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also decrease due to another demographic factor – a skewing of the ratio of reproducing males to females<sup>2</sup>. The more unequal the sex ratio, the lower the effective population size. While the

sex ratios of polygynous mammals are naturally female-biased in most instances due to a variety of reasons, the selective hunting of males would further exacerbate this situation. Among Asian

elephants (*Elephas maximus*), only the males possess tusks (there are also tuskless males) and thus are selectively targeted by poachers for their ivory<sup>3</sup>, resulting in very skewed sex ratios.

While ivory poaching has been a problem in most southern Indian populations<sup>3</sup>, several reports suggested that Periyar Tiger Reserve in Kerala is one of the worst affected<sup>4</sup>. We therefore initiated studies on the status, ecology and behaviour of elephants in Periyar to address several conservation concerns. Among the aspects we have studied are estimates of elephant population numbers, population structure and demography, simulation modelling of tusk harvest by poachers, and interrelationships of skewed sex ratio and changes in social behaviour. In this commentary we would like to summarize the present status of Periyar's elephants, the impact that ivory poaching has made on the population, and its demographic, genetic and conservation implications.

Periyar Tiger Reserve (777 km<sup>2</sup>) in Kerala state is constituted around a lake, with a waterspread of 26 km<sup>2</sup>, created by a dam constructed across the Periyar river in 1895. The vegetation of the reserve consists of tropical wet evergreen and semi-evergreen forests, interspersed with moist deciduous forests and grasslands. Periyar was amongst the first Project Tiger Reserves declared in 1973, and more recently designated as an Elephant Reserve (No. 10) under India's Project Elephant<sup>5</sup>.

A rapid survey was carried out at Periyar during March–May 1994, when density estimates were made and data on population structure obtained. We continued observation on the population structure and demography of elephants from June 1994 to June 1995 and during February–April 1997. A vegetation map of Periyar Tiger Research (PTR)<sup>6</sup> formed the basis of our survey and stratification of the reserve for the purpose of sampling. The density of elephants was estimated using the line transect, indirect count method described elsewhere<sup>7,8</sup>. A total of 64 transects was cut in different habitat types, and data analysed separately for each habitat type and also for areas around the lake (i.e. 0.5 km from the lake shore) and away from the lake. The daily defaecation rate of elephants was taken to be 16.3 (CV of 10%) based on data from wild elephants at Mudumalai<sup>9</sup>, while the daily dung decay rate of 0.013/day (CV of 10%) from calculations at Parambikulam Sanctuary<sup>10</sup> where the climate and vegetation are in part similar to Periyar. Dung and elephant densities estimates were calculated for each habitat type using the programs TRANSECT<sup>11</sup>, and GAJAH which uses a Monte Carlo method described in detail elsewhere<sup>12</sup>. Elephants were aged by field techniques for constructing the population age structure<sup>3</sup>. Population structures were also obtained during another phase of field work during February–April 1997.

The total number of elephants in the sanctuary was found to be 1166 (95% confidence limits of 641–2115) during our 1994 survey. This is comparable to the estimates of 800 elephants (within high use areas alone) during 1978 through indirect count<sup>13</sup>, 935–1100 during 1987–89 by Chandran<sup>4</sup> and dung densities in Thekkady Range during the 1993 census by Kerala Forest Research Institute<sup>14</sup>.

Using direct elephant sightings, the adult male to female ratio was found to be 1:101 in the present study. Of the 5 adult males recorded, only two were tuskers and the rest were makhnas. It is possible that we may have missed another tuskier according to local reports. The time series data on population structure across the various studies during the period 1969–97 clearly brings out a decline in the proportions of males in the population (Table 1). Concurrently, the numbers of males in the population would have also declined in the absence of any significant increase in the total population size. The population size is unlikely to have increased much, at least during the latter half of the above period (1969–97), because of a clear decline in recruitment into the population (discussed below).

Some of the data from previous studies such as Kurup<sup>15</sup> and Chandran<sup>4</sup> cannot be directly compared with ours because the former do not clearly define the various categories (calf, juvenile, sub-adult and adult) either in terms of

**Table 1.** Comparison of age structures and sex ratios of elephant populations in southern India

	Female (% population)				Male (% population)			
	Calf	Juvenile	Sub-adult	Adult	Calf	Juvenile	Sub-adult	Adult
Periyar 1969	1.2	19.0*		51.5	1.2	19.0*		8.0
Periyar 1978–80**	?	?	?	?	?	?	?	3.1
Periyar 1981–82	7.2	6.6†	8.1	56.7	7.2	6.6†	6.7	0.8
Periyar 1987–89	8.8†		18.5	60.2	8.8†		3.3	0.5
Periyar 1994–95	2.1	10.2	25.1	51.9	1.8	4.9	3.5	0.5
Periyar 1997	4.9	8.4	11.6	60.4	4.9	5.6	3.7	0.5
Satyamangalam-Chamarajanagar 1981–83	3.6	10.6	18.5	35.3	3.6	14.3	6.8	7.4
Mudumalai-Bandipur 1994	3.5	10.8	14.5	37.2	3.5	15.7	10.8	4.0

Note that classification into various age categories at Periyar during 1969 (ref. 15), 1978–80, 1981–82 (ref. 13) and 1987–89 (ref. 4) are not directly comparable with the rest of the data (Ref. 3 and our observations). See text for details.

\*Combined data for juveniles and sub-adults.

\*\*Data on herd classification not available for Periyar during 1978–80.

†Juveniles have not been sexed during 1981–82. Therefore equal numbers of males and females have been assumed.

‡Combined data for calves and juveniles.

age or actual sizes, while we have defined these as calf (<1 yr), juvenile (1–5 yr), sub-adult (5–15 yr) and adult (>15 yr) based on size criteria<sup>3</sup>. Even if the definitions of elephant categories are not directly comparable, the distinct decline in the juvenile, sub-adult and adult male categories can be seen over this time period.

The ratio of adult male to female seems to have progressively skewed from about 1:6 (1969) to 1:19 (1977–79) and then skewed substantially to 1:71 (1980–82) reaching a peak of 1:122 (1987–89). It is important to remember that skewing of the adult sex ratio will proceed at a geometric rate with the progressive death of one sex, and thus the death of one or a few adult males will skew the ratio substantially as their numbers reduce in the population.

Interestingly, both the sub-adult and males categories seem to have reached very low frequencies even by 1987–89 when Chandran<sup>4</sup> studied this population, and have not changed much over the next five years. These data indicate that ivory poaching began during the 1970s itself, with the adult male segment being targeted and then moved down to the sub-adult category by the 1980s. Severe poaching is indicated during the period prior to 1987 when even juvenile males have not been spared. Computer simulation modelling of elephant demography indicates that 336–388 tuskers of various ages have been killed and 3256–3334 kg of tusks harvested by poachers over the period 1974–94 (ref. 16).

Another demographic effect of the high rates of poaching and extreme skew in adult sex ratios is a decline in the birth rate of the population. Our 1994–95 data indicated that the average fecundity was only 0.075/adult female/year as compared to between 0.20 and 0.25 for the more productive populations in southern India<sup>3</sup>. The most likely cause of the fecundity decline is an Allee effect<sup>17</sup>. With an extremely low number of adult males in the populations, a substantial proportion of females coming into estrus would not be detected and mated. Another possible reason for the low numbers of calves and juveniles seen at Periyar is that females may have stopped reproducing under conditions of extreme stress

(poaching), or infant mortality may have been very high, as may have happened in an African elephant population at Ruaha, Tanzania<sup>18</sup>. The decline in recruitment into the population is not because of inter-annual variations in births as seen elsewhere in the south<sup>3</sup> but a phenomenon which has persisted for several years as seen from the low numbers of juveniles in the 1994–95 age structure. Our 1997 observations, however, showed an increase in births with a fecundity rate of 0.16/adult female/year, still lower than the potential rate. It is possible that 1997 represents a genuine upswing in reproductive rates or that our limited sampling during three dry months represents only a single clan at Periyar.

Another aspect of reproduction at Periyar that has been observed is the presence of several barren adult females. Such female elephants show no sign of mammary gland activity and, further, have retracted nipples indicating that they have not reproduced or may be incapable of reproducing. This has also been noted by another experienced elephant observer (D. K. Lahiri-Choudhury, pers. commun.). It is possible that an alteration of reproductive physiology in female elephants is related to the near absence of adult males in the population over an extended period of time. This aspect requires further study, possibly through monitoring metabolites of reproductive hormones in faeces<sup>19</sup>.

The present situation of the elephant population at Periyar clearly calls for further research and active management. The elephant population here can possibly withstand the drastic reduction in the genetically effective population size ( $N_e$ ), because this reduction has occurred over a single elephant generation (about 20 years). In theory, a one generation reduction of  $N_e$  to 20+ still retains about 98% of the original (prior to the poaching spate) heterozygosity, assuming random sampling of individuals. Allelic diversity could, however, be expected to suffer greater decline, with rare alleles having a high probability of being lost during a population bottleneck<sup>20</sup>. Obviously the poaching of male elephants has been selective, at least in the initial years, and thus the genetic erosion could have been more serious<sup>21</sup>.

Management options for Periyar would include the translocation of adult male elephants from other populations with surpluses, in order to increase the genetically effective population size to 50 or above. This could be achieved by increasing the number of adult males from the present 6 to 13 individuals. Apart from increasing  $N_e$ , this would also serve to stimulate the birth rate of the population. Several questions would arise about such a proposed translocation. First of all, there is the question of protection of translocated bulls from poachers. From this angle, it may be better to translocate tuskless bulls (makhnas) into Periyar, given that ivory poaching is likely to be a continuing problem<sup>22</sup>. If breeding makhnas are translocated, the frequency of alleles for tusklessness would increase. Available data on captive elephant breeding (RS, unpublished) indicate that females are also carriers of the genes for tusks. Among sons born to females mated by a makhna, a certain proportion would thus still be tuskers (heterozygous genotype). It may thus be prudent to translocate makhnas or a mixture of makhnas and tuskers until protection from poachers is ensured.

The next aspect to be considered is that of the genetic consequences of introducing males from a population (such as Assam, where surplus makhnas are most likely to be available) which has been isolated from Periyar for a long period of time. Related to this is the health (parasite and disease) status of translocated bulls. Could elephants in Periyar have evolved resistance to certain local parasites against which elephants from another population may not have resistance? Could the translocation of such bulls disrupt locally-adapted gene complexes at Periyar? This calls for basic studies on patterns of genetic variation and levels of divergence among the elephant populations at Periyar and elsewhere. Concurrently, there have to be studies on the parasite and health status of elephants in these populations. If bulls are translocated into Periyar, it would be advisable to do this in stages after careful monitoring of these bulls through radio-telemetry to study breeding and possible conflict with people. It is time that such an elephant management programme is initiated at Periyar. The current status of

this important elephant population warrants immediate management action.

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