

Modelling the effect of age-specific mortality on elephant *Loxodonta africana* populations: can natural mortality provide regulation?

Leigh-Ann Woolley, Robin L. Mackey, Bruce R. Page and Rob Slotow

Abstract The historical regulation of African elephant *Loxodonta africana* populations could provide guidelines for management efforts and decisions in areas where elephant numbers are now increasing. However, there are few detailed records of the natural mortality processes of the past. Therefore, we modelled elephant population growth to evaluate possible effects of age-specific mortality. Model projections indicated that an annual mortality of 17.1% of juveniles or 10.5% of adults would be sufficient to prevent population growth. For age classes below or just at sexual maturity (i.e. 0-3, 4-7, 8-11) 37.5% annual mortality of one of these classes was required to achieve 0% population growth. These mortality levels are much higher than those reported in southern Africa today. Simulations of episodic mortality events (e.g. droughts) indicated that such events would need to occur every 16 years at a severity that would

cause the mortality of all infants and weaned calves (0-7 years old), as well as 10% of adults and subadults (8-60 years old) to prevent long-term population growth. An 8-year frequency required the mortality of 84.7% of infants and weaned calves. Historically, it is possible that high drought mortality and frequency, and high predation levels, may have reduced population growth significantly but current mortality rates and frequencies are insufficient to constrain long-term average population growth at 0%. The natural limitation of existent elephant populations through mortality is therefore unlikely, indicating a need for active management of the increasing elephant populations in southern Africa.

Keywords Demography, elephant management, growth rates, *Loxodonta africana*, mortality, population model, southern Africa.

Introduction

There is concern over the current rate of increase of African elephant *Loxodonta africana* populations in southern Africa. Past maximum annual elephant growth rates have been estimated at up to 7% (Hanks & McIntosh, 1973; Calef, 1988) but more recent studies indicate that short-term rates of growth can be much higher. Van Jaarsveld *et al.* (1999) calculated average annual growth rates of up to 15%, and Mackey *et al.* (2006) showed that annual growth rates of 10-15% were not uncommon in nature reserves in South Africa.

Up to the mid 1990s culling was promoted as a management tool for elephant populations confined to conservation areas in southern Africa (Buechner *et al.*, 1963; Glover, 1963; van Wyk & Fairall, 1969). However, there is now again debate over the impact of high numbers of elephants and the possible need to reduce populations. This creates a conservation dilemma, with the impact of

high elephant densities on biodiversity being in contrast with the elephant's more precarious status beyond southern Africa (Baxter & Getz, 2005; Mabunda, 2005; Owen-Smith *et al.*, 2006). The lack of evidence for density dependent responses in elephant populations (Gough & Kerley, 2006) suggests the current high rates of population growth may not slow down under natural conditions. Although density feedbacks must inevitably influence population growth, it is uncertain at which stage this occurs in different elephant systems (Owen-Smith *et al.*, 2006). Maximum population growth rate can be maintained in large-bodied mammals until the point when forage resources can no longer support the population (Fowler & Smith, 1973; Fowler, 1981). However, because of their long generation times elephant populations can lag in their response to changing forage availability, theoretically causing oscillations in the numbers of elephants and forage rather than the achievement of an equilibrium (Caughley, 1976).

The direct study of long-term mortality is difficult in a long-lived mammal and few studies have documented elephant populations over a long timescale (Whitehouse & Hall-Martin, 2000; Moss, 2001; Wittemyer, 2001; Wittemyer *et al.*, 2005). Natural mortality in large, well-established, free-ranging elephant populations is age-dependent, with

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the youngest being most susceptible to dry season impacts (Dudley *et al.*, 2001; Moss, 2001). For example, all calves <8 years of age died during a drought over 1991-1993 in the lowveld of Zimbabwe (Leggatt, 2003), and a drought in 1994 killed 5-9% of the elephant population of Hwange National Park, Zimbabwe, with the highest frequency of mortality occurring in the youngest age class (Dudley *et al.*, 2001). Elephants in some parts of the Kalahari Sands region of Hwange National Park may be entirely dependent on sub-surface drinking water during the dry season and droughts (Weir, 1971), digging craters to reach water, and mortality in the youngest age-class in 1994 was influenced by whether elephants could reach this water. Whereas nursing calves can rely on milk for hydration, juvenile weaned calves die from dehydration when the water table drops below the level reachable by their trunks (Conybeare & Haynes, 1984).

In addition to drought and senescence other, less common, causes of elephant mortality include disease, injury, and predation by lions and humans (Corfield, 1973; Laws *et al.*, 1975; Walker *et al.*, 1987; Moss, 2001; Dudley *et al.*, 2001; Wittemyer *et al.*, 2005). Generally, little mortality can be attributed to disease, except in Etosha where endemic anthrax causes mortality in all age classes (Lindeque & Turnbull, 1994). Predation by lions most commonly involves juvenile elephants (Ruggiero, 1991; Wittemyer *et al.*, 2005). Injury and human predation mainly affect adults, with poaching for ivory having reduced numbers of large adult elephants in the 1970s and 1980s, especially in East Africa (Ottichillo *et al.*, 1987; Moss, 2001; Wittemyer *et al.*, 2005).

Because any long-term consequences of high elephant densities have not yet been observed there are scientific uncertainties surrounding elephant management. Nevertheless, decision-makers are again looking for ways to manage the overpopulation of elephants in southern African nature reserves, with the need to evaluate the long-term effects of mortality on population growth being of particular importance. In the absence of direct evidence of the long-term effects of mortality we therefore used a mathematical population model with various scenarios to gauge the magnitude of mortality required to bring about a zero population growth rate. This enabled us to (1) examine the age-specific mortality levels required to prevent long-term population growth, and (2) simulate age-specific mortality resulting from drought events.

Methods

The model

We used a probabilistic age and state model, based on the model of Wu & Botkin (1980), incorporating aspects

of elephant life history and the following demographic parameters: maximum expected lifespan, female age at sexual maturity, average calving interval for the population, age at menopause, sex ratio of newborns, and age-specific probabilities of survival. The number of individuals of different ages and biological states were transitioned through a matrix in which the number of individuals of each age was recorded in the rows and states in the columns, i.e. males (first column); sexually immature females (second column); sexually mature but not pregnant females (third column); pregnant females in the first or second year of pregnancy (next two columns), females in the first, second, third or fourth year post-parturition anoestrus (next four columns). Males aged and died, but were not transitioned through specific states as it was assumed that sexually mature males were always present in the population and thus conception was not limited by the presence of mature males. All parameters other than the maximum expected lifespan and average period of anoestrus were input as probabilities for each age and state (i.e. probability of sexual maturity, probability of conception, probability of survival, and the sex ratio or probability of being born female). Menopause was included as a probability of conception in older individuals, and variations in mortality as the probability of survival in different ages and states. For this simulation the state of the individual was assumed not to influence mortality. The number of individuals dying and/or conceiving in each cell of the matrix was determined by comparing the input probability value with a value obtained from a random number generator that produced a normal distribution of values between 0 and 1. The model was thus stochastic in nature but input probabilities were kept constant over the period of simulation. The population was recorded at the end of each year of a simulation. The statistical variation introduced by the probabilistic approach was determined by repeating each simulation 500 times and the means and standard deviations calculated from these replicate simulations.

Population parameters

A lifespan of 60 years was used in all simulations (Hanks & McIntosh, 1973; Wu & Botkin, 1980; Whyte *et al.*, 1998), along with a moderate estimate of menopause at 50 years of age (Hanks & McIntosh, 1973; Wu & Botkin, 1980; Owen-Smith, 1988; Woodd, 1999; Moss, 2001). Female age at sexual maturity was set to 10 years (Smuts, 1975; Moss, 2001; Mackey *et al.*, 2006) and a mean calving interval, or period of time between consecutive births for females averaged over all females in the population, of 4 years was used (Eltringham, 1982; Owen-Smith, 1988; Whyte *et al.*, 1998; Whitehouse & Hall-Martin,

2000; Moss, 2001). A birth sex ratio of 1:1 was used (Laws *et al.*, 1975; Calef, 1988; Whitehouse & Hall-Martin, 2000; Moss, 2001). The probability of female conception has been found to vary with age, with lowest conception in the youngest and oldest individuals (Wu & Botkin, 1980; Dominy *et al.*, 1998). However, Mackey *et al.* (2006) concluded that variation in the age-specific probability of conception had little effect on model projections of population growth; we therefore chose to simplify our model by using a probability of conception of 1 for all individuals of breeding age.

Simulations

A hypothetical initial population was created by running two females each of 6, 7 and 8 years old (i.e. a total of six females) through the model using the population parameters above. When the population age structure was constant with time (i.e. population size was increasing at a constant rate, and survivorship and fecundity rates were constant), this population size and structure was selected as the initial population, which consisted of 759 individuals, with juveniles (0-9 years old) comprising 54% and adults (10-60 years old) 46% of the population.

Using the initial population, simulations were run over 300 years, so as to include at least 10 generations and allow enough time to evaluate long-term trends. To examine the potential effects of different age-specific mortality regimes several mortality schedules were simulated, with mortality occurring from year 21 onwards after allowing 20 years for the initial effects of the population parameters to occur. Mortality scenarios were run until the population reached a 0% population growth rate over the 280 year time period after mortality was initiated. The percentage annual mortality of the following age classes, required to achieve 0% total population growth over 280 years, was examined: overall population mortality; adult (10-60 years old) mortality; juvenile (0-9 years old) mortality; mortality in 10-year age classes; and mortality in 4-year age classes. The grouping of individuals into 10-year age classes was to separate the juvenile (0 to 9 years old) from the adult age classes. Further division into 4-year age classes added more biological relevance to age divisions, as it divided the young portion of the population into infants (0-3 years), weaned calves (4-7 years) and subadults (8-11 years). The weaned calf class was set at 4 years because calving interval (in this case 4 years) usually determines the average age at which a calf is weaned, with almost all calves suckling until the birth of the next calf, or just a few months thereafter (Lee & Moss, 1986).

To evaluate the measure of dispersion of results due to the probabilistic nature of the model, 95% confidence

limits of the mean population growth rate were calculated from the means and standard deviations obtained from replicate simulations (Zar, 1974). Population growth rate was calculated using the standard equation for exponential population growth (Begon & Mortimer, 1986): % population growth = $(e^r - 1) * 100$, where $r = (\ln N_{t2} - \ln N_{t1}) / t$, and N_{t1} and N_{t2} are population size at the beginning and end of the time interval in question, respectively, and t is the length of the time span in years.

We examined the frequency of episodic mortality events required to prevent population growth when 100% mortality occurred in each age class. The same age classes used in the annual mortality scenarios above were used in the evaluation of episodic mortality. A drought event was then simulated at a frequency of 16 years (the average cyclic frequency of rainfall occurring in southern Africa; Tyson *et al.*, 1975; Louw, 1982; Reason & Rouault, 2002). The levels of mortality required in infant and weaned calf (0-7 years), as well as subadult and adult (8-60 years) age classes, to give a long-term population growth rate of 0%, were examined. The mortality levels required with a drought frequency of 8 years were also assessed. Age at sexual maturity was then adjusted to 14 years of age and calving interval to 5 years to examine the effect of these reproductive delays on the mortality required to prevent long-term population growth at a frequency of 16 years.

Drought events were simulated as single year occurrences of high mortality, as an alternative to multiple year occurrences of low mortality. The intensity and duration of drought affects the levels of drought-related mortality experienced by elephant populations (Dudley *et al.*, 2001) and the frequency of elephant drought mortality occurs most prolifically after some years of drought-related resource restriction, resulting in a mortality event (Moss, 2001). The longevity of the elephant, the low mortality among adults even under poor conditions, the ability to exploit browse effectively when necessary and a unique combination of life history traits affect the elephant's ability to respond immediately to temporal variability in environmental conditions (Fowler & Smith, 1973; Moss, 2001; Wittemyer *et al.*, 2007).

The sensitivity of model projections to adjustments in mean calving interval, female age at sexual maturity, initial population size and structure was assessed by varying each of these parameters separately whilst keeping all else constant. Mean calving interval was adjusted to 3, 5 and 6 years, female age at sexual maturity was adjusted to 12 and 14 years, and initial population structure was adjusted to be adult biased by taking 349 individuals (46% of baseline initial population size) from the juvenile age class and adding it to the adult age class with an even spread of individuals in each year, and vice versa for a juvenile biased initial population size.

Results

The achievement of 0% population growth is the focus of all mortality scenarios. The levels of mortality giving this growth rate are sectioned into annual and episodic mortality events, as well as different age classes. The frequencies of specific episodic events, and the level of mortality of different age classes during these episodic events, are central to the results presented.

Annual age-specific mortality

The mortality of the age classes (i.e. entire population, adults and juveniles, and 10-year and 4-year age classes) required to give 0% population growth are given in Fig. 1. The percentage age-specific mortality required to pro-

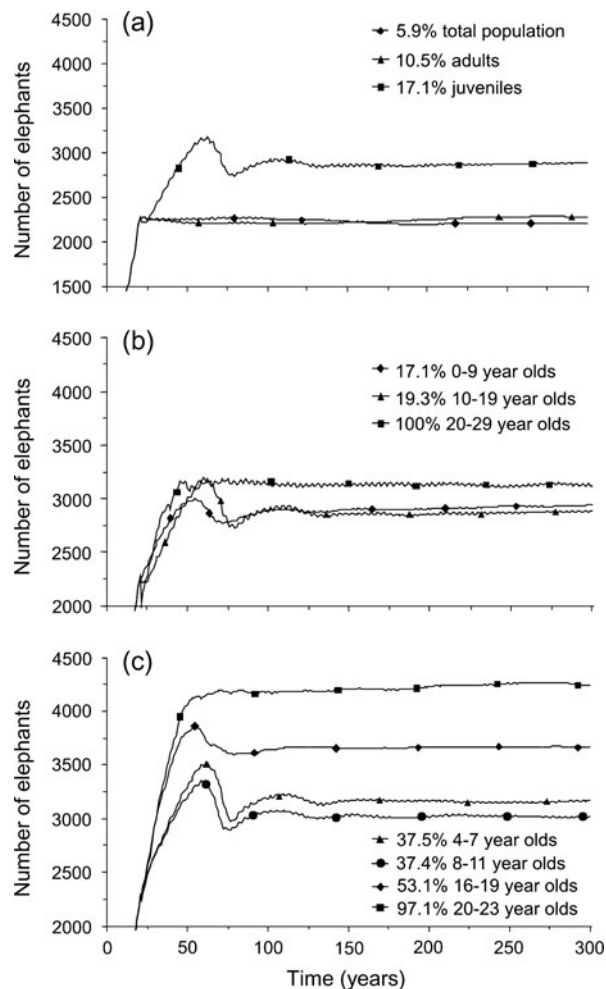


Fig. 1 Change in projected elephant population size over 300 years under the following annual age-specific mortality scenarios: (a) Total population mortality, adult (10-60 year old) mortality, and juvenile (0-9 years) mortality; (b) 10-year age classes; (c) 4-year age classes (population size at 37.5% mortality of 0-3 and 12-15 year age classes fell between the 4-7 and 8-11 year age projections and therefore, to reduce clutter, were not included in this figure).

duce the curves in Fig. 1 are presented in Table 1 and outlined below.

It was projected that 5.9% annual mortality of the entire population across all ages was required to achieve 0% population growth, whereas the annual mortality of 10.5% of adults (10-60 years old) or 17.1% of juveniles (0-9 years old) was required to achieve the same result. The effectiveness of mortality in 10-year age classes for controlling population growth differed amongst age classes. The annual mortality of 19.3% of 10-19 year olds would result in 0% population growth. However, 100% annual mortality of individuals in the 20-29 year age class was required to level off population size. For 10-year age classes above this (i.e. 30-39; 40-49 etc.) 100% annual mortality of individuals was insufficient to reduce population growth to 0%.

Within individual 4-year age classes below and just at sexual maturity (i.e. 0-3; 4-7; 8-11 years), 37.5% annual mortality was required to achieve 0% population growth. An annual mortality of 41.4% of 12-15 year olds, or 53.1% of 16-19 year olds, or 97.1% of 20-23 year olds resulted in a levelling off of population size. Annual mortality of 100% of individuals in age classes >30 years (i.e. 30-39; 40-49, etc.) was insufficient to reduce population growth to 0%.

Mortality of age classes >20 years achieved 0% growth more quickly than that of age groups <20 years. However, the percentage mortality required to achieve 0% growth in age classes >20 years, as well as the average population size attained, and the variability of this population size, was higher than in classes below 20 years.

The variability of results due to the stochastic nature of the model is indicated by the 95% confidence limits of

Table 1 Percentage mortality required of each age class, mean population size obtained, and the time, since mortality was implemented, required to achieve 0% mean population growth rate, and the 95% confidence limits of the mean population growth rate.

Age class (years)	Mortality required (%)	Mean population size (\pm SD)	Time (years)	95% CL
0-60 (entire population)	5.9	2,226 \pm 26	5	0.04
10-60 (adults)	10.5	2,238 \pm 29	5	0.03
10-year age classes				
0-9 (juveniles)	17.1	2,848 \pm 142	150	0.02
10-19	19.3	2,915 \pm 112	150	0.01
20-29	100.0	3,128 \pm 167	60	0.02
4-year age classes				
0-3	37.5	3,030 \pm 177	150	0.02
4-7	37.5	3,161 \pm 162	150	0.02
8-11	37.4	3,022 \pm 131	150	0.01
12-15	41.4	3,080 \pm 125	150	0.01
16-19	53.1	3,664 \pm 210	100	0.01
20-23	97.1	4,200 \pm 339	100	0.02

mean population size and growth rates (Table 1, Fig. 2). The mortality of 5.9% of the entire population resulted in a population growth rate confidence interval of ± 0.04 (Table 1). Population growth rate confidence limits from age-specific mortality scenarios were <0.04 (Table 1). The 95% confidence limit of the mean population size, calculated from 500 replicate simulations of 5.9% annual mortality of the entire population, did not coincide with 95% confidence limits calculated similarly from 5.8 or 6.0% annual mortality of the entire population (Fig. 2a). Confidence limits showed slight overlap for adult and juvenile mortality scenarios but this disappeared with increasing simulation time, as well as a 0.1% change in percentage mortality either side of that required to give 0% population growth (Fig. 2b,c). Therefore, results can be considered statistically reliable, although few replications at slightly lower or higher levels of mortality may result in 0% population growth.

Episodic mortality

When mortality occurred from discrete events on an episodic, rather than annual, basis, it was found that 100% mortality of the adult age class was required at

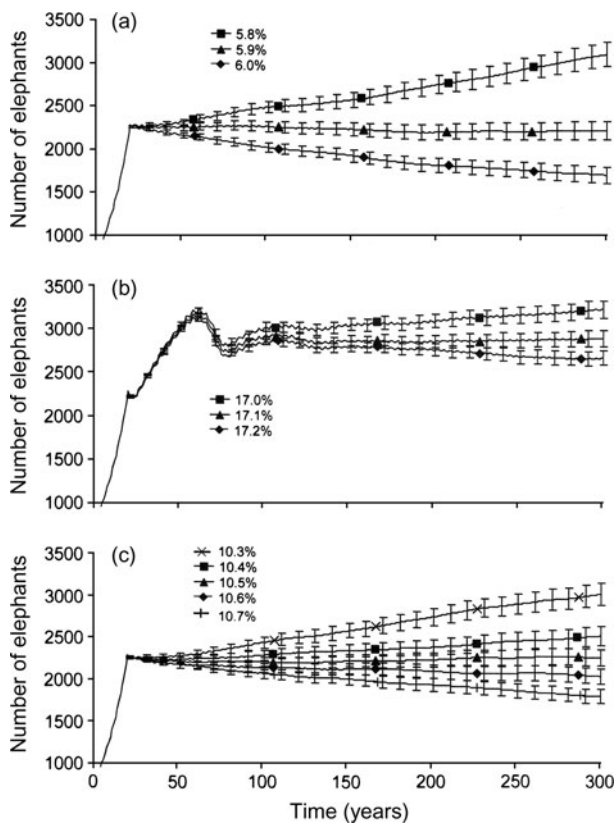


Fig. 2 Mean population size \pm 95% confidence limits over 300 years resulting from: (a) annual total population mortality, (b) annual juvenile mortality, and (c) annual adult mortality.

a frequency of 18-19 years to produce 0% long-term population growth (Fig. 3a) and 100% juvenile mortality was required at a frequency of 13 years (Fig. 3b). The episodic mortality of 10-year age classes could not be examined for classes >20 years, as a mortality rate of 100% was required on an annual basis to prevent growth of the population. A frequency of 11 years was sufficient to prevent long-term population growth if 100% of the 10-19 year age class occurred (Fig. 3b), whereas 100% mortality in 4-year age classes at a frequency of 4-5 years was required (Fig. 3a).

Episodic mortality at a frequency of 16 years resulted in 0% long-term population growth if there was 100% mortality of infants and weaned calves (0-7 years) and 10% of the rest of the population (Fig. 4). An 8-year frequency required the mortality of 84.6% of infants and weaned calves (0-7 years old) to give an overall 0% population growth and cycling about a constant mean population size of 2,743 (\pm SD 455). If age at sexual maturity was adjusted to 14 years of age and calving interval to 5 years, the mortality of 100% of infants and weaned calves every 16 years, or 78% of infants and weaned calves every 8 years, was sufficient to prevent long-term population growth.

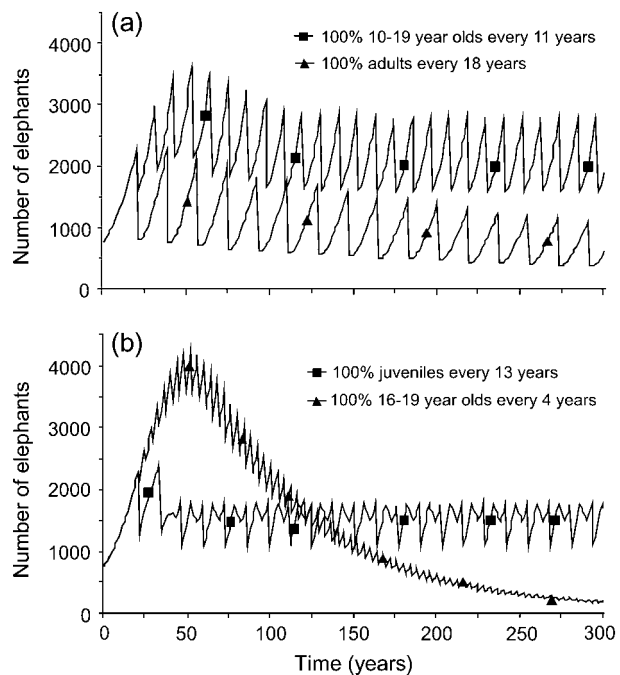


Fig. 3 Change in projected elephant population size over 300 years when the following episodic mortality events occur: (a) Adult mortality at a frequency of 18 years giving a mean population size of 956 (\pm SD 422), or mortality of 10-19 year olds every 11 years giving a mean population size of 2,153 (\pm SD 509). (b) Juvenile mortality every 13 years giving a mean population size of 1,532 (\pm SD 245), or mortality of 16-19 year olds every 4 years.

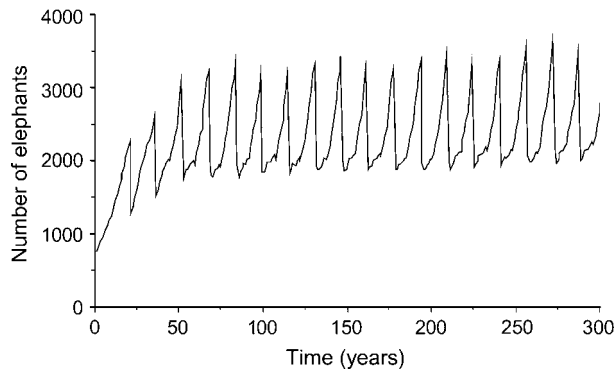


Fig. 4 Change in projected elephant population size over 300 years with 100% mortality of infants and weaned calves (0-7 year olds) and 10% of the rest of the population at a 16-year frequency, giving a mean population size of 2,253 (\pm SD 528).

Model robustness

Model projections of age-specific mortality were most sensitive to a change in mean calving interval and, to a lesser extent, age at sexual maturity (Table 2). Model projections were not sensitive to population age structure. In age classes with individuals >20 years, mortality requirements for 0% growth tended towards 100%.

Discussion

With the recent trend of increasing elephant populations across southern Africa, decision makers are attempting

to take past population patterns into account when implementing elephant management plans (Mabunda, 2005). The historical limitation of free-ranging elephant populations may have been driven by a combination of factors. It is not known whether predation by large cats or prehistoric predators may have influenced elephant population dynamics in the past but human predation has had a significant impact on elephant population size since prehistoric times (Kay, 2002; Surovell *et al.*, 2005). Episodic events, such as drought, have influenced both past and present elephant mortality patterns (Walker *et al.*, 1987; McKnight, 2000; Dudley *et al.*, 2001).

Senescence and predation are forms of mortality that could occur throughout any year. Model projections from this study indicate that an annual mortality of 5.9% of the entire elephant population would be required to reduce the long-term population growth to 0%. In contrast to this, a mean annual mortality rate of just 0.4% was found in small fenced reserves in South Africa (Slotow *et al.*, 2005), 3.2% in the Kruger National Park (Whyte, 2001) and *c.* 3% in Amboseli National Park, Kenya, which was averaged over 27 years that included both drought and high human impacts (Moss, 2001). The average annual mortality rate over 1998-2003 for Samburu and Buffalo Springs National Reserves, Kenya, was 2.6% (Wittemyer *et al.*, 2005). If predation was historically common it may have been a limiting factor for elephant population growth in the past. However, in southern Africa today predation on elephants occurs

Table 2 The sensitivity of the model to changes in mean calving interval and age at sexual maturity as the percentage change from baseline mortality requirements.

Age class (years)	Baseline (%) ¹	Sensitivities ² (% change from baseline)				
		Calving interval (years)			Age at sexual maturity (years)	
		3	5	6	12	14
0-60 (entire population)	5.9	+1.3	-0.9	-1.4	-0.4	-0.8
10-60 (adult)	10.5	+3.7	-2.2	-3.1	-1.5	-2.6
10-year age classes						
0-9 (juvenile)	17.1	+2.3	-2.7	-3.2	-0.6	-0.6
10-19	19.3	+3.7	-2.8	-3.8	-1.8	-2.4
20-29	100.0	*	0.0	-14.2	0.0	-67.4
30-39	*	*	*	*	*	*
4-year age classes						
0-3 (infants)	37.5	+4.0	-4.3	-6.0	-1.3	-1.4
4-7 (weaned calves)	37.5	+4.0	-4.3	-6.0	-1.3	-1.3
8-11 (subadults)	37.4	+4.1	-4.2	-5.9	-1.2	-1.2
12-15	41.4	+9.4	-6.2	-7.9	-4.6	-5.2
16-19	53.1	+43.8	-9.8	-12.6	-7.0	-12.9
20-23	97.1	*	-6.1	-48.5	-9.5	-61.7
24-27	*	*	*	96.4	*	*
28-31	*	*	*	*	*	*

¹Projected percentage mortality required to achieve 0% population growth using the baseline population parameters of a 4-year calving interval and 10-year age at sexual maturity

²+, an increase from the baseline; -, a decrease; *, 100% mortality in a particular age class was not sufficient to cause zero population growth. If baseline percentage of 100% was insufficient and a result was obtained after adjustment of sensitivity parameters, neither + nor - is shown.

rarely and accounts are generally anecdotal, with known accounts of predation on elephants by lions mainly involving juveniles (Ruggiero, 1991). In the Samburu and Buffalo Springs National Reserves 23.8% of calf mortalities recorded over 1998-2003 were attributed to lion and these mortalities accounted for only 4% of total population mortality (Wittemyer *et al.*, 2005). These levels of predation on juvenile elephants do not reach the projected 17% annual mortality rate of this age class required to achieve 0% population growth. Therefore, the current elephant mortality rate due to senescence and predation is unlikely to control elephant population size.

In southern Africa there is considerable decadal variability in drought events, with a 16-20 year cycle in total rainfall (Tyson *et al.*, 1975; Louw, 1982; Reason & Rouault, 2002; Rouault & Richard, 2005). The realization of modelled projections of mortality of all adults every 18 years, or all juveniles every 13 years, is therefore very unlikely. Adult mortality at such a high level is unrealistic, and a severe drought causing the mortality of all juveniles would be uncommon at a frequency of 13 years. Little natural adult elephant mortality has been recorded during drought events but juvenile mortality is usually high (Haynes, 1987; Dudley *et al.*, 2001; Moss, 2001). A drought frequency of 16 years, in accordance with the rainfall cycle of the southern African region, was projected to require the death of all infants and weaned calves, as well as 10% of adults and subadults. These levels of mortality would perhaps be possible in an extremely severe drought event, such as that which led to the die-off of at least 7,000 elephants (15% of the Tsavo East elephant population) during an extreme drought in 1970-1971 (Corfield, 1973). However, severe droughts do not occur with any regularity, or at frequencies ≤ 16 years (Rouault & Richard, 2005).

Separately, predation and drought mortality are unlikely to have controlled elephant population growth historically but if, in combination, the resulting mortality occurred at high levels and frequencies (i.e. regular, severe droughts causing the death of juveniles and adults, together with high predation levels) this may have contributed significantly to historical control of elephant populations. In southern Africa today, however, reported rates of mortality due to senescence, predation and drought are not high enough to control elephant population size.

There are few options left for decision makers in areas with high elephant densities and population growth rates. In general, either higher mortality rates can be introduced via culling, or simulated by live removal of elephants, or populations can be left to increase at current rates, with the expectation that density feedbacks will eventually reduce the population growth rate to zero. However, it has been recommended that any

measures be applied through differential management of the specific situation, with each assessed independently and suitable measures taken according to what is possible, e.g. removal of elephants from sensitive areas, restriction of surface water in sensitive areas, biochemical contraception of elephant populations in small, or fenced reserves (Owen-Smith *et al.*, 2006).

The matriarchal social system of the elephant must be considered if culling or removals occur, with the possibility that sex- and age-specific mortality would be better options. An adult female has an extremely strong bond with her suckling calf, whereas weaned calves have looser bonds with their mothers and other members of the family group (Moss & Poole, 1983). Predation of weaned elephant calves by lion is common because of these weakened bonds (Ruggiero, 1991; Wittemyer *et al.*, 2005). Mortality of weaned calves is also common during drought periods (Dudley *et al.*, 2001; Moss, 2001). Thus the mortality of weaned calves may have a significant role in the natural mortality pattern.

High temporal variation in juvenile survival typically drives population growth rates in predator-free systems, although growth rates are more sensitive to changes in adult survival (Saether, 1997; Gaillard *et al.*, 1998, 2000). In systems where large predators are present adult, as well as juvenile, survival responds to environmental variability due to interactions between resource availability, population size and predation pressure (Owen-Smith *et al.*, 2005). Our model projections indicated that adult mortality was very important in the short-term achievement of 0% growth but a higher percentage of individuals were required to die in these age classes (>20 years) than in juvenile age classes (<20 years) to achieve the same result. The mortality of 100% of individuals >30 years old was insufficient to reduce population growth to 0%. This is easily understandable if the mean generation time is *c.* 15-20 years, with animals >30 years old having a low influence on the growth rate of the population. Juvenile mortality was important in maintaining population size at a lower average level, as well as causing less fluctuation in population size about this average than that obtained from the mortality of adult age classes. Therefore, whereas it is more common to find high juvenile mortality in elephant populations (Laws, 1969; Corfield, 1973), adult mortality can cause a significant shift in bringing about a more immediate reduction in population growth.

Mortality impacts can be significant during times of resource limitation but female fecundity and reproductive limitations can also play a significant role. Wittemyer *et al.* (2007) suggest that demographic fluctuations in African elephant populations are not driven by the classic juvenile mortality pattern observed in many ungulate populations but by the relationship between

female fecundity and ecological stochasticity. Density feedbacks are expected to affect elephant population growth through possible influences on female fecundity and reproductive delays caused by competition for available resources at high elephant densities (Dobson, 1993; Sinclair, 2003; Owen-Smith *et al.*, 2006). Reproductive delays are evident in some populations that live in extreme conditions, such as those of Namibia, where a mean calving interval of 5 years and age at first calving of 11–20 years seems to be sufficient to curb population increase (Leggatt, 2003). Our model projections indicated that an increase in mean calving interval and female age at sexual maturity caused a decrease in mortality requirements to prevent elephant population growth. Therefore, in combination with density-dependence, stochastic environmental events can have a significant impact on the limitation of elephant populations.

The effects of episodic mortality events require long-term assessment over hundreds of years, as elephant population sizes may historically have varied significantly in the short-term, with mean population size evident only on assessment of many episodic mortality events. Model projections indicated that while long-term average population growth may be constrained at 0%, oscillations of population size about an overall mean may have high amplitude, resulting in high short-term variability in population size. In the case of episodic mortality events, modelled populations varied by >1,000 elephants (mean \pm 500), which totalled *c.* 40% of mean population size. Annual mortality rates reported over short periods will therefore not reliably indicate the real mortality losses over extended periods.

Historically, it may have been possible that a combination of high drought mortality and predation kept elephant population growth in check. Today, however, artificial waterholes minimize the effects of resource limitation and dehydration due to drought, elephants are well protected from human predation, and reserves are resource-rich, resulting in rapidly increasing populations. Our modelled projections of elephant population growth suggest that the current level and frequency of natural mortality in southern Africa is insufficient to prevent long-term growth of the elephant populations of the region. Therefore, interventions to increase mortality or introduce reproductive delays are needed if population growth is to be prevented.

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