A demographic model to predict future growth of the Addo elephant population

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An age-structured demographic model of the growth of the Addo elephant population was developed using parameters calculated from long-term data on the population. The model was used to provide estimates of future population growth. Expansion of the Addo Elephant National Park is currently underway, and the proposed target population size for elephant within the enlarged park is 2700. The model predicts that this population size will be reached during the year 2043, so that the Addo elephant population can continue to increase for a further 44 years before its target size within the enlarged park is attained.

Key words: elephant, Addo, demographic model, age structure, future population growth

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Introduction

The Addo Elephant National Park (AENP) currently provides a refuge for over 285 elephants. This population, which stems from just 11 individuals when the park was created in 1931, is the second largest elephant population in South Africa and the southern-most elephant population on the African continent (excluding the three remaining elephants in the Knysna State Forest). The population is one of few undisturbed elephant populations, as it has not been culled and has suffered no poaching since the fencing of the park in 1954. Not only is the Addo elephant population of great importance in conservation terms, it is also extremely valuable in socio-economic terms (Geach 1997). Situated in the poor Eastern Cape Province of South Africa, the AENP attracts nearly 100 000 visitors annually, bringing substantial economic benefits to the region. The elephants are the major draw-card for tourists visiting the park (a recent survey showed that 88 % of visitors come to Addo primarily to see the elephants, Geach 1997) and are, undisputedly, the flagship species of the AENP.

A recently proposed expansion of the AENP, to form a "Greater Addo National Park", would increase the elephant's area from the current 103 km² to 3400 km², providing habitat to support approximately 2700 elephants (Kerley & Boshoff 1997). Clearly such an expansion would not only benefit the elephants—an elephant population above 2500 individuals should be both genetically and demographically viable (Armbruster & Lande 1993), but would also benefit a multitude of other species, whilst additionally providing all the socio-economic advantages of the expansion of a highly successful eco-tourism venture. Land purchase is already underway, and expansion of the park will take place in stages.

As the flagship species of the AENP, estimates of the elephants' future population growth are essential for managers planning the time frame and extent of land purchase. This paper describes an age-structured demographic model of the growth of the Addo elephant population, and this model is used to make predictions of future population growth.

Methods

Demographic parameters influencing elephant population growth include age of female sexual maturity and reproductive senescence, age-specific female fecundity, inter-calf interval, and age- and sex-specific mortalities. These parameters were calculated for the Addo elephant population based on a reconstruction of the population's history (1976 - 1998) in which the life history of every elephant within the park was traced, and birth dates, dates of death and maternal relationships documented (Woodd & Hall-Martin *in prep.*).

A simple model for population growth incorporating these demographic parameters was set up on a computer spreadsheet. The population was segregated by sex and divided into 62 year classes from 0 (calves of less than one year) to 61 years old (the oldest recorded age of an elephant in Addo). Each year the number of calves born was calculated by multiplying the total number of cows of reproductive age (above the age of sexual maturity, but below the age of reproductive senescence—female fecundity between these ages is treated as constant) present in the population two years earlier (elephant gestation is 22 months) by the inverse of the inter-calf interval. A 1:1 sex ratio of new-born calves was applied (complying with actual data: of the 258 calves born in AENP between 1976 and 1998, 126 were male, 126 were female, and six were unsexed). In successive years the number of individuals in each age/sex class was calculated by multiplying the number of individuals in the previous age class of the same sex by the age/sex specific mortality.

The model was run starting with an initial population identical to the known Addo elephant population at the end of 1976. Four calves of the appropriate age and sex (two males aged two and three, and two females both aged three) were removed from the model population in 1979, in order to take account of the four calves translocated to Pilanesberg in that year (Anderson 1993). Annual population sizes calculated by the model were compared to known actual population sizes for the years 1977–1997, and the model was then run for a further 100 years in order to predict future population sizes for this period.

The model population's age structure in successive years was compared. The population was divided into age and sex classes using the same categories as for age- and sex-specific mortality (Table 1) and the percentage of the population in each age/sex class at the end of each year calculated. Time taken to reach a stable age distribution (no further fluctuations to the nearest 0.1 % in all age/sex classes) was determined.

Results

The demographic parameters used in the model are given in Table 1. Starting with the known December 1976 Addo elephant population, annual population sizes predicted by the model closely match actual population sizes for the years 1977-97 (Fig. 1).

Population sex ratios predicted by the model also closely match observed sex ratios (actual population sex ratio at the end of 1997 = 1 male : 1.18 females; sex ratio predicted by the model = 1 male : 1.23 females. The number of males and females in the 1997 model population is not significantly different to the expected number based on the actual sex ratio at that time: chi-square = 0.704; $P > 0.1$).

The model population reaches a stable age distribution by 2045. Thereafter, a doubling time of 13.6 years is observed, equivalent to 5.2 % annual population growth. Prior to 2045 the population's doubling time fluctuates between 13 and 14 years.

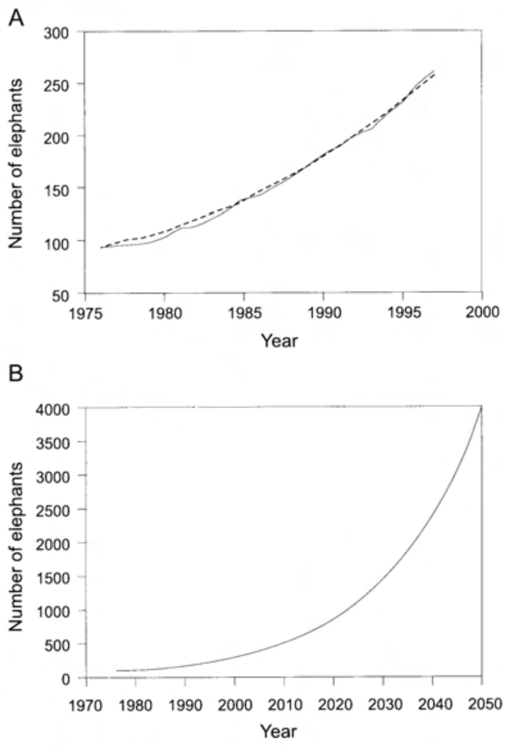

Fig. 1. A demographic model predicting future population growth for the Addo elephant population. A: model population growth (———) in comparison to observed population growth (———) for the period 1976 – 1997; B: projected population growth up to the year 2050.

Table 1

Demographic parameters for the Addo elephant population, based on data for the period 1976 – 1998

Age of first conception:	11.2 years		
Intercalf interval:	3.8 years		
Age of reproductive senescence:	49.2 years		
Age and sex-specific mortalities:	Age class	Male	Female
	0	0.062	0.062
	1 - 9	0.009	0.001
	10 - 19	0.020	0.004
	20 - 29	0.031	0.003
	30 – 44	0.051	0.012
	45 – 59	1	0.016
	60+		1

The model predicts that a population size of 500 will be reached during the year 2010, a population size of 1000 will be reached during the year 2023, and a population size of 2700 will be reached during the year 2043 (Fig. 1).

Discussion

The simple model developed here predicts that the Addo elephant population will reach 2700 elephants, the estimated carrying capacity of the Greater Addo National Park, during the year 2043. Therefore, if the Greater Addo National Park becomes a reality, the elephant population can continue to increase at its current rate for a further 44 years, to a size which should be both genetically and demographically viable (Armbruster & Lande 1993), without threats of perceived over population and negative impact on the habitat. This period allows time for further research on alternative methods of population control so that if in the future a reduction of population growth is deemed necessary, park authorities will be in a better position to consider all alternative options for management.

Data suggests that the sub-tropical thicket vegetation found within the current elephant area cannot support elephant densities greater than two elephants/km² without unacceptable loss of vegetation biomass and species diversity (Hall-Martin *unpubl. data*). Therefore, efforts should be made to plan the park's expansion so as to maintain elephant density below this level. The model presented here can be used to provide projections of population size and hence calculate the area required by the population in future years.

However, it should be remembered that the results obtained from any modelling used to predict future population trends should always be treated with caution. Such models can be useful to give an idea of possible population growth, but the assumptions should be fully understood and reliance should not be placed on the exact figures produced, given all the unavoidable uncertainties of the future.

A number of assumptions have been made in developing this model. The mortality rate within each age classes is assumed to be constant, and the fecundity of all breeding females is treated as equal. These assumptions have been made primarily in order to simplify calculations. Variation in mortality within the given age classes is minimal, so that the use of mean values for these parameters will have a negligible effect. Although female fecundity is not constant between the attainment of sexual maturity and reproductive senescence (a peak is observed in the 25-29 year age class - Woodd & Hall-Martin *in prep.*) the use in the model of the mean age of sexual maturity and mean inter-calf interval will take into account variations in fecundity. Given the very low mortality of females throughout the adult age classes, the assumption of a constant female fecundity will make very little difference to the outcome of the model (if mortality amongst teenagers had been particularly high, so that few females reached the age of peak fecundity, incorporation of age specific fecundity would have been more relevant).

The model also assumes that all demographic parameters are constants. Although evidence for density dependence in elephant populations has been observed (Buss & Smith 1966; Laws 1969) and the high adult male mortality of the Addo elephants (Hall-Martin 1987) may be density related (*unpubl. data*), no density dependence has been incorporated into this model. The primary aim of developing this model was to project probable population growth as the park expands, and not to consider the impact on future reproductive and mortality rates of an increasing density resulting from continued growth of the population within the current restricted range. Therefore, incorporating density dependence into the model was not considered appropriate. It is assumed that the average density of the population in future years as the park expands is the same as the average density for the period from which the parameters were derived (population density for the period 1976-1998 ranged from 1.7 - 4.0 elephants/km² as the population grew and the park was enlarged (on four occasions) to accommodate the expanding population).

It is additionally assumed that future environmental conditions experienced by the population do not, on average, differ from conditions experienced by the population over the past 22 years. Although elephant reproduction and mortality are both influenced by environmental conditions (Corfield 1973; Moss 1988), future conditions cannot reliably be predicted and so it is not appropriate to incorporate environmental factors into this model.

The age-structured model presented here provides projections of future population sizes of the Addo elephant population that will be of benefit to managers, particularly as the expansions of the AENP are planned. Since the Addo elephant population has not yet reached a stable age distribution, a simple exponential model increasing at a constant growth rate would be inadequate to predict future population growth. An age-structured model also provides a useful framework upon which to base further investigations of the population's dynamics, the key parameters influencing population growth and the effects of changes in both demographic parameters and environmental conditions.

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