Chapter 5

The Population Demography of the Maputaland Elephants

Introduction

Elephants in southern Africa are no longer as widespread as they once were. Their distributional range has been shrunk and fragmented by human activities (Gillson & Lindsay 2003). Continued fragmentation may influence the viability of the remaining populations (see Burkey 1989, 1999), and van Jaarsveld, Nichols & Knight (1999) argued that the probabilities of extinction for small populations of elephants will increase due to constraints imposed on demographic and genetic variables. The medium and long-term viability of the elephant populations of southern Africa may be challenged at certain locations by further loss of range. Fragmented populations also may go extinct faster than continuous populations even when overall population size is the same (Burkey 1999).

The elephant population of Maputaland is probably a fragment of a population that, less than a century ago, extended to the south, north and west (see Chapter 2). More recently (during 1989), this population was further fragmented when an electrified fence was constructed along the northern boundary of the TEP. The fence divided the range of the Maputaland elephant population into two distinct units, one enclosed in the TEP and another roaming freely across the eastern parts of southern Mozambique, focused on the Maputo Elephant Reserve (MER).

For the 15 years preceding the present study there has been no exchange of elephants between the MER and the TEP. Fragmentation may have reduced the number of individuals in the MER (see Chapter 3) and skewed the sex ratio of the adult elephant population of TEP to favour males (KwaZulu-Natal Nature Conservation Service 1999). Based on the small population paradigm (Caughley 1994), it is expected that a fragmented elephant population in Maputaland is less likely to persist than one that is continuous. This assumption would be particularly valid if the population sizes of the two fragments remain below that considered as viable (see Ambruster & Lande 1993; van Jaarsveld *et al*. 1999). Current estimates of population size are 204 elephants in Maputo Elephant Reserve (Ntumi 2002), and 179 elephants in Tembe Elephant Park (see Chapter 4). Here I evaluate whether the demography of these two small isolated sub-populations predict persistence over the next five to 50 years. If the sub-populations are to persist, population growth estimates derived from survival and fecundity schedules will be greater than or equal to zero. The risk of population decline will then be low.

An understanding of the demographic parameters of these two populations may also contribute to future management decisions. I evaluate the effects of fragmentation on the demography of the two sub-populations and the likely outcomes for the population biology of a reunited elephant population if the TEP and MER are linked through the development of a Transfrontier Conservation Area (TFCA).

Methods

Surveys

I surveyed the elephant population in the TEP during an 18-month field study from January 2001 to June 2002. The whole of the Park was covered during regular, systematic, road and waterhole surveys as described in Chapter 4. I then identified and photographed herds and individual bulls. I also measured the shoulder heights of 32 bulls using an Impulse range-finder (Laser Technology Inc. 7070 South Tucson Way, Engelwood, CO 80112, USA).

I was part of a team that surveyed the MER elephant population on 26th October 2002. We covered the area of the MER through regularly spaced transects that was flown in a south-north direction. For this we used two flights of seven micro-light aircraft, flying abreast, each surveying a strip width of 400m, at an average flying height of 100m. For each of the two flights one additional micro-light followed behind and recorded the location, number of individuals, sex and number of calves in each group of elephants encountered by the flight. We photographed all herds and individuals encountered using 35mm Canon EOS500 camera fitted with a 28-80mm lens (Cannon Inc. 30-2 Shimomaruko 3-chome, Ohta-ku, Tokyo, Japan) loaded with 100 ASA colour slide film.

Data reduction to derive age related population variables following age determination was based on a method developed at CERU by Dr Sam Ferreira and Prof. Rudi van Aarde. Here I summarise the approach based on the descriptions of Ferreira *et al*. (2003, 2004), Ferreira, Shrader & van Aarde (2004) and van Aarde, Ferreira & Shrader (2004a, 2004b).

Age determination

For breeding herds in both Tembe Elephant Park and Maputo Elephant Reserve I measured the back length of the elephants from digitised 35mm slides using a Digimatic 500 digital calliper (Mitutoyo, Sakado, Takatsu-ku, Kawasaki-shi, Kanagawa-ken, Japan). I measured back length from where the ears join the head to the base of the tail (Croze 1972). Shoulder heights of bulls were entered into an age prediction model constructed from the shoulder-height/age relationship recorded from

203 male elephants culled and measured in the Kruger National Park[10]. The model (y=133.3$x^{0.209}$, r^2=0.90) is based on the shoulder heights (y) measured during culling operations and ages (x) derived using tooth eruption criteria of Laws (1969). Ages of males were estimated as:

$$x = 10^{\left(\frac{\log(y/133.3)}{0.209}\right)}.$$

For breeding herds I determined the ages of individual elephants from the relationship between the ratio of back length to mean adult female back length and known age (♂: y=0.48$x^{0.258}$, r^2=0.89, ♀: y=0.49$x^{0.208}$, r^2=0.78, y= ratio, x=age, data from known-age individuals from Amboseli National Park[11] and Addo Elephant National Park[12]). Ages of males were estimated as:

$$x = 10^{\left(\frac{\log(y/0.48)}{0.258}\right)},$$

while those of females were estimated as:

$$x = 10^{\left(\frac{\log(y/0.49)}{0.208}\right)}.$$

Deriving population age and sex structures

Once the age of individual elephants was determined (see age determination) I grouped them in four year composite age classes (0$\leq$4, >4$\leq$8, >8$\leq$12, >12$\leq$16) and a single adult age class for elephants >16 years. When sex could not be determined for elephants in herds, half were considered as female.

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[10] Unpublished data kindly provided to Professor Rudi van Aarde (CERU) by Dr Ian Whyte, Kruger National Park, PB X402, Skukuza 1350, South Africa.

[11] Unpublished data kindly provided to Professor Rudi van Aarde (CERU) Dr Phyllis Lee and Cynthia Moss, Amboseli Elephant Research Project, P.O. Box 15135, Nairobi, Kenya.

[12] Unpublished data, (CERU), University of Pretoria.

Estimating reproductive variables

From the breeding herds photographed I could assess which calves were associated with which females. This allowed me to estimate the age at first calving by plotting the proportion of female's within the age categories with calves (p_r) against the age of a female (a_j) where that females' age was determined from the ratio of its back length to mean adult female back length. Using models developed by CERU (*e.g.* see Ferreira et al. 2004) I predicted the mean age at first calving ($\bar{a}_i$) for the population by fitting:

$$p_r = p_{min} + [(p_{max} - p_{min})/(1+10^{(k_{50}-a)c})],$$

where 'p_{min}= the minimum proportion of cows with calves (set at zero), p_{max}= maximum proportion of cows with calves, k_{50}= the age where the rate of increase in the proportion of cows with calves is the highest, and c = a constant defining how fast proportions will change from maximum to minimum' (Ferreira *et al.* 2004). I estimated mean age at first calving ($\bar{a}_i$) where 50% of the females had calved and 50% had yet to calve. I estimated variance by allowing the relationship coefficients to vary within their estimates and repeated the model 50 times to get estimates not constrained by small sample sizes and variances not constrained by large sample sizes.

I determined calving interval from the birth rate. Birth rate was calculated as the number of calves < 1-year old divided by the number of females with a calf and calving interval was taken as the inverse of this birth rate. This method reflects the mean calving interval for the population from a single sample.

For each of the two populations I constructed age-specific fecundity schedules by estimating the proportions of females that had calved at specific ages. I estimated age specific fecundity (m_x) by multiplying the proportion of females that calved in each age class (age_t) by the mean birth rate, multiplied by sex ratio at birth (assuming a ratio of 0.5, see Moss 2001).

Estimating age specific survival

I estimated age-specific survival rates ($s_{0\text{-}1}$, $s_{1\text{-}4}$, $s_{5\text{-}16}$, $s_{>16}$) by constructing a Leslie-matrix using hypothetical survival rates and estimates of fecundity, following those constructed by CERU (*e.g.* Ferreira *et al*. 2004). A residual sum of squares (RSS) approach was used 'to estimate age-specific survival rates by progressively changing hypothetical survival rates until the residual sum of squares are minimised when the predicted stable age distribution of the Leslie-matrix approximated recorded standing age distributions' (Ferreira *et al.* 2004). Two constraints on variation in survival rates were imposed on the model. First, it was assumed that younger animals experienced higher mortality than older animals. Secondly, observed calving interval estimated from the age difference between consecutive calves is affected by survival to puberty at ~12 years. To estimate variance values were recalculated after allowing parameters to vary within 95% confidence intervals and re-calculated following the re-assignment of ages each time the model was re-run. An estimate of population increase (λ) was derived from the dominant eigenvalue calculated for matrix L following the residual sum of squares solution of each reiteration. This eigenvalue was converted to an exponential rate of increase r as $r = \ln \lambda$. The modelling procedure was repeated 50 times from which estimates of means and variances were obtained for age-specific survival rates and population growth rates.

Observed mortalities

For TEP I recorded known mortalities from an ivory register kept for the Park, from data supplied by the regional ecologist (W.S. Matthews *pers. comm.*[13]), and from carcasses that I located in the field. For the Maputo Elephant Reserve the only available data for elephant mortality was a carcass count conducted during an aerial survey in 1999 (I.J. Whyte *pers. comm.*[14]). The age of the elephants that died was not recorded but based on the size of their ivory they were considered as adult, sub-adult or young.

Population Growth

To predict population growth I used single population models in RAMAS Ecolab 2.0 software (Applied Biomathematics, 100 North Country Road, Satauket, NY 11733, USA). The populations of the TEP and the MER were modelled using the demographic variables (initial abundance, survival-fecundity growth rate (r_s), survival (l_x), standing age stricture (S_x) and the standard deviation of r estimated for the fragments. The two fragments were combined and modelled using the demographic variables from each fragment. I modelled population growth using the survival-fecundity rate of increase:

$$r = \frac{\log_e l_x - \log_e S_x}{x}$$

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[13] Mr W.S. Matthews, Regional Ecologist, Tembe Elephant Park, PB. 356, Kwangwanase, KwaZulu-Natal.

[14] Dr I.J. Whyte, Kruger National Park, PB X402, Skukuza 1350, South Africa.

Initial simulations were single iteration deterministic models (Akçakaya, Burgman & Ginzburg 1999) for 50 years. Simulations which include demographic stochasticity were then run for each population for 1000 iterations for time periods of 5, 10, 15, 20, 30 and 50 years. The risk of population decline was determined as the probability that a population would fall below the initial population size (x) at least once during the time period. The risk of population increase was determined as the probability that a population would exceed an abundance x at least once during the time period. A summary of predicted abundance over time served as a summary of population trend for each population (Akçakaya *et al*. 1999).

Intra and inter fragment comparisons

I used the G-test (Fowler & Cohen 1992) applied to an r x c contingency table to analyse age distributions between the sexes for each of the sub-populations and to compare age and sex distributions between the sub-populations. To evaluate sex ratios for age classes <16 years old and age classes >16 years old for each of the population fragments I applied the χ^2 test (with Yates' correction applied for one degree of freedom). To evaluate differences between the population fragments for age at first calving, mean calving interval and survival I used the t-test. All statistical evaluations followed Fowler & Cohen (1992) and were calculated using Excel spreadsheet models.

Results

Demography

Age specific fecundity (m_x) for the two fragments differed. Fecundity was higher for elephants living in the MER than for those living in the TEP fragment (Table 5.1).

Table 5.1. Mean age specific fecundity (female live births per female, Caughley 1977), calculated by multiplying the proportion of females that calved in each age class by the mean birth rate, corrected for a sex ratio at unity at birth. Values for the Tembe Elephant Park were estimated from ground-based observations, and those for the Maputo Elephant Reserve from aerial observations. The values are based on 50 iterations for each age class.

Age class (years)	**Tembe Elephant Park** m_x	**Maputo Elephant Reserve** m_x
0-≤1	0.00	0.00
>1-≤4	0.00	0.00
>4-≤8	0.00	0.00
>8-≤12	0.096	0.11
>12-≤16	0.11	0.17
>16-≤20	0.10	0.22
>20-≤24	0.12	0.20
>24	0.12	0.19

For elephants in the TEP the mean age at first successful calving was 11.5 years, with an inter-calving interval of 4.2 years (Table 5.2). Here the age distribution did not differ between sexes across age classes ($G_4 = 8.98$, $P = 0.06$) (Fig. 5.1a). The sex ratio for elephants <16 years old did not differ from unity ($\chi_1^2 = 0.57$, $P = 0.45$), but favoured males for elephants >16 years old ($\chi_1^2 = 14.6$, $P < 0.01$).

For the first year of life survival was 0.89 and annual survival rate between 1-4 years of age was 0.99. From 5-16 years survival rate was also 0.99, the same as that for adults. The survival and fecundity recorded here predict that, under current conditions, the population will grow at a rate of 4.64% per year (Table 5.2).

For elephants in the MER the mean age at first calving was 9.8 years, with an inter-calving interval of 2.2 years (Table 5.2). Here the age distribution did not differ between sexes across age classes ($G_4 = 0.75$, $P = 0.94$) (Fig. 5.1b). The observed proportion of adult females (>16 years) to males was 0.57 (Table 5.2), and did not differ from unity ($\chi_1^2 = 2.92$, $P = 0.09$). For elephants <16, sex ratio also did not differ from unity ($\chi_1^2 = 0.07$, $P = 0.78$).

Table 5.2. Demographic variables (mean ± SE based on 50 iterations) for elephants in the Tembe Elephant Park (based on ground surveys) and for those living in Maputo Elephant Reserve (based on aerial observations).

Demographic Variable	**Tembe Elephant Park**	**Maputo Elephant Reserve**[15]
Rate of population increase (%)	4.6 ± 0.63	3.1 ± 1.1
Age at first calving (years)	11.49 ± 0.54	9.77 ± 0.5
Calving interval (years)	4.17 ± 0.79	2.21 ± 0.15
Proportion of adult ♀ (> 16 years)	0.29 ± 0.06	0.57 ± 0.06
Survival 0 – 1 year	0.90 ± 0.117	0.82 ± 0.012
Survival >1 – ≤ 4 years	0.99 ± 0.011	0.94 ± 0.022
Survival > 4 – ≤ 12 years	0.99 ± 0.010	0.95 ± 0.019
Survival > 12 – ≤ 20 years	0.99 ± 0.010	0.96 ± 0.019
Survival Adult > 20 years	0.99 ± 0.010	0.97 ± 0.022

I estimated first year survival at 0.82 while annual survival between 1-4 years of age was estimated as 0.94 (Table 5.2). Annual survival from 5-16 was 0.95 and adult annual survival for elephants >16 years of age was estimated as 0.97 (Table 5.2). The estimated survival and fecundity rate predict that the population will grow at a rate of 3.05% per year (Table 5.2).

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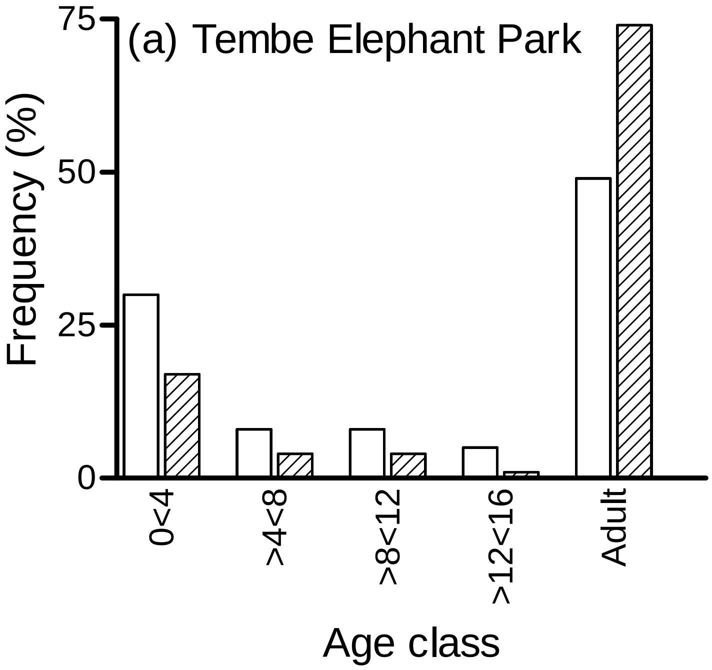
[15] The demographic assessment in MER is constrained by sample size (<100 individuals for which age was estimated and included in the analysis) and therefore must be considered with caution. Studies on the population are continuing.



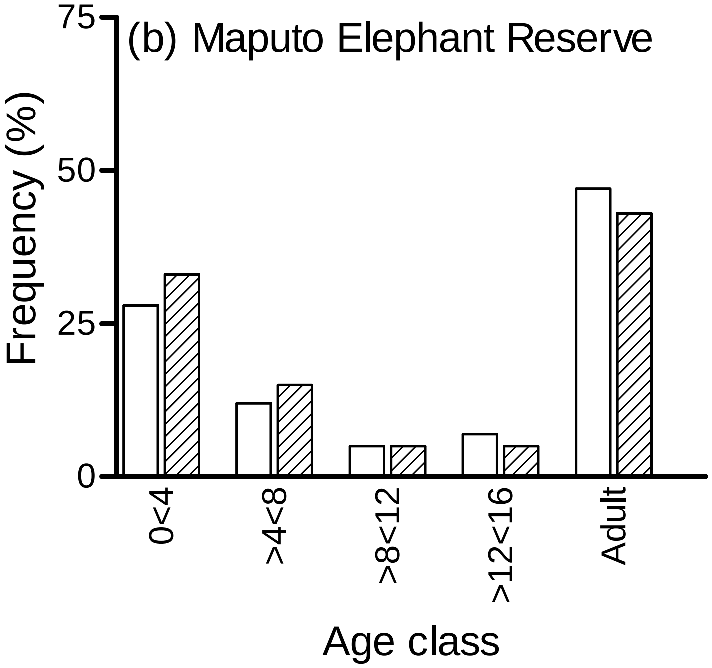


Figure 5.1. Sex specific age distribution of elephants in (a) the Tembe Elephant Park (n=163) and (b) the Maputo Elephant Reserve (n=131). Males are indicated by shaded bars and females by open bars. For Tembe Elephant Park estimates were derived from ground-based observations and for Maputo Elephant Reserve from observations of elephants during an aerial survey.

The sex and age structures of the elephant populations of TEP and MER differed for some age and sex classes (Fig. 5.1). The age distribution of females was similar ($G_6 = 1.91$, $P = 0.93$), but that for males differed significantly ($G_4 = 19.73$, $P<0.01$) (Fig. 5.1.). For males <16 years old the distribution amongst age classes were similar ($G_3 = 1.88$, $P = 0.60$) (Fig. 5.1).

Age at first calving for the two fragments differed significantly ($t_{98} = 9.18$, $P<0.001$), as did mean inter-calving interval ($t_{98} = 17.24$, $P<0.001$). Calf survival during the first year was significantly lower in the Maputo Elephant Reserve than in Tembe Elephant Park ($t_{98} = 3.18$, $P<0.01$), as was annual survival for all age classes (1-$\leq$4 years $t_{98} = 14.40$, $P<0.001$, >4-$\leq$12 years ($t_{98} = 13.94$, $P<0.001$, >12-$\leq$20 years $t_{98} = 11.42$, $P<0.001$, adults >20 $t_{98} = 6.62$, $P<0.001$). The rates of population increase also differed significantly ($t_{98} = 9.18$, $P<0.001$) (Table 5.2).

Observed mortalities

Between 1989 and 2002, 51 mortalities were recorded for elephants in Tembe Elephant Park, of which 41 were adult bulls (Table 5.3). Cause of death was not determined for 45% of mortalities, 27% resulted from elephants destroyed as wounded or problem animals and 8% (all bulls) were shot by safari hunters. The remaining 20% (all bulls) died from fighting.

Table 5.3. Elephant mortalities recorded for Tembe Elephant Park between 1989 and 2002. For elephants recorded as found dead, cause of death could not be determined. Shot elephants were hunted (n=4) or destroyed as problem animals or wounded animals. Elephants recorded as killed in fights may be the result of male/male aggression. The information that led to these records could not be validated. For the five elephants found dead during the two year study no evidence of injury from fighting could be determined. The information was extracted from the ivory and elephant mortality register held by the conservation manager at Tembe Elephant Park.

Class	**Found dead**	**Shot**	**Died in fight**	**Total**
Male	14	17	10	41
Female	6	1	0	7
Young (unsexed)	3	0	0	3
Total	23	18	10	51

In the Maputo Elephant Reserve 11 elephant carcasses were recorded during a two-day aerial survey in 1999. The year and cause of death was not established for these elephants, neither was age or sex (I.J. Whyte *pers. comm.*[16]).

Population Growth

Under deterministic simulations with no variation in demographic variables, both population fragments grow exponentially. Starting with a founder population of 179 elephants in the TEP, the fragment would reach 225 in five years, 281 in 10 years, 353 in 15 years, 443 in 20 years, 700 in 30 years and increase to more than 1736 elephants in 50 years. The MER fragment would number 238 in five years, 276 in 10 years, approach 320 in 15 years, exceed 372 in 20 years, increase to more than 502 in 30 years and 914 elephants in 50 years.

Simulations that included demographic stochasticity (run for 1000 iterations) yielded estimates of average, minimum and maximum population size (± 1 SD) for TEP and MER (Table. 5.4).

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[6] Dr I.J. Whyte, Kruger National Park, PB X402, Skukuza 1350, South Africa.

Table 5.4. Predictions of population size (mean±SD) and range from minimum to maximum for Tembe Elephant Park and Maputo Elephant Reserve. Values are derived from demographic models using the demographic variables calculated for each population.

Time (years)	**Tembe Elephant Park**		**Maputo Elephant Reserve**	
	Size	Min-Max	Size	Min-Max
0	179	NA	205	NA
5	224±10	190-253	237±14	194-280
10	281±18	231-338	275±23	216-348
15	352±26	276-446	319±30	233-425
20	442±36	356-563	370±39	246-514
30	695±64	521-909	498±61	344-679
50	1721±178	1207-2295	907±132	585-1348

The simulations suggest that the TEP fragment will double in 15 years, triple in 25 years and approach 10 times the initial population size in 50 years. For the MER fragment the model indicates that the sub-population will double in 23 years, triple in 37 years and quadruple in 47 years.

Modelling of population size suggests a high probability of the fragment increasing in numbers. There is a 25% probability that the elephant population in TEP will exceed 230 individuals in five years (Table 5.5). The probability that the TEP population will exceed 320 elephants in 15 years is 90% (Table 5.5).

For the MER fragment the modelling of population increase (Table 5.6) suggests a 75% probability of the fragment exceeding 300 elephants in 15 years. The probability of the population exceeding 740 elephants in 50 years is 90%.

Table 5.5. The probabilities of the elephant population of the Tembe Elephant Park attaining population sizes in determined time intervals.

	Predicted Population size (x)			
Time (years)	**Probability of reaching population size**			
	0.25	**0.5**	**0.75**	**0.90**
5	232	224	217	211
10	295	282	270	260
15	372	355	337	322
20	466	442	418	397
30	745	696	654	617
50	1840	1720	1615	1454

Table 5.6. The probabilities of the elephant population of the Maputo Elephant Reserve attaining population sizes in determined time intervals.

	Predicted Population size (x)			
Time (years)	**Probability of reaching population size**			
	0.25	**0.5**	**0.75**	**0.90**
5	249	239	231	219
10	292	278	262	245
15	342	323	302	274
20	401	374	349	311
30	546	500	464	408
50	992	897	815	743

Discussion

Both populations in Maputaland are presently increasing in numbers. This suggests that the populations will persist, at least in the short to medium term (between five and 50 years).

The demographic variables used in the present study were derived from a rapid elephant population assessment (REPA) technique that CERU has developed (e.g. see Ferreira *et al.* 2004). CERU is addressing the limitations imposed by hypothetical survival rates for this novel technique. Further refinements will include sensitivity analysis to quantify the impact of age specific survival for intrinsic population growth rates. The demographic variables presented in this chapter may therefore be considered as preliminary approximations.

Prior to the fencing of TEP the Maputaland elephant population was probably already relatively small (see Chapter 3), isolated and fragmented into two populations. Regular movements of elephants along the Futi River that connects these sub-populations did occur before fencing elephants into the TEP (Klingelhoeffer 1987; Hall-Martin 1988; Ostrosky 1988). The two populations may have been exposed to different factors that could influence their demography. Elephants in the TEP have been fenced off and actively protected for the past 15 years The MER on the other hand supports a relatively unprotected, open population and poaching, emigration and immigration could dictate growth rates. Survival probabilities of older elephants are lower in MER than TEP, suggesting that emigration and or poaching may have affected the former is population. Few elephants are present elsewhere in southern Mozambique suggesting that emigration is not a main factor (Ntumi 2002). Poaching has long been reported in the MER (Tello 1973) and has continued until recently (de

Boer *et al*. 2000), and therefore, it is likely that poaching has reduced survival rates for elephants in the Reserve.

The demographic variables for the two sub-populations differ, probably because of the different management regimes under which elephants live. The 15 years of intense protection afforded to elephants in the TEP is equivalent to a quarter of an elephant's lifespan and exceeds the age at first calving (varying between 9.8 and 11.5 years) for the sub-populations. Consequently any effects of fragmentation on population dynamics will only start to manifest now. While calving interval may have changed the consequences for population growth are yet to be detected. Nonetheless the analysis presented clearly illustrates that fragmentation into theoretically open and closed populations has resulted in substantially different demographics. Elephants in the MER have a lower age at first calving, shorter inter-calving interval and higher fecundity rates than those in TEP, but survival rates are lower than Tembe's. The population growth rate for the MER is less than that of TEP due to lower survival rates in the Reserve. At equal survival the sub-population now living in the MER population would grow faster than that of the TEP.

In spite of the demographic and genetic constraints imposed by low population numbers (e.g. van Jaarsveld *et al.* 1999), such constraints are presently of little importance. Both the Tembe Elephant Park and Maputo Elephant Reserve sub-populations are increasing at rates typical for other populations not constrained by small populations (see Table 5.7).

Based on published data the elephant population of the TEP increased at 8.3% per year following its fencing (Chapter 3), a value nearly double that derived from demographic variables. For elephants in the MER the rate of increase of 3.05% per year based on survival-fecundity schedules also is lower than the exponential rate of

4.4% per year between 1979 and 1999 (see Chapter 3). Estimates of population growth rates based on survival-fecundity schedules were calculated from observed age distributions, therefore are different from those based on extrapolation from a series of population size estimates, where the population size estimates may be unreliable (see Chapter 3).

The calving interval for elephants in TEP is similar to that for other populations but the value for the MER is shorter than those of other populations (Table 5.7). Ages at first calving for TEP and the MER are lower than those for other populations (Table 5.7), but within the range of values for first reproduction for the species (7 – 15 years: see Laws & Parker 1968; Douglas-Hamilton 1972; Hanks 1972; Smith & Buss 1973; Smuts 1975). The inter-calving interval and age at first reproduction in TEP does not appear to be affected by their containment or the relatively high population density of elephants in the Park (Chapter 4), as has been shown for other populations (Laws 1969; Hanks & McIntosh 1973).

In the MER where elephants are less confined, age at first calving and calving interval are lower than in TEP or elsewhere. The MER fragment may be recovering from reduced numbers, a high ratio of adult females and low population density. Population density may, however, be high locally, as they do not use all areas available to them (Fairall & van Aarde 2004b). The relatively short calving interval recorded for elephants in the MER may be influenced by the effects of a birth pulse if the 'one-off' survey conducted coincided with a high proportion of females calved.

The contribution of adults to the elephant population in the TEP is higher than that recorded for elephants in the MER (present study) and populations elsewhere (Dunham 1988; Lindeque 1991; Bhima & Bothma 1997; Moss 2001; Whitehouse & Kerley 2002). Prior to fencing, elephants, especially bulls, may have moved into TEP to escape persecution in Mozambique thereby reducing the proportion of older animals in the MER. The possibility of the TEP being a 'bull area' can not be discounted, however, as yet the concept of bull areas is not supported by published accounts, If poaching was as high as has been suggested the higher ratios of young elephants in the MER indicate a population recovering from persecution and where older animals and their dependant young experienced high mortality. Higher rates of mortality for elephants in the youngest age classes in the MER could be influenced by the inexperience of younger mothers. Male bias and fewer females present when fragmentation occurred may have influenced the TEP population.

The predicted exponential increase for elephant population size (see Table 5.5) ignores the potential consequences of density dependence. Density dependent limitations may alter exponential growth rates, giving rise to lower population sizes in the future than I have calculated. The information needed to parameterise population growth is beyond the scope of this study but earlier work on elephant population dynamics (Laws 1969b; Laws, Parker & Johnstone 1975) suggests that both calving interval and age at sexual maturity increase with density. Van Jaarsveld *et al*. (1999) modelled density dependent changes in elephant numbers but failed to determine mechanisms other than culling that influenced population trend. Arguments supporting density dependent restrictions on elephant population growth lack quantative data and it appears that in southern Africa, most newly founded small populations or populations recovering from disruptions are growing exponentially (Blanc *et al.* 2005; Slotow *et al.* 2005).

The rate of population growth of the elephant population in the TEP suggests that potential negative impacts of high elephant densities in a fenced conservation area could increase in the medium to long term unless survival rates decrease and length of calving interval increases. The elephant population of the MER may not be restricted by available space for elephants (Ntumi 2002) especially with the inclusion of the Futi Corridor. I conclude, therefore that reuniting the Maputaland elephant population is ecologically viable and desirable if a conservation area can be established between the Tembe Elephant Park and the Maputo Elephant Reserve.

Table 5.7. Population rates of increase, age at first calving and inter-calving interval estimated for elephants across Africa. Estimates given are those available in the literature. For the Tembe Elephant Park and the Maputo Elephant Reserve, estimates from this study are given in bold.

Area	**Yearly rates of population increase (%)**	**Age at first calving**	**Calving interval**
Addo[1]	5.53 ± 2.82	13.0 ± 2.03	3.8 ± 1.29
Amboseli[2]	2.17	14.1 ± 0.36	4.5
Etosha[3]	NA	13.3-15.3*	3.8
Kasungu[4]	1.0	13*	3.3
Kruger[5]	NA	14*	4.5 ± 0.49
Kruger[6]	5.8	14*	3.8
Lake Manyara[7]	3.7	13	3.9-4.6
Liwonde[8]	3.6	NA	2.8
Luangwa Valley[9]	NA	16*	3.5-4.0
Mana Pools[10]	NA	15-16*	3.8 ± 0.8
Maputo Elephant Reserve	**3.05 ± 0.11**	**9.77 ± 0.50**	**2.21 ± 0.15**
Tembe Elephant Park	**4.64 ± 0.06**	**11.49 ± 0.54**	**4.17 ± 0.79**
Tsavo[11]	NA	13-17*	5 ± 1.8
Asian Elephant[12]	NA	17.5*	4.6 ± 1.07

[1]Whitehouse & Hall-Martin 2000; [2]Moss 2001; [3]Lindeque 1988; [4]Jachmann 1986; [5]Smuts 1975; [6]Whyte 2001; [7]Douglas-Hamilton 1972; [8]Bhima & Bothma 1997; [9]Hanks 1972; [10]Dunham 1988; [11]McKnight 2000; [12]Sukumar 1989

* Approximate estimates calculated as age at first conception or mean age at puberty plus 22 months gestation