

Impact of poaching on an Asian elephant population in Periyar, southern India: a model of demography and tusk harvest

R. Sukumar^{1,2}, Uma Ramakrishnan² and J. A. Santosh¹

¹Centre for Ecological Sciences, Indian Institute of Science, Bangalore-560012, India

²Asian Elephant Conservation Centre, Indian Institute of Science, Bangalore-560012, India

(Received 18 December 1997; accepted 15 July 1998)

Abstract

Ivory poaching has been a serious problem in Asian elephant (*Elephas maximus*) populations. Reliable records of elephants killed and ivory harvested are generally unavailable. We have used a simulation modelling approach to estimate the numbers of male elephants killed and the quantities of ivory harvested over a 20 year period (1974–94) in the Periyar Reserve of southern India. The age-structured Leslie matrix projection model was modified for this purpose by considering three segments (female, tusked male and tuskless male), relating fecundity to adult sex ratio and iteratively simulating tusked male mortality rates so as to match the observed elephant population structure at Periyar. Four different scenarios of poaching all gave very similar results. We estimate conservatively that 336–388 tuskers have been poached and 3256–3334 kg of ivory harvested by poachers over the 20 year period. The maximum harvest came from the 10–20 year age class. Trends in various demographic parameters such as population numbers, tusked male to tuskless male ratios and female fecundity are described. The implications of ivory poaching and the extremely skewed sex ratios for the conservation and management of the elephant population at Periyar are discussed.

INTRODUCTION

Poaching of elephants for ivory has been a serious conservation issue not only in African elephant (*Loxodonta africana*) populations (Western, 1987; Douglas-Hamilton 1988; Poole & Thomsen, 1989; Dublin, Milliken & Barnes, 1995) but also in Asian elephant (*Elephas maximus*) populations (Sukumar, 1989; Menon, Sukumar & Kumar, 1997). Unlike the African elephant, where both sexes generally possess tusks, only males in the Asian elephant have tusks. The proportion of male Asian elephants having tusks varies widely among populations, from over 90% in southern India to under 10% in Sri Lanka (Kurt, 1974; Sukumar, 1989).

Although ivory poaching is widespread in Asian countries where substantial proportions of male elephants are tuskers, one region which has been particularly affected in recent times is southern India (Sukumar, 1989). The southern Indian elephant populations constitute the largest regional concentrations of elephants in Asia (Sukumar & Santiapillai, 1996). Given the very high proportion of tusked male elephants here, the southern Indian region was also home to perhaps the largest numbers of tuskers until recent times. This has changed with

the spate of ivory poaching over the past two decades. Periyar Tiger Reserve in the south has been one of the worst affected by poaching (Chandran, 1990).

Selective hunting of male elephants for tusks has several consequences for the population. Sex ratios become increasingly female-biased, genetic variation is eroded, and demographic changes may occur through decreases in female mating success. There may also be attendant changes in social organization and behaviour in the population. We have been investigating these aspects in southern Indian elephant populations of the Eastern Ghats (1981–83), Mudumalai-Bandipur (since 1987) and Periyar (since 1994).

Official records of elephant mortality, in particular of ivory poaching, are often deficient, and can underestimate considerably the true extent of this phenomenon. Our objective was to get an estimate of the minimum number of elephants poached for ivory in Periyar over a given time period, the age distribution of elephants killed and the quantities of ivory harvested by the poachers. We explore these questions through simulation modelling of the dynamics of the elephant population.

STRUCTURE OF THE POPULATION DYNAMICS SIMULATION MODEL

The age structure of the population of elephants in Periyar Tiger Reserve during 1994–95 (Ramakrishnan *et al.*, 1998)

All correspondence to: R. Sukumar. Tel: +91-80-334 3382, 309 2786; Fax: +91-80-331 1280, 331 5428; E-mail: rsuku@ces.iisc.ernet.in.

reveals a substantial depletion of the male segment of the population (Fig. 1) when compared to a simulated one under stable age distribution with no poaching (see below), or other populations in southern India such as the Eastern Ghats during 1981–83 (Sukumar, 1989) and Mudumalai-Bandipur (unpublished data). We had reason to believe that this depletion of males was due largely to poaching during the past 20 years. This reasoning was based on observations of Periyar's elephants recorded by Krishnan (1972 and pers. comm.), data on elephant population structure for Periyar during 1969 by Kurup (1971), which showed an adult male to female ratio of about 1:6 compared with 1:122 by 1987–89 (Chandran, 1990) and 1:101 by 1994–95 (this study). Asian elephant populations not under much pressure from ivory poaching, as in Sri Lanka (Kurt, 1974) or Sumatra (Santiapillai & Suprahman, 1986), have adult male to female ratios of about 1:3, suggesting that a ratio of 1:6 at Periyar during the early 1970s was indicative of low levels of poaching until that period. The observed age structure during 1994 could have been the result of different scenarios of poaching operating previously. Our goal was thus to model various scenarios, and compare the simulated population structures with the observed population structure during 1994.

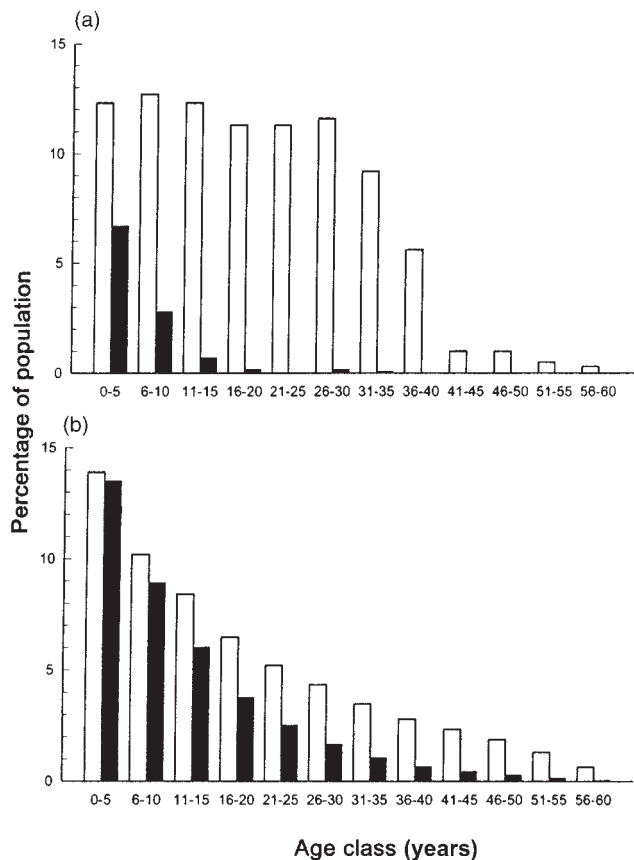


Fig. 1. Age structure of the male and female segments of the elephant population (a) observed at Periyar Reserve during 1994–95 and (b) simulated age structure under stable age distribution with no poaching assuming differential natural mortality between the sexes and an adult (>15 years) male to female ratio of about 1:3. ■, males; □, females.

We used an age-structured, matrix projection model (the Leslie matrix, see Pielou, 1977), with a discrete time step of 1 year for simulating the dynamics of the elephant population. In our model we modified the basic Leslie model to incorporate matrices for the female, tusked male and tuskless male (*makhna*) segments of the population.

The starting population (base year 1974) was taken to be 1000 individuals, based on population estimates from Periyar (Vijayan, 1980; Ramachandran, Nair & Easa, 1986; Karoor, 1990; Ramakrishnan *et al.*, 1998). The age structures of the male and female segments of the starting population were assumed to be similar to that reported by Sukumar (1989) for another southern Indian elephant population. The structure was slightly modified to change the adult male to female ratio from 1:5 (in Sukumar, 1989) to 1:6 as indicated by Kurup's (1971) data from Periyar. Among males the proportion of *makhnas* in the different age classes was again based on data from southern India summarized by Sukumar (1989), which indicated that *makhnas* constitute about 4% of juvenile classes and about 8% of the adult segment.

Fecundity rates

Births were taken to be probabilistic events. The fecundity rate (m_x) of a female aged x was dependent on her maximum potential fecundity at age x , and the adult sex ratio of the population at the time of conception (2 years prior to actual birth). Age-specific maximum fecundity was based on data in Sukumar (1989) and Sukumar, Krishnamurthy *et al.* (1997) and was taken to be 0.225 for ages 16–50 years and 0.2 for 51–60 years (Table 1).

Long-term demographic data from the Mudumalai-Bandipur population of elephants in southern India (unpublished data) indicated that birth rates are not depressed up to adult (>15 years) male to female ratios of about 1:20. With a large proportion of female elephants being already pregnant or in lactational anoestrus, the operational sex ratio for the purposes of mating in such a population would actually be much less skewed, being about 1:5 to 1:10. The precise adult sex ratio at which a reduction in conceptions and birth rate of the population begins to occur would obviously depend on population density, social organization and reproductive seasonality (Sukumar, 1989). For the present study, we assumed that the birth rate would be constant until an adult male to female ratio of 1:25, after which it would decline exponentially. Our demographic data from Periyar indicated that with an adult sex ratio skewing to about 1:100 the average fecundity rate had fallen to 0.075/adult female/year, or about one-third of the 'normal' fecundity rate (0.22) seen in other southern Indian populations. We thus used a drop factor (d), for adult female (F) to adult male (M) ratios greater than 25, to calculate this decline in Periyar as follows:

$$d = \exp(0.3134 - (0.0147 \times (F/M))), \quad (1)$$

$$m_x = m_x \times d. \quad (2)$$

A 1:1 ratio of male to female calves was assumed at

Table 1. Age specific schedules of female fecundity and female and male annual mortality under natural conditions and under the different poaching Scenarios (2–5).

Age class (years)	Female fecundity	Female mortality	Male mortality								
			Natural	Scenario 2		Scenario 3		Scenario 4		Scenario 5	
				Constant	Initial low	Later high	Background	Spurts	Background	Spurts	
<1	0.000	0.10	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	
1–3	0.000	0.04	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	
4–5	0.000	0.04	0.06	0.15	0.06	0.15	0.06	0.10	0.06	0.10	
6–10	0.000	0.015	0.08	0.25	0.15	0.25	0.20	0.35	0.15	0.35	
11–15	0.000	0.015	0.08	0.35	0.20	0.35	0.30	0.60	0.20	0.60	
16–20	0.225	0.03	0.08	0.35	0.20	0.35	0.30	0.60	0.20	0.60	
21–50	0.225	0.015	0.08	0.40	0.20	0.40	0.30	0.60	0.25	0.60	
51–60	0.200	0.10	0.15	0.40	0.20	0.40	0.35	0.70	0.25	0.60	

See text for further details.

birth. The male calves born had to be further divided into (potential) tuskers and *makhnas*. This requires detailed knowledge of the pattern of genetic inheritance of tusks in elephants, an aspect that is unknown at present. Dobson *et al.* (1992) used a simple, single-locus, two-allele model of tusk inheritance in African elephants (in which both the sexes have long tusks), while Tiedemann & Kurt (1995) used a similar model for the Asian elephant (in which only the male can possess long tusks) by assuming that the trait is not expressed in females. While an explicit population genetics model incorporating allelic inheritance would be essential to model the longer term (centuries or several elephant generations) changes in tusk inheritance patterns in an elephant population, our objective was to model the rates of poaching and ivory harvest on a short time scale (20 years, which is less than one elephant generation) using a simpler demographic model that would adequately reflect the tusker:*makhna* dynamics over this short period.

We therefore approached the problem of setting up our model in the following manner. Assume that an elephant population is not under any serious pressure from selective poaching of tuskers. Further assume that the population is under Hardy–Weinberg equilibrium with respect to allelic frequencies for tusk inheritance. With a single-locus, two-allele (T and t) model, the homozygous dominant (TT) and heterozygous (Tt) individuals are assumed to be tuskers, and homozygous recessive (tt) individuals are *makhnas* among males. The tusks are not expressed in females.

If we assume that *makhnas* constitute 4% and tuskers the remaining 96% of the male segment, a simple calculation based on the Hardy–Weinberg law indicates that the frequency of the two alleles are $T = 0.8$ and $t = 0.2$, and further that the genotypic frequencies are $TT = 0.64$ (tuskers), $Tt = 0.32$ (tuskers) and $tt = 0.04$ (*makhnas*). The genotypic frequencies are similar to the above among females in the population. Assuming random mating and no selective advantage for tuskers or *makhnas*, even if all tuskers (TT and Tt) were to be removed from the population at a given point in time, the male offspring resulting from matings between *makhnas* and females would be divided into 80% tuskers and 20% *makhnas*.

Data from Periyar during 1974–94 and some of our observations there during intermediary years show that all adult tuskers have not disappeared during this period. We can thus expect that the percentage of male calves born in the population that are tuskers would be greater than 80% of the male segment. We thus decided to use a simple assumption that 80% of all newborn males are tuskers, and divided the remaining 20% into tusker and *makhna* calves in proportion to the ratio of adult tuskers and *makhnas* (potential fathers) in the population at the time of conception (2 years prior to birth).

A tusker may also have a mating advantage over *makhnas* based on considerations of sexual selection and female choice (Watve & Sukumar, 1997). However, there are no field data to support such an expectation at present (D. K. Lahiri-Choudhury, pers. comm.). We therefore neglected this factor in our model. For the first 2 years of the model run we divided the male calves into 96% tuskers and 4% *makhnas* based on observed tusker to *makhna* ratios in southern Indian populations suffering only marginally from ivory poaching (Sukumar, 1989).

Mortality rates

Female age-specific mortality rates were based on long-term demographic data from the Nilgiri-Eastern Ghats population in southern India (Sukumar, 1989, and unpublished results). Typically, the mortality rates are high (8% or more per annum) during the first year, come down to about 4% during the juvenile years (1–5 years) and are very low (1.5%) during the subadult (5–15 years) and adult (>15 years) stages. Higher mortalities associated with the risks of first calving (during ages 15–20 years) and old age (>50 years) are also indicated. These female mortality rates, associated with the normal age-specific fecundity rates indicated above, result in population growth rates of about 2% per annum (intrinsic $r = 0.02$) assuming deterministic dynamics.

The main aspect of modelling was obviously to determine male mortality rates. We estimated these rates iteratively in the following manner.

First, the baseline ‘natural’ mortality rate of male elephants in the population, assuming the absence of ivory poaching but including some deaths during

conflict with people (deaths during crop raiding, for instance, see Sukumar, 1989), was assumed to be similar to that operating in Sri Lanka, where most male elephants are tuskless and thus poaching for ivory is negligible at present. The adult male to female ratio in this elephant population is about 1:3. A simulation was run in which age-specific male mortalities were adjusted so as to obtain a stable age distribution (Fig. 1) with an adult male to female ratio of about 1:3. These age-specific mortality rates were then fixed as the 'natural' mortality rates for males (Table 1, see also Sukumar, 1989).

Second, for each different scenario of poaching (i.e. constant mortality rate or fluctuating rates over the 20 year period) we simulated the baseline 1974 population (1000 individuals, adult male to female ratio of 1:6) over the next 20 years. The mortality rates for *makhnas* were fixed as those (simulated to operate) in the Sri Lankan population (Table 1). Mortality rates of tuskers were iteratively increased so as to obtain, at the end of 20 years, an adult male to female ratio of approximately 1:100. While increasing the male mortality rates it was assumed that male tuskers are susceptible to poaching only from age 3 onwards.

At each time step (annually) we considered the number of male elephants in each age class (1 year) that would have died under each of the two mortality rates, the natural rate and the increased rate. The difference was taken as the number that had died in each age class each year due to poaching. This was summed over the 20 year period of the simulation to give an estimate of the total number of elephants poached for ivory. Thus:

$$T^* = \sum_{i=1}^{20} \sum_{j=4}^{60} T_{ij} (p'_j - p_j), \quad (3)$$

where T^* is the number of tuskers of all ages ($j = 4 - 60$) poached over all years ($i = 1 - 20$); T_{ij} is the number of tuskers that survived from age $j - 1$ to age j in year i in the absence of poaching; p'_j is the probability of tuskers aged j surviving to age $j + 1$ in the absence of poaching, and p_j is the probability of tuskers aged j surviving to age $j + 1$ in the presence of poaching.

Five scenarios were considered (see Table 1). Maximum longevity of individual elephants was taken to be 60 years in all cases.

Scenario 1: This was the 'control' scenario in which it was assumed that no poaching occurred during the first 19 years. The starting population of 1000 individuals with an adult male to female ratio of 1:6 was simulated using the male mortality rates assumed to be the 'natural' rates. At the end of 19 years the simulated male age structure was compared with the observed 1994 age structure at Periyar, and the difference or 'missing' males in each age class assumed to have been poached during the last (20th) year. This obviously was not the scenario that had occurred at Periyar because the paucity of adult males had been recorded long before 1994.

Scenario 2: In this scenario the enhanced male mortality rates were taken to be constant over the 20 year period of the simulation. The starting population was 1000 individuals with a sex ratio of 1:6 during 1974.

Scenario 3: The rates of mortality due to poaching were taken to be low during the first 5 years, and then high during years 6–20. The reasoning behind this was that a constant mortality rate implied very high harvests of males during the first 2 years (thus, with a 40% mortality rate of adults, the adult male segment would have been reduced to 36% of the original numbers by the end of the second year, assuming no transition of individuals from the subadult classes). It was more realistic to assume that even if poachers killed a substantial number of elephants in the initial years, the mortality rates these represented were still on the lower side because of the large numbers of males to begin with. As the number of males was reduced in the population the rates of mortality would increase if poachers continued to harvest equal numbers of individuals each year. Other conditions were similar to those in the previous scenario.

Scenario 4: In this scenario we assumed a certain background rate of mortality due to poaching, and enhanced mortality rates due to spurts of poaching during years 5, 10 and 15 of the simulation. All other conditions were similar to those in the previous two scenarios.

Scenario 5: This was similar to Scenario 4, but with enhanced mortality due to spurts in poaching during years 2, 5, 8, 11, 14 and 17.

In order to estimate the quantity of ivory harvested by poachers each year, from each age class, and from the population over the 20 year period, we used figures for the mean weights of tusks for each age class from Sukumar, Joshi & Krishnamurthy (1988) and Sukumar (1989). For each individual killed we took the weight of a pair of tusks for the calculation.

RESULTS

Trends in population numbers

The total population size under all scenarios increases initially and then declines slowly under Scenarios 2–5 (Fig. 2). The final population sizes under all scenarios, with the exception of Scenario 5, are higher than the initial sizes by year 20. In the absence of poaching (Scenario 1, not illustrated) the number of females increases steadily from the initial size of 723 to 928 individuals by year 19. Under the four scenarios (2–5) of poaching the number of females in the population initially increases until year 10–12, and then stabilizes or declines (Fig. 2) as adult sex ratios become extremely skewed and the fecundity rates decline steeply.

Trends in the number of males are more variable (Figs 2 and 3). Under Scenario 2 the total number of tuskers

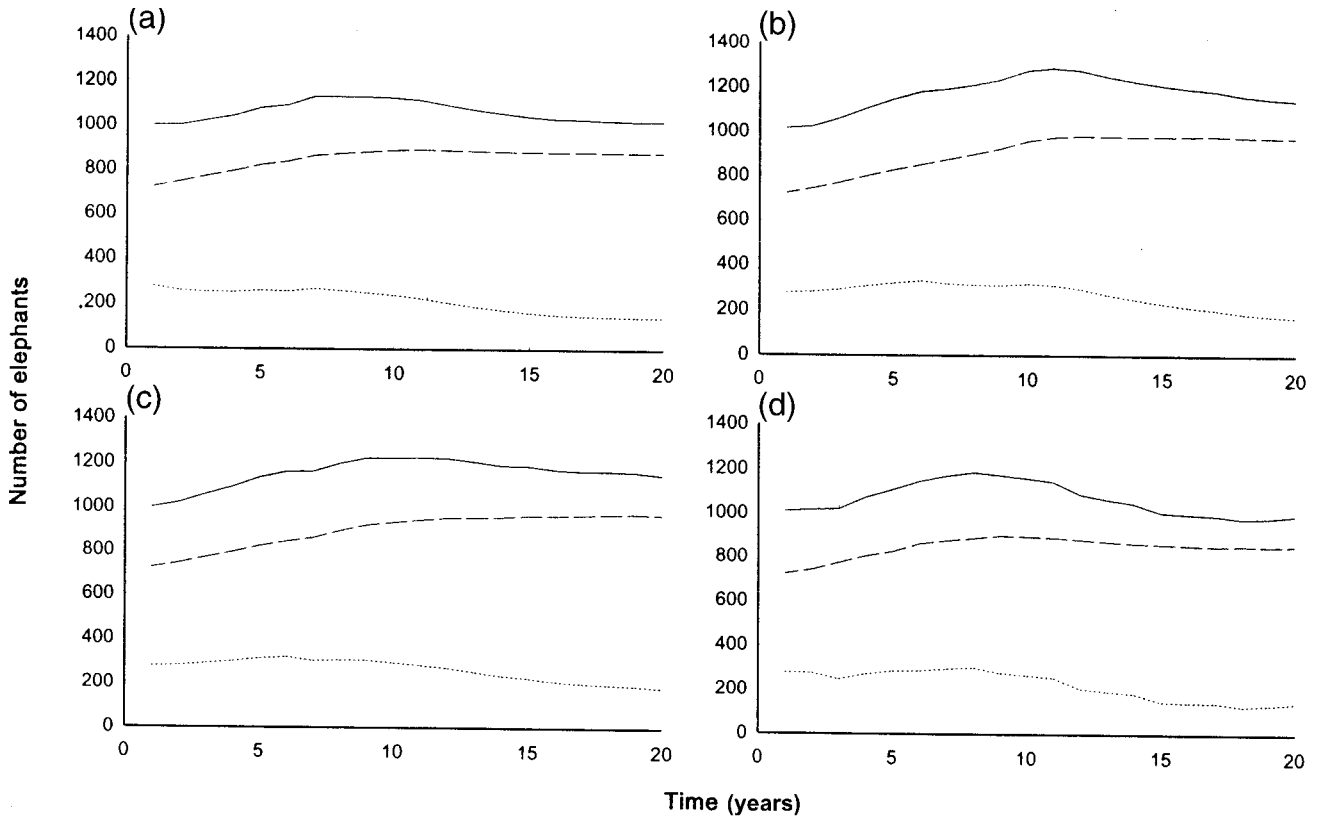


Fig. 2. Simulated trends over a 20 year period (1974–94) in: —, total population size of elephants; ---, total females; and ..., total males under different scenarios of poaching at Periyar. (a) Scenario 2; (b) Scenario 3; (c) Scenario 4; (d) Scenario 5.

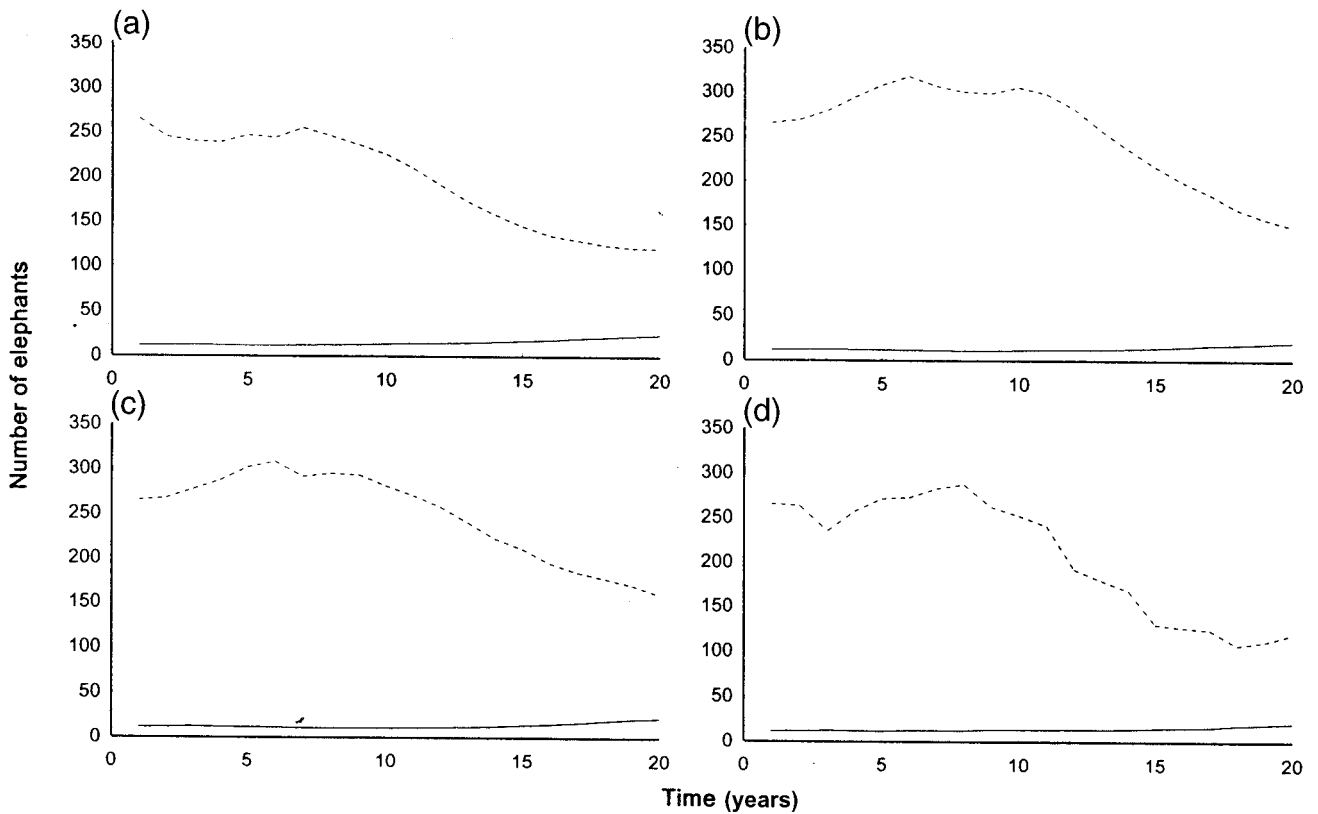


Fig. 3. Simulated trends over a 20 year period in total numbers of tusked males (tuskers, ---) and tuskedless males (*makhnas*, —) under different poaching scenarios at Periyar. (a) Scenario 2; (b) Scenario 3; (c) Scenario 4; (d) Scenario 5.

remains relatively steady or declines only marginally until year 8, when it then declines noticeably. Under Scenario 3 the number of tuskers actually increases, largely due to increases in calf and juvenile classes, until year 10, before starting to decline. Under Scenario 4 the tusker segment also increases until year 6, and

declines later. Scenario 5 with several poaching spurts shows fluctuations in tusker numbers for the first 8 years before starting to clearly decline. The total number of *makhnas* increases gradually from about 10 individuals to reach about 20–24 individuals by year 20 in all the scenarios.

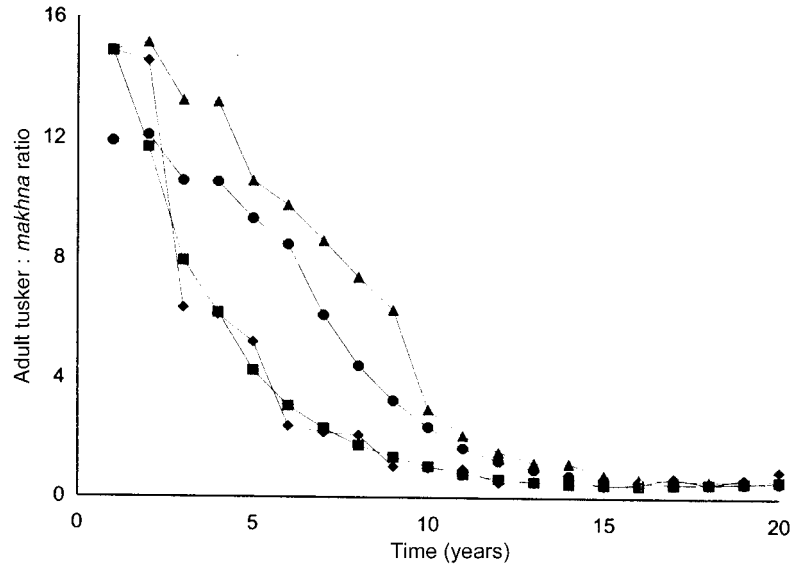


Fig. 4. Simulated trends over a 20 year period in the adult (>15 years) tusker to *makhna* ratio under different poaching scenarios at Periyar. ■, Scenario 2; ●, Scenario 3; ▲, Scenario 4; ◆, Scenario 5.

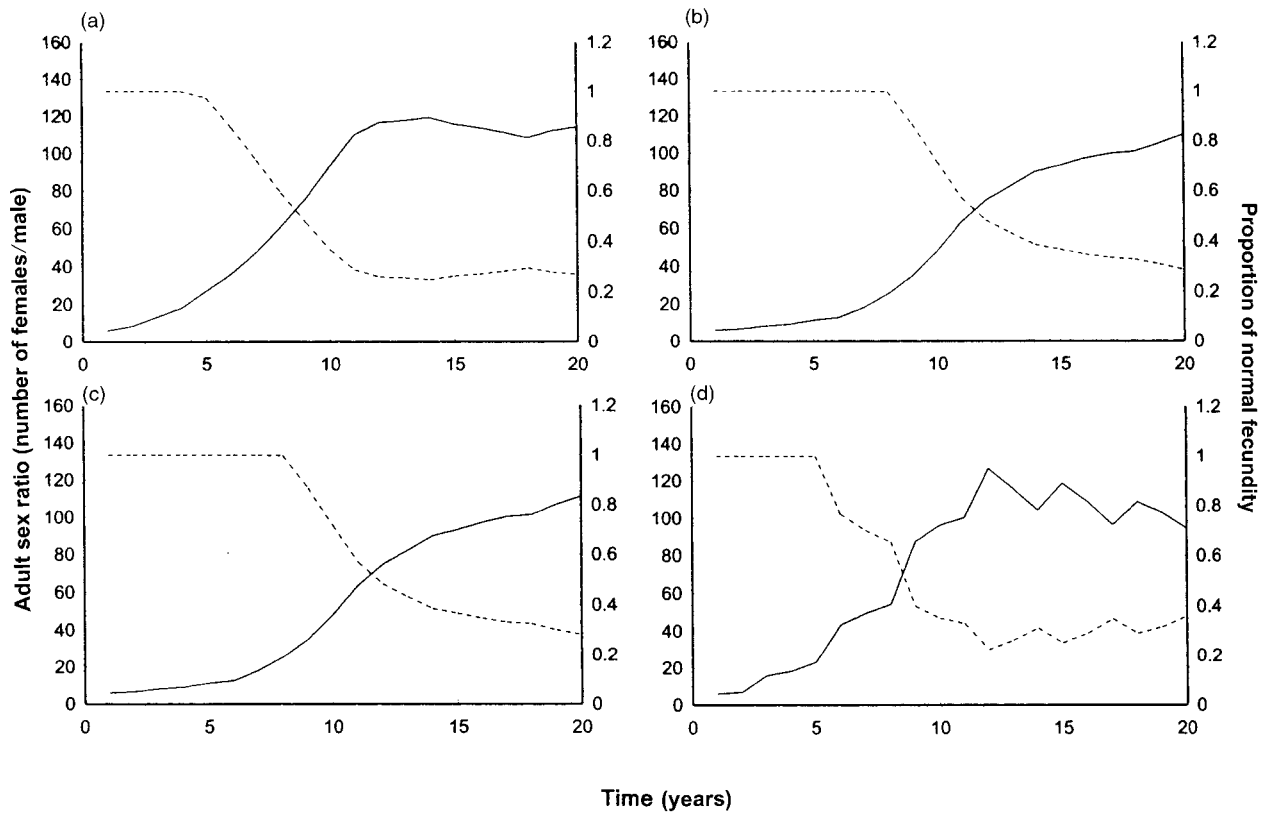


Fig. 5. Simulated trends over a 20 year period in the adult (>15 years) female to male ratio (—), and proportional reduction in average female fecundity from the normal fecundity (---). (a) Scenario 2; (b) Scenario 3; (c) Scenario 4; (d) Scenario 5.

The ratio of adult (>15 years) tuskers to *makhnas*, beginning at 23:1, changes rapidly to 1:1 between years 10 and 14 and changes further to 0.6:1 by year 20, in Scenarios 2, 3 and 4 (Fig. 4). In Scenario 5, with spurts in poaching, this ratio reaches 1:1 by year 10 and fluctuates thereafter at between 0.5 and 1 adult tusk per *makhna*. This compares well with the observed adult tusk:*makhna* ratio of 1:1 (3 tuskers and 3 *makhnas* recorded during the study).

Trends in adult sex ratio

The ratio of adult (>15 years) males to females skews from the initial ratio of 1:6 to a peak of about 1:120 between years 12 and 14 under Scenarios 2 and 5, before dropping back to about 1:114 and 1:95, respectively, by year 20 (Fig. 5). In Scenario 3 and 4 the ratios climb steadily to their peak of about 1:110 by year 20. Sex ratios would have become even more skewed but for the presence of a few adult *makhnas* in the population.

Trends in female fecundity

The initial fecundity rate of about 0.22 begins to drop when the adult sex ratio becomes more skewed than a ratio of 1:25 between years 5 and 8 in the different

poaching scenarios (Fig. 5). Fecundities reach a low of about 21–25% of the initial rates anywhere between years 12 and 20, corresponding to the sex ratios attaining their peak skewness. By year 20 the average female fecundity is still only about 30% of the initial rate.

Age distribution of poached elephants

As the number of older tuskers in the population declines with poaching, there is a shift towards a harvest of younger tuskers. After year 10 the poaching is confined almost exclusively to tuskers under 20 years of age (Fig. 6).

Numbers of poached elephants and ivory harvested

The distribution of poaching over the 20 year period is obviously related to the mortality patterns initially defined for the different scenarios, and no real significance should be attached to these results, except that the number of tuskers killed broadly declines with time.

Under Scenario 1 the number of tuskers ‘missing’ at the end of year 20 is 435 individuals over all age classes. The number of tuskers simulated to be poached during the 20 year period under Scenarios 2, 3, 4 and 5 are 372, 388, 336 and 340, respectively (Fig. 7). The age

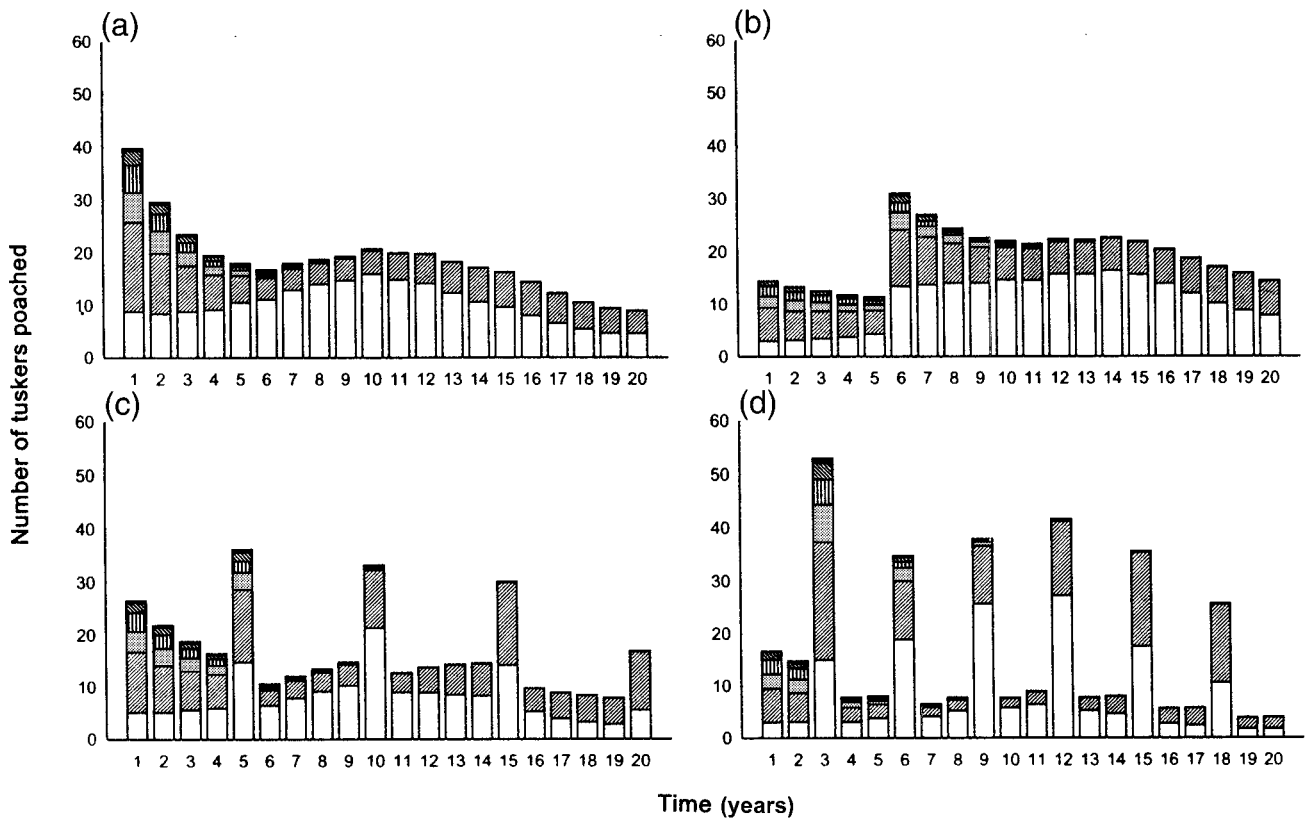


Fig. 6. Simulated numbers of tuskers poached in the different age classes each year over a 20 year period under various poaching scenarios at Periyar. Age classes are: □, 1–10 years; ▨, 11–20 years; ▩, 21–30 years; ▪, 31–40 years; ▮, 41–50 years; ■, 51–60 years. (a) Scenario 2; (b) Scenario 3; (c) Scenario 4; (d) Scenario 5.

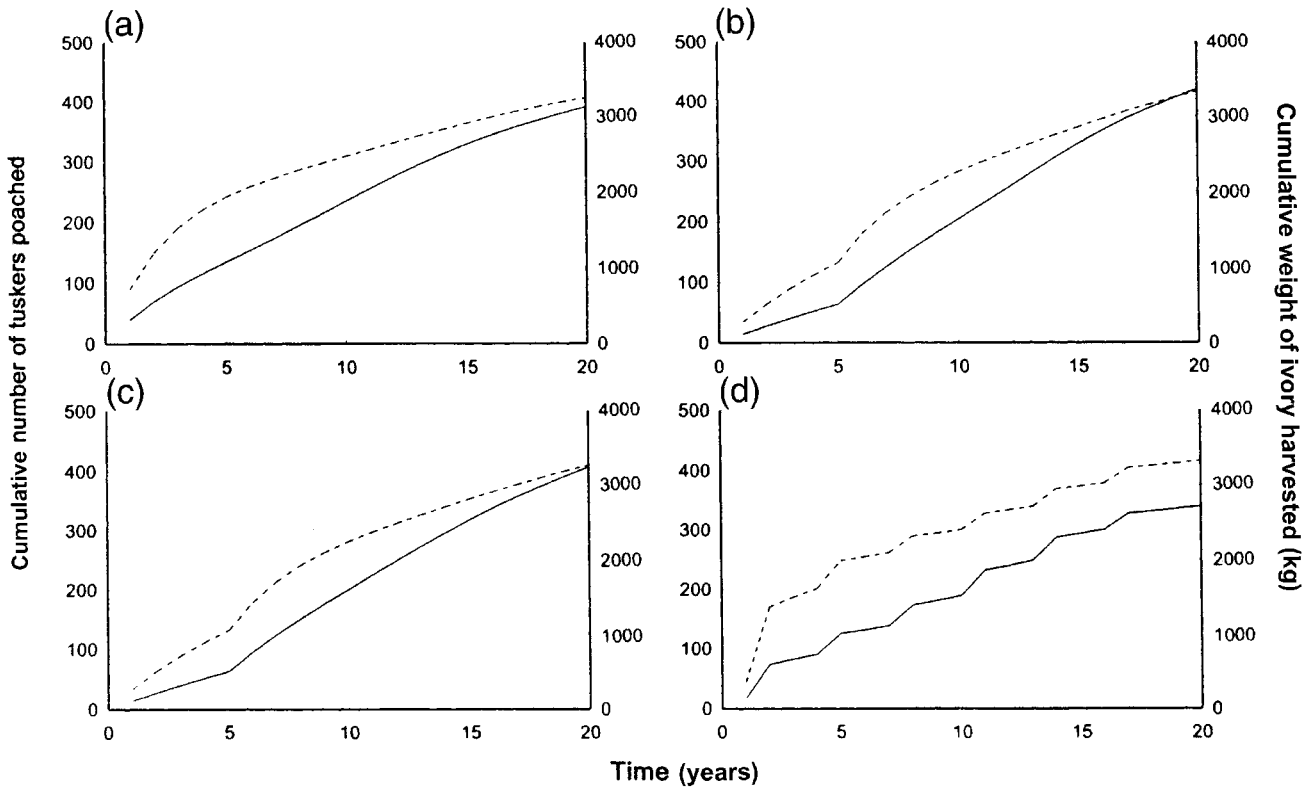


Fig. 7. Cumulative numbers of tuskers poached (—) and cumulative weights of ivory harvested (---) over a 20 year period under different poaching scenarios at Periyar. (a) Scenario 2; (b) Scenario 3; (c) Scenario 4; (d) Scenario 5.

distribution of poached elephants over this period is shown as an average of these four scenarios in Fig. 8. The harvest by poachers is predominantly in the younger age classes, with an average of 188 and 133 tuskers killed in the <10 years and 10–20 year age classes, respectively.

The quantity of ivory estimated to have been removed by poachers is 3147 kg under Scenario 1. Under the other scenarios there is a remarkable similarity in the quantities simulated to be harvested, being 3256 kg, 3334 kg, 3280 kg and 3328 kg under Scenarios 2, 3, 4 and 5 respectively (Fig. 7). The quantities of ivory obtained from the different age classes over the 20 year period of the simulation are averaged for the last four scenarios in Fig. 8. The maximum harvest of ivory (1358 kg on average) comes from the 10–20 year age class. The mean weight of a pair of tusks declines from about 16.5 kg during the first year (1975) of harvest to 6.7 kg by year 20 (1994) (Fig. 9)

DISCUSSION

Before the significance of the results are discussed, we should consider how realistically the model behaves by comparing the age structures of males and females from the simulated populations under the different scenarios with the observed age structure of the Periyar population during 1994–95. This comparison between the simulated and the observed data is summarized in Table 2.

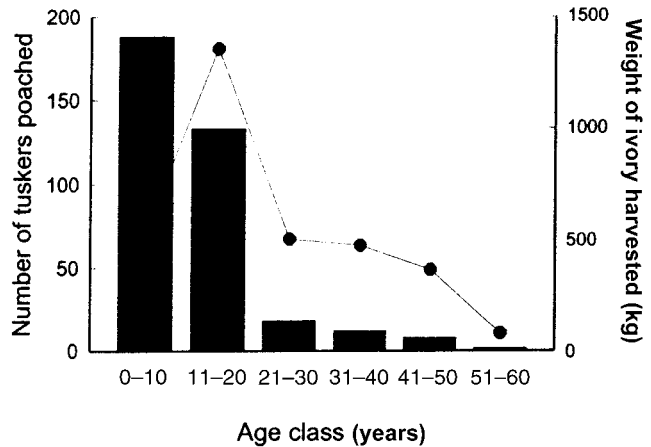


Fig. 8. Total numbers of tuskers poached (■) and weight of ivory harvested (●) from the different age classes averaged over the four scenarios of poaching at Periyar.

Given the complexities of simulating demography in populations with unstable age distributions, the overall match between the simulated and observed data is extremely good. Thus, in all simulated populations the proportion of adult males is about 0.5% of the population, which is what we aimed to achieve in the first place, on the basis of our observed data. In achieving this the simulated proportions of adult females also closely matched the observed data. This varies from 50.1% to 58.7% in the simulated populations, compared with

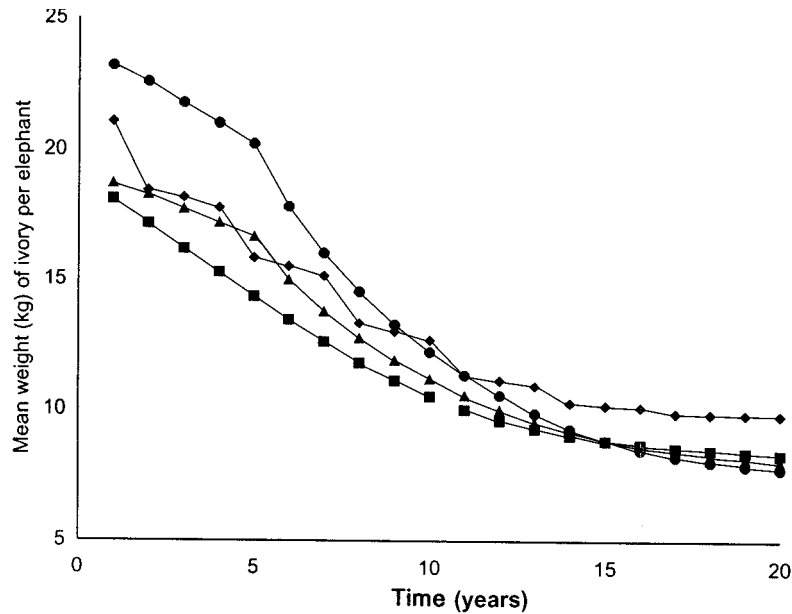


Fig. 9. Trends in mean weights of ivory harvested over 20 years under the four poaching scenarios at Periyar. ■, Scenario 2; ●, Scenario 3; ▲, Scenario 4; ◆, Scenario 5.

51.9% in the observed population (Scenarios 3 and 4 match the observed figure very closely). Simulated and observed subadult females are also similar, with observed juvenile females being in slight excess of the corresponding simulated figures. The proportion of calves, which reflects the fecundity of the population, is also very closely matched between the simulated (4.0–5.0% for both sexes combined) and observed figure (3.9%) by year 20. Overall, Scenarios 3 and 4 match the observed age structures best, while Scenarios 2 and 5 match the total population size estimated for 1994, and also replicate the time series data on adult sex ratios by matching the 1:122 ratio reported by Chandran (1990) during 1987–89.

The observed numbers and proportions of juvenile and subadult males in the population are, however, somewhat deficient when compared to the simulated figures for these age classes. This indicates that ivory poaching of these younger age classes may be more serious than is shown by our estimates. Furthermore, the number of *makhnas* in the juvenile and subadult classes simulated by the model under the different scenarios is still slightly in excess of that observed in the population. There is of course the possibility that we may have slightly underestimated the number of young males in the population

through failure to recognize some young *makhnas* within family groups in the field.

What is the significance of ivory poaching from Periyar to the overall trade in illegal ivory in India? Data on ivory poaching in India are still very deficient and are only now beginning to emerge on a countrywide scale (Menon *et al.*, 1997). On the regional scale for southern India an estimate of 1800 kg of ivory harvested by poachers each year during 1980–87 was made by Sukumar (1989). Our simulated figures give an average estimate of 153 kg of ivory harvested each year from Periyar during the same period. Thus, the Periyar population may have provided just under 10% of the total ivory taken illegally in southern India during the 1980s. With high rates of poaching during the 1970s, the age structure of the male segment at Periyar had obviously shifted to younger animals with a corresponding reduction in mean tusk weight. The mean tusk weight of poached ivory for the Nilgiri-Eastern Ghats elephant population during 1980–87 was calculated to be 9.5 kg per tusk, compared with only 3.9 kg (simulated figures) per tusk for Periyar during this time. The possibility of poachers and ivory traders shifting their attention from a depleted area to a more lucrative one has been discussed by Sukumar (1989). Thus, Periyar may have been

Table 2. Observed (1994–95) and simulated age structure (percentage) under the various poaching Scenarios (2–5) for the Periyar elephant population

Age class	Observed		Scenario 2		Scenario 3		Scenario 4		Scenario 5	
	F	M	F	M	F	M	F	M	F	M
Calf (<1 year)	2.1	1.8	2.3	2.3	2.1	2.1	2.0	2.0	2.5	2.5
Juvenile (1–5 years)	10.2	4.9	7.2	6.5	7.2	6.4	8.2	7.4	6.4	5.9
Subadult (5–15 years)	25.1	3.5	19.7	4.7	25.2	5.8	24.0	5.9	18.2	5.1
Adult (>15 years)	51.9	0.5	56.8	0.5	50.7	0.5	50.1	0.5	58.7	0.6

a more important source of ivory to the illegal trade during the 1970s, after which the poachers shifted to other populations with larger numbers of tuskers.

The skewed adult sex ratio at Periyar is the most disparate recorded for any major Asian elephant population or, for that matter, any African elephant population. With an adult sex ratio of 1:101 and a total population of 1166 (605 adult females, 6 adult males), the genetically effective population size (N_e) considering only the female-biased sex ratio, is calculated to be 24. Thus, N_e is at best only 2% of the total population and 4% of the breeding population, assuming that all adults are potentially capable of breeding. Compared with this, N_e may be 40% and 77% of the total and adult populations, respectively, in Sri Lanka (Sukumar, 1995).

The demographic and genetic consequences of a skewed sex ratio may be even more serious in Periyar. Field observations indicate that, apart from a much lower average fecundity in the population, a certain proportion of females aged >15 years may be reproductively barren. Certain family groups consist of only subadult and adult females with no young below the age of 7 years. The large females show no signs of mammary gland activity and have retracted nipples. It is possible that the reproductive physiology of such females has been disrupted, similar to that of many female elephants kept in zoos. Such family group compositions and female condition have never been observed by us in the course of over 17 years of observation of elephants in the Nilgiris and Eastern Ghats, where adult males are much more common. The relationship between the disruption of the reproductive physiology in females and the paucity of adult males in the population is not clear. Population growth rates calculated from the simulations indicate an overall increase over the first 10 year period but a general decline over the next 10 years. The growth rates are between -1.5% and -0.6% per annum for the whole population or between -0.5% and +0.4% for the female segment of the population under the various scenarios.

In any case, the present demographic situation of elephants at Periyar calls for remedial management measures. Habitats outside the Periyar Reserve should also be surveyed for the possible presence or absence of subadult and adult male elephants. Apart from ensuring that they are protected against ivory poaching, there is a need for augmenting the adult male segment by translocating bulls from other areas into Periyar. If females also carry genes for tusks, the potential for the birth of tusked males in future in the population would largely remain intact. Combined with an increase in N_e through the translocation of bulls, after genetic and health screening, the population can be nursed back to a healthy, viable one.

Acknowledgements

This study was funded by the Ministry of Environment and Forests, New Delhi. Funding for the preliminary survey was provided through the IUCN Asian Elephant Specialist Group by the Calgary Zoological Society and Wildlife Preservation Trust International. We thank the

Forest Department of Kerala for research permissions at Periyar. A. K. Bharadwaj and James Zackariah are especially thanked for their assistance during the field work.

REFERENCES

- Chandran, P. M. (1990). Population dynamics of elephants in Periyar Tiger Reserve, Kerala. In *The proceedings of the elephant symposium*: 51–56. Karunakaran, C. K. (Ed.). Thiruvananthapuram: Kerala Forest Department.
- Dobson, A., Mace, G. M., Poole, J. & Brett, R. A. (1992). Conservation biology: the ecology and genetics of endangered species. In *Genes in ecology*: 405–430. Berry, R. J., Crawford, T. J. & Hewitt, G. M. (Eds.). Oxford: Blackwell Scientific.
- Douglas-Hamilton, I. (1988). The great East African elephant disaster. *Swara* **10**: 8–11.
- Dublin, H. T., Milliken, T. & Barnes, R. F. W. (1995). *Four years after the CITES ban: illegal killing of elephants, ivory trade and stockpiles*. A report of the IUCN/SSC African Elephant Specialist Group.
- Karoor, J. J. (1990). Some aspects of the ecology and behaviour of Asiatic elephants in the Periyar Tiger Reserve, Kerala. In *The proceedings of the elephant symposium*: 97–104. Karunakaran, C. K. (Ed.). Thiruvananthapuram: Kerala Forest Department.
- Krishnan, M. (1972). An ecological survey of the large mammals of peninsular India. The Indian elephant. *J. Bombay Nat. Hist. Soc.* **69**: 297–315.
- Kurt, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In *The behaviour of ungulates and its relation to management*: 618–634. Geist, V. & Walther, F. (Eds.). Morges, Switzerland: IUCN Publications, New Series no. 24.
- Kurup, G. U. (1971). A preliminary ecological survey of the Periyar Wildlife Sanctuary, Kerala State. *Cheetal* **13**: 5–18.
- Menon, V., Sukumar, R. & Kumar, A. (1997). *A God in distress: threats of poaching and the ivory trade to the Asian elephant in India*. Bangalore: Asian Elephant Conservation Centre. New Delhi: Wildlife Protection Society of India.
- Pielou, E. C. (Ed.) (1977). *Mathematical ecology*. New York: Wiley-Interscience.
- Poole, J. & Thomsen, J. B. (1989). Elephants are not beetles: implications of the ivory trade for the survival of the African elephant. *Oryx* **23**: 188–189.
- Ramachandran, K. K., Nair, P. V. & Easa, P. S. (1986). Ecology of larger mammals of Periyar Wildlife Sanctuary. *J. Bombay Nat. Hist. Soc.* **83**: 505–524.
- Ramakrishnan, U., Santosh, J. A., Ramakrishnan, U. & Sukumar, R. (1998). The population and conservation status of Asian elephants in the Periyar Tiger Reserve, southern India. *Curr. Sci.* **74**: 110–113.
- Santiapillai, C. & Suprahman, H. (1986). *The ecology of the elephant (Elephas maximus L.) in the Way Kambas Game Reserve, Sumatra*. WWF/IUCN 3133 Final report, Bogor, April 1986.
- Sukumar, R. (1989). *The Asian elephant: ecology and management*. Cambridge: Cambridge University Press.
- Sukumar, R. (1995). Minimum viable populations for Asian elephant conservation. In *A week with elephants*: 279–288. Daniel, J. C. & Datye, H. (Eds.). Bombay: Bombay Natural History Society. New Delhi: Oxford University Press.
- Sukumar, R., Joshi, N. V. & Krishnamurthy, V. (1988). Growth in the Asian elephant. *Proc. Indian Acad. Sci. (Anim. Sci.)* **97**: 561–571.
- Sukumar, R., Krishnamurthy, V., Wemmer, C. & Rodden, M. (1997). Demography of captive Asian elephants (*Elephas maximus*) in southern India. *Zoo Biol.* **16**: 263–272.
- Sukumar, R. & Santiapillai, C. (1996). *Elephas maximus*: status and distribution. In *The Proboscidea: evolution and palaeoecology of elephants and their relatives*: 327–331. Shoshani, J.

- & Tassy, P. (Eds). New York: Oxford University Press.
- Tiedemann, R. & Kurt, F. (1995). A stochastic simulation model for Asian elephant *Elephas maximus* populations and the inheritance of tusks. *Acta Theriol. suppl.* **3**: 111–124.
- Vijayan, V. S. (1980). Status of elephants in Periyar Tiger Reserve. In *The status of the Asian elephant in the Indian sub-continent*: 31–34. Daniel, J. C. (Ed.). IUCN/SSC Report. Bombay: Bombay Natural History Society.
- Watve, M. G. & Sukumar, R. (1997). Asian elephants with longer tusks have lower parasite loads. *Curr. Sci.* **72**: 885–888.
- Western, D. (1987). Africa's elephants and rhinos: flagships in crisis. *Trends Ecol. Evol.* **2**: 343–346.