Chapter 7

Synthesis

General Introduction

In this thesis I investigated the population biology of two isolated fragments of a population of the savanna elephants that live in part of Maputaland. Their demographies may have been affected by the differences in the management regimes to which they have been subjected. I therefore compared fecundity and survival schedules of these fragments and tried to determine if differences will influence viability and the prospects of reuniting these fragments through the development of a Transfrontier Conservation Area (TFCA).

Elephant numbers have declined over the past 150 years (Owen-Smith 1988) and elephants currently occur in fragmented populations, many of which have been compressed into smaller areas than those they used to inhabit. This has been attributed to anthropogenic factors (Georgiadis et al. 1994; Hanks 2001) and the elephant population of Maputaland is no exception.

Small and fragmented populations are of concern because the probability of extinction increases exponentially with decreasing population size or with a decrease in area occupied by a population (Burkey 1989; Hanski 1999). Populations are more likely to survive in contiguous tracts than when subdivided (Burkey 1999). Fragmentation may, however, improve the survival of a protected sub-population when a population is heavily persecuted. This may have been the case in Maputaland where the decision was made to fence part of the population into the TEP (Ostrosky 1987, 1989; Hall-Martin 1988). Fragmented populations are more likely to go extinct
but where they do increase they may have negative impacts on their habitats (Herremans 1995; Cumming et al. 1997). These negative impacts can be especially prevalent when elephant populations are confined to fenced reserves (Cumming et al. 1997; Johnson, Cowling & Phillipson 1999; Lombard et al. 2001).

Small populations are at risk of inbreeding depression and even in larger populations there can be a gradual loss of genetic variability (Franklin 1980). With decreasing population size the magnitude of effects on population dynamics, of demographic stochasticity, environmental stochasticity, genetic stochasticity and natural catastrophes may increase (Shaffer 1987). In small populations (10s to 100s) demographic stochasticity can result in a population decline and lead to extinction. Environmental stochasticity also effects population size and in a variable environment any loss in population size proportionally increases the chances of population extinction (Shaffer 1987). To ensure long-term (100 years) population survival population sizes of hundreds to thousands of individuals are needed (Shaffer 1987). Given the limited resources available to conservation in southern Africa and competing land uses (Hanks 2001; Wynberg 2002; Western 2003), maintaining such large populations in single units may prove to be difficult in practice.

Recommended minimum population sizes have been questioned (Caughley 1994). The concept of a minimum viable population is a ‘slippery notion’ and the ‘50/500 rule’ (Franklin 1980; where 50 animals is enough to stave off inbreeding depression and an effective population size of 500 animals is the lower limit to allow evolutionary process to fully function) are genetic concepts that have little to do with effective population sizes (Caughley 1994). He also asserts that populations have behavioural and demographic adaptations for coping with stochastic events.
Caughley’s (1994) assertion is supported by the demographics of the elephants of Addo Elephant National Park (AENP). This population grew relatively slowly between 1930 and 1960 (Whitehouse 2002), from an estimated population size of 11 animals in 1931 (Woodd 1999). Growth rate increased from the 1960’s onwards resulting in 324 elephants by 2000 (Whitehouse 2002). While the decrease in genetic variation in this population may be attributed to a bottleneck there are no signs of inbreeding depression (Whitehouse & Harley 2001). Fecundity is high and mortality is low (Whitehouse & Hall-Martin 2000). As both the sub-populations in Maputaland are far larger than the founder population of AENP inbreeding depression should not be apparent, and indeed the demographic variables reported in Chapter 5 give no indication of reduced reproductive output.

Biologists are concerned that the effects of fragmentation and isolation of conservation areas in the landscape and there is realisation of the importance of interaction between conservation areas (Siegfried, Benn & Gelderblom 1998 and references therein). Movement between population fragments is important for species that need large areas. This may well be the case for elephants and many African conservation areas may be spaced too widely apart to allow interchange (Siegfried et al. 1998). Increased migration is, however, not always beneficial for population persistence in fragmented populations (Gruntfest, Arditi & Dombrovsky 1997). There are also significant difficulties in establishing wildlife corridors for elephants (Johnsingh & Williams 1999; Osborn & Parker 2003). TEP and the Maputo Elephant Reserve (MER) are not too far apart to allow interchange of individual elephants or herds, only the fence prevents elephants migrating between sub-populations as evidenced by the data from satellite collars fitted to individuals in both sub-populations. In the case of the Maputaland TFCA the proposed linkage between the
two fragments (see van Aarde & Fairall 2001) is larger than the TEP. This area therefore may be considered as an additional conservation area that will link the TEP to the MER rather than a wildlife corridor.

To persist in the longer-term (1 000 years), elephant populations require reserve sizes of a minimum 2500km² in order to maintain effective population size of 500 animals (Armbruster & Lande 1993). This prediction is based on high mortality rates and high environmental stochasticity in a relatively arid environment. Such conditions certainly do not prevail in Maputaland (see Chapter 2 & Chapter 5). Furthermore the concept of effective population size of 500 elephants is probably flawed (Caughley 1994). Elephant populations in other areas are likely to require smaller areas to permit population persistence (Armbruster & Lande 1993) as evidenced for the Addo Elephant National Park and supported by the analysis presented here.

Where elephants occur in small parks their numbers can soon exceed desired levels (Dominy, Ferguson & Maddock 1998). When elephants become too numerous they need to be managed but the methods currently available are far from ideal. Contraception has yet to prove a practical solution (van Aarde, Whyte & Pimm 1999) and culling is controversial and can enhance population growth rates (Dominy et al. 1998; van Aarde et al. 1999; Pimm & van Aarde 2001), thereby contributing to the problem it is meant to solve.

**Enumeration of elephant populations**

Small populations of elephants tend to be under-estimated (Whitehouse et al. 2001; Barnes 2002). The methods used to estimate population sizes for the elephants of Maputaland have consistently underestimated true population size especially when
populations were small (Chapter 3). Given the previously discussed concerns over small populations it is important that small populations are not undercounted. To manage elephants population size should be known. If populations are declining then research focused on determining why the population is declining should be implemented. Increased protection or decreased utilisation may be needed or alternatively animals could be introduced to the population to increase numbers. If populations are increasing culling, contraception or translocation may be needed.

The present thesis is part of a research programme of the Conservation Ecology Research Unit that aimed at addressing several commonly held beliefs regarding the elephants of Maputaland and the reserves in which they occur. Some 69% of the population in the TEP apparently comprised free-ranging bulls (KwaZulu-Natal Nature Conservation Service 1999), and it was believed that the population numbered some 120 to 130 elephants (despite aerial surveys yielding estimates far less than this; see Matthews 2000). The suggested overabundance of adult bulls was used to justify sport hunting in the TEP and four bulls were shot in 1998. For the MER it was assumed, although there has been little investigation to support the assumption, that the population is biased towards females, with fewer males due to poaching (Ntumi 2002). My research does not support these notions and perceptions built on casual observations should not be used as a basis to manage populations. The sub-population of elephants in the TEP indeed has an adult sex ratio that favours bulls, but not to the extent previously accepted. Apparently few breeding herds lived in the Park when the fence was erected. For the TEP my estimates yield larger populations then those previously determined by helicopter surveys and through ‘informed guesses’.
Given the relatively high mortality rate among older bulls, high survival rates for females, a more even sex ratio in younger age classes and the population growth rate, it appears likely that the bias towards older bulls observed in TEP is decreasing as population size increases. I did not find the MER population to be as biased towards females as previously estimated by regional conservation authorities. The mark-resight methods I have applied (see Chapter 4) have not been used previously to estimate elephant numbers. Based on my studies these models are applicable to elephants especially in landscapes where other methods are inadequate.

Implications of small population size and fragmentation for elephants

Of the 200 elephant populations listed for southern and eastern Africa by Blanc et al. (2003), 106 (53%) comprise <250 elephants and some 76% (n=153) consist of <1 000 elephants. Only 30 populations (27%), exceed 2 000 individuals. Of the 200 populations, 83 are restricted to areas less than 1 000 km² and an additional 24 to areas <2 000 km². Some 54% of populations (n=107) therefore occur in areas <2 000 km². Only a quarter of elephant populations (n=48) live in areas >5 000 km² (Blanc et al. 2003). We therefore cannot ignore small populations as they are a reality for conservation in the modern era and so we must develop management regimes that may be based on Caughley’s small population paradigm (Caughley 1994).

Some 384 elephants live on the coastal plains of Maputaland (Chapter 4). The Kruger National Park (KNP) that is situated to the north of Maputaland, supports more than 10 000 elephants (see Blanc et al. 2003). The Limpopo National Park that adjoins the KNP has a population of about 150 elephants (Blanc et al. 2003). As the fence between KNP and Limpopo is removed, the KNP/Limpopo population will eventually be reunited. The population is large as is the conservation area over which

South of Maputaland elephants from KNP have been introduced to small, isolated conservation areas. These populations are relatively small (Mkuzi Game Reserve, n=28, Greater St. Lucia Wetland Park, n=31, Pongola Nature Reserve, n=33, Itala Nature Reserve n=61, Hluhluwe-Umfolozi Game Reserve n=310, see Blanc et al. 2003). In the smaller reserves key management issues relate to small population size, perceived sex and age distributions and the effects of elephants on other species of conservation concern (Slotow et al. 2000).

The key management issues for Maputaland are that there is the possibility of increasing landscape area available to elephants, reuniting a fragmented population and providing a linkage for regional elephant populations. Although the overall population for southern Mozambique and KwaZulu-Natal is less than 1 000 elephants the sub-populations of TEP and the MER represent almost 50% of this total. While the conservation of a population of less than 500 elephants might be considered of low priority compared to larger regional populations the importance of the Maputaland elephants, other than their potential to act as surrogates for the wider conservation of the region, is that they would to provide a link between the large population of the KNP and smaller populations occurring in KwaZulu-Natal in which landscapes managed for conservation and tourism are increasing.

Armbruster & Lande (1993) suggest a ‘minimum effective population size’ for elephants of 500 individuals in a minimum reserve size of 2500km$^2$. The minimum population size they propose is based on genetic variability assumptions (Franklin 1980) that are questionable (Caughley 1994). The population and reserve sizes proposed by Armbruster & Lande (1993) would, according to them, provide a 99%
probability of persistence for 1 000 years and includes both demographic and environmental stochasticity. Predicting the population viability of any species or conservation area over a 1 000 year time frame and with such a high probability of persistence may not be realistic (see Armbruster and Lande 1993). While conservation agencies should strive for extensive conservation areas and large populations, it must be recognised that such conditions may be the exception rather than the rule. The establishment of smaller conservation areas and small populations may be more practical. Where possible these smaller conservation areas and populations should be linked.

Some reserves with small founding populations have been expanded to accommodate increasing elephant populations, (e.g. Addo was 103 km$^2$ in 1999, but will increase to 3400 km$^2$ as the Greater Addo National Park; Woodd 1999). Many southern African parks have a high edge to interior ratio, so factors operating outside these Parks are expected to have a large impact on management. Surrounding land use needs to be considered in the management of such protected areas (Siegfried et al. 1998).

The number of individuals within a population may determine the long-term survival of the population (Lande & Barrowclough 1987). Small, closed populations may be depleted of genetic variation. When genetic variation decreases the fitness of the individuals in the population may decrease due to inbreeding depression. This may compromise adaptability and evolutionary potential (Ralls et al. 1986; Lacy 1993). It is important, therefore, that the potential loss of genetic diversity and subsequent threats to population viability in small fragmented populations is considered in their management (Amos & Hoelzel 1992; Whitehouse & Harley 2001).
Even relatively few animals exchanging between sub-populations is preferable to the total isolation of populations. Where natural exchange is not possible, managers can move animals between populations (Whitehouse & Harley 2001). The conservation goal of the reunification of the two Maputaland sub-populations should be to ‘re-establish spatial heterogeneity in the distribution of individuals and environmental conditions, with regular movement and dispersal’ (e.g. Gruntfest et al. 1997).

The recovery of space for elephants

Removing the fence that induced the fragmentation can restore the spatial integrity of the population in Maputaland. The Maputaland elephant population, as with many elephant populations in southern Africa, occurs across an international border. Worldwide about one-third of all areas of high biodiversity straddle international boundaries (Westing 1998). In Africa the elephant when used as a flagship species can highlight these areas and attract interest and funding. Countries with better resources can aid their neighbours in conserving common resources. This, however, might prove increasingly difficult if the current trend in reduced funding for conservation by southern African countries continues (Hanks 2001; Wynberg 2002; Smith et al. 2003; Western 2003).

An exciting concept to recover spatial integrity for elephant populations is that of TFCAs (Westing 1998; Hanks 2001; Wynberg 2002). Transfrontier conservation initiatives aim to expand the area under conservation by linking protected areas with other areas in the land use mosaic (Hanks 2001). TEP is a protected area as is the MER. The cross border linkage provided by the Futi Corridor would include different land use options including subsistence agriculture and fishing, forestry, natural
resource extraction and community conservation areas. While there are political and socio-political challenges to be overcome (de Boer & Baquete 1998) the linkage would alleviate the constraints that humans impose on elephant movement in Maputaland.

The recovery of population dynamics across space is desirable as large areas are spatially more heterogeneous and habitat types not found in smaller areas may be included in larger areas (vegetation mosaic hypothesis; Short & Turner 1994). Single, large, continuous conservation areas are preferable to multiple smaller conservation areas (Soulé & Simberloff 1986; Schwartz 1999). At the scale of species, populations, communities, ecosystems and landscapes there is a need to conserve ecological patterns and processes (Poiani, Richter, Anderson & Richter 2000). This can only be achieved through the conservation of large areas and, therefore, conservation areas should represent regional features (van Jaarsveld et al. 1998).

When elephants are confined to small fragments of the landscapes in which they formally lived this can lead to competitive interactions and intensified aggression (Berger & Cunningham 1998; Slotow et al. 2000; Whitehouse & Hall-Martin 2000) as is suggested by the number of mortalities from male/male fights recorded for TEP (Chapter 5). The inclusion of the Futi Corridor and the lower population density of elephants in southern Mozambique compared to TEP will give more room for males to disperse, or spread females over wider area, thereby reducing male/male competition.

The importance of elephants in the landscape

At the landscape scale the ecology of Maputaland could change if elephants were to disappear. Elephants can affect their environment (Dublin, Sinclair & McGlade 1990;
Lock 1993; Cumming et al. 1997; Trollope et al. 1998; van de Vijver, Foley & Olff 1999). Elephants can be ‘ecosystem engineers’ which can change, maintain or modify their habitat and influence the availability of resources to other organisms (Jones, Lawson & Shachak 1997) and an ‘interactive species’ who’s removal can lead to significant changes in their ecosystem (Soulé, Estes, Berger & Del Rio 2003).

The ecology of Maputaland appears to be driven by water (soil moisture), and the effects of fire (Matthews et al. 2001) but where elephants occur they may contribute to fire derived effects. The sand forests of Maputaland are of high conservation value because they support most of the regions endemic species (van Wyk 1994; Matthews 2001). No change in forest structure due to elephant impact has yet been determined (R.A.R. Guldemon & R.J. van Aarde in prep.). Elephants predominantly use open and closed woodlands that support fewer endemics and are more robust to elephant impacts. Whether elephants are present or absent in Maputaland the ecosystems are predominantly driven by fire, which is usually anthropogenic and more frequent than natural fires (Matthews et al. 2001).

This study may prove useful for the conservation of small, fragmented elephant populations. Habitat fragmentation negatively affects vertebrate population dynamics (Robinson et al. 1992) and, therefore, detailed population analyses are needed in studies of fragmented habitats (Robinson et al. 1992). The methods applied to study the demography of the Maputaland elephants were chosen specifically in response to the challenges posed by a population for which very little reliable information was available, and where the elephants were known to habitually frequent areas of extensive forest, woodlands, thickets tall reed-beds and grassland. The two sub-populations are larger than previously thought (see Chapter 3), the adult sex ratio was not significantly biased to females in Maputo Elephant Reserve. Demographic
parameters are significantly different between the population fragments and may have diverged due to different conditions imposed on the two sub-populations. In the case of adult elephants the Tembe Elephant Park is biased towards bulls. Although fragmentation has led to significant differences in demographic parameters this may not be due to fragmentation itself given the long generation time of elephants. It may be due to the different management regimes that are in place. Both sub-populations are increasing, the less protected population (MER) at a lower rate than the well protected one (TEP). The elephant population of MER may be increasing at a lower rate due to higher mortality because of less protection in Mozambique. In addition to being confined within a fully fenced area, the TEP supports a smaller portion of adult cows than the MER, therefore reproductive output maybe lower although population growth rate is higher due to increased survival in TEP.

The TEP being fully fenced and intensively protected is representative of conservation areas in South Africa, including those in other areas of KwaZulu-Natal. The MER is more representative of conservation areas outside South Africa. Although not fenced, elephant distribution is determined by human density and activity (Hoare & du Toit 1999; de Boer et al. 2000). There has been some illegal use, protection is not strict and resources available to manage the MER are severely limited. These two scenarios are, therefore, broadly typical of those operating in the region.

This study is of importance to elephant conservation and management because the landscapes available to elephant populations may be increasing as illegal hunting declines, protected populations in confined areas are increasing in population size and previously fragmented populations are reunited. Small reserves will need more intensive management than larger reserves and this increases the cost of conservation in small reserves. As small reserves are unlikely to support viable populations of
elephants, populations will have to be managed as meta-populations unless they are linked to other landscapes available to elephants.

The utility and impact of TFCAs’ for conservation objectives in general and elephant populations specifically, is open to discussion. The TFCA concept implies that conservation areas will be expanded and linked. Ecological theory predicts that large contiguous areas are preferable to small fragmented ones. The positive implications for elephant conservation therefore are apparent (see Bulte et al. 2004).

Elephants have recently been confined to relatively small areas by human encroachment and have come into conflict with people. As populations increase in numbers and populations are reunited elephants returning to areas from which they have been excluded will present managers with new problems.