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MINIMUM VIABLE POPULATIONS FOR ASIAN ELEPHANT CONSERVATION

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(With a text-figure)

The dynamics of an elephant population was simulated using the stochastic model VORTEX, to determine its probability of survival under different scenarios of birth and death rates, sex ratios, population sizes, environmental variation and catastrophes. Initial population sizes were varied from 15 to 75 individuals, potential (deterministic) intrinsic growth rates (r) from 0 to 0.02 (by adjusting birth and death probabilities), adult male to female ratio from 1:4 to 1:16, environmental variation from 20% to 40% (SD) of death rates. Two types of catastrophes were also incorporated into the model. All simulations were run 1000 times for 100 years.

The results showed that a population of 100-200 elephants, depending on demography, sex ratio and ecological pressures, would have a high (>99%) probability of survival for 100 years in the face of demographic and environmental stochasticity, and possibly genetic erosion in the short term. The goal of managers could thus be to maintain these minimum sizes in small isolated populations for short term conservation; in the long term much higher numbers would be needed to maintain the evolutionary potential of a population.

INTRODUCTION

It is common knowledge that the smaller the size of a species population the higher the risk of it becoming extinct. This extinction need not be caused merely by deterministic ecological processes such as habitat destruction or hunting but also by chance factors operating on birth and death processes. Thus in a small population all the mature females may fail to reproduce in a given year drawing it into the "extinction vortex", or all the individuals may die within a short time span due to chance alone.

For small populations it is thus meaningless to talk of average birth, death or population growth rates. Deterministic models of population dynamics provide a reasonably robust approximation of average long-term demographic trends in large populations. These models are, however, quite inadequate for small populations in which not only demographic stochasticity but environmental and genetic stochasticity or catastrophes may also drive the population to extinction, even though life table analysis may indicate that the population has on average a positive growth rate.

Small population biology is especially relevant to the conservation of Asian elephants. Loss and fragmentation of habitat, a process that still

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continues, has given rise to numerous small, isolated elephant populations in most Asian countries (Sukumar 1989, Santiapillai and Jackson 1990).

Definitions

It is important to first define some of the terms such as "population viability analysis", "population vulnerability analysis", "minimum viable population" and "effective population size" commonly used in the conservation biology literature on small population biology. Desai (1991) while discussing these with reference to elephants, for instance, wrongly uses the term "minimum viable population" when the appropriate term would have been "effective population size".

1. Population viability analysis (PVA) is a process that evaluates data and models for a species population in order to give a probability that it will survive for an arbitrarily chosen time into the future (Boyce 1992). PVAs usually rely on simulation methods using a computer because analytical methods are extremely complicated and beyond the comprehension of most biologists (and perhaps the average mathematician). PVA thus encompasses the concept of minimum viable population and provides useful inputs to management decisions for a population (see Soulé 1987 for a review).

2. Population vulnerability analysis is the negative appellation of population viability analysis.

3. Effective population size (N_e) is the number of animals that would yield the same amount of genetic drift as it were an "ideal" constant population under random mating, equal sex-ratio and random distribution of offspring among parents. Only reproductive animals are considered for computing N_e. Thus, if the adult sex ratio is equal, the effective population size is the same as the total number of adults (N_a). With skewed sex ratios, however, the value of N_e progressively becomes smaller than N_a. N_e is equal to $4(N_m \times N_f)/(N_m + N_f)$, where N_m and N_f are the number of breeding males and females respectively.

4. Minimum viable population (MVP) is that which has a pre-defined probability of surviving for a given period of time. The continued survival of a population can be expressed only in probabilistic terms (Shaffer 1981). Thus, the MVP is usually expressed as that which has a 95% (or 99%) chance of surviving to 200 (or 1000) years. The MVP thus varies from one species to another and from one population to another, depending on their peculiar demographic, environmental and genetic factors, and most important, on one's personal definition of MVP in probabilistic terms. A population ecologist may define MVP as one that has a 99% chance of surviving for 1000 years (cf. Shaffer 1981); a

reserve manager may deem it to fit to continue *in situ* conservation measures for a population that has a 90% chance of surviving for 100 years.

Population viability analysis is thus a process that can yield different values of minimum viable population (Boyce 1992). The results I report in this talk are based on preliminary analyses and provides a first approximation of the MVP in Asian elephants. For this I used the programme VORTEX (Lacy 1993) which has capabilities for modelling demographic, environmental and genetic stochasticity, catastrophes and trends in carrying capacity.

Stochastic Modelling

Most of the population parameters, such as birth and death probabilities, used in the modelling are based on data obtained from my study of the Nilgiri - Eastern Ghats population in southern India (Sukumar 1989 and unpublished results). Female elephants were assumed to begin reproduction at 15 years and continue to do so until 60 years of age. In a given year 80% of the adult male segment was in the breeding pool.

Population processes are modelled as discrete, sequential events, with probabilistic outcomes determined by Monte Carlo simulation. Demographic stochasticity is modelled by taking birth and death probabilities as corresponding to observed average annual rates obtained from field data. In the first round of modelling, birth probability was taken as 0.20 to 0.22/mature female/year, while annual age-specific death probabilities were varied as follows:

Female elephants: 10-15% (age 0-1 year), 4-8% (age 1-5 years), 2-3% (age 5-15 years) and 1.5 - 3.2% (above 15 years).

Male elephants: 15% (0-1 year), 8% (1 - 5 years), 6-16 % (5 - 15 years), 6 - 16% (above 15 years).

The parameters were adjusted so as to yield a desired growth rate and sex ratio under a deterministic life table analysis.

Environmental stochasticity is modelled as variation in annual birth and death probabilities by sampling binomial distributions, with the standard deviation (SD) specifying the annual fluctuations. Two populations were simulated, one with a SD equal to 20% and another equal to 40% of the average probabilities of death. SD in fertility was taken to be 5.0 and 10.0 for the two populations respectively, the later reflecting the variance observed in the study population (also see Douglas-Hamilton 1972).

Two types of catastrophes were modelled, the first (such as a severe drought) with a 2% probability of reducing reproduction to 60% and survivorship to 80% (see Corfield 1973 for drought-related mortality at

Tsavo) of the normal values, and the second (such as a disease epidemic) with a 0.5% probability of reducing survivorship to 75% of the normal value.

The carrying capacity (k) was set at 150 (SD=30); this was much higher than the initial sizes of simulated populations. There was no trend projected in carrying capacity. For many elephant populations this would obviously decrease in the future as their habitat is constricted.

Age and sex-structure of the initial population were adjusted to begin with the stable age distribution. Adult sex ratios at stable age distribution under the first scenario were in the range of 1 adult male for every 3-4 adult female, representative of a natural population not under any serious threat from ivory poaching. These were later varied by increasing male mortality so as to result in adult M:F ratio of 1:8 and 1:16.

Inbreeding depression was incorporated using a "Heterosis model" in which homozygotes have reduced juvenile survival as compared to heterozygotes. In the absence of specific data for elephants the median value of 3.14 lethal equivalents per diploid genome for mammals reported by Ralls *et al.* (1988) was used.

Simulations were run 1000 times for 100 years for scenarios without inbreeding depression and 500 times for 100 years with inbreeding incorporated (inclusion of inbreeding depression slows down the simulation process considerably and it is usually not practical to run simulations 1000 times unless a very fast computer is available).

RESULTS

Fig. 1a & b show the probability of survival for 100 years as a function of population size for populations with different intrinsic or deterministic growth rates (r) from 0 to 0.02 as calculated from life table analysis of the female segment of the population. The actual growth rate based on stochastic dynamics would, of course, be lower than the deterministic rates.

To ensure a 99% probability of survival for 100 years, the minimum population sizes required are about 25-30 for one growing at r=0.02 (about 2% per year) and 65-80 for those growing slowly at r=0.005 (0.5% per year) or remaining stable. When the probabilities of the two types of catastrophes are doubled for the population with deterministic r=0.02, a population of 45 animals has a 99% of surviving for 100 years.

The survival probabilities for the two populations with low and moderate levels of environmental variance were hardly distinguishable. This implies that a long-lived K-selected mammal such as the elephant is relatively well buffered against environmental stochasticity.

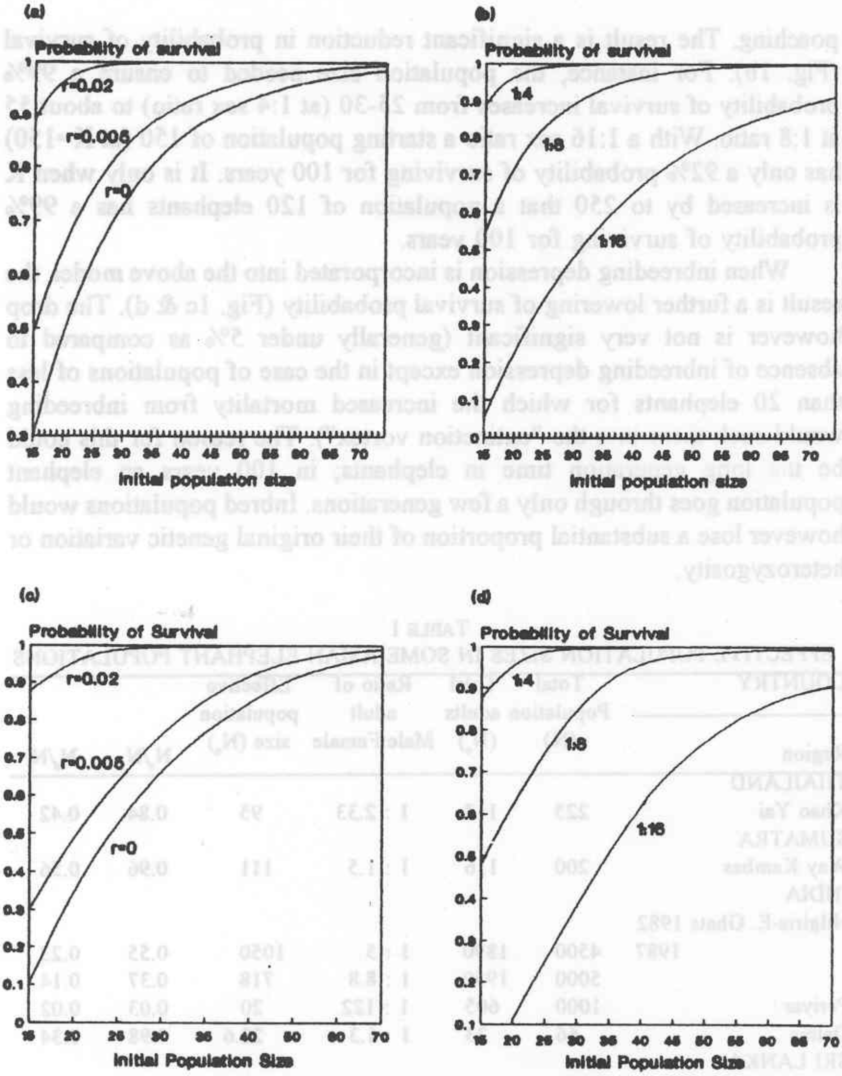

Fig.1. Probability of survival for 100 years as a function of initial population size for populations with: a) Deterministic growth rate r =0.02, 0.005 and 0, adult sex ratio of M:F = 1:4, without inbreeding depression. b) Adult sex ratio of M:F = 1:4, 1:8 and 1:16, deterministic growth rate r = 0.02, without inbreeding depression. c) Same conditions as a) but with inbreeding depression. d) Same conditions as b) but with inbreeding depression.

For the population potentially increasing at r=0.02, the male mortality rates were increased so as to result in more skewed adult sex ratios (adult male : female ratio going from 1:4 to 1:16) at stable age distribution. This would reflect the trends seen in many Asian (Sukumar 1989) and African elephant populations (Poole & Thomsen 1989) suffering from ivory poaching. The result is a significant reduction in probability of survival (Fig. 1b). For instance, the population size needed to ensure a 99% probability of survival increases from 25-30 (at 1:4 sex ratio) to about 55 at 1:8 ratio. With a 1:16 sex ratio a starting population of 150 (at K=150) has only a 92% probability of surviving for 100 years. It is only when K is increased by to 250 that a population of 120 elephants has a 99% probability of surviving for 100 years.

When inbreeding depression is incorporated into the above model, the result is a further lowering of survival probability (Fig. 1c & d). The drop however is not very significant (generally under 5% as compared to absence of inbreeding depression except in the case of populations of less than 20 elephants for which the increased mortality from inbreeding would suck them into the "extinction vortex"). The reason for this could be the long generation time in elephants; in 100 years an elephant population goes through only a few generations. Inbred populations would however lose a substantial proportion of their original genetic variation or heterozygosity.

TABLE 1

EFFECTIVE POPULATION SIZES IN SOME ASIAN ELEPHANT POPULATIONS

COUNTRY Region	Total Population (N)	Total adults (N_a)	Ratio of adult Male:Female	Effective population size (N_e)	N_e/N_a	N_e/N
THAILAND						
Khao Yai	225	113	1 : 2.33	95	0.84	0.42
SUMATRA						
Way Kambas	200	116	1 : 1.5	111	0.96	0.56
INDIA						
Nilgiris-E. Ghats 1982						
1987	4500	1890	1 : 5	1050	0.55	0.23
	5000	1950	1 : 8.8	718	0.37	0.14
Periyar	1000	605	1 : 122	20	0.03	0.02
Dalma	66	23	1 : 1.3	22.6	0.98	0.34
SRI LANKA						
Ruhuna-Yala	521	275	1 : 2.9	211	0.77	0.40

The above figures [illegible] population sizes and structures reported in Dobias (1985), Santiapillai and Widodo [illegible] Sukumar (1989), Chandran (1990), Datye (1993) and Anon (1993). The figures probably represent minimum population sizes. The figures for Nilgiris-E. Ghats have been updated from earlier estimates, while the effective population size for Ruhuna-Yala would be higher as the elephants are linked to other populations in the north.

Table 1 gives the total and effective population sizes for some representative Asian elephant populations for which data on population structure are available. The adult sex ratio varies considerably among these populations depending on the extent of poaching of males for tusks

(Sukumar 1989). The most skewed sex ratios occur in parts of southern India; in particular a ratio of 1:122 reported for Periyar (Chandran 1990) means a drastic reduction in effective population size to a ridiculously low figure of 20 even though the total population size may be about 1000 elephants. Such populations are in serious danger of losing genetic variation through drift and inbreeding if this situation persists.

DISCUSSION

"Rule of thumb" estimates of minimum viable population based on theoretical considerations of population genetics (Franklin 1980, Frankel and Soule 1981) have been criticized as being too vague or generalized to be applied to any species. Although originally based on genetical considerations, the well known figures of N_e of 50/500 for short-term versus long-term conservation are probably of appropriate magnitude for several vertebrates as revealed from empirical studies (Boyce 1992). For instance, $N_e < 50$ has been clearly shown to be insufficient for certain mammalian and bird species (whose populations are known to have become extinct). Several simulation studies of the larger "K-selected" mammals also show that N_e in the range of 50-100 is needed for a population to be safe from purely demographic and environmental stochasticity driving it to extinction.

The genetically effective population size (N_e) of 50 suggested as the minimum number to keep inbreeding below a tolerable 1% per generation can thus be taken as a useful guide for management. This would, of course, translate into a higher total population size depending on the adult sex ratio and the proportion of pre-reproductives in the population. The EPS as a percentage of the total population varies widely in Asian elephant populations depending largely on the extent of poaching of males for ivory. This may be only about 2% in Periyar, southern India (where ivory poaching has been a serious problem) to 50% or more in Sumatra and southeastern Sri Lanka (where ivory poaching is not a threat).

In summary, a total population of 100-300 elephants, depending upon demography, sex ratio and ecological pressures, would not only have a high (>99%) probability of survival for the next 100 years in the face of demographic and environmental stochasticity, but also be safe in the short-term from genetic erosion. The goal of managers could thus be to maintain these minimum sizes in isolated elephant populations until other options emerge in the future.

Let me emphasize that the figures given above are the minimum sizes recommended for *short-term* conservation of populations that are not under any serious danger of losing their habitat. Such populations would still be unable to survive serious catastrophes. A PVA incorporating progressively higher levels of mortality for 10-year, 50-year and 250-year drought cycles for African elephants in semi-arid regions indicates that a population of about 3000 elephants (or a reserve size of about 2500 sq km, assuming an equilibrium density of 1.2 elephants/sq km) may be needed to ensure a 99% probability of persistence for 1000 years (Armbruster and Lande 1993). There is no historical evidence that such severe droughts could affect Asian elephant populations found largely in medium to high rainfall areas. However, the long-term consideration would certainly indicate elephant populations above 1000 individuals from the demographic view point.

To maintain the *long term* evolutionary potential of a population, much larger population sizes than $N_e = 50$ would be required. The much quoted N_e of 500 (Franklin 1980) again translates into a total population in the range of 1000-3000 individuals depending on population structure. If such sizes cannot be maintained, several small populations may have to be managed as meta-populations through artificial translocation of individuals. Before any such management is undertaken we have to understand the genetics of elephant populations and the link between genetics and evolutionary process.

This brings us to the question of minimum viable area for elephant conservation. The answer to this depends on the carrying capacity of the habitat or the density of elephants maintained under equilibrium conditions. An equilibrium density of 0.5 elephant/sq km, typical of many deciduous habitats in Asia, would indicate minimum areas of 200-600 sq km for short-term and 2000-6000 sq km for long-term conservation based on above figures of MVP. If equilibrium density is more likely to be 0.1 elephant/sq km, as in some tropical rain forest, the minimum area needed would be five times larger (also see Sukumar 1989).

If small elephant populations continue to lose habitat and come into conflict with people their viability would of course be further compromised. In such instances it would be meaningless to come up with estimates of minimum viable populations. PVAs can however be carried out for individual populations where data exists not only on demographic and environmental variables but also socio-economic factors likely to impinge on them. The result of such an exercise would not be estimates of MVP but of the viability of a population in probabilistic terms. PVAs can thus assist a manager in decision making; is it worthwhile to spend money in maintaining an elephant population in the "wild" or would a better option be to translocate it to a more viable habitat or take it into captivity?

PVAs can also be combined with other aspects of elephant management as, for instance, in dealing with the problem of populations in conflict with people (Sukumar 1991).

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