Demography of Captive Asian Elephants (*Elephas maximus*) in Southern India

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Historically, the Asian elephant has never bred well in captivity. We have carried out demographic analyses of elephants captured in the wild or born in captivity and kept in forest timber camps in southern India during the past century. The average fecundity during this period was 0.095/adult female/year. During 1969–89, however, the fecundity was higher at 0.155/adult female/year, which compares favorably with wild populations. There was a seasonality in births with a peak in January. The sex ratio of 129 male to 109 female calves at birth is not significantly different from equality, although the excess of male calves born mainly to mothers 20–40 years old may have biological significance. Mortality rates were higher in females than in males up to age 10, but much lower in females than in males above age 10 years. The population growth rate, based on the lower fecundity over the century, was 0.5% per year, and based on the higher fecundity during 1969–89, was 1.8% per year. The analyses thus showed that timber camp elephants in southern India could potentially maintain a stationary or increasing population without resorting to captures from the wild. Breeding efforts for elephants in zoos can thus profitably learn from the experience of traditional management systems in parts of Asia. Zoo Biol 16:263–272, 1997.
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INTRODUCTION: ELEPHANT BREEDING PROGRAMS

The Asian elephant (*Elephas maximus*) was probably first tamed about 4,000 years ago by the people of the Indus Valley civilization [Carrington, 1959]. Since that time, the animal has played a pivotal role in the religious, cultural, political, and economic life of the peoples of Asia.

There are < 50,000 Asian elephants remaining in the wild and ~ 15,000 in captivity [Sukumar, 1989; Santiapillai and Jackson, 1990]. The major reasons for the decline of wild populations have been loss of habitat and capture for domestication. For instance, during the past century alone, up to 100,000 elephants may have been captured from the wild all over Asia [Sukumar, 1989], a level of exploitation that was clearly unsustainable. In the past many kings and chieftains maintained large numbers of elephants in their armies; thus the Mauryan Emperor Chandragupta (4th century BC) had 9,000 elephants in his army. Many centuries later, the Moghul Emperor Jehangir (17th century AD) is reputed to have held 12,000 elephants in his stables.

Historically, stocks of captive elephants have been maintained almost entirely through replenishment from the wild. Reproduction in captivity was negligible, with the result that rulers had to resort regularly to obtaining elephants from wild populations. Because a quarter of the total population of Asian elephants is held in captivity—in temples, timber camps, nature reserves, and zoos, it is clear that proper maintenance and breeding of tame elephants are important for the conservation of the species.

Many zoos in the West have breeding programs for elephants, but these populations are declining. For instance, the North American zoo population of Asian elephants is currently declining (in the absence of any imports) at a rate of ~ 8% per year [Tuttle, 1989]. However, many of the captive populations kept under different management regimes, such as logging camps, seem to have better breeding success [Toke Gale, 1974]. We have been studying the captive elephants kept in forest camps in southern India, for which reliable records extending back several decades exist. Among various aspects we have examined in these elephants are patterns of growth, morphometry, reproduction, and management [Sukumar et al., 1988; Krishnamurthy and Wemmer, 1995a,b]. In this report, we present the results of a demographic analysis of southern Indian captive elephants, which offer useful lessons for captive breeding programs for the species.

MATERIALS AND METHODS
Forest Camp Elephants

The Forest Department of Tamilnadu State (formerly the Madras Presidency) has been capturing and maintaining elephants for the past 130 years or so. These animals have been used mainly for logging operations in the past and for taking tourists inside parks. The captive elephants also have been sold to temples and zoos.

Two major forest camps are maintained today, one at Theppakadu in Mudumalai Wildlife Sanctuary and another at Varagaliyar in Anamalai Wildlife Sanctuary (now the Indira Gandhi National Park). The elephants are maintained as mixed herds consisting of adult females, calves, and males of various ages, thus mimicking the social structure of wild elephant herds. The camps are usually located inside or adjoining a forest area, near a perennial water source such as a stream or a river. Apart from the natural fodder the elephants get from the forests, they are also given supplemental feed twice a day. The rations are fixed by the attending veterinarian based on the sex and age of the animal and its workload.

The elephants are thus able to socialize both when they are in the camp and when they are let out for foraging in the forest at night. The forests are also home to wild elephants, and captive cows thus have the opportunity to mate with both cap-

tive bulls and wild bulls. Significant numbers of calves born in captivity have been sired by wild bulls.

We scrutinized records of several hundred elephants captured or born in captivity since the late 19th century in the Madras Presidency/Tamilnadu State. We had access to a near-total record of elephants captured or born after 1925. These elephants have been kept in captivity for varying periods of time, in some cases for > 50 years, making this database one of the most comprehensive for any captive elephant population in the world.

Demographic Analyses

The entire database could not be used in the analyses for a number of reasons. Many of the elephants that had been captured could not be aged sufficiently accurately for our purpose if they had already reached their asymptotic shoulder heights at the time of capture. Further, some of them were kept in captivity for only a few months before they were sold, making it meaningless to include them in the analyses. We therefore selected elephants for the analyses by the following procedure.

All elephants born in captivity whose date of birth was known were included. In some cases, the sex of the calf was not known and thus had to be discarded for computing sex ratios, but nevertheless could be still used in calculating fecundities of the adult cows. Of the elephants captured, only those kept in captivity for 4 years or more were selected. These were aged from their shoulder heights by procedures described elsewhere [Sukumar et al., 1988]. However, calves born in captivity to all females were used in computing overall sex ratio at birth, although these were not considered in computing fecundities.

Our final data set included 202 females, 215 males, and 24 (all newborns) of unknown sex. Of these, 261 elephants were born in captivity; the remaining were captured from the wild. The data represent a total of 2,811 female-elephant years and 2,749 male-elephant years in captivity.

We used the demographic modelling program PEDDEMO [Bingaman and Ballou, 1986] for much of the basic computation of age-specific fecundity, age-specific survivorship and population growth projections, and adapted the outputs for presenting the results. Age-specific fecundity (m_x) is the average number of female offspring (in practice, taken as half the total offspring) produced by an individual female aged x. Age-specific survivorship (l_x) is the probability of a newborn individual surviving to age x. The instantaneous rate of population change r is computed iteratively from the Euler equation $\Sigma\ l_x m_x e^{-rx} = 1$. Population growth projections are based on the well-known Leslie matrix method [Pielou, 1977].

RESULTS
Fecundity

The earliest age at which a female gave birth was at 13 years, 4 months, by a cow named Meenakshi, who herself was born in captivity and thus her age known accurately. Thus suggests that she was sexually mature by about age 11–11.5 years. This record of calving is, however, exceptional, as no other cow in captivity has calved before the age of 15 years. The next earliest age at first calving was by Vasanthi (captured when she was < 6 months old) at age 15 years. All the other cows have either calved for the first time well after age 15 years or

even beyond age 20 years. The oldest authenticated age at which a cow calved was by Tara at age 62 years.

There have been three instances of twin calves out of 261 calves born in captivity, a twining rate of ~ 1%.

Figure 1 gives the average annual fecundity rates for females of different age classes, pooled together for the entire study period of about a century. The per capita annual fecundity rises from 0.062 at age 15–20 years to 0.116 at age 35–40 years, with only a marginal reduction thereafter until age 50 years. Beyond this age, the peaks and troughs are probably due to low sample sizes (there are few cows living into these ages), and thus the values should be interpreted cautiously. The mean per capita birth rate (male and female offspring) of 0.095 calves/year translates into an intercalving interval of 10.5 years.

However, a very different picture of fecundity arises when the data are considered only for the last 20 years of the study period (Nov 1969 to Nov 1989). During these years there were 28 cows that were in the sexually mature age class (15–65 years for our purpose) for at least part of the period. The 355 sexually mature elephant years these cows represent resulted in a total of 55 births, or a per capita birth rate of 0.155 calves per year or 63% higher than the average over the entire period.
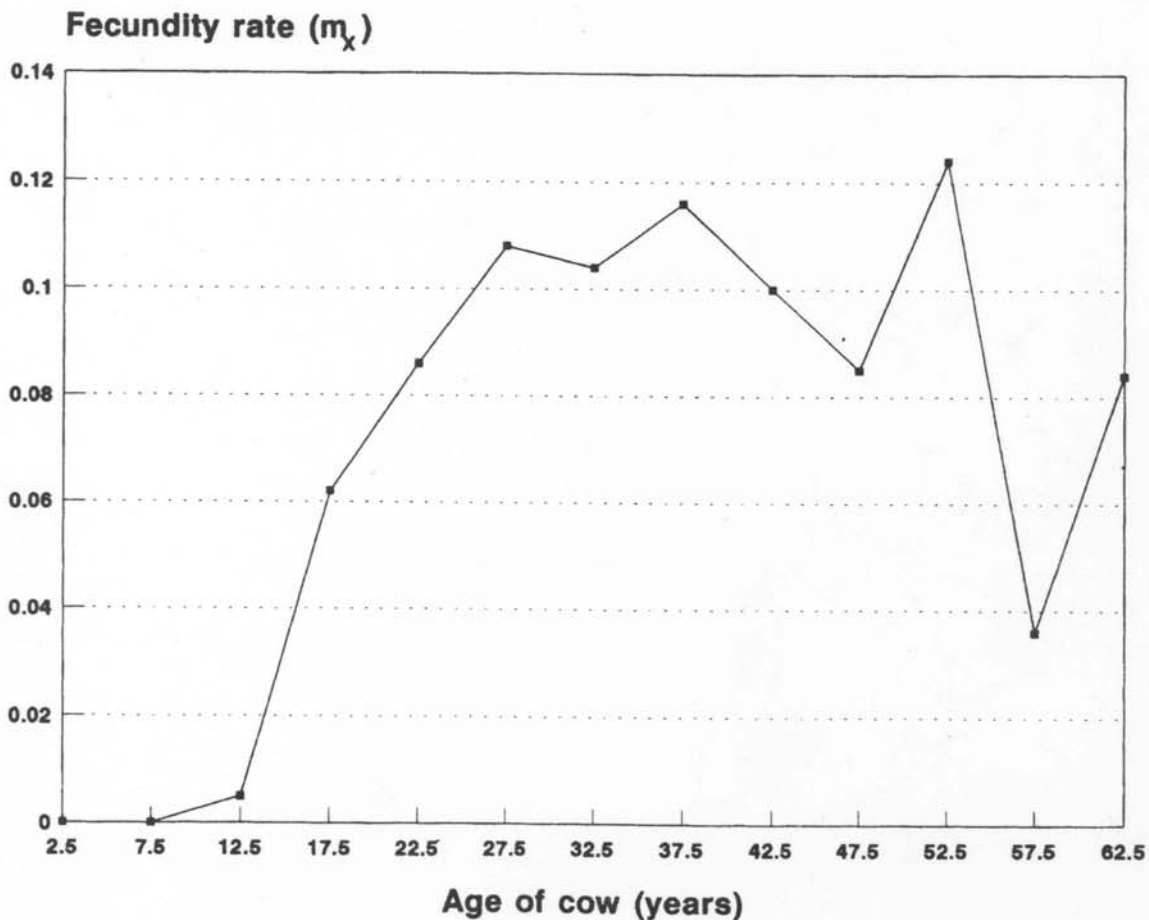

Fig. 1. Age-specific fecundity rates (m_x) in captive Asian elephants. The rates are expressed as mean number of offspring of both sexes born to a female per year. Females have been placed in 5 years age classes and the midpoint of the class interval shown in the figure.

This clearly indicates that reproduction in captivity was relatively poor during the earlier part of the century, but has substantially increased in recent years.

Sex Ratio

Out of 238 calves for which the sex was known, there were 129 male and 109 female calves or a male:female ratio of 1.18:1. This is not statistically significantly different from a 1:1 ratio (Chi-square = 1.68, $P>0.05$). The sex ratio of calves born to cows of different age classes is given in Figure 2. We used a subset of only 108 male and 79 female calves for this analysis, because the ages of the mothers of other calves could not be determined. For none of the age classes does the ratio depart significantly from equality, although it is of interest to note that cows in the 20–40 year age class distinctly produced larger numbers of male calves.

Seasonality in Births

When the 261 births are classified month-wise (Fig. 3), it is seen that there is clear seasonality in births during December-February, with a peak in January.

Mortality

The average annual mortality rates for different ages are given in Table 1 and plotted as survivorship curves (based on survivorship at intervals of 5 years) for male and female segments of the captive population in Figure 4.
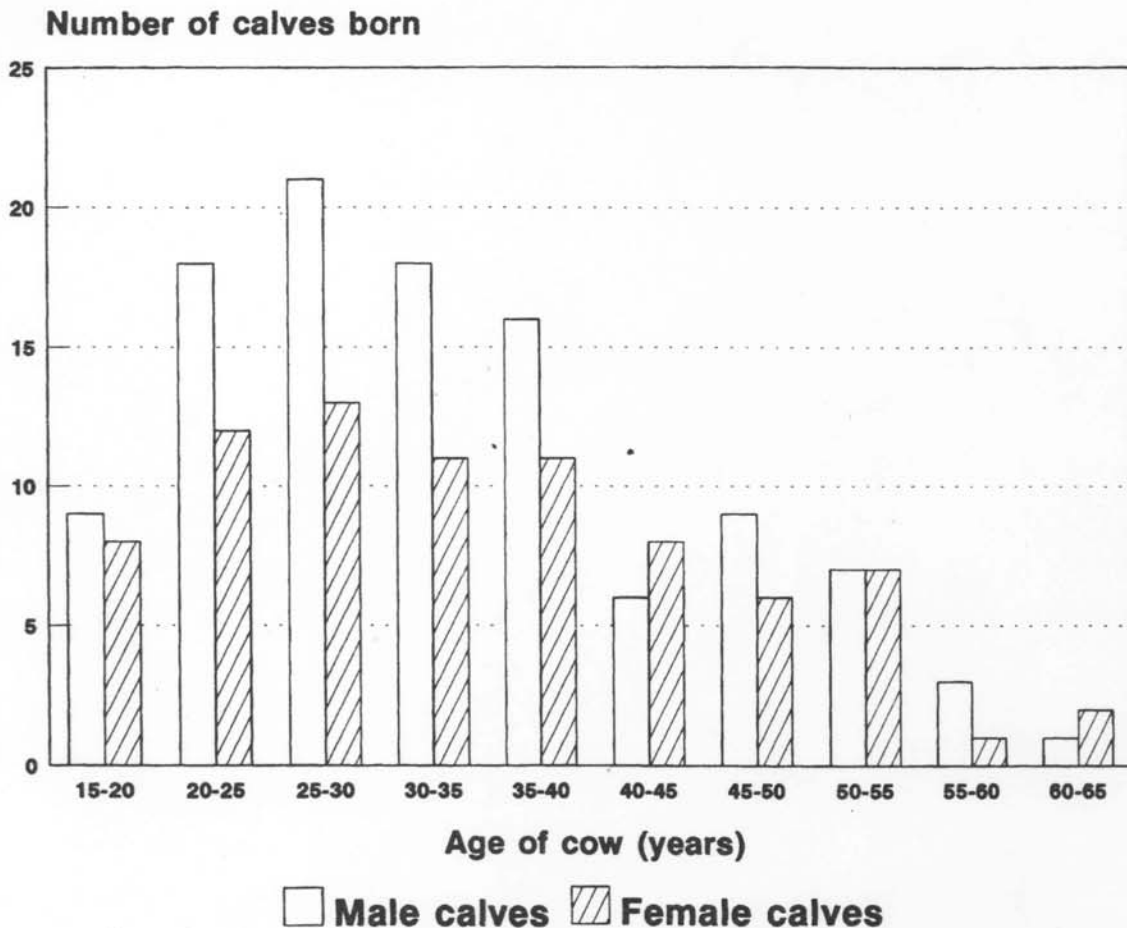
Number of calves born

Fig. 2.   Number of male and female calves born to captive elephants of different ages.
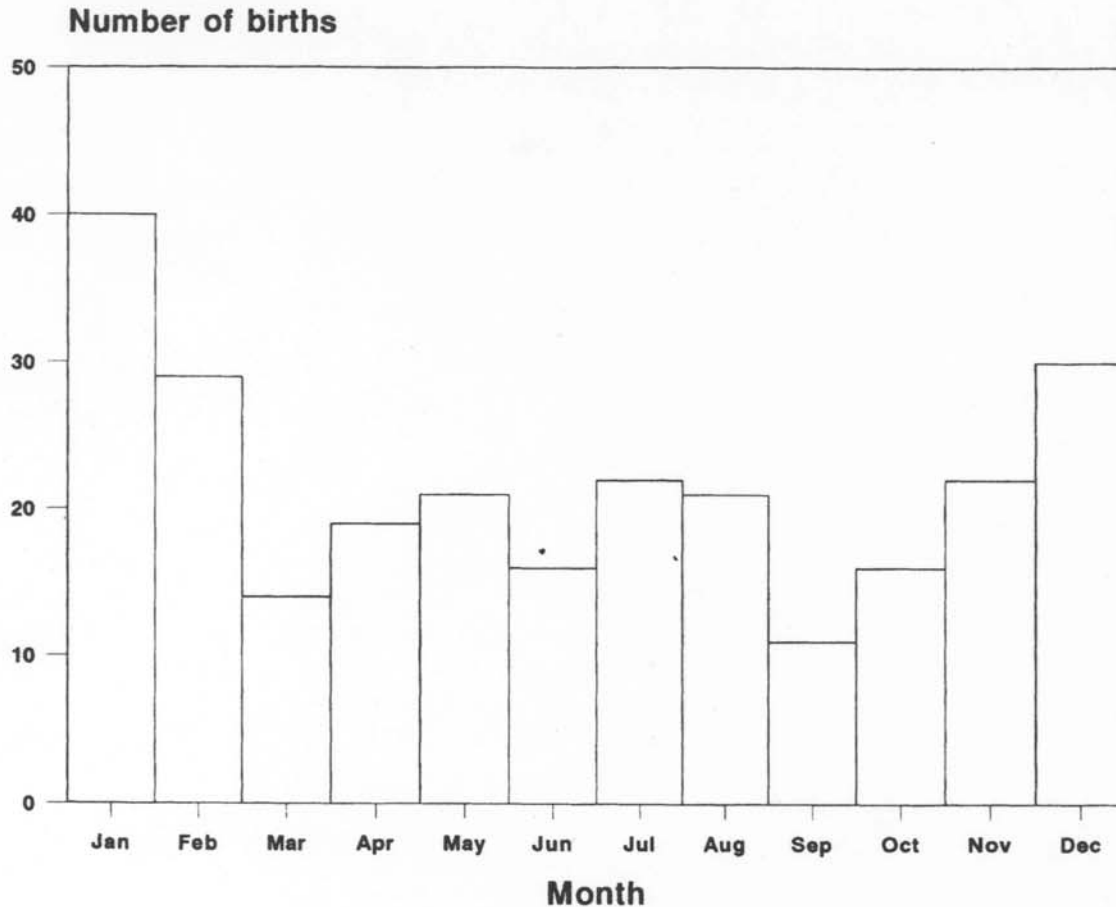
Number of births

Fig. 3. Frequency distribution of elephant calves born during different months of the year. Data have been combined for the entire study period.

During the first year of life, mortality rates are high, being 24% for females and 16% for males. The relatively higher female mortality (compared to male mortality) continues until age 10 years, beyond which the two rates are not very different until 20 years of age. From 20 years onward, the mortality rate in males is signifi-

TABLE 1. Mean annual mortality rates in percentage of male and female elephants*

| Age (years) | Male | | Female | |
	Mortality rates	n	Mortality rates	n
0–1	15.5%	123	23.8%	109
1–2	3.7%	81	10.5%	67
2–5	1.9%	115	5.3%	76
5–10	0.9%	255	1.8%	116
10–20	0.13%	789	0.0%	510
20–40	0.9%	1117	0.16%	1264
40–60	3.8%	258	1.1%	593
60–80	21.4%	11	7.2%	76

*n refers to the number of individuals at risk (of death), expressed as the number of elephant years over the age class interval.
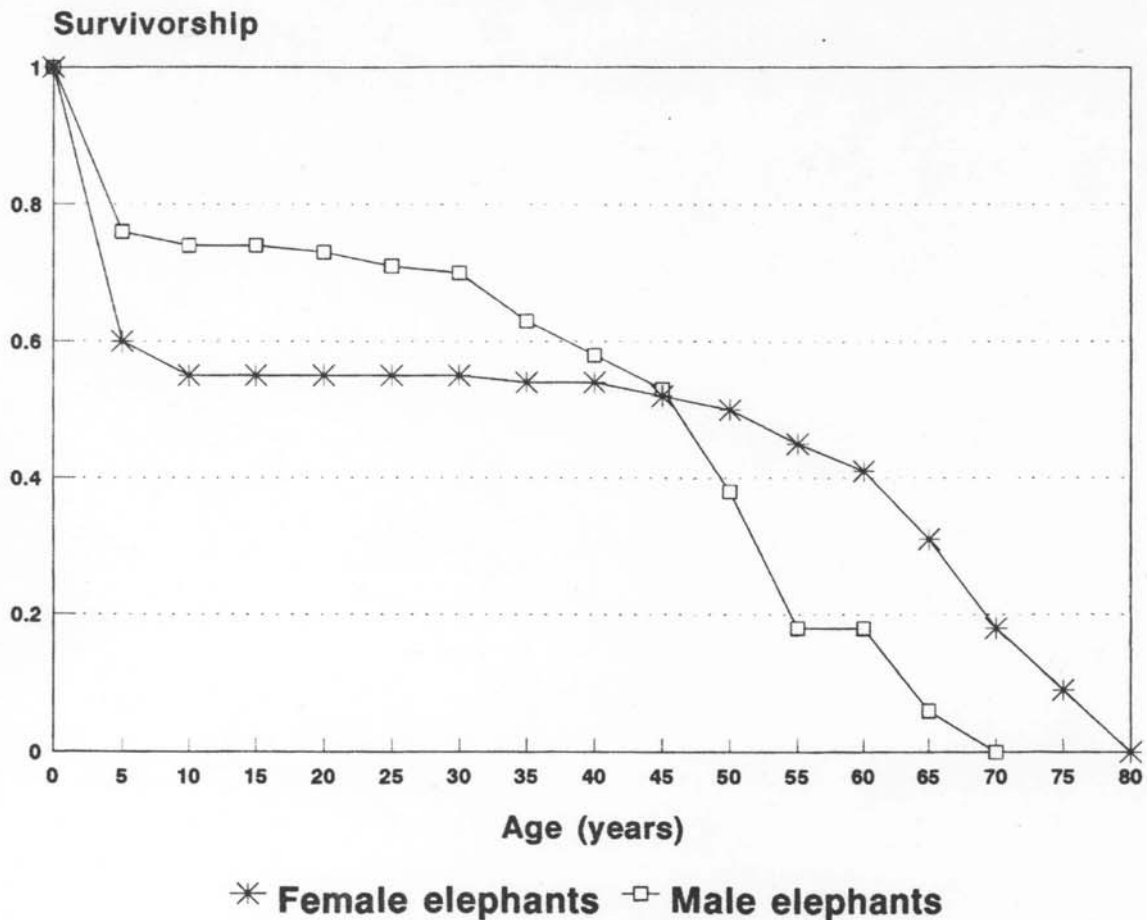
Survivorship

Fig. 4. Survivorship in male and female elephants expressed as the proportion of newborn individuals surviving to a particular age. Survivorship values have been plotted at the end of every fifth year only.

cantly higher than in females. Overall, the risk of death in captive elephants is low between the age of 5 and 60 years, being generally under 2% per year, with the exception of males in the 40–60 age class. We took 80 years as the maximum potential longevity of an elephant. The oldest elephant in our records was a cow named Peri that died at an estimated age of 79 years.

Population Growth Rate and Modelling

The intrinsic growth rate r of the captive population over the entire study period as computed by the Euler equation, using the above age-specific fecundity and mortality rates for the female segment (age 0–80 years), was 0.005. This indicates that the captive elephant population can be stationary or even potentially grow slowly even in the absence of any immigration from the wild population.

The population's intrinsic growth rate computed after incorporating the fecundity rates for the last 20 years (1969–89) of the study is 0.018, or a growth rate of 1.8% per annum. A 20-year age-structured population projection for the female segment, based on fecundity during 1969–89 and mortality rates over the entire study period, predicts a slight increase over a 16-year period (base year = 1989) followed by a slight decrease. There are considerable fluctuations in the age structure, notably

in the proportions of elephants above 10 years, but a remarkable constancy in the numbers of individuals below 10 years (Fig. 5).

DISCUSSION

The captive elephant population shows a number of demographic features that are in variance with those observed in wild populations. The average fecundity of the captive population (0.095 calves/adult female/year) is substantially lower than that for a wild population (0.21 calves/adult female/year) in southern India [Sukumar, 1989]. However, the fecundity observed during the past two decades in the captive population (0.155/adult female/year) compares much more favorably with wild populations both in Asia and in Africa [Laws et al., 1975; Sukumar, 1989]. The low fecundity of the earlier years could have been imposed by social barriers to reproduction as a consequence of management practices. The elephants were used mainly for logging operations and consequently the cows may have been much more segregated from bulls, both captive and wild, than they are at present. The nutritional status may also have been inadequate, given the heavy workload during earlier years. In recent years the workload for the elephants has diminished considerably due to the reduction in logging.
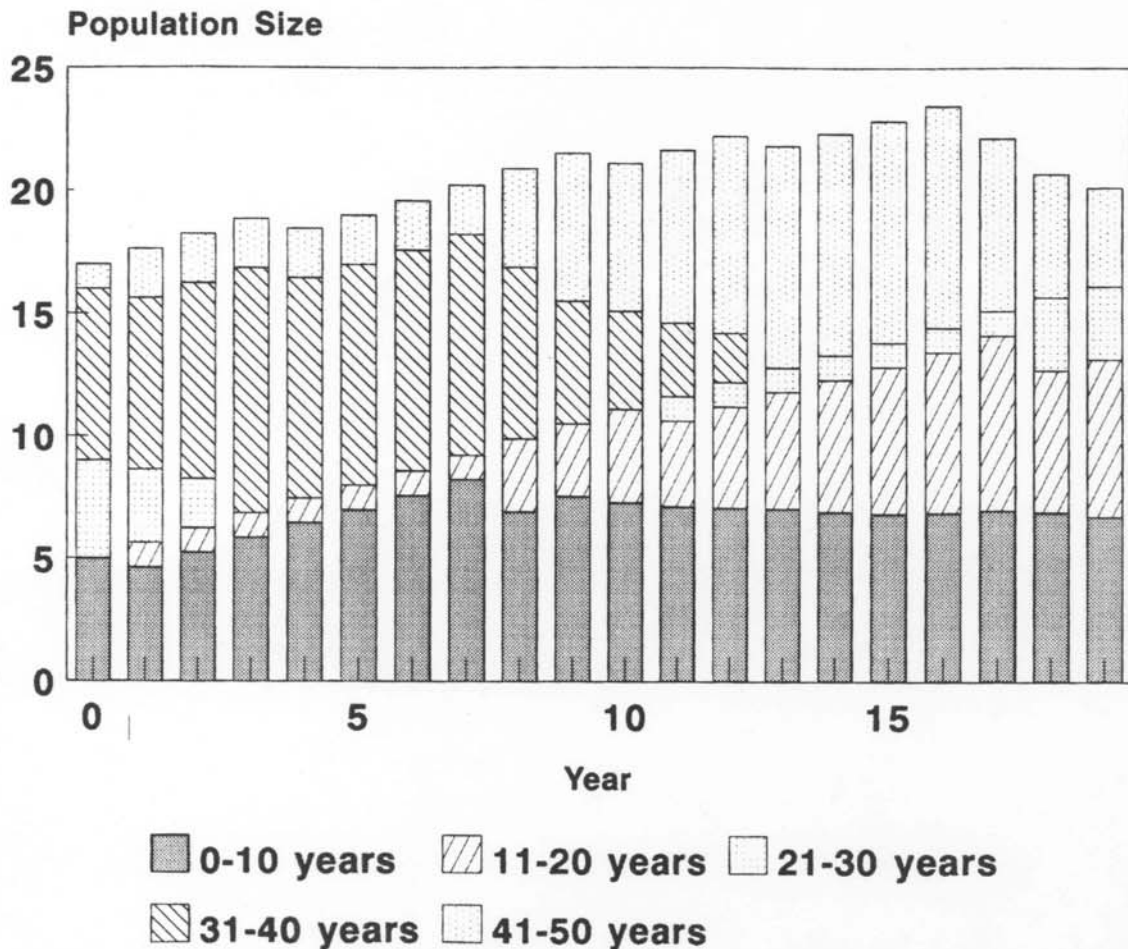

Fig. 5.   A 20-year age-structured population projection of female elephants. The projections are based on calculated age-specific survivorship for the entire study period and age-specific fecundity during 1969–89. An age range of only 0–50 years is considered in these projections.

The peak in births during the month of January, at the beginning of the dry season, was unexpected. This indicates that conceptions peaked during September-October (assuming a mean gestation period of 20–21 months), three to four months after the onset of the southwest monsoon, or just at the onset of the northeast monsoon. In some wild elephant populations, a seasonal peak in births has been observed at the beginning of the wet season, when nutritious forage would be ensured for the lactating mother, a pattern that would be favored by natural selection [Laws et al., 1975; Hanks, 1979; Eltringham, 1982]. It is possible that under captive conditions such natural patterns could be obscured for various unknown reasons.

Although the sex ratio at birth is not statistically significantly different from 1:1, the excess of male calves may nevertheless have some biological significance. A male-biased sex ratio at birth seems pronounced for mothers in the 20–40 age class when they could be expected to be in relatively good condition. This may conform to the Trivers and Willard [1973] model of adaptive variation in offspring birth sex ratio. According to this model, in a polygynous species for which the males have higher variation in lifetime reproductive success than females, a mother in good condition should invest preferentially in sons because a high-quality male is likely to enjoy high reproductive success. Such a pattern has been observed for several species, e.g., in caribou by Thomas et al. [1989], in mule deer by Kucera [1991], although contradictory evidence also exists from other studies [Robinette et al., 1973; Skogland, 1986].

The higher female mortality compared to male mortality during the juvenile years is also different from patterns observed in wild elephant populations. As a general rule, the males suffer higher mortality than do females in polygynous species showing a marked sexual dimorphism [Trivers, 1985]. Studies of African elephant populations have revealed that the mortality of males exceeds that of females during the subadult stage, for there is little difference in mortality rate between fully adult elephants [Laws, 1969; Laws et al., 1975]. In a wild Asian elephant population in southern India, for example, the males had a death rate that was twice as high as that for females during the first year [Sukumar, 1989]. A possible explanation for the observed difference under captive conditions is that female calves may be relatively neglected in health care, as they have lower economic value. This may not be deliberate or obvious, but may accrue to a subtle difference in the upbringing of juvenile elephants.

The relative stability in age structure projections, the slightly positive population growth rate over the time-scale of a century, and the strongly positive population growth rate during the past two decades in the southern Indian captive elephants is of considerable interest for captive breeding programs. All these testify to the successful breeding of elephants under captive conditions in state-controlled elephant camps. We attribute the success of these camps to stability of living conditions and good husbandry, as well as the availability of sires, either from the captive population or in the form of males living wild in adjacent forests. Surpluses of captive bred elephants are regularly available from these camps and could serve as a more important source of animals for captive populations in other parts of the world.

Zoos of the Western world could profit from greater familiarity with traditional systems of domestic elephant management and husbandry and might even examine the possibility of entering into partnerships with forest department elephant camps for the broader purposes of captive propagation.

CONCLUSIONS

1. Demographic analyses of captive Asian elephants kept in forest timber camps in southern India showed relatively high fecundity and low mortality as compared to captive populations elsewhere. Availability of wild bulls for siring calves is undoubtedly important in contributing to the high birth rate.

2. This captive population of elephants could be intrinsically stationary or even show an increasing trend in the absence of captures from the wild.

3. The experience of breeding timber camp elephants under traditional management systems could provide useful lessons for breeding programs in zoos.

ACKNOWLEDGMENTS

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