The demography of a fragmented population of the savanna elephant (*Loxodonta africana* Blumenbach) in Maputaland

By

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I haue rid vpon an elephant ſince I came to this Court, determining one day (by Gods leaue) to haue my picture expreſſed in my next Booke, ſitting vpon an Elephant,

Tom Coriate ‘Traveller for the English Wits: Greetings’ (1616).

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Abstract

The savanna elephant is a flagship species for conservation in Maputaland, a biologically diverse centre of endemism. At present Maputaland's elephants are fragmented into two sub-populations, those confined to the Tembe Elephant Park (TEP) and those roaming across the Maputo Elephant Reserve (MER) and along the Futi Corridor. Fragmentation may have affected the sub-populations by skewing age and sex ratios, decreasing survival, isolating the sub-populations, and restricting landscape selection.

My evaluation of historical population estimates suggest that the size of the elephant populations has been under estimated both before and after the construction of an electrified fence that fragmented the population. The application of a series of mark-recapture models to sight-resight data collected in TEP resulted in a population estimate of 179 (95% CI=136-233). The Bowden's estimator was the most suitable model under prevailing conditions.

My results confirmed that small populations of elephants are difficult to census in closed habitats. Estimates derived from aerial counts significantly under-estimated minimum population size determined from a registration count. Estimates derived from mark-recapture models approach or exceed those from registration counts.

Both population fragments are increasing in numbers: TEP's at 4.6% per year, MEP's at 3.1% per year. Demographic variables are significantly different, age at first calving is 11.5 years and 9.9 years, and calving interval is 4.2 years and 2.2 years for TEP and MER respectively. Age distribution was similar for females but not for males, as TEP showed a bias for adult males.

At the population level bulls in TEP favoured sand forests while breeding herds preferred reedbeds, but these preferences did not prove to be statistically significant. Individual bulls appeared to select for closed woodland landscape type but no statistical significance could be determined.

My study highlights the inconsistencies inherent in using historical data to determine population trends. Caution must be used when management decisions are based on such estimates. Sight-resight models are suitable for the enumeration of elephant populations. My results do not support landscape selection in elephants. The differences between population variables for the sub-populations are probably due to age and sex ratios imposed when the population was fragmented and the different levels of protection afforded to the sub-populations.

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For me researching and writing this PhD has been similar, I imagine, to conducting a long and arduous ocean voyage. At times is has been plain sailing, at others storms have raged and tempests have been endured. I hope I have charted some unknown waters on the way and improved understanding for those who sail after me. I have been very fortunate on my voyage to have Rudi van Aarde as my captain. He has kept me off the rocks, reset my compass on many occasions and taught me the ways of the academic seas. Fortunately I never had to mutiny, nor did he have to keel-haul me, though I believe I came close to walking the plank a few times. If I now approach dry land it is thanks to his perseverance and trust in my abilities.

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La luta continuar.

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Chapter 1

Introduction

My study is one of several conducted between 1999 and 2004 in the Maputaland region under the auspices of the University of Pretoria's Conservation Ecology Research Unit. In this dissertation I focus on the demography of the two principal sub-populations of savanna elephants (*Loxodonta africana*) living in the region. This study uses well established techniques to estimate the sizes of the two sub-populations. The synthesis of this information will contribute to the design of a Transfrontier Conservation Area (TFCA) in the region that will reunite the population fragments and, therefore, enable the population to function as a single entity. The present chapter puts my study into context with the recent history of the savanna elephants and provide a rationale for this investigation.

The Maputaland area of northern KwaZulu-Natal and southern Mozambique has been identified as an important area of biological diversity and is characterised by relatively high levels of endemism (White 1983; van Wyk 1994). In accordance with recent conservation ideologies directed at so called 'hotspots' (Myers, Mittermeier, Mittermeier, de Fonseca & Kent 2000), a very high percentage of global terrestrial biodiversity can be protected on a small proportion of the Earth's land surface (Mittermeier, Myers & Thomsen 1998). As such an area, Maputaland deserves priority attention to afford protection to all its biota.

This area, with the addition of eastern Swaziland, has been identified as an ideal place in which to establish a TFCA which would strive to conserve the biological diversity, increase the level of protection awarded to the area, improve the social and economic welfare of local communities and increase the capacity of the national partners to manage natural resources (van Aarde 1999; Hanks 2001). Its importance is further enhanced as the TFCA would span from mountains to the ocean and so include a great diversity of habitat types.

Perhaps the most important biological factor available to allow the TFCA concept to work in this region is the presence of the savanna elephant. The elephant fits the criteria for it to be considered a 'flagship species', defined as a species that attracts public interest (Simberloff 1998; Caro & O' Doherty 1999; Williams, Burgess & Rahbek 2000). Elephants can also be considered a 'keystone species', *i.e.* a species whose importance in its ecosystem's functioning is far greater than would be expected from its biomass and abundance (Mills, Soulé & Doak 1993; Boswell, Britton & Franks 1998; Caro & O' Doherty 1999; Jordán, Takács-Sántas & Molnár 1999). The elephant is an animal of popular interest, is able to generate tourist income and is attractive to funding agencies and donors.

Elephants presently occur on both sides of the South Africa/Mozambique frontier in Maputaland and these animals were previously considered as belonging to one population (Hall-Martin 1980, 1992; Klingelhoeffer 1987). Events over the last 20 years have fragmented this population into at least two sub-populations through the construction of electric fences. The existing population fragments are located in the Tembe Elephant Park (TEP) in South Africa and the Maputo Elephant Reserve (MER) in Mozambique. Prior to my study estimates for TEP were 130 elephants, with up to five breeding herds present (although survey techniques used suggested a population far below this figure; see Matthews 2000) and an estimate of 205 elephants for MER (de Boer & Baquete, 1998; de Boer, *et al.*, 2000; Ntumi 2002).

These estimates were suspected to be unreliable and very little was known about sex ratios, although they were understood to be heavily male biased in TEP with far more bulls than females (69% of the TEP population was estimated to be adult bulls; KwaZulu-Natal Nature Conservation Service 1999). De Boer *et al.* (2000) stated that the population in MER then comprised mainly of breeding herds with a very low incidence of lone bulls.

At the onset of the present study very little reliable information was available, therefore, on population variables such as sex and age structures, fecundity rates and survival schedules. A study dedicated to elephant demography would, therefore, be a prerequisite for efforts directed at the conservation management of the species in the Maputaland region.

Due to changes in the political climate and the cessation of military conflict in Mozambique the situation in the region has changed dramatically. It may now be possible to reunite the two population fragments. The linkage would be provided by the Futi Corridor, an established elephant dispersal route, and would be conducted as part of the proposed TFCA. Although habitat corridors can be species specific and may not stop species loss (Boswell *et al.* 1998), in the case of Maputaland the proposed corridor is an established elephant route and is large enough to effectively unite TEP and MER sub-populations. The removal of the elephant-proof fence between TEP and the Futi drainage line could effectively reunite the elephant sub-populations and the landscapes in which they occur. It may be possible, therefore, to use the reunification of the elephant population, at species level or fine scale, to ensure the restoration of the Maputo/Futi/Tembe ecosystem at landscape level or coarse scale (Schwartz 1999). As fragmentation of elephant populations is common in southern Africa, I give an outline of the history of fragmentation and its inherent problems.

The distribution of elephants in the pre-colonial (pre circa 1840) era

During pre-colonial times elephants were distributed throughout Africa where landscapes were favourable (Owen-Smith 1988; Spinage 1994). Prior to the nineteenth century people probably did not have the technology to hunt elephants at levels that would have affected their distribution (Alpers 1975). In the pre-colonial era elephants were hunted for meat and ivory using pits, weighted spears and axes (Alpers 1975). In southern Mozambique they were also exposed to specialist elephant hunters (Hedges 1978 cited in Merrett & Butcher 1991). In response to the decimation of human populations in many areas of Africa by war, slavery and disease elephants may have been more numerous and widespread at the onset of the colonial period than before (Selous 1925; Adams & McShane 1992). The commercial ivory hunters who decimated elephant populations and fragmented their distribution came later and were at the forefront of the colonisation of Africa (Selous 1925).

The distribution of elephants in southern Africa during the colonial period (1840s-1960s)

Prior to the arrival of European settlers, elephants inhabited ‘woodlands’ from the Cape Province to the Sudan (Fitzsimonds 1920). Elephants had long been hunted for ivory, and populations may already have been depleted at the onset of the colonial period (Alpers 1975; Milner-Gulland & Beddington 1993; Whyte 2001). During the colonial period commercial hunting for ivory with increasingly advanced rifles and the expansion of European settlement (with associated habitat transformation) accelerated elephant population decline in Africa, and caused their range to contract (Fitzsimonds 1920; Selous 1925; Kittenberger 1929; Cumming *et al.* 1990; Milner-

Gulland & Beddington 1993). The elephant hunter H.A. Bryden predicted that the rate of ivory extraction in the late 1800s would cause the extinction of elephants in southern Africa (Bryden 1889). The spread of traders, use of fire arms, and ability to haul large volumes of ivory on ox-wagons almost validated his prediction, as elephants were nearly exterminated from southern Africa in the period of 60-70 years preceding 1900 (Bryden 1903) as "before the resistless march of the railway and the man with the breechloader the game inevitably disappears" (William Finaughty, elephant hunter, in Tabler 1957). By the turn of the nineteenth century elephants were 'scarce' south of the Zambezi River and in large areas of east Africa (Kittenburger 1929) and rare over most of southern, eastern and western Africa (Owen-Smith 1988).

Colonial authorities, in response to the widespread loss of large mammals, introduced hunting restrictions and established game reserves and parks. In 1858 the Cape Colony issued strict protection measures for elephants. This was followed in 1860 and 1876 with protection measures ordered for elephants in the Addo Bush the Knysna Forest respectively. This did not, however, halt their persecution (Skinner & Smithers 1990). At the turn of the nineteenth century the elephant populations of South Africa had been fragmented into four small populations: the Addo bush (now Addo Elephant National Park, proclaimed in 1931 with a population of 11 elephants, see Hall-Martin 1980), Knysna Forest in the former Cape Colony, the Sabie Game Reserves (proclaimed in 1898, re-proclaimed as the Kruger National Park in 1926, see Whyte 2001) in the former Transvaal and in Maputaland, Natal (Fitzsimonds 1920; Haagner 1920).

Game protection initiatives were tabled for continent-wide control under the Convention for the Preservation of Wild Animals, Birds and Fish, held in London in 1900. Although Rhodesia (now Zimbabwe) passed its first game laws in 1902

(Skinner & Smithers 1990) and by 1920 elephant hunting was controlled by colonial governments in 'most, if not all, of the African States' (Fitzsimonds 1920), these initiatives proved ineffective. In the 1890s the first colonial game reserves were established in South Africa, with other colonial administrations following suit, *e.g.* the Wankie (Hwange) National Park, Rhodesia, in 1930 and The Maputo Elephant Reserve, Mozambique, in 1932.

The distribution of elephants in Maputaland

The elephant population of Maputaland was hunted commercially from at least the 1850s (Merrett & Butcher 1991), with large scale hunting for ivory in the Delagoa Bay (Maputo) hinterland, Tongaland (Maputaland) and Zululand (Northern KwaZulu-Natal) between 1850 and 1875 (Baldwin 1863; Leslie 1875; Bryden 1889; Merrett & Butcher 1991). Considered common in these areas at the beginning of the 1850s, elephants in northern Natal/Zululand were largely hunted out by the 1880s (Bruton & Cooper 1980; Merrett & Butcher 1991) with a 'few' around St. Lucia and only remaining 'in numbers' in Maputaland (Sclater 1900). In 1918 "Zululand's last elephant was found dead" but "occasionally elephants cross the Zululand border from Portuguese territory" (Fitzsimonds 1920). Haagner (1920) reported that populations were present in southern Mozambique, "especially Gazaland and Mapotoland, where herds of varying size still exist, but which the farmers in the neighbourhood seem determined to exterminate".

The population must have recovered, as large numbers of elephants were present in Maputaland in recent historical times. Smithers & Tello (1976) reported that over 500 were killed between the Maputo River and the Swaziland border in the 1940s as a crop protection measure. During the 1940s elephants were also observed in the Ingwavuma district in South Africa (Lugg 1970). Elephants from Gaza repopulated the Kruger National Park from about 1900 after European hunters almost exterminated them between 1880 and 1896 (Whyte 2001). By the 1970s Smithers & Tello (1976) considered elephants in Maputaland as increasing and ‘abundant’ in the Maputo Elephant Reserve, after the banning of professional meat and ivory hunting in Mozambique in the early 1960s.

The distribution of elephants in the post-colonial era

Independence came to most African states in the 1960s and 1970s. Post independence, European conservation models which stress the economic value of wildlife were initially maintained, often ignoring the associated costs and creating social tensions (Parker 1983). More recently new models for conservation have been developed which better address the conservation needs of Africa (*e.g.* Hanks 2001; Western 2003). Where colonial attempts to conserve elephants were successful, by independence some countries faced the problem of too many elephants in conservation areas, leading to vegetation change (e.g. Buechner *et al*. 1963; van Wyk & Fairall 1969; Laws 1970; Barnes 1983) with potential impacts on species composition (Owen-Smith 1988). In response to local over-abundance elephant control programmes were instituted (Laws, Parker & Johnstone 1975; Hanks 1979; Whyte, van Aarde & Pimm 1998; van Aarde, Whyte & Pimm 1999). Outside of protected areas elephant populations continued to decline due to the expansion of human agricultural activity (Parker & Graham 1989a) and the inability of governments to control human competition with elephants (Parker & Graham 1989b).

During the 1970s and 1980s many countries in Africa experienced civil war and ethnic strife, fuelling the killing of elephants (Douglas-Hamilton 1987). By the

1970s concerns of elephant population decline were voiced but data to support the decline was lacking (Douglas-Hamilton 1987; Barnes *et al*. 1999). It has been estimated that in 1979 about one million elephants existed covering a range of some 7.3 million km^2 (Spinage 1994). These elephants were found in many fragmented sub-populations (Douglas-Hamilton 1987). Marked declines in elephant populations due to illegal hunting for ivory continued in the 1980s in east, west, central and some parts of southern Africa, although populations increased or stabilised in Botswana, Zimbabwe and South Africa (Douglas-Hamilton 1987; Thouless 1999). In 1976 the African elephant was placed on Appendix II of the Convention of International Trade in Endangered Species of Flora and Fauna (CITES). By 1987 estimated elephant range was reduced to 5.9 million km^2 (Spinage 1994) and in 1990 the African elephant was moved to Appendix I of CITES. Blanc *et al*. (2003) estimate that present elephant range covers 5 346 000 km^2, of which 35% is known range and 65% is possible range.

South Africa has recently experienced a significant increase in areas managed for conservation (Wynberg 2002). This increase includes areas under private ownership and these areas are important contributors to the protection of biodiversity in the country (Wynberg 2002). As a result elephant range has increased, as animals were translocated on to state and private land, or elephant range has expanded into areas contiguous with parks (*e.g.* the Klaserie, Timbavati and Sabi Sands private reserves adjacent to Kruger National Park; see Hall-Martin 1992). Although private landowners have changed from agriculture or ranching to wildlife as a land use option the motive is usually profit (Duffy 2000). Some private conservation areas support small elephant populations sourced from the Kruger National Park (Hall-Martin 1992), and may be of little conservation value unless intensively managed.

Despite the frequent failure of western approaches to wildlife conservation in post-colonial Africa (Parker 1983), perhaps most notably for the elephant, western interests, especially protectionist NGOs, continue to try and dictate conservation practice (Adams & McShane 1992; Bonner 1993; Gibson 1999; Duffy 2000), recommending areas are set aside for elephants. Western conservation organisations have subsequently been accused of imperialism or of wanting to re-colonise Africa (Adams & McShane 1992; Gibson 1999).

Partly in response to claims of imperialism, and partly as a result of a more holistic approach to conservation, a new paradigm of ecosystem conservation, which includes humans as an integral part of the system has been identified (Parker 1983; Gibson 1999; Duffy 2000). This paradigm needs to address the fact that elephants and humans are unable to co-exist above certain human population densities (the absolute density is dependent on local conditions, see Parker & Graham 1989b) and that human population increase is one of the leading causes of elephant population decline (Douglas-Hamilton 1987; Parker & Graham 1989a). If areas are set aside for elephants there is concern that reserves would become island ecosystems in a sea of transformed habitat (Owen-Smith 1988). Rather than setting aside 'island' populations of elephants, perhaps there is a greater need for conservation models for national parks and other areas that are broader and integrate conservation with other land uses (Parker 1983; Hanks 2001; Wynberg 2002).

The consequences of fragmentation for elephants

The fragmentation of landscapes and populations is of concern to conservation managers and scientists (Lande 1988; Burkey 1989; Cutler 1991; Robinson *et al.* 1992). Small fragmented populations are at greater risk of extinction from demographic and environmental stochasticity and less likely to survive than larger populations that are less restricted spatially (see Terborgh & Winter 1980; Diamond 1984; Burkey 1989, 1999 and references therein).

The use of surrogate species in conservation biology may be a short cut to monitor or solve conservation problems (Caro & O' Doherty 1998), but Simberloff (1998) identified problems posed by a single species approach and proposed that we aim for ecosystem conservation. He acknowledged, however, that it is hard to define the ecosystem system and its function so perhaps the use of surrogates can be justified. The assumption underlying the use of surrogates is that if we protect the surrogate we can adequately conserve regional biota (Andelman & Fagan 2000). There is little evidence to support the use of umbrella or flagship species, and that, as a minimum, surrogate species must spatially co-occur with a large proportion of other species in the area of interest (Andelman & Fagan 2000).

The long-term population persistence of elephants is probably dependent on an initial population size exceeding 400 individuals (van Jaarsveld *et al.* 1999) and isolated populations smaller than this have experienced reduced genetic diversity (Whitehouse & Harley 2001). In South Africa only Kruger National Park and adjacent areas exceed a population size of 400 elephants (Hall-Martin 1992), although the founder population was probably much smaller and numbers increased due to immigration from Mozambique (Whyte 2001). The only elephant populations in South Africa/southern Mozambique that are not recently derived from the Kruger population are those of Maputaland and Addo Elephant National Park.

The Maputaland coastal plains are of importance as a biodiversity 'hotspot' (Myers *et al.* 2000) and many endemics/near endemics co-occur with the elephant populations (van Wyk 1994). We propose that the presence of elephants can afford other species conservation that they might not otherwise have. Elephants fit the criteria of a flagship species because they can be used to "anchor a conservation campaign because it arouses public interest and sympathy" (Simberloff 1998) and are a species that stands for, or promotes, conservation in a general or regional sense (Mittermeier *et al*. 1998).

The presence of the African elephant as a flagship species might be a key factor in the conservation of the biodiversity of Maputaland. Early in the planning phase, the Peace Parks Foundation (PPF) identified the importance of elephants to the TFCA. It is significant in this case that the elephant was not used to determine the importance of Maputaland as a biodiversity 'hot spot' (Mittermeier *et al*. 1998), but used as a flagship species to attract funding, support and interest.

While ecosystem management is better than the conservation of flagships, in the case of Maputaland, perhaps, the flagship can enable ecosystem protection, especially by using elephant ranges to determine the ecosystem boundaries (Fairall & van Aarde 2004a). The elephant can be used as a flagship to draw attention or raise funds, but the status of elephants does not necessarily reflect the health of an ecosystem, as the removal of larger vertebrates can cause a wave of further extinction (Pimm 1991). For instance in South Africa the decline of elephants has resulted in forestation of large areas of savanna habitat, leading to localized extinction of several species of grazing antelope (Owen-Smith 1989).

Re-connecting fragmented elephant populations

If fragmentation has negative effects for elephant conservation then the ideal solution to the problem of fragmented elephant populations is to reunite, *i.e.* de-fragment, them. This may be facilitated through the establishment of TFCAs. In most countries in the world, and in countries that were former colonies in particular, international borders are politically determined and not ecological or physical boundaries. This is especially evident in Africa where many international borders are straight lines.

In Southern Africa there are seven TFCAs in development between South Africa and its neighbours. Of these seven potential TFCAs two include the linking of conservation areas in South Africa and Mozambique; the Lubombo TFCA and the Limpopo (Gaza-Kruger-Gonarezhou) TFCA. The Lubombo Transfrontier Trilateral Protocol, between Mozambique, South Africa and Swaziland, and the Lubombo-Tembe-Futi TFCA Protocol between Mozambique and South Africa, both signed on 22nd June 2000 (Peace Parks Foundation 2004), are aimed at establishing a TFCA between the signatories including areas currently inhabited by the Maputaland elephant populations, and removing the fence which currently fragments the elephant population.

While the establishment of TFCAs is usually seen as beneficial to conservation activities it is possible that some attempts could be detrimental in the long term if communities are marginalised or displaced, or communal property rights are not established (Metcalfe 1999; Mayoral-Phillips 2000; Wynberg 2002). Elephants should not, therefore, be used as an excuse to establish TFCAs where it might not be beneficial for the ecosystem, or in response to an elephant problem on one side of an international boundary.

Chapter 2

Study Area

Introduction

Maputaland is located at the southernmost end of the Mozambique Coastal Plain. This plain extends from Somalia in the north to northern KwaZulu-Natal, South Africa, in the south (Watkeys, Mason & Goodman 1993). It encapsulates an area of about 26,734 km^2 defined as the Maputaland Centre of Endemism (see van Wyk 1994). This centre is bordered by the Inkomati-Limpopo River in the north, the Indian Ocean in the east, the Lebombo Mountains in the west and the St. Lucia estuary to the south. Biogeographically the northern boundary of the centre is not as clearly defined as the other borders (van Wyk 1994). Earlier authors (*e.g.* Moll 1978; Bruton & Cooper 1980) considered Maputaland as an area of 5,700 km^2 in north-eastern KwaZulu-Natal. These authors clearly did not always consider areas beyond South Africa in their descriptions.

There has been some contention over the name Maputaland, formerly known as Tongaland in South Africa (Bruton 1980). Nevertheless this now seems largely settled and the name Maputaland is taken to be politically acceptable (van Wyk 1994) and is generally accepted on both sides of the South Africa/Mozambique border. Maputaland is the northern part of the Maputaland-Pondoland Region, a more arbitrarily defined area of about 200 000 km^2 of coastal belt between the Olifants-Limpopo River in the north (24^{o}S), to the Great Kei River (33^{o}S) in the south, bounded to the west by the Great Escarpment and to the east by the Indian Ocean (van Wyk 1994). For the present study fieldwork focused in the Tembe Elephant Park in

South Africa, with some surveys also being undertaken in the Maputo Elephant Reserve in Mozambique (Fig. 2.1).

Tembe Elephant Park

The northern boundary of the Tembe Elephant Park (TEP) forms the international border between South Africa and Mozambique. It is part of the Maputaland Centre of Endemism and extends over an area of about 300 km^2 (Matthews *et al*. 2001). It was proclaimed in 1983 (Gazette Notice Nº 73 of 1983) and re-proclaimed in 1993 (Gazette Notice Nº 11 of 1993), largely under the direction of the local people, with land for the Park allocated by Chief Mazimba Tembe (Sandwith 1997). The Park belongs to the Tembe Tribal Ward but is administrated on their behalf by Ezemvelo KwaZulu-Natal Wildlife. The people that lived in the area before the proclamation of the Park moved out, but retain the right to use some of its natural resources (Sandwith 1997). The Park was game fenced along its western, southern and eastern borders in 1983 and the northern border was fenced during 1989 in response to a perceived elephant poaching problem in adjacent Mozambique (Hall-Martin 1988; Ostrosky 1988). This fence stopped elephants from either moving in or out of the Park thereby fragmenting the elephant population of Maputaland.

Maputo Elephant Reserve (Reserva dos elefantes do Maputo)

The Maputo Elephant Reserve (MER) is located in the south east of Mozambique, below the Maputo Bay. The Reserve of 794km^2 was gazetted in 1932 and its current boundaries were finalised under the Diploma Legislativo Nº 22314 of 1969 (DNAC 2001).

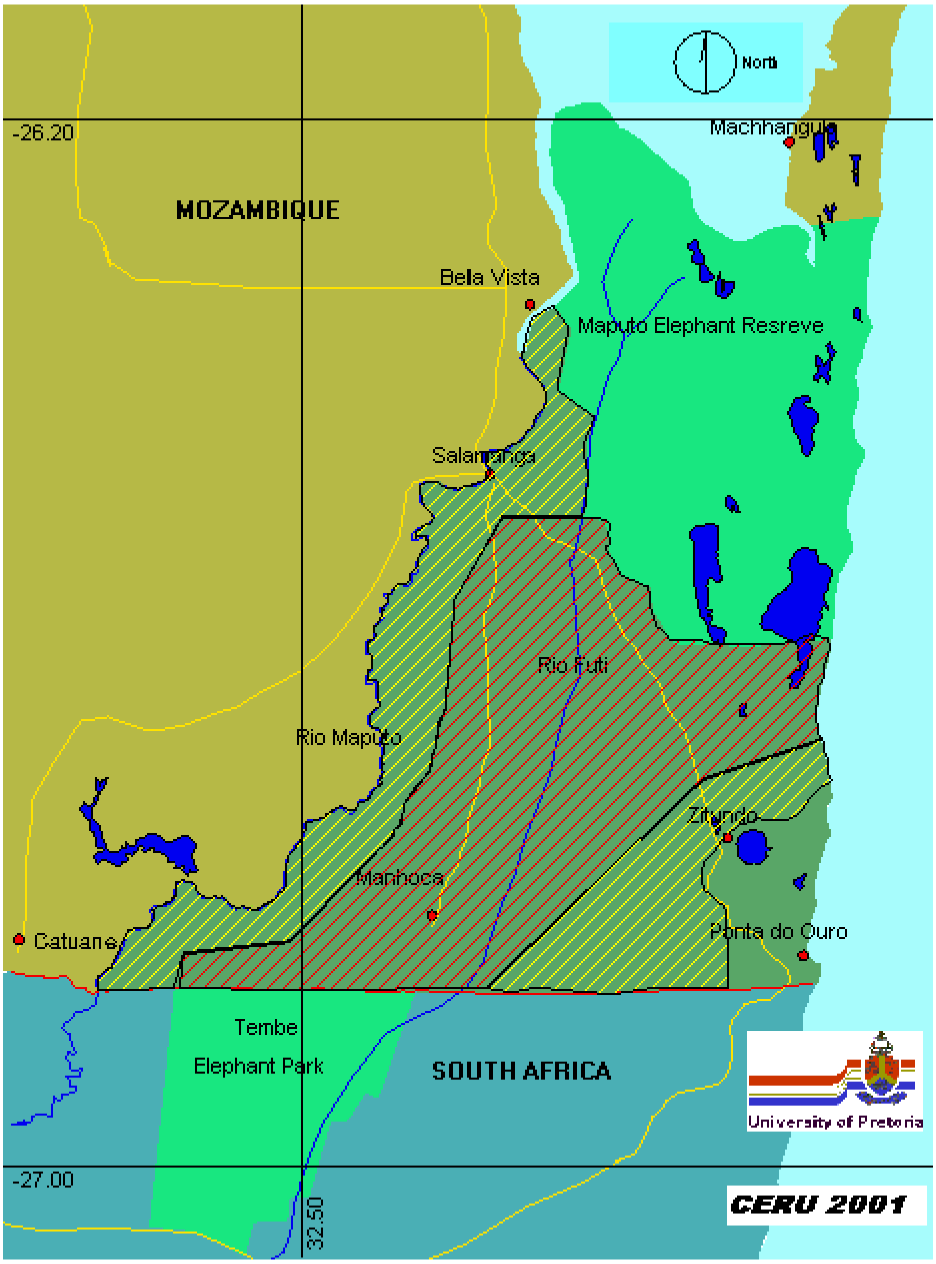

Figure 2.1. The elephant study centred on the Maputo Elephant Reserve and the Futi River Corridor, cross hatched in red, and Tembe Elephant Park in South Africa. The areas cross hatched in yellow are the proposed Community Conservation Development Areas (see DNAC 2001).

The Maputo Bay forms its northern boundary and the high water mark of the Indian Ocean delineates the eastern border. The western boundary largely follows the Maputo River as far as the town of Bela Vista, then heads eastwards in the direction of the Futi River (Rio Futi), before heading southwards along the road between Salamanga and Ponta do Ouro (DNAC 2001). The southern boundary goes east from the main road, and cuts through Lake Piti at 26°36'S. The Reserve is unfenced except for a 26 km distance along the western boundary close to Bela Vista (de Boer & Ntumi 2001). People continued to live in the Reserve after it was gazetted. Currently some 75 households exist within in the MER and the Futi Corridor totaling approximately 450 people (Els, Kloppers & van Aarde 2004; Fairall & van Aarde 2004a). This figure is far lower than the estimated 5 000 – 10 000 people reported to have lived there during the 1970s (DNFFB 1997). While law forbids the extraction of natural resources, collection of plant material has always been permitted (de Boer & Baquete 1998; Soto, Munthali & Breen 2001).

The Futi River Corridor

The Futi River in southern Mozambique runs from the north-east of TEP into the Maputo Elephant Reserve. The proposed Futi Corridor (DNAC 2001; van Aarde & Fairall 2001) is an area of 688 km^2 centred on the Futi River. In 1969, the time of the most recent delineation of the MER, the area south of the Reserve, east from the Rio Maputo to the ocean, and south to the border with South Africa was given a measure of protection as a Zona Vigilancia. The status of such a protected area in Mozambican legislation is unclear (DNAC 2001; van Aarde & Fairall 2001). The Futi area provides a natural linkage between the TEP and the MER and contains permanent fresh water and seasonal pans. The alignment of the proposed corridor has been identified to protect elephant range and habitat and to minimise elephant/human conflict (DNAC 2001; van Aarde & Fairall 2001), which has occurred in the area (de Boer & Baquete 1998; Soto *et al*. 2001).

The south-western areas of the proposed Futi Corridor contain different vegetation than other areas in the TEP/MER complex and so are included to attain the exceptionally high biodiversity value of the proposed TFCA (DNAC 2001).

DNAC propose a 'Core Conservation Area (CCA)' which would extend the area of formal conservation provided by MER from 790 km^2 to 1,520 km^2 flanked by two 'Community Conservation Development Areas (CCDAs)' covering an additional 693 km^2 which would act as buffer zones (DNAC 2001).

The Physical Environment

Geography

Maud (1980) and Watkeys, Mason & Goodman (1993) described Maputaland as almost flat and as a coastal plain that rises no higher than 150m. High rising dunes fringe the coastline. Palaeo-dunes in the hinterland form north-south ridges that were formed by a retreating coastline (Watkeys *et al.* 1993).

The Tembe Elephant Park is generally flat with two main dune ridges that run through it in a north to south direction. At 129m above sea level, the peaks on these ridges are among the highest on the coastal plain of Maputaland (Matthews *et al.* 2001). The Maputo Elephant Reserve is also generally flat with undulating dunes, the tallest of which reaches 104 metres (de Boer & Baquete 1998).

The coastal plain formed during the break-up of the Gondwana super-continent. Since then the plain has been exposed to rising and falling sea levels and the deposition, erosion and reworking of marine sands and silts. The oldest rocks occur in the Lebombo Mountains. These rocks date from the Jurassic Period and the geology gets progressively younger towards the coast. The Maputaland coastal plain consists of Quaternary sands. Most of these are redistributed sands and alluvium from river systems. These more recent geological features cover the Quaternary (youngest), Tertiary, Cretaceous and Karoo (oldest) sequences.

Watkeys *et al*. (1993) distinguish the Lebombo Mountains and the coastal plain landscapes and divide the coastal plain into undulating terrain, sandy ridges, coastal lake systems, coastal dunes and river-related systems. The Lebombo Mountains follow a north-south line, are up to 13 km wide and reach a maximum height of over 700m. Their western scarp is steep and to the east they slope gently. Both coastal and inland dunes are vegetated and the coastal dunes are among the largest vegetated coastal dunes in the world.

The rivers of Maputaland are of a simple drainage model (Cooke & Doornkamp 1990 cited in Watkeys *et al*. 1993), in that they have eroding headwaters, a water-sediment transport zone, and depositional lowlands. The three types of river identified for Maputaland are; large rivers with eroding headwaters lying to the west of the Lebombo Mountains, smaller streams with sources starting in the mountains, and streams with sources on the coastal plain. Rivers mainly run in a north-south direction determined by the presence of sandy ridges. The Pongolo River starts in South Africa and joins the Usutu River from Swaziland in Ndumo Game Reserve. It flows into Mozambique as the Maputo River and enters the Indian Ocean in Maputo Bay where it forms a large estuary. The Pongolapoort Dam restricts the flow of the Pongolo River and has a significant impact on the river and the associated floodplain and pans (Begg 1989). The Muzi swamps and adjacent wetlands are other important hydrological features and their surface area fluctuates with rainfall and other hydrological events. The swamps have some permanently waterlogged areas and other seasonally waterlogged areas occur (Begg 1989). The Muzi drainage becomes the Futi River in Mozambique and flows into the MER where it ends in a swampy delta that does not reach the Indian Ocean.

Maputaland is covered in yellow and grey soils. The soils are hydromorphic, mainly mesotrophic mixtures of sands and loams and are relatively infertile and leached. The alluvial systems of rivers, pans and floodplains are associated with more fertile red clay and duplex soils (Schulze 1982; Watkeys *et al*. 1993; Pollet *et al*. 1995). The higher lying and older south western dunes have higher clay content than the lower gradient dunes in the north and east and are consequently more fertile (Matthews *et al*. 2001). Along the Muzi Swamp, clay rich duplex soils have formed (Matthews *et al*. 2001) and these may continue along the Futi River as it drains the Muzi Swamps in a northerly direction into Mozambique.

During the dry winter period natural water in the TEP is limited to the Muzi swamp system. Seasonal pans occur, mainly close to the swamp, but also at Ezinaleni, Mahlasela, Vukazini and Sinzangwane. The Park's Management artificially replenishes the last three pans. The chemical composition of the lakes and pans in the MER varies and changes seasonally in response to rainfall (de Boer *et al*. 2000; Pollet *et al*. 1995). Some of these pans and lakes are brackish and saline.

Climate

Maputaland is a transitional sub-tropical area with warm temperatures and no winter frost. Climate varies from moist sub-tropical coastal eastern area to a moderately dry sub-tropical inland western area (Maud 1980). Schulze (1982) describes the region as warm to hot, humid and sub-tropical. Summers are hot and wet, winters warm and dry (van Wyk & Smith 2000). Temperatures range between 4°C and 45°C (Schulze 1982), with a daily maximum of 20°C to 24°C, depending on location (Schulze 1997). Mean monthly temperature at Lake Sibaya, in the south of Maputaland, varies between 11.5°C in July to 28.7°C in January (Maud 1980). The mean annual temperatures in the Tembe area range between 20°C and 22°C, with mean daily maximum temperatures for the summer months (December-February) varying from 28°C to 30°C. The mean daily minimum temperature for winter months (June-August) is less than 10°C (Schulze 1997).

Humidity and evaporation are high. In summer humidity often exceeds 80%, and during winter it usually ranges between 50% and 60%. Evaporation exceeds precipitation for all months except December, January and February (Schulze 1997). Rain falls throughout the year but is highly variable. In the Tembe Elephant Park rainfall peaks from September to March and troughs from May to August (Fig. 2.2) (Official records, Tembe Elephant Park[1]) and between 25% and 35% of rainfall can occur during the 'dry' winter months (Schulz 1982). Mean annual rainfall ranges from 900mm in the southeast to 500mm in the northwest, (Schulze 1982; Pollet *et al.* 1995), with a consistent decrease from east to west, in an inland direction.

The western plains receive 500 to 600 mm rain per annum and rainfall increases in the mountains, with the Lebombo ridge receiving 800 to 1 000 mm per year (Schulze 1982, 1997). The Tembe Elephant Park is located in the 700-800 mm rainfall area (Schulze 1982, 1997). Average rainfall is highly variable, both within the summer rainfall season and from year to year.

Tropical cyclones that move down the Mozambique Channel sometimes reach the area and are often associated with exceptionally high rainfall. Values then can be

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[1] EKZN, Tembe Elephant Park, P.B. 356, Kwangwanase, KwaZulu-Natal.

twice as high as the annual mean rainfall (Pollet *et al*. 1995). Dry years get less than half the mean annual rainfall. Thus rainfall is seasonally predictable but variable with the coefficient of variation increasing from 20% in the east to more than 30% in the west (Schulze 1997). The climate of the MER is comparable to that of the TEP, although along the coast rainfall and humidity are higher than inland (Maud 1980). There is little data available for the MER but in general, there is a hot wet season between October and March, and a cooler and relatively dry season from April to September. Rainfall is between 690-1 000m (DNFFB 1994 cited in de Boer et al. 2000).

Biodiversity

Cowling & Hilton-Taylor (1994) identified Maputaland as a biodiversity 'hot-spot'. They based this on the high species richness, high occurrence of endemics and threats to the habitats of the region. About 9% of the 2,500 species of vascular plants identified for the region are endemic to the Maputaland centre of plant diversity (van Wyk & Smith 2000). It is highly likely that more endemic species will be identified as research intensifies in the region (van Wyk & Smith 2000). Matthews *et al*. (2001) identified eight major plant communities in the TEP. These include sand forest, closed woodland on clay based soils, woodland of deep sandy areas, clay based soils, woodland of deep sandy areas, grassland associated with sand forest, grassland on clay-rich soils, grassland associated with swamp/marsh/pan areas, aquatic vegetation of marshes/pans, and reed-beds of the Muzi Swamp.

De Boer *et al.* (2000) recognised six vegetation communities in the MER; mangroves in the Maputo Bay and river deltas; dune vegetation of pioneers, thicket and forest; grass plains, parts of which are seasonally inundated; forest on old dunes similar to the sand forest of the TEP; open woodland and riverine vegetation of reedbeds and riverine forest. A recently constructed landscape map for the Futi Corridor region recognises 13 landscape units (Fairall & van Aarde 2004b) (Fig. 2.3). Two of these are endemic to Maputaland. These 13 landscape units are based on species composition (Table 2.1). The primary vegetation communities in the Futi Corridor are open woodlands, closed woodlands, woody grasslands, sand forest, swamp forest, hygrophilous grassland and reedbeds (Fairall & van Aarde 2004b). Fairall & van Aarde (2004b) used a supervised classification of a LANDSAT image to develop a landscape map for the area. They used the vegetation classes described by Pollet *et al.* (1995), and Matthews *et al.* (2001). They also included information from a map of the MER prepared by the Department of Biological Sciences of the University of Eduardo Mondlane (Fig. 2.3).

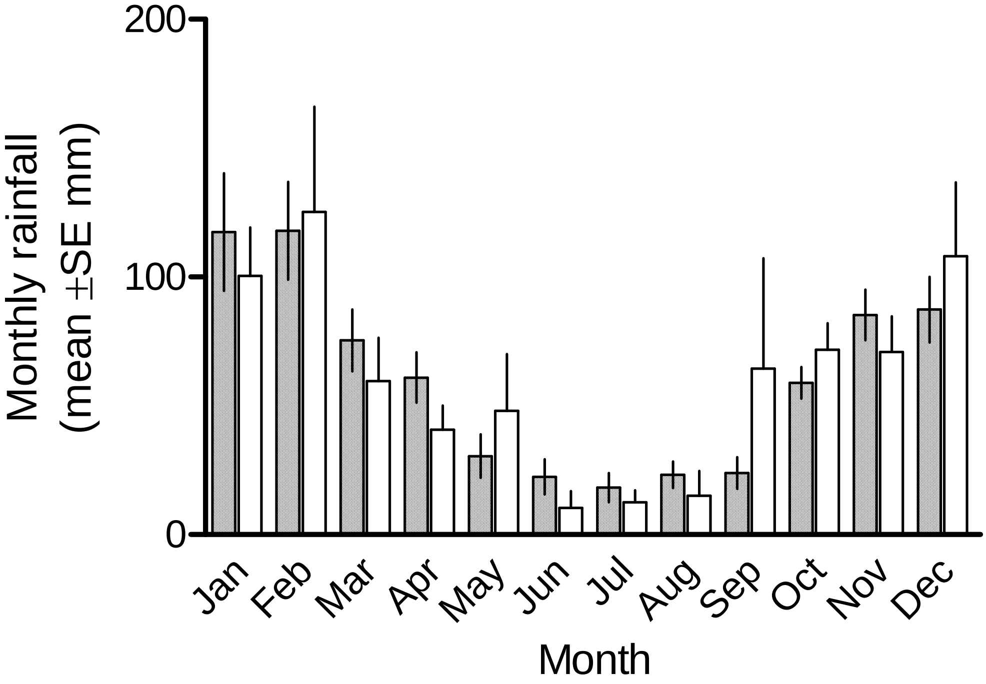

Figure 2.2. Mean monthly rainfall for the Tembe Elephant Park (clear bars, n=39 years, Official records, Tembe Elephant Park) and for Bela Vista (striped bars, n=7 years, Mozambican National Meteorological Institute Maputo 1999) at the southern and northern sectors of the study area. The seasonal pattern holds for the rainfall stations surrounding the study area, although the amount varies.

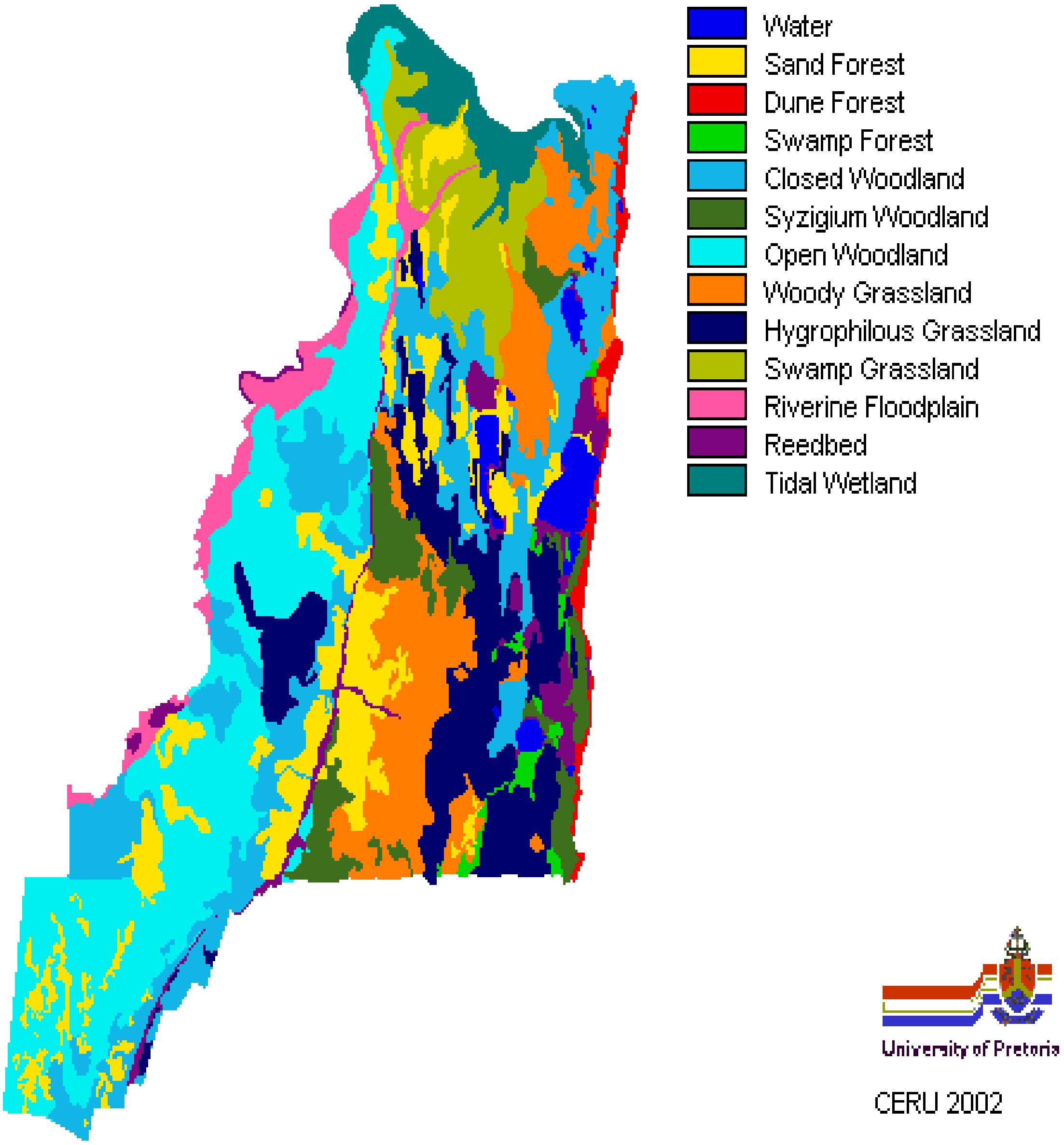

Figure 2.3. Landscape map of the study area constructed by Fairall & van Aarde (2004b) and derived from supervised classification of a LANDSAT image using all spectral bands. The map is based on information provided by Pollet *et al*. (1995), the University of Eduardo Mondlane (2000) and Matthews *et al*. (2001).

Table 2.1. The landscape units occurring in the Maputaland study area as determined by Fairall & van Aarde (2004b). The total area covered by each landscape type, its percentage of the total study area of 2100 km^2, and the number of patches it occupies are indicated, with a range of patch sizes and the dominant plant species occurring.

Landscape unit	**Area (km$^{2)}$**	**% of study area**	**Number of patches**	**Patch size & Location**	**Dominant plant species**
Water	NA	NA	NA	Ephemeral pans to 3,000 ha Lake Piti Inter-dune depressions	Reedbeds *Phragmites australis,* Bulrushes *Typha latifolius,* sedges *Cyperus* species and water lilies *Nymphaea* spp.
Sand Forest	301	14.3	55	0.6 – 33.1 km^2 Dune crests and higher lying sandy soils Occurs as forms of forest & thicket	Tree species include *Dialium schlechteri, Cleistanthus schlechteri, Hymenocardia ulmoides, Newtonia hildebrantii, Balanites maughamii, Pteleopsis myrtifolia Ptaeroxylon obliquum,* shrubs include *Drypetes arguta, Croton pseudopulchellus*, *Cola greenwayi* and *Psydrax fragrantissima* Vegetation type is endemic to Maputaland
Dune Forest	34	0.8	NA	Coastal band on coastal dunes	Seaward side: *Mimusops caffra*, *Diospyros rotundifolia* and *Euclea natalensis*. Landward side: *Apodytes dimidiata, Celtis africana, Acacia kosiensis* (formerly *karroo*) and *Strychnos* spp.
Swamp Forest	23	1.1	12	Inundated marshy conditions around Lake Piti & south of Lake Satine au Sotiba	*Voacanga thoarsii, Ficus tricopoda, Rauvolfia caffra, Macaranga capensis*, and *Syzigium cordatum*
Closed Woodland	444	21.1	13	0.7 – 53.2 km^2 Includes closed woodlands of TEP and woodlands of MER and comprises a range of different plant communities	Species occurring throughout the landscape include *Strychnos madagascariensis, Dichrostachys cinerea, Acacia burkei, Spirostachys africanus, Afzelia quanzensis, Albizia adiantifolia, Sclerocarya birrea* and *Combretum molle*. Grasslands supporting *Panicum maximum*, *Digitaria eriantha*, *Brachycloa* and *Eragrostis* spp. cover the areas between trees
Syzigium Forest	126	5.9	11	1.8 – 33.2 km^2 Mainly south east Mozambique	Dominated by *Syzigium cordatum*, tree species such as *Trichilia emetica, Albizia adiantifolia, Sclerocarya birrea and Bridelia micrantha occur.* May form a mosaic with *Hyparrhenia dissolute* and *Themeda triandra* grasslands in dry areas and with *Imperata cylindrica* in wet areas

Table 2.1 (continued).

Open Woodland	523	24.8	NA	Western side of study site Occurs as dry bushveld between Maputo & Futi Rivers	Trees & shrubs: *Strychnos madagascariensis*, *Strychnos spinosa, Acacia burkei, Sclerocarya birrea, Combretum molle, Terminalia sericia, Garcinia livingstonei, Vangueria infausta* and *Albizia versicolor* Denser grass cover than closed woodland including *Andropogon gayanus, Themeda triandra, Diheteropogon amplectens, Digitaria eriantha* and *Aristida* spp.
Woody Grassland	283	13.4	9	1.2 – 145.5 km^2 Woody component grows underground	Geoxylic suffrutex species such as *Salacia krausii, Eugenia mossambicensis, Dichapetalum cymosum and Parinari capensis.* Grass cover very dense and dominated by *Themeda triandra.* In some areas palms *Hyphaene coriacea* and *Phoenix reclinata* dominate to form “Palm Veld”. *Syzigium cordatum* occurs as isolated trees or bush clumps and is sometimes associated with *Terminalia sericia* This vegetation type is endemic to Maputaland
Hydrophilous Grassland	323	15.4	12	1.4 – 207 km^2 Low-lying seasonally inundated area in the southeast and central parts of the study area	True grassland with species such as *Ischaemum fasciculatum, Eragrostis lappula, Imperata cylindrica* and *Dactyloctenium germinatum* and in the wetter areas *Hemarthria altissima* and *Acroceras macrum*
Swamp Grassland	130	6.1	NA	Situated within boundaries of MER in the north	*Typha latifolius, Phragmites australis and Juncus* species. *Hemarthria altissima* recorded but area is not typical grassland
Riverine Floodplains	96	4.3	NA	Narrow strips of vegetation next to the Maputo and Futi Rivers	Floodplains covered in *Phragmites australis, Typha latifolius, Juncus* species and *Cyperus papyrus*. Riparian forests on riverine floodplains consist of trees such as *Ficus sycomorus, Kigelia africana, Syzigium cordatum* and *Trichilia emetica*
Reedbeds	84	3.8	NA	Along the Maputo and Futi Rivers. Extensive beds associated with some lakes	*Phragmites australis*, with some *Typha latifolius* and *Cyperus papyrus* in and along the slow flowing Futi River. Reedbeds associated with lakes are almost pure stands of *Phragmites australis*
Tidal Wetlands	95	4.3	NA	Shore of Maputo Bay	*Avicenna marina* and *Rhizophora mucronata* mangroves. Tidal area behind mangroves covered predominantly in *Phragmites australis* reeds and some salt marsh species

The sand forest is a major community containing many species endemic to Maputaland. It is associated with dunes and includes 42 endemic/near-endemic species in the Tembe Elephant Park of which 27 have been identified only in sand forest (Matthews *et al*. 2001). The closed woodlands mainly occur on the clay-rich soils of the 'bottomlands' of dunes and bordering the Muzi Swamp. In this community 20 endemic/near-endemic species were found in the Tembe Elephant Park, ten of which occur only in this vegetation type (Matthews *et al*. 2001). Woodlands of deep sandy areas dominate the Tembe Elephant Park and contain 37 endemic/near-endemic species (Matthews *et al*. 2001). Woodlands occur as closed woodland and thicket, ecotonal closed woodland, open woodland and sparse woodland (Matthews *et al*. 2001).

Maputaland has an exceptionally rich herpeto-fauna with 112 species/subspecies of reptiles, 23 of which are endemic (Bruton & Haacke 1980) and 45 frog species, three of which are endemic (Poynton 1980). Maputaland is also considered a biodiversity hotspot for freshwater fish (Skelton 2001). Bruton and Kok (1980) reported that 67 species of fresh water fish are found here, 12 of which are endemic to Maputaland (Davis, Heywood & Hamilton 1994). In a recent survey of the MER and the Futi Corridor 43 species were reported (Bills 2001). As with the flora, more intensive surveying may result in an increase in the recorded numbers of these mostly cryptic species. The invertebrate fauna of Maputaland is poorly understood; at least 257 species of butterflies are known to occur here (Davis *et al*. 1994).

Bird diversity follows the same trend as other vertebrates though in more spectacular numbers. At least 472 species have been recorded for the Maputaland region of which 4 species are endemic and 43 subspecies are either endemic or near-endemic (Davis *et al*. 1994). In the Maputo Elephant Reserve alone at least 340 bird species have been recorded (Parker & de Boer 2000).

Of the 102 mammal species/sub-species recorded in the region 14 are endemic. Game eradication programmes before the 1920s apparently depleted the large mammal fauna on the South African part of Maputaland, as did hunting with black powder guns and snares by local people (Lugg 1970). Military activities depleted game in southern Mozambique from the 1940s onwards and may have been responsible for the extermination of wildebeest in southern Maputo province (Smithers & Tello 1976). Populations of large mammals survived in the Ndumo Game Reserve and the Tembe Elephant Park was extensively restocked with such species between 1985 and 1996 (Sandwith 1997).

In southern Mozambique 11 species of large mammals (cheetah *Acinonyx jubatus*, lion *Panthera leo*, wild dog *Lycaon pictus*, white rhinoceros *Ceratotherium simum*, black rhinoceros *Diceros bicornis*, zebra *Equus burchelli*, blue wildebeest *Connochaetes taurinus*, impala *Aepyceros melampus*, African buffalo *Syncerus caffer*, kudu *Tragelaphus strepsiceros*, and waterbuck *Kobus ellipsiprymnus*) were reported as extinct in the living memory of local people (Tello 1973). All of these have been reintroduced to the Tembe Elephant Park, with the exception of wild dog and cheetah. Of the other 14 large mammal species present in Tembe (spotted hyaena *Crocuta crocuta*, leopard *Panthera pardus*, side-striped jackal *Canis adustus,* African elephant *Loxodonta africana,* bush pig *Potamochoerus porcus*, hippopotamus *Hippopotamus amphibius*, red duiker *Cephalophus natalensis,* common duiker *Sylvicapra grimmia*, suni *Neotragus moschatus*, nyala *Tragelaphus angasii*, bushbuck *Tragelaphus scriptus* and reedbuck *Redunca arundinum*), 12 are known to occur in the Maputo Elephant Reserve, with the status of the leopard and spotted hyaena not known

(Oglethorpe 1997). Giraffe *Giraffa camelopardalis,* and eland *Taurotragus oryx* have been reintroduced to the Tembe Elephant Park (Sandwith 1997), while waterbuck and kudu were reintroduced into the MER (Ntumi 2002).

The People

The people living in the study area belong to the Tsonga-speaking cultural group (Felgate 1982), and the people living in Matutuine Province of southern Mozambique speak the Ronga dialect of the Tsonga group (Junod 1962). Neighbouring cultural groups are Nguni-speaking Zulus and Swazis whose cultures and language differ markedly to those of the Tsongas (Felgate 1982).

The Tembe clan has been living in the study area since at least 1554 (Bryant 1965), and is still the dominant clan in the area. The Tembe clan used to live in the area bounded by Maputo Bay in the north, the Maputo River in the west and the present day Ubombo District in KwaZulu-Natal (Felgate 1982).

Over the last 200 years four major events shaped the socio-political and economic situation of the people living in Maputaland. The first of these events emanated from the Zulu people fleeing through the area during Shaka's wars. This disrupted cultural life, gave rise to Nguni people settling among the Tembes (Felgate 1982), and saw the establishment of the kingdom known as Gaza.

European colonisation at the turn of the 18th Century further disrupted life for people living in Maputaland (Axelson 1967). The Portuguese in Mozambique and the British, who then controlled Natal, tried to gain control of Maputaland over a long period. The colonial border between South Africa and Mozambique was finalised in 1875, when the French president (MacMahon) awarded all land between Delagoa Bay and the current border to Portugal.

The colonial boundary split the Tembe clan between two colonial authorities despite appeals for redress in 1889 (Bulpin 1966; Axelson 1967). Initially the Tembe *nkosi* retained his rule over the entire clan, but after trouble with the Portuguese, the then *nkosi* Ngwanase fled to Natal. Initially he and his descendants maintained their rule over the Tembe clan. The Portuguese colonial administration, however, strengthened its authority over southern Mozambique in 1940. Thereafter it became more difficult for the *nkosi* to exert influence from his base in South Africa. The Portuguese colonial administration then largely replaced the traditional systems of governance (Felgate 1982). Portuguese became the *lingua franca* for most Mozambicans, though certain socio-cultural elements of the traditional system, such as the *izinduna* (local headmen), continued to function across the region (Felgate 1982).

The third major disruption experienced by the Tembe people came in the form of the Mozambican War of Independence from 1964 to 1974. Although mainly fought in the northern provinces of the country the war had a devastating effect on the Mozambican economy. After Portugal surrendered Mozambique to FRELIMO in 1975, FRELIMO implemented socialist policies that further eroded the powers of traditional leaders (Newitt 1995).

Civil war broke out in 1980 between the ruling FRELIMO party and RENAMO. This was the fourth major disruption to the regions' inhabitants. Civil war lasted 12 years and disrupted all aspects of life for people living in Mozambique. Country-wide, about 50% of the rural people were displaced, many emigrating from southern Mozambique to Swaziland and South Africa (McGregor 1998; Hatton, Couto & Oglethorpe 2001). A large part of Mozambican Maputaland became depopulated (de Boer & Baquete 1998; Fairall & van Aarde 2004a) as about 60% of the residents moved out of the Matutuine district (Els *et al*. 2004).

The civil war resulted in the destruction of most of the infrastructure across southern Mozambique. This severely negatively influenced the local economy (Hatton *et al*. 2001). People have recently started to return to the area (Soto *et al*. 2001; Fairall & van Aarde 2004a), but the Tembe people in both South Africa and Mozambique live in a region that has little infrastructure. Most households depend on subsistence farming and the collection and sale of natural resources (de Boer & Baquete 1998; Tyburski 2003; Els *et al*. 2004).

Efforts to improve living conditions amongst the people are generally small scaled and supported by non-government agencies. The development of a Transfrontier Conservation Area in the region could catalyse economic development and improve existing conservation programs (van Aarde 2004).

Chapter 3

Evaluating historical estimates of population size for the elephants of Maputaland

Introduction[2]

The elephant population of Maputaland has a recent history of fragmentation. Since 1989 part of the population has been fenced into the Tembe Elephant Park that adjoins the southern boundary of Mozambique. The unfenced fragment of the population, however, continues to roam freely across southern Mozambique's Maputo Elephant Reserve and the Futi Corridor (an area either side of the Futi River). Here they occasionally associate closely with humans but continue to be legally protected (Soto, Munthali & Breen 2001). Maputaland is earmarked for the development of a transfrontier conservation area that will reunite the elephant and other wildlife populations occurring in the region (Wynberg 2002). Maputaland supports an exceptionally high number of species (van Wyk 1994) and elephants, as surrogates for the conservation of regional biota (see Caro & O'Doherty 1998; Simberloff 1998), may well affect the success of the development of a cross border conservation initiative in Maputaland. An understanding of historical events driving trends in the abundance of elephants may benefit future initiatives to conserve and manage the reunited population as a single unit.

The status of the elephant population of Maputaland has never been accurately assessed and surveys have been infrequent and unsystematic (see Tello 1973; Hall-

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[2] Chapter 3 has been drafted as an independent publication and much of the information provided here therefore repeats that in Chapter 1.

Martin 1980; Ward 1986; Matthews 1994, 2000; de Boer *et al*. 2000). Many of these earlier estimates (e.g. Thompson 1978; Hall-Martin 1980; Klingelhoeffer 1987; Matthews 2000) are little more than ‘educated’ guesses. In spite of this these are some of the only data that can be used to evaluate past and future trends in population numbers.

Large numbers of elephants must have been present in recent times as Smithers & Tello (1976) reported that over 500 were killed between the Maputo River and the Swaziland border in the 1940s as a crop protection measure. Large scale hunting for ivory was conducted in Maputaland from the 1850s (Baldwin 1863; Leslie 1875) and in northern Natal elephants were largely hunted out by the turn of the century (Bruton & Cooper 1980).

Smithers and Tello (1976) regarded the elephant population as increasing after the closure of professional meat and ivory hunting in the early 1960s. By then the Maputaland population was separated from the Gaza populations, which were then continuous with those of the Kruger National Park. They reported elephant as ‘abundant’ in the Maputo Elephant Reserve during the early 1970s.

With the onset of civil war in Mozambique attempts to count elephant populations in Mozambique ceased and uncontrolled hunting became common (Hatton, Couto & Ogelthorpe 2001). The perception of large scale hunting of elephants in southern Mozambique influenced the fragmentation of the Maputaland elephant population as conservation authorities sought to protect elephants in Tembe Elephant Park (Hall-Martin 1988; Ostrosky 1989). Conflict in Mozambique also led to humans moving out of southern Mozambique (Ogelthorpe 1997; Hatton *et al.* 2001).

Attempts to census the elephants living in the Tembe Elephant Park (TEP) were more frequent but the difficulties of aerial surveying elephants in such a thickly vegetated habitat (Caro 1999; Walsh & White 1999; Whitehouse, Hall-Martin & Knight 2001; Jachmann 2002) led to inconclusive population estimates. Here I use estimates of population size derived from a total count, using non-overlapping transects (by helicopter) for the Maputo Elephant Reserve (MER) and the Futi Corridor (Ntumi 2002) and ground surveys using sight-resight models (see Chapter 4) to interpret earlier estimates based on realistic population growth rates.

Methods

Earlier estimates of population size

I extracted estimates of population size from the papers and reports of Hall-Martin (1986), Ward (1986, 1987, 1988, 1989, 1990), Klingelhoeffer (1987), Ostrosky (1988 *pers. comm.* Matthews[3]), Matthews (1992, 1993, 1994, 2000) and Ntumi (2002). Of the earlier estimates few are based on properly structured surveys, or are based on methods described by de Boer *et al*. (2000), Matthews (2000) and Ntumi (2002). For the Maputo Elephant Reserve, only six estimates of population size were attempted between 1970 and 1999 (Tello 1973; Klingelhoeffer 1987; de Boer *et al*. 2000; Ntumi 2002; Matthews *pers comm.*[1]).

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

Population growth rates

I extracted population estimates from published and unpublished reports. These estimates were transformed to natural logarithms ($\log_e$) and used to derive intrinsic rates of population change using linear regression analysis (see Caughley 1977).

Modeling of population size

I determined minimum possible population sizes for the fragments and for the combined population and used a spreadsheet (Excel 2000) model to derive population sizes. The minimum number of animals alive at the time of the last estimate (1999 for southern Mozambique, 2002 for Tembe Elephant Park) were used to estimate past population sizes using the equation:

$$N_0 = \frac{N_t}{e^{rt}} \qquad (1)$$

where N_t = the known population size and r = intrinsic of rate increase (Caughley 1977). The population growth rates (r) used ranged from 7%, the maximum modeled for closed elephant populations (Calef 1988), to 3%, within the lower rates reported from east Africa (Douglas-Hamilton 1972; Moss 2001). An intermediate rate of 5% was used as reported for elephants in the region (Kruger National Park; Whyte, van Aarde & Pimm 1998, and Zimbabwe; Craig 1989), similar to the 5.23% reported by Whitehouse & Hall-Martin (2000) for Addo Elephant National Park. Although I used 7% as the maximum growth rate other studies (Craig 1989; Whyte *et al.* 1998; Whitehouse & Hall-Martin 2000) suggest that a more realistic maximum population growth rate is close to 5.5%, higher than the 4% suggested as close to the maximum by Hanks & McIntosh (1973).

To model the Maputaland population as a single entity I added the 1999 population estimate for southern Mozambique to the 2000 estimate for TEP. My estimates of population size are based on minimum observed population size for MER (Ntumi 2002) and a sight-resight model for TEP (as described in Chapter 4).

Results

Earlier estimates of population size

The earliest published estimate of the size of the elephant population of the Maputo Elephant Reserve (Tello 1973) yielded 350 elephants (Table 3.1). In 1970 Tello (1973) identified 280 elephants and estimated that the population in Mozambican Maputaland did not exceed 350 elephants. For 1972 Tello estimated that 269 elephants occurred in the Maputo Elephant Reserve (cited as *pers. comm.* in Klingelhoeffer 1987).

The elephant population of the Maputo Elephant Reserve apparently declined from 269 in 1972 to 80 in 1979 (K.N. Tinley, *pers. comm.* in Klingelhoeffer 1987) with displaced animals moving into the Maputo flood plain, the Futi floodplain and into South Africa. Klingelhoeffer estimated the population of 'northern Tongaland' to fluctuate between 50 and 150 elephants at the time of his research (1979 to 1981) before the Tembe Elephant Park was established (Klingelhoeffer 1987). An estimate of 150 elephants for southern Mozambique for 1995 given to the Mozambique authorities in a 1995 report by Ostrosky & Matthews (W.S. Matthews, *pers. comm.*[4]), seems to be a guess rather than based on an actual survey.

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

Table 3.1. Summary of population estimates for southern Mozambique and Tembe Elephant Park based on information extracted from published and unpublished papers and reports.

Year	Population size	Survey method	Source
Southern Mozambique			
1970	350	Ground survey	Tello 1973
1972	269		Klingelhoeffer 1987
1979	80	Educated guess	Klingelhoeffer 1987
1995	150	Educated guess	W.S. Matthews*
1998	180	Unstructured helicopter count	De Boer *et. al.* 2000
1999	205	Helicopter Transects	Ntumi 2002
Tembe Elephant Park			
1947	40	Guess	Lugg 1970
1971	16	Educated guess	Ostrosky 1988*
1973	25	Educated guess	Anon. 1978*
1974	40	Educated guess/Fixed Wing	Thompson 1978
1976	30	Educated guess/Helicopter	Hall-Martin 1980
1980	60	Fixed Wing /Aerial photo	Hall-Martin 1986
1981	75	Educated guess	Klingelhoeffer 1987
1984	39	Count-Helicopter	Ward 1986
1985	32	Count-Helicopter	Ward 1986
1986	35	Helicopter transects	Ward 1986
1987	41	Helicopter transects	Ward 1987
1988	56	Helicopter transects	Ward 1988
1988	104	ID Photo kits	Ostrosky 1988*
1989	54	Helicopter transects	Ward 1989
1990	48	Helicopter transects	Ward 1990
1992	85	Helicopter transects	Matthews1992
1993	54	Helicopter transects	Matthews1993
1994	71	Helicopter transects	Matthews1994
1996	106	ID Photo kits	W.S. Matthews*
2000	74	Helicopter transects	Matthews 2000
2000	130	Educated guess	Matthews 2000
2002	167	ID Photo kits	Present study
2002	179	Recapture models	Present study

**Pers. comm.*, W.S. Matthews, Regional Ecologist, Tembe Elephant Park, PB.356, Kwangwanase KwaZulu-Natal.

An unstructured helicopter survey conducted over two days in October 1998, while collars were fitted to elephants, yielded a minimum number alive estimate of 180 animals (de Boer *et al*. 2000). While not intended as a complete survey it covered the Futi floodplain and the Maputo Elephant Reserve in southern Mozambique. An attempt at a total count, using non-overlapping transects, flown with a helicopter and conducted over five days during October 1999, covered an area of 1270km^2 and yielded a minimum number alive estimate of 205 elephants (Ntumi 2002).

Twenty one estimates of population size have been made for elephants in the TEP between 1947 and 2000 (Table 3.1). KwaZulu Nature Conservation officers reported 17 of these in internal reports. Four estimates were supplied by the regional ecologist (W.S. Matthews, *pers. comm.*[5]).

The 1947 estimate is questionable as it is based on a descriptive statement that 'about' 40 elephants came into the area at night 'having travelled a great distance' (Lugg 1970), based on the recollections of a magistrate in Ingwavuma District in the late 1940s. The timing of this estimate coincides with an elephant extermination programme in adjacent areas of southern Mozambique (Smithers & Tello 1976).

For the Tembe Elephant Park the first 'educated guesses' are based on ground surveys and are given for 1971 and 1973. Between 1974 and 2000, 14 aerial transect surveys were conducted, two by fixed wing aircraft and 12 by helicopter. Prior to the 2002 estimate (Chapter 4), two estimates were based on the identification of known animals. Two further estimates were based on educated guesses (Table 3.1). Aerial surveys used transect sampling based on the method of Norton-Griffiths (1978), but were not standardized and did not yield estimates of their accuracy or precision. Waterhole counts, where water points are flown-over at mid-day when elephants are thought to concentrate at them, were used in an attempt to support the transect counts.

My estimates for 2002 are based on sight-resight models and yielded a population size of 179 (compared to 167 individual elephants identified as a 'known to be alive' estimate during the sight-resight research programme) for Tembe Elephant Park, with a 95% confidence interval for the Park of between 136 and 233 elephants (see Chapter 4).

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

Trends in population size and growth rates

The estimates of the size of the elephant population of southern Mozambique declined from 350 to 80 animals between 1970 and 1979. Since then estimates have increased to 205 in 1999 (Table 3.1). The data for the Tembe Elephant Park suggests a relatively small population in the 1970s and early 1980s that, thereafter, increased to the present level (Table 3.1).

A linear regression analysis on transformed ($\log_e$) population estimates of the southern Mozambique elephant population yielded an annual rate of decline of 1.2% per year[6] ($y = 28.42–0.012x$, $r^2=0.09$, $F_{1,4}=0.41$, $P=0.56$) between 1970 and 1999. A similar analysis for the Tembe Elephant Park's population suggests an increase from 1971 to 2002 of 5.6% per year ($y = 0.056x-106.8$, $r^2= 0.71$, $F_{1,20} = 49.76$, $P<0.001$).

From 1970 to 1979, the last population estimate for southern Mozambique before fragmentation, estimates of population size for southern Mozambique declined by 16.6% per year ($y = –0.1664x–333.7$, $r^2=1.0$, $F_{1,1} = 487.9$ $P< 0.05$) and from 1979 to 1999 increased at 4.4% per year ($y= 0.044x–83.31$, $r^2=0.98$, $F_{1,2}=106.4$, $P< 0.05$).

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[6] This value and all later estimates of intrinsic population growth rate should be treated with caution since they are based on population estimates of unknown accuracy and precision.

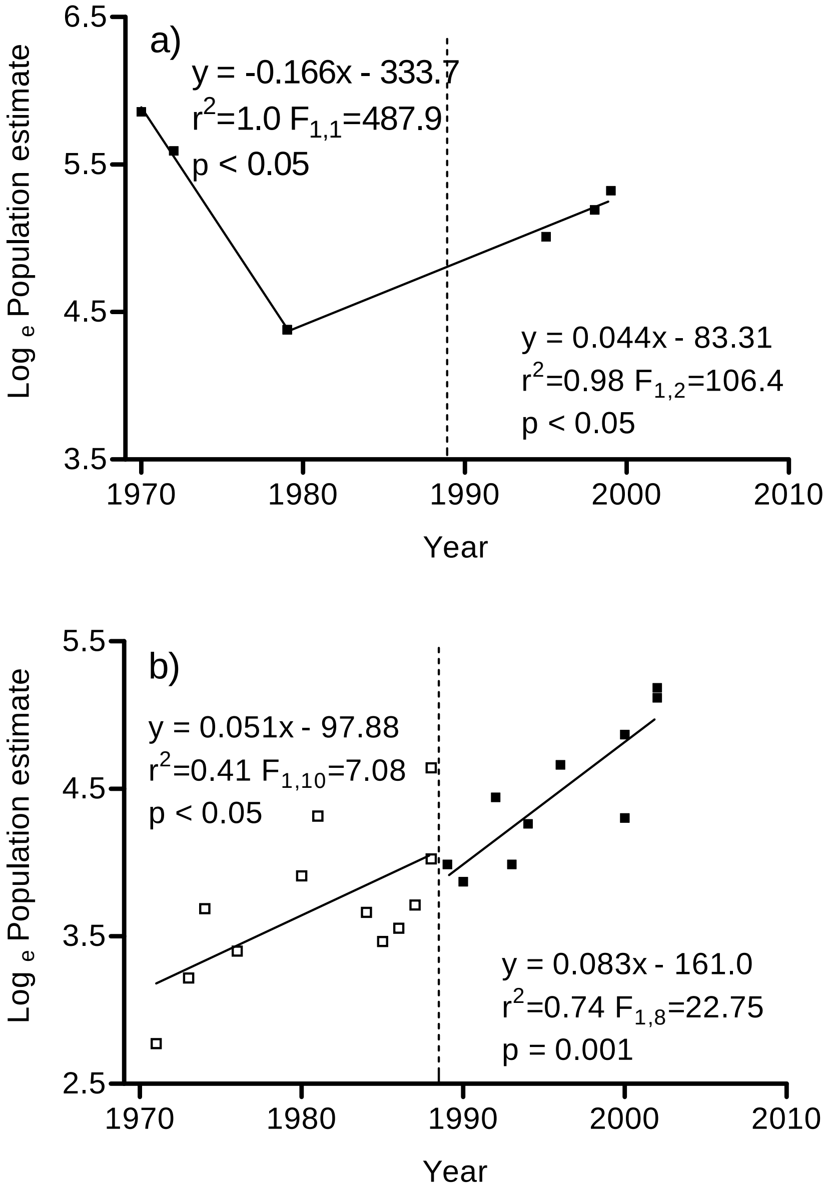

Figure 3.1. Population growth rates for (a) southern Mozambique and (b) Tembe Elephant Park calculated from linear regression analysis of $\log_e$ transformed population size estimates. For the southern Mozambique population estimates are indicated by shaded squares. The left hand slope shows population decline between 1970 and 1979 of approximately 16.6 % per year and the right slope shows population increase from 1979 to 1999 of 4.4% per year. For the Tembe Elephant Park, open squares indicate population estimates up to 1988; shaded squares indicate population estimates from 1989. The curve on the left of the graph shows population increase between 1971 and 1988 of 5.1% year and the curve on the right shows population increase from 1989 to 2002 of approximately 8.3% per year. The stippled vertical line indicates fragmentation of the population.

The southern Mozambique population may, therefore, have been increasing at the time the Maputaland population was fragmented through the fencing of the Tembe Elephant Park.

The annual rate of population increase for the TEP between 1971 and 1988 was 5.1% ($y = 0.05127x–97.88$, $r^2=0.41$, $F_{1,10}=7.08$, $P< 0.05$) and after fencing apparently increased to 8.3% per year ($y = 0.08293x–161.0$, $r^2= 0.74$, $F_{1,8}= 22.75$, $P= 0.001$) (Fig. 3.1b).

Retrospective modeling of population size

Retrospective extrapolation for the southern Mozambican elephant population starting from a minimum population size of 205, with rates of change ranging from 3% to 7% per year suggests that earlier estimates dramatically under-estimated population size. My extrapolations suggest that at a maximum potential growth rate of 7% the population would have been >190 in 1998, >150 in 1995 and numbered a minimum of 100 animals when separated from the South African fragment in 1989 (Table 3.2).

The minimum possible population size in 1979 would have exceeded the 50 animals proposed. At a growth rate of 5% the population would have numbered 195 animals in 1998, 168 in 1995, 124 when fenced from South Africa and 75 animals in 1979 (Table 3.2). At a growth rate of 4.4%, as predicted by linear regression of the post-1979 estimates, the predicted population sizes were 196 for 1998, 172 for 1995 and 132 in 1989 when fenced from South Africa (Table 3.2). At a growth rate of 3% population size would have been 199 animals in 1998, 182 in 1995 and 152 when fenced from South Africa with a minimum population size in 1979 of 113 animals (Table 3.2).

Table 3.2. Population sizes extrapolated from the most recent minimum estimates (in bold) for the elephant population fragments of Maputaland. The minimum estimates are 205 elephants for southern Mozambique, 179 elephants for Tembe Elephant Park and 339 elephants for the combined population in 1999. Growth rates (r) were from lower range estimates (3%), intermediate (5%) and maximum (7%) published for elephants, and estimates of growth from linear regression analysis. Estimates for years prior to those in bold were extrapolated from the most recent estimates. Population estimates for years after those in bold are based on extrapolations of varying intrinsic population growth rates. The population has been fragmented since a fence was completed around Tembe Elephant Park in 1989.

Area	**Year**					
Southern Mozambique	2002	1999	1998	1995	1989	1979
Estimate	NA	**205**	180	150	NA	80
r=0,044*	234	**205**	196	172	132	85
r=0.03	224	**205**	199	182	152	113
r=0.05	238	**205**	195	168	124	75
r=0.07	253	**205**	191	155	102	51
Tembe Elephant Park						
Estimate	**167**	74[A]	106[B]	71[C]	54	60
r= 0.083 & 0.051*	**167**	131	120	93	57	34
r=0.03	**167**	153	148	135	113	33
r=0.05	**167**	144	137	118	87	53
r=0.07	**167**	135	126	102	67	84
Maputaland						
Estimate	NA	**279[D]**	NA	256[E]	NA	140[F]
r=0.03	371	**339**	329	301	251	186
r=0.05	394	**339**	322	278	206	125
r=0.07	418	**339**	316	256	168	84

* based on a linear regression analyses of $\log_e$ transformed estimates

[A] data for 2000, [B] data for 1996, [C] data for 1994, [D] TEP 2000 estimate plus MER 1999 estimate, [E] TEP 1996 estimate plus MER 1995 estimate, [F] TEP 1980 estimate plus MER 1979 estimate

For the TEP retrospective extrapolation suggests that population estimates after the fencing have consistently under-estimated the true population size for elephants. For earlier estimates to be valid the elephant population in the TEP would have to have attained a growth rate in excess of the biological maximum for the species given by Calef (1988). Extrapolation shows that at potential growth rate of 7% the population would have been 130 in 1999 and >100 in 1996. The population would have numbered a minimum of 67 animals when separated from the southern Mozambique population in 1989 (Table 3.2). A population growth rate of 5% predicts that there were more than 140 animals in 1999, nearly 120 in 1996 and 87 when fenced into South Africa (Table 3.2). At a rate of population increase of 3% the population would have numbered more than 150 animals in 1999, 135 in 1995 and more than 110 when fenced into South Africa in 1989 (Table 3.2).

For the combined population of Maputaland the minimum population size of 339 animals in 1999 suggests that at Calef's (1988) maximum growth rate of 7% the population would have been >310 in 1998, >250 in 1995 and numbered a minimum of 168 animals in 1989 (Table 3.2). The minimum possible population size in 1979 would have been 84 should the population have been growing at 7% per year. The consequences of lower rates of increase are illustrated in Table 3.2. My extrapolation suggests that the Maputaland elephant population comprised of between 371 and 418 elephants in 2002 (Table 3.2).

Discussion

Problems have been identified when comparing historical estimates to determine trends, as counting methods change (Eltringham 1977; Dublin & Douglas-Hamilton 1987; Hall-Martin 1992; St. C. Gibson, Craig & Masogo 1998; Rookmaaker 2002). Furthermore, estimates of population size and trend detection tend to increase as methods improve (Laws 1969a; Barnes 2002). The biases in aerial counts are different year on year, as environmental conditions differ even when time of year is controlled for (Redfern *et al*. 2002). Bias in censuses can also mask large changes in population sizes from year to year (Redfern *et al*. 2002).

Eltringham (1977) identified problems in determining population trends from aerial surveys even when relatively large numbers of surveys were available. Census data with unknown bias should not, therefore, be used to determine management actions (van Jaarsveld, Nicholls & Knight 1999; Redfern *et al*. 2002).

Despite the difficulty of interpreting population trends from historical data, this type of data has been used in an attempt to predict population persistence (van Jaarsveld *et al*. 1999) and promote elephant population control measures or range expansion (Hall-Martin 1992). St. C. Gibson *et al*. (1998) dismiss population estimates from non-standardised methods as ‘not useful in analysis of trends’ and emphasised the importance of standardised surveys for predicting trends. Historical estimates from non-standardised methodologies are often, however, all that is available (Rookmaaker 2002).

Different aerial methods were used to enumerate the elephant population of Tsavo (Laws 1969a), and the difficulty in interpreting such data is further highlighted by Ottichilo’s assertion that, for Tsavo between 1967 and 1970, there were ‘probably more than 35 000 elephants present’ because the population estimate was 35 000 in

1974, following 6 000 elephant deaths recorded during the 1970-1971 drought (Ottichilo 1986).

For the Serengeti-Mara region long term population estimates from 1958 to 1977 show an increasing elephant population until 1965 followed by a long period of population stability, then increase in elephants in the Masai Mara Game Reserve and a significant decline in the Serengeti National Park (Dublin & Douglas-Hamilton 1987). In their study Dublin & Douglas-Hamilton (1987) only calculate population change between the means of 1965-1977 estimates and a 1984 estimate. They concluded that the Mara population increased by 19% between 1977 & 1984, and the Serengeti population experienced a 52% decline during the same period, and that elephants moved from the Serengeti to the Mara (Dublin & Douglas-Hamilton 1987).

For the Kasungu National Park, Malawi, Bhima, Howard & Nyanyale (2003) analysed trends in elephant numbers from historical data collected between 1969 and 1998 using different methods. They did not interpret population change other than stating that the population declined between the 1970s and 1998 (Bhima *et al*. 2003).

These studies highlight that even where survey data has been collected relatively frequently the determination of trend, and even population size, is often crude but frequently the only information available (Rookmaaker 2002). I faced a similar situation determining population trend for Maputaland where until recently information on the size of the Maputaland elephant population, and on the factors influencing it, has been either lacking or inadequate. From my analysis it appears that many earlier estimates were little more than guesses, or derived from aerial counts conducted under poor surveying conditions. These estimates would have been of little value to managers especially considering that past under-estimates inflated future growth rates. Incorrect estimates could solicit overreactions from managers responsible for controlling the consequences elephants may have for enclosed parks (Cumming *et al*. 1997; Trollope *et al*. 1998; van Aarde, Whyte & Pimm 1999; Whyte *et al*. 1999; Matthews *et al*. 2001).

It appears that the elephants of southern Mozambique may not have been as threatened as was feared some 10 to 15 years ago (Klingelhoeffer 1987; Hall-Martin 1988; Ostrosky 1989; World Bank 1996). Based on the maximum rate of change at least 100 elephants remained in Mozambique when the fence was constructed during 1989. The population must therefore have exceeded the 1979 estimate of Klingelhoeffer (1987) and the 1995 estimate of 150 of W.S. Matthews (*pers. comm.* [7]), especially if poaching was as high as has been suggested (Hall-Martin 1988; Ostrosky 1989).

My extrapolations also suggest that estimates for the TEP were constantly lower than that implied by realistic maximum intrinsic growth rates of 5.5%. The apparent steep population decline from shortly before Mozambican independence in 1975, to the onset of civil war in 1980 and on into the mid-1980s is probably due to an overly pessimistic population estimate by Klingelhoeffer (1987).

People abandoned former elephant range during the war years (Ogelthorpe 1997; Soto *et al*. 2001) and their numbers within the MER declined from 10 000 before the war to fewer than 1 000 in the mid-1990s (Ogelthorpe 1997; Fairall & van Aarde 2004b). By the mid-1990s only 5 000 to 8 000 people remained between the Maputo River and the coast (World Bank 1996). The human population in the area may have freed elephants from competition for landscapes with people and domestic animals (Parker & Graham 1989a). The elephant population living here may even have started to recover during the civil conflict.

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

For the TEP aerial surveys have constantly under-estimated true population size. At best the available data may have given an indication of changes in population size but the wide confidence limits would have masked real growth trends. This would have rendered the censuses cost inefficient and of limited value to conservation management. The underestimation of population size from recent aerial surveys seems to be due to the undercounting of breeding herd members. This applies especially to those animals that concentrate in the north-east of the Park where vegetation is dense and where canopy cover is high.

Before the international border was fenced annual population trends were almost certainly influenced by the migration of elephants in and out of Tembe Elephant Park (Klingelhoeffer 1987; Ostrosky 1987, 1989; Hall-Martin 1988). Their movement into the Park may have increased due to persecution in southern Mozambique (Ostrosky 1987). Aerial surveys consistently yield fewer than 100 elephants for the Tembe Elephant Park (Ward 1989, 1990; Matthews 1992, 1993, 1994, 2000), the three registration counts based on ID profiles, however, all produced estimates >100 (Matthews *pers. comm.*[8]; see Table 3.1). I conclude that most historical estimates were considerably lower than that reflected by the trend I derived from realistic values of intrinsic population growth.

At present the densities of elephants in Tembe Elephant Park (0.56 km^2) exceed that for southern Mozambique (0.14 km^2) and the Maputo Elephant Reserve (0.26 km^2). The restoration of former elephant range through a transfrontier conservation initiative in the region would most probably reinstate the historical roaming patterns of these elephants.

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

Chapter 4

Estimating abundance for a savanna elephant population using mark-resight methods: a case study for the Tembe Elephant Park, South Africa

Introduction[9]

Savanna elephants and fire affect vegetation (Dublin, Sinclair & McGlade 1990; Lock 1993; Cumming *et al*. 1997; Trollope *et al*. 1998; van de Vijver, Foley & Olff 1999). Elephants confined to the Tembe Elephant Park (hereafter TEP) in South Africa are well protected, and their apparent increase may have negative consequences for sensitive vegetation types such as sand forests that support high levels of endemicity (van Wyk 1994; Matthews *et al*. 2001). The future management of this population may involve its inclusion in a transfrontier conservation area (World Bank 1996). Through this action traditional migratory patterns may be reinstated thereby reducing local pressure on sensitive ecotypes within the Park. Knowing the number of elephants present within the Park therefore has considerable conservation implications.

The techniques used to estimate population size or densities for medium to large mammals living in wooded areas are poorly developed (Caro 1999). For African elephants (*Loxodonta africana*), census methods such as dung counts (Walsh & White 1999; Walsh *et al*. 2001), aerial surveys (Whitehouse, Hall-Martin & Knight 2001; Jachmann 2002; Khaemba & Stein 2002), and calling patterns (Payne, Thompson &

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[9] Chapter 4 has been drafted as an independent publication and much of the information provided here therefore repeats that in Chapter 1.

Kramer 2003) are often inadequate for small populations in dense habitats. Although aerial survey methods are well developed for open habitats (for review see Craig 1993), indirect methods are used for elephants occurring in dense habitats (for review see Barnes 1993). Whitehouse *et al.* (2001) showed that for small populations (~250) aerial surveys underestimate numbers. This problem increases with increasing population size (Whitehouse *et al.* 2001). Under such conditions, where the use of other methods is unviable, the use of mark-recapture methods could be evaluated (Walsh & White 1999). To the best of my knowledge such a method has not been applied to elephants.

Earlier attempts to count elephants in the TEP were based on aerial surveys similar to those traditionally used across much of Africa (*i.e.* Buechner *et al.* 1963; Laws 1969a; Eltringham 1977; Ottichilo 1986, 1999; St Gibson, Craig & Masogo 1998; Whitehouse *et al.* 2001; Jachmann 2002). A total count based on helicopter survey at the onset of my study yielded 65 elephants for the Park (Matthews 2000). However, a mid-day count at water holes from the same helicopter the following day yielded 74 elephants. Neither of these counts provided confidence limits. My study was designed, therefore, to evaluate the validity of a variety of mark-recapture models (see Krebs 1999) to estimate population size when applied to a confined population of elephants. The advantage of my approach is that mark-recapture procedures provide an opportunity to determine accuracy and precision for estimates derived from mark-recapture models and compare these to a registration count (where the number of known individuals are counted and registered during repeated survey), given the assumption that registration count and the mark-recapture estimates are independent. These estimates may have implications for the design of programmes to determine population size.

Materials and Methods

Study Site

The TEP covers an area of about 300 km^2 in northern KwaZulu-Natal, South Africa. Mean annual precipitation for the region is 800-1 000 mm (Schulze 1997) but is highly variable. Mean annual temperature is 20-22^{o}C. The Park's northern boundary forms the international border with Mozambique and it is surrounded by an elephant-proof fence. Situated in the Maputaland Centre of Endemism (van Wyk 1994), TEP is considered vital for the protection of regional biodiversity. There are few other protected areas in the region conserving stands of endemic-rich sand forests (van Wyk & Smith 2001). The confinement of elephants to the TEP since 1989 is artificial and may have negative consequences for sensitive vegetation communities within the Park.

Methods

I was an observer on an attempted total count using a helicopter during the last week of August, 2000. Twenty five parallel north/south orientated transects, 1km apart, of between 3km and 23km long, totalling approximately 380km, were flown at ~40 knots, at an altitude of 90m above ground level. The count was completed in two sessions, one early morning and one late afternoon. Permanent water bodies in the Muzi swamp and artificially supplemented water holes (n=4) were flown the following day between 12h00 and 14h00, the hottest part of the day.

I used a modification of Caughley's 'sequence of decisions by which a technique for estimating abundance can be chosen' (Krebs 1999) to select mark-recapture methods to determine population size. As elephants during the study were "marked" through the recording of their unique markings and thereafter resighted, all methods are hereafter referred to as mark-resight methods (see Minta & Mangel 1989).

An advantage of this mark-resight method is that animals do not have to be physically captured and handled. It allows for the post-hoc manipulation of data for both the continuous marking of the population, and non-continuous marking, as required by Bowden's estimator (Krebs 1999). Mark-resight techniques allow for the use of many mark-resight models and for accuracy and precision to be estimated (Pollock 2000).

My mark-resight protocol was based on individual identification using features such as ear markings and tears, tail characteristics, tusk form, wear and breakages, trunk and other scars (see Douglas-Hamilton 1972; Croze 1974; Jachmann 1980; Whitehouse & Hall-Martin 2000; Moss 2001). Each identifiable feature was considered a 'mark' on that individual, and all individuals carried multiple marks. These marks are considered permanent although additional marks may have been added during the study. Identification was aided by profiles including photographs and field drawings kept on references files. Elephants could be positively identified as 'marked' or 'unmarked' at time of observation. Where models allowed, unmarked animals, once encountered and marked, were added to the 'marked' population.

For elephant bulls an initial marking programme, where bulls were identified throughout the Park, was conducted over four months, during which 52 individuals were 'marked' and their identification profiles compiled. This period of familiarization facilitated accurate individual identification. The 'marking' event was then followed by 14 resighting events, each lasting 10 days each, at intervals of seven days over a period of nine months, therefore the attempt at total registration took 13 months. During each of these events the entire Park was covered by vehicle using a road network, divided into 20 sections covered by five routes. Sessions were conducted morning and afternoon, avoiding the heat of mid-day when elephants are known to be less active (Wyatt & Eltringham 1974). Resighting sessions included observations at the two main permanent water points in the Muzi swamp and the semi-permanent pan in the south of the Park. Elephants encountered during these resighting sessions, either along the routes or at waterholes, were noted as 'marked' or 'unmarked'.

I compiled group identification keys for family groups using a similar method to that used for bulls. During an initial marking period of two months, eight adult cows from different groups were 'marked' including three fitted with satellite/radio collars as part of another study. Once herds could be recognised by the identification of a 'marked' adult cow the remaining members were identified as described using the protocol of Moss (2001). Identifying features of herd animals were repeatedly noted to improve estimates of herd size. The population estimate for breeding herds is based on the repetitive enumeration of individual groups and Bowden's estimator (Krebs 1999) calculated from the sighting frequencies of the eight marked cows.

My registration count, directed at determining the total number of elephants in the population, is not reliant on a set of assumptions (Caughley & Sinclair 1994). As the sum of all the animals identified during the study it gives an estimate of the animals known to be present in the research area but is not considered a total count as new animals were recorded until the last cycle.

Data analyses

Closed Population Estimators

Mark-resight models for closed populations provide estimators that are robust to variation in capture probabilities, especially when the assumption of a closed population is valid (Kendall 1999). The assumption of a closed population is valid for this fenced population.

I used Seber's modification of the Petersen method (Seber 1982) for a single marking and a single recapture event to reduce potential bias in overestimating population size (Krebs 1999). I also assessed the data using the Schnabel method (an extension of the Petersen method) that makes the same assumptions as the Petersen method, but it is easier to identify violations of these assumptions. Here marking occurs at each of the sampling times, and only two types of individuals need be identified, marked and seen once or more before, and unmarked and not seen before (Krebs 1999).

The Schumacher-Eschmeyer estimator (referred to as the Schumacher method) is a robust and useful ecological model for multiple censuses of closed populations (Seber 1982) and allows for the non-random capture of marked and unmarked individuals (Koper & Brooks 1998). The population estimate is obtained from the slope of the linear regression of the assumed significant relationship between the proportion of animals marked (y) and those previously marked (x) (Koper & Brooks 1998). For my study this relationship was significant ($y = 0.113x+0.214$, $r^2= 0.69$, $F_{1,12}=6.70$, $P<0.001$).

Open Population Estimators

I used the Jolly-Seber model that also allows for the estimation of parameters such as survival. This type of open population estimator is, however, of more use for long-term programmes where populations cannot be assumed as closed (Pollock *et al.* 1990).

Model Assumptions

Generally as models become more complex they make more assumptions. For some models compliance with these assumptions can be tested for (see Table 4.1). As the equal catchability assumption is the Achilles' heel of all estimates that uses marked animals (Krebs 1999), a combination of open (Jolly-Seber) and closed (Schnabel) methods has been developed (Pollock 1982).

The Robust Capture-Recapture design allows for relatively unbiased estimates when the underlying assumptions of models are not met (Pollock 1982; Pollock *et al.* 1990; Nichols 1992), and avoids relying solely on sensitive Jolly-Seber models (Pollock *et al.* 1990; Krebs 1999).

Frequency of capture analysis operates on the number of animals caught once, twice three times and so on over several capturing sessions (see Caughley 1977). These data form a zero-truncated frequency distribution of captures, the missing zero-class representing the unknown number of animals that were never caught. The analysis estimates the frequency of zero-classes from the shape of the truncated distribution. While the Poisson estimate is reliant on constant catchability, the negative binomial estimate allows for unequal sighting (Caughley 1977).

Table 4.1. Assumptions of the mark-recapture (resight) models used to estimate population size for the Tembe Elephant Park (see Caughley 1977, Krebs 1999). Bowden's Estimator is the model with the fewest constraints when a population is closed.

	Model							
Assumption	Petersen	Schnabel	Schumacher	Jolly-Seber	JS Robust	Bowden	Poisson	Negative Binomial
Population is closed	Yes	Yes	Yes	No	No	Yes	No	No
All animals have same probability of sighting in first sample	Yes	Yes	Yes	Yes	Yes	Yes	No	No
Marking does not affect catchability	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Marks are not lost	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Sighting probabilities are equal	Yes	Yes	Yes	Yes	No	No	Yes	No
All marks are recorded in subsequent samples	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes

Bowden's estimator is a frequency of capture model, and is an extension of Petersen type population estimators developed from the Minta-Mangel model (Minta & Mangel 1989) and is available on the program NOREMARK (White 1996a) and MARK-RECAPTURE (Krebs 1999). It is a frequency of capture model that can be used for populations where individuals can be identified as marked. It is designed for closed populations and relaxes the assumption that all individuals have the same resighting probability (Krebs 1999). White (1996b) recommends the use of Bowden's estimator when there is heterogeneity of sighting probabilities. Additionally, it does not require that the entire study area be searched during the sighting period and applies even when some animals are always seen in large groups and frequently observed, while lone animals are rarely sighted (Bowden & Kufeld 1995). If mortality or emigration is independent of an animal's marked status this model remains valid.

The assumption that the population is closed was valid as TEP is fully fenced. There was effectively no recruitment to be considered as newly born calves are easily recognised and not included in the database used for estimating population size. Five adult males died during the two years of the study (see Chapter 5), some of which might have been marked, and this could have reduced the number of marked animals. Bowden's estimator, however, allows for losses providing they are independent of the mark status of the animal (Bowden & Kufeld 1995). The assumption of equal catchability is usually violated in field studies (Pollock *et al*. 1990) and can be tested for in some models. To attempt to comply with this assumption, animals were sighted and marked throughout the Park using all available roads and hides, thereby covering all areas utilised by elephants. Resighting locations and a satellite tracking study indicated that elephants move extensively throughout TEP and therefore could be encountered on any road or at any hide. Compliance with the assumption that marking does not affect catchability was ensured because a non-invasive marking method was used. A zero-truncated Poisson test (Krebs 1999) showed unequal sighting probability, as is usual under field conditions (Eberhardt 1969; Seber 1986; Pollock *et al*. 1990). The Bowden's estimator and Pollock's robust design relax the assumption of equal catchability so avoid this assumption. The Robust design allows relatively unbiased estimates to be obtained when the assumption of equal catchability is not met (Pollock 1982; Nichols 1992).

The use of naturally occurring, permanent features unique to the elephants that are known to persist over the long term (Douglas-Hamilton 1972; Croze 1974;

Jachmann 1980; Moss 2001) ensured that marks were not lost. The assumption that all marks are recorded at each subsequent observation was not violated as elephants had sufficient marks to ensure that they could be identified.

Analysis

I analysed the resight data under eight different mark-resight models using the software MARK-RECAPTURE (in Programs for Ecological Methodology 2nd Edition Krebs 1999). I used least squares linear regression analysis (Sokal & Rohlf 1995) to illustrate trends in the accuracy and precision of the models when effort increases. I used the small sample unbiased Akaike information criterion (AIC_c) to evaluate fit and complexity for the resight models used (see Johnson & Omland 2004 and references therein).

Results

Population Size

The helicopter count yielded a population estimate of 65 elephants. Of these 25 were bulls and 19 were cows. Twenty one elephants were classified as sub-adults or younger elephants for which sex could not be assigned from the air. The 65 elephants occurred in 20 groups (sightings). The mid-day water hole count yielded 74 elephants, 29 bulls, 14 cows and 31 sub-adults or younger.

From the registration count I identified 75 bulls, 52 of these before the resighting sessions. During the 14 sighting sessions I encountered 42 of the 52 pre-identified bulls and an additional 23 bulls. Of the 52 pre-identified bulls 10% were observed in the last four cycles (two months) of the study. For the 23 additional bulls, 17% were recorded in the last four cycles. From observations of the eight marked cows in breeding herds and the recognition of known adult cows and their attendant young, before, during and after resighting sessions, I identified 92 elephants in ten family units. When I combined observations of breeding herds and bulls I obtained a 'known-to-be-alive' count of 167 elephants for TEP.

The resighting sessions yielded 65 different bulls on 189 occasions. After 14 sessions, all population estimates for bulls, except for the negative binomial (n=87, 95% CI=65-126), were lower than that obtained using the registration count (Poisson (n=70, 95% CI=55-86), Bowden's estimator (n=67, 95% CI=60-74), Jolly-Seber (n=63, 95% CI=3-123), Schumacher (n=61, 95% CI=54-69), Schnabel (n=59, 95% CI=49-73), Robust (n=55, 95% CI=45-79), Petersen (n=38, 95% CI=27-79)) (Fig. 4.1a). Only the Poisson and Bowden's models yielded estimates close to the registration count.

The only sight-resight model suitable for estimating the population size of the breeding herds was Bowden's estimator. Other models require all animals to be identified as marked or unmarked upon capture (sighting). This could not be determined for all animals at every breeding herd observation. The Bowden's estimator allowed population estimates when some marked animals are not identified at every sighting (Bowden & Kufeld 1995).

The 14 sighting events yielded marked cows on 16 occasions and all of the marked cows were sighted at least once. When all sightings of breeding herds post-marking are included, breeding herds were sighted on 37 occasions and all marked cows were sighted at least three times each. The estimates for breeding herds, both for sighting events and when all sightings are considered exceed the 'known to be alive' estimate (Fig. 4.1b).

The Bowden's estimator (all breeding herd sightings) yielded an estimate of 179 elephants for the Park (Fig. 4.2), 4% higher than the number of animals known to be alive for the population. For sighting sessions, the Bowden's estimator under-estimated the registration count for bulls by 11%, and over-estimated the breeding herd registration by 15%.

For the total population Bowden's estimator exceeded the waterhole count by 60% and the registration count by 6.7%. The helicopter survey under-counted the Bowden's estimator by 65% and the registration count by 61% (Fig. 4.2).

Influence of effort on estimates

I used least squares linear regression analysis to determine the influence of effort on the estimates and here consider accuracy in terms of the match of an estimate generated by a given model to the population size, as deduced from the registration record compiled for the population.

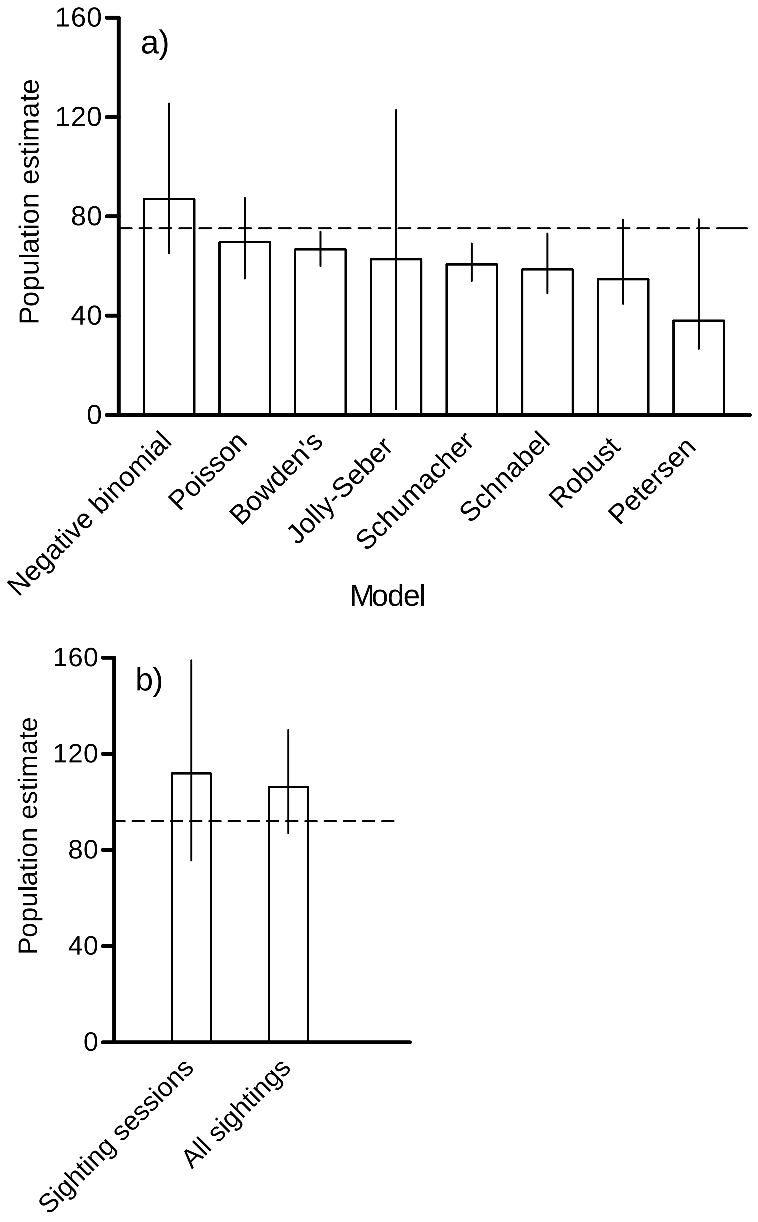


Figure 4.1. Population estimates for sight-resight models for (a) elephant bulls and (b) elephant breeding herds in the Tembe Elephant Park. For breeding herds only Bowden's estimator was used. Estimates for bulls are based on 14 sighting sessions. For breeding herds population size was determined from 14 sighting sessions, indicated as 'sighting sessions' and from all post marking observations, indicated as 'all sightings'. Bars indicate population estimate, vertical lines indicate 95% confidence intervals. Dashed line denotes the number determined by registration counts.

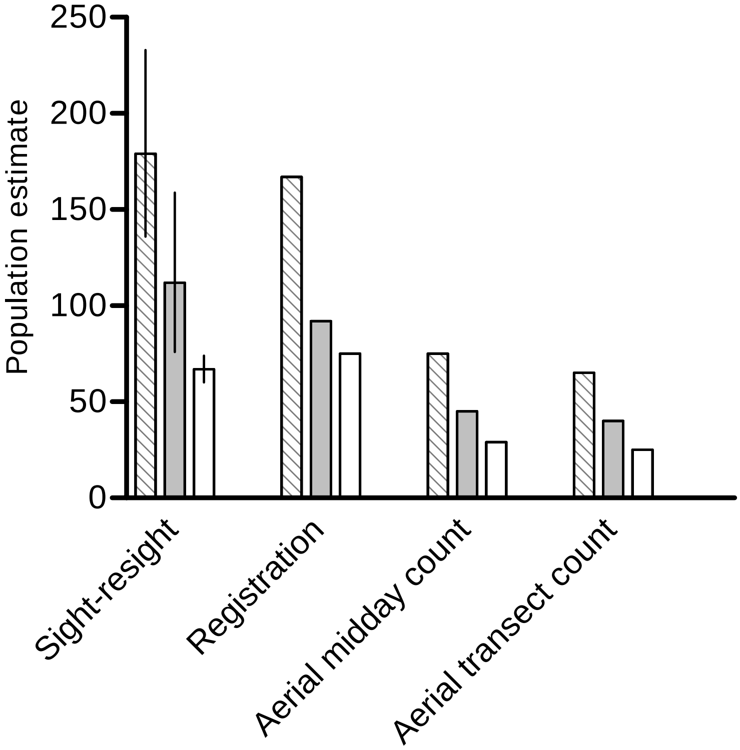


Figure 4.2. Comparison of population estimates determined from the Bowden's estimator (sight-resight method), registration count and two aerial counting methods. Total population estimates are indicated by bars with lined fillings, animals in breeding herds by shaded bars and bulls by open bars. Vertical lines indicate 95% confidence intervals.

For bulls the estimate generated by the negative binomial model was not affected by effort (y=57.39+2.637x, r^2=0.32, $F_{1,10}$ = 4.60, P=0.058) but for all other models estimates improved with increasing effort (Poisson, y=50.61+1.220x, r^2= 0.70, $F_{1,10}$= 23.20, P<0.001, Bowden's, y=60.65+0.577x, r^2=0.70, $F_{1,12}$ =28.36, P<0.001, Jolly-Seber, y=10.41+3.392x, r^2=0.51, $F_{1,10}$ = 10.44, P<0.05, Schumacher, y=37.71+1.737x, r =0.86, $F_{1,10}$=63.64, P<0.0001, Schnabel, y=37.45+1.619x, r^2=0.90, $F_{1,10}$=91.73, P<0.0001; Fig. 4.3 a-f).

Limiting the analysis to data collected during structured resighting sessions, estimates did not improve with increasing effort (y=83.18+2.901x, $F_{1,5}$=4.63, P=0.084; Fig. 4.4a). When all observations of breeding herds are included in the analysis, however, estimates of population size improve with increasing effort (y=76.33+1.013x, $F_{1,35}$=49.28, P<0.0001; Fig. 4.4b).

The influence of effort on precision

Effort only affected the width of the 95% confidence interval for the Schnabel model (y=50.79-2.016x, $F_{1,10}$ =5.669, P<0.0001; Fig. 4.5 f). For all the other models the width of the confidence limits did not change with increased sighting effort (negative binomial, y=89.31-2.534x, $F_{1,10}$=0.93, P=0.357, Poisson, y=28.98+0.227x, $F_{1,10}$=3.50, P=0.091, Bowden's, y=17.46-0.041, $F_{1,12}$=0.08, P=0.776, Jolly-Seber, y=17.74+3.995x $F_{1,10}$=2.01, P=0.199, Schumacher, y=23.35-0.535x, $F_{1,10}$=1.06, P=0.327; Fig. 4.5 a-e).

For breeding herd observations during resighting events the width of the 95% confidence interval also showed no significant improvement with increased effort over time (y=75.40-1.330x, r^2=0.09, $F_{1,5}$=0.51, P=0.509; Fig. 4.6a). However, when lumping the data for all breeding herds the width of the 95% confidence interval decreased significantly with increasing sampling effort (number of sightings)(y=146.70-2.315x, r^2=0.58, $F_{1,35}$=72.94, P<0.0001; Fig. 4.6b).

Evaluation of resight models

Based on the Akaike information criterion (AIC_c) the Bowden's model (AIC_c=0.87) is the most suitable when sample sizes are small. This is followed by the Schnabel (AIC_c=0.10), Schumacher (AIC_c=0.03) and Poisson (AIC_c=0.01) models. The Jolly-Seber (AIC_c=0.00) and negative binomial (AIC_c=0.00) models were the least suitable of the models I evaluated. The factors which have the largest impact on model suitability, when viewed across all models are that all animals have the same probability of sighting in the first sample, marks are not lost, marking does not affect catchability and that the population is closed.

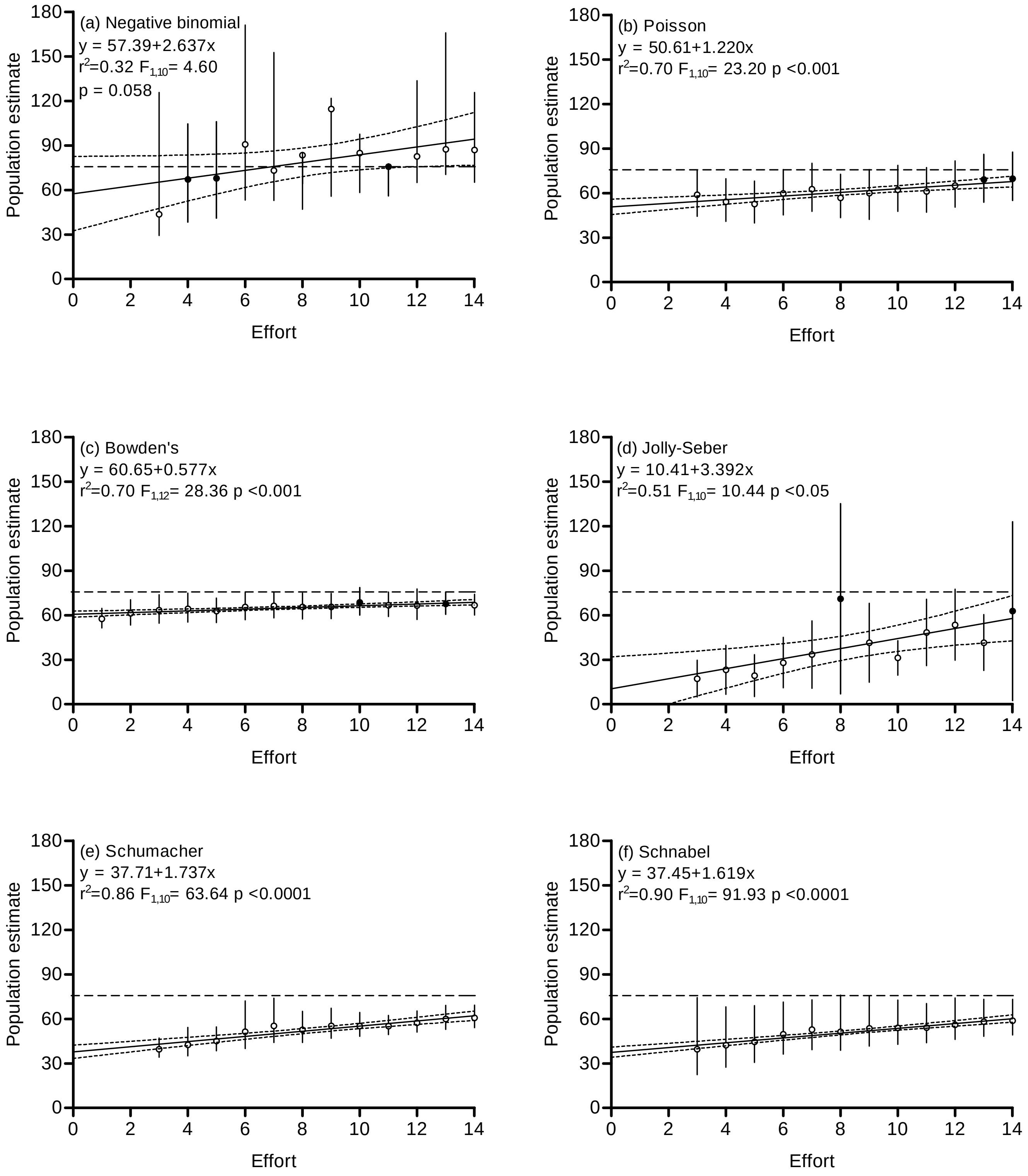


Figure 4.3. Legend on next page.

Figure 4.3. The influence of survey effort on population estimates for bulls from sight-resight models over 14 sighting events. Points indicate population estimate and vertical lines denote the 95% confidence intervals. Solid points indicate estimates that are within ten percent of the registration count (dashed horizontal line). Solid diagonals are regression lines fitted through least squares regression analysis and dotted lines are their 95% confidence intervals. The F-values test for deviation from zero of the slopes of the regression lines.

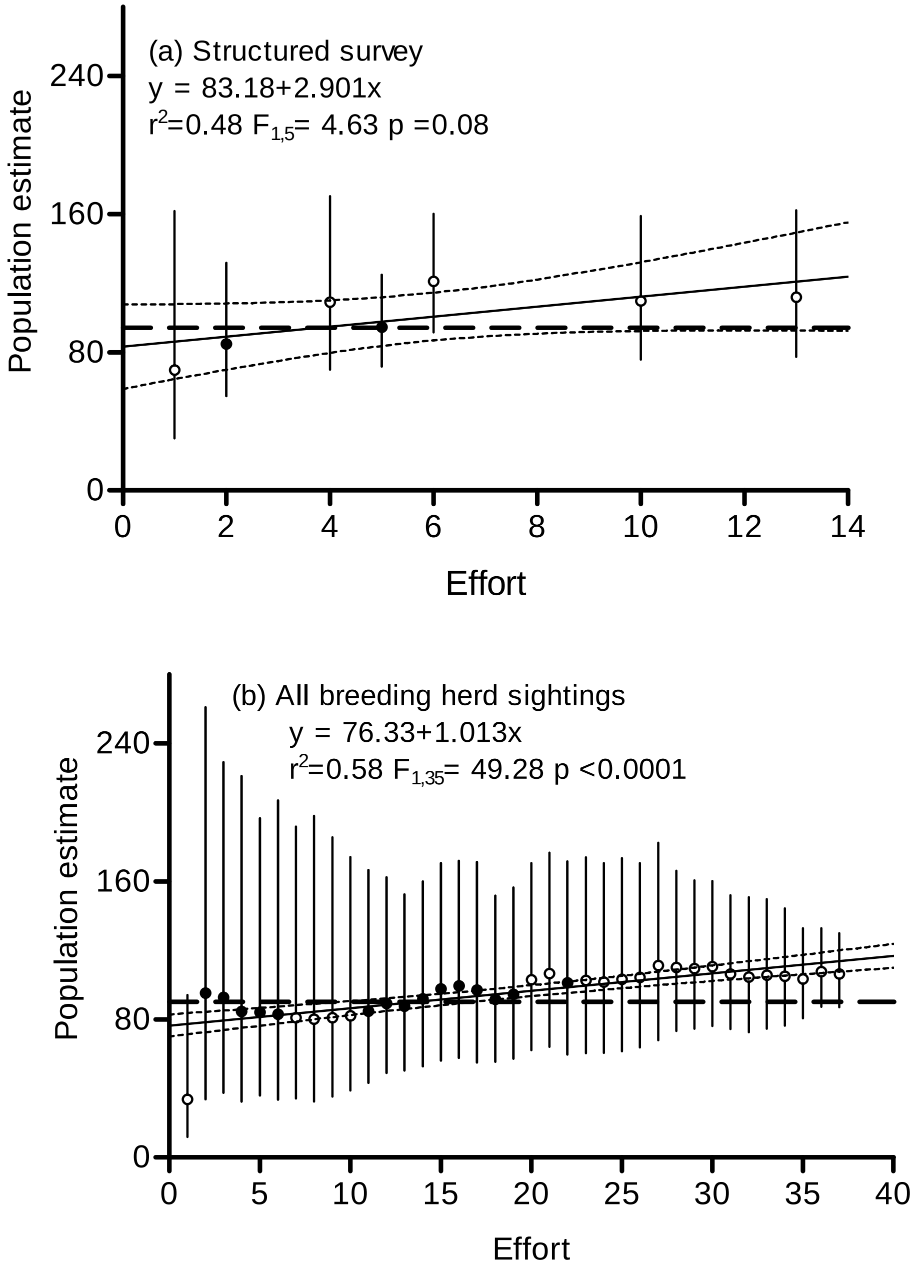


Figure 4.4. The influence of survey effort on population estimates for elephants in breeding herds using the Bowden's estimator for (a) 14 resighting sessions on structured surveys and (b) for all post-marking sightings of breeding herds. Circles indicate population estimates. Solid circles are within 10% of the registration count (dashed horizontal line). Vertical lines indicate 95% confidence intervals of the population estimates. Regression lines were fitted through least square regression analysis (dotted lines present the 95% confidence intervals). The F-values test for deviation from zero of the slopes of the regression lines.

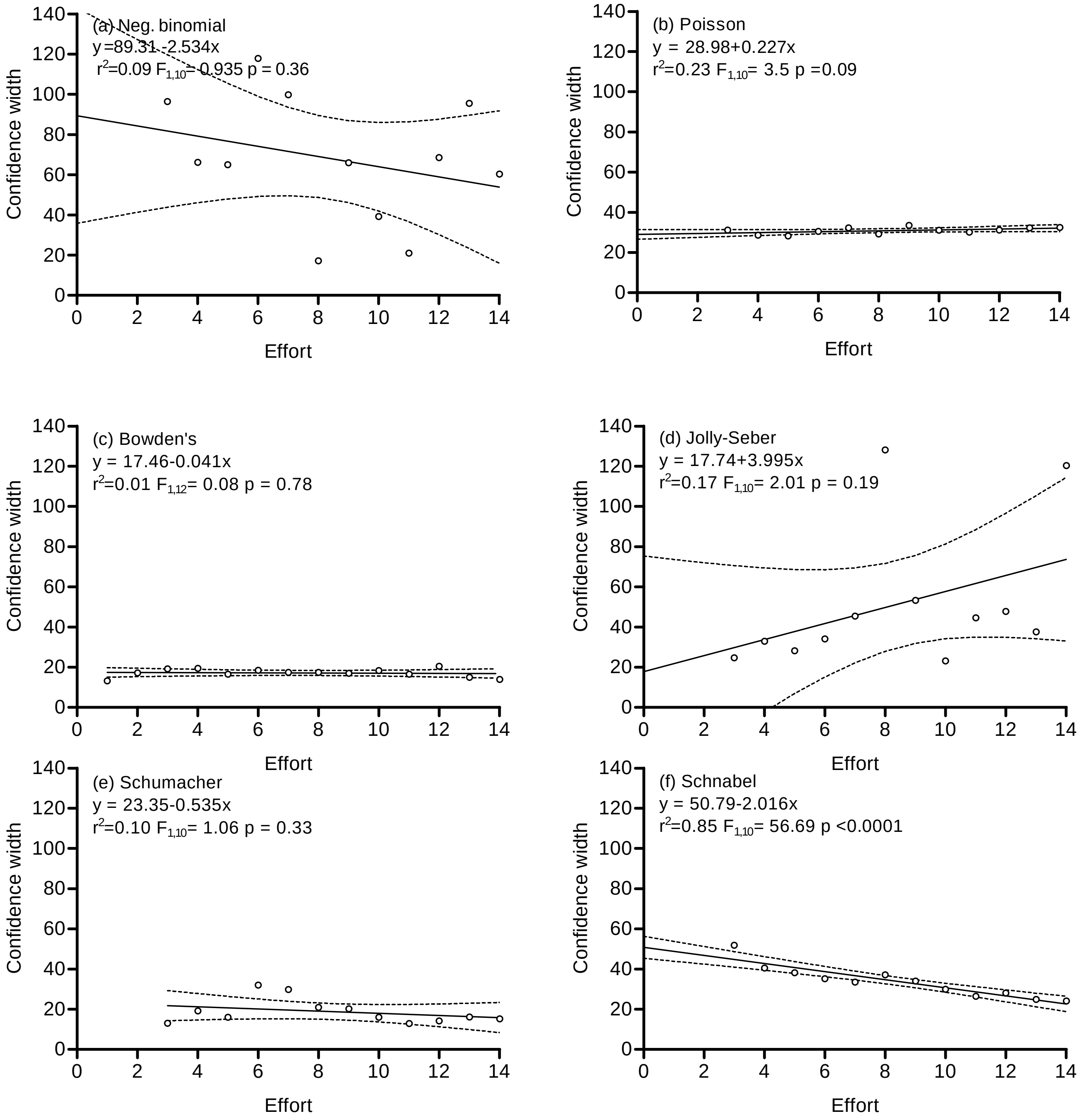
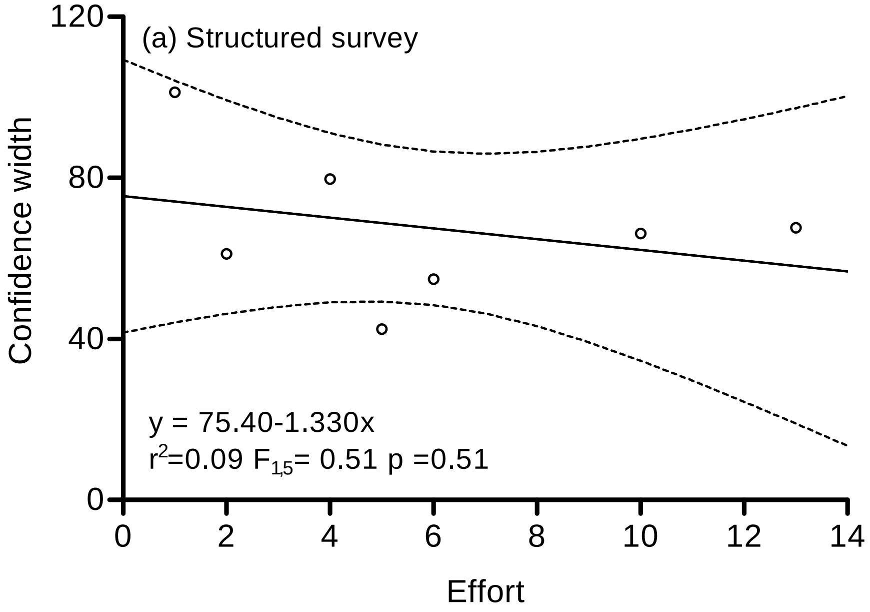


Figure 4.5. Legend on next page.

Figure 4.5. The influence of sampling effort on the width of the confidence limits of estimates of population size for bulls. Least squares linear regression analyses were used to evaluate change in the 95% confidence intervals for sight-resight models as effort increased through the number of resighting sessions. Models are (a) negative binomial, (b) Poisson, (c) Bowden's, (d) Jolly-Seber, (e) Schumacher and (f) Schnabel.



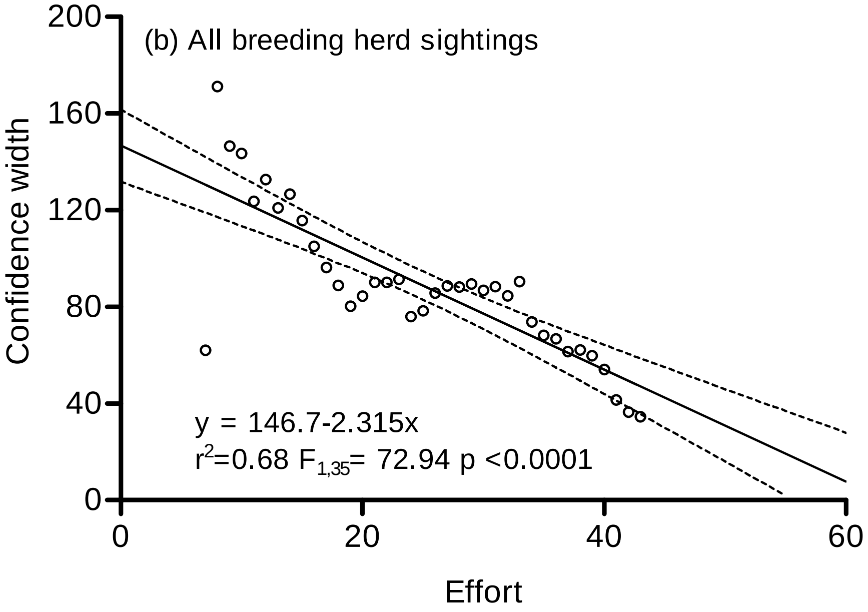


Figure 4.6. The influence of sampling effort on the width of the confidence limits of estimates of population size for elephants in breeding herds. Figures show least squares linear regression analysis of 95% confidence intervals for breeding herds for the Bowden's estimator, where (a) effort constitutes 14 resighting sessions and (b) effort comprises of all post-marking sightings of breeding herds.

Discussion

Capture-recapture models often are used to estimate abundances (e.g. Krebs 1999; Nichols 1992; Pollock 1991, 2000; Pollock *et al*. 1990; Seber 1982, 1986, 1992 and references therein). These models have been used to estimate abundance for a wide range of large mammals including bottle nose dolphins *Turslops truncatus* (Wilson, Hammond & Thompson 1999), bison *Bison bison* (Minta & Mangel 1989), tigers *Panthera tigris* (Karanth & Nichols 1998), mountain sheep *Ovis canadensis* (Neal *et al*. 1993) and moose *Alces alces shirasi* (Bowden & Kufeld 1995), but have not been applied to elephants.

This study suggests that some mark-resight models may yield population estimates similar to those derived from registration counts for a closed population of elephants. Model selection, however, is important as the violation of assumptions reduce their utility. Such methods may still be better than enumeration methods because mark-resight models are less biased than those based on the minimum-number-alive method (Krebs 1999).

A zero-truncated poisson test (see Krebs 1999) indicated that for elephant bulls the assumption of equal catchability was violated in my study, this compromised five of the eight models used (Table 4.1). The Jolly-Seber model proved least effective because it is specifically designed for open populations and where catchability is equal (Krebs 1999). It yielded wide confidence intervals that did not improve with increased effort. The Petersen model was the simplest model I tested and the low number of sightings and subsequent resightings could have compromised the model's performance, as could its sensitivity to unequal catchability (see Minta & Mangel 1989; Seber 1992). The negative binomial model was the only model I used that produced an estimate higher than the registration counts. The remaining models all produced estimates lower than the known population size but with confidence limits that were closer to the minimum number known to be present through registration counts. All the models I used yielded estimates closer to the known population than the aerial surveys. The Bowden's estimator, Schumacher method and the Schnabel method provided underestimates of the registration count at the upper 95% confidence limit although these were small.

For breeding herds my estimate of population size using the Bowden's estimator exceeded the registration count, though the lower confidence limit included the known population estimate. The estimate of total population size (bulls and breeding herds) from the Bowden's estimator, derived from resighting sessions, is close to the registration count and precision improved when I included all post-marking observations. This method yielded an estimate in which the 95% confidence intervals overlapped the registration count. My estimates of total population size from the Bowden's estimator are closer to the number of elephants known to be present in the area than those yielded by aerial surveys. The Bowden's estimator allowed me to use all sightings of marked animals, which, in the case of the breeding herds improved precision (a narrower confidence limit) although the estimate of population size was similar.

The effort expended on sighting sessions is important when designing a mark-resight study. For the breeding herds, the number of observations during sighting sessions was insufficient to provide a significant improvement in the population estimate and confidence interval. With increased effort both population estimates and confidence intervals improved significantly. For bulls all the models tested with the exception of the negative binomial estimate, showed an increased precision with increasing effort. Only the Schnabel model showed a significant narrowing in confidence interval with increased effort over 14 sighting sessions.

Of the models tested, the Bowden's estimator was the most suitable model for determining population size under the conditions prevailing during my study. The Bowden's estimator showed the highest probability that it was the best model of those selected (AIC_c weight), and is designed for closed populations. The model's ability to function without an assumption of equal catchability is a key attribute, and it was the only model tested that is not dependent on all marks being recorded in subsequent recapture (resighting) events. It therefore was the only model that could be applied to the breeding herd in the population. While the precision of estimates did not improve with increased effort for the bulls, for the breeding herds the precision of the estimate did improve with increased effort (number of observations). The Petersen, Schumacher and Schnabel models are dependent on an assumption of equal catchability and could be compromised by the violation of this assumption in this study. The Petersen model was the simplest model tested and relies on a single marking event and a single recapture event. It yielded a population estimate (38 bulls) far below the registration count (75 bulls). The only model tested that showed an increase in the precision of the population estimate with increased effort was the Schnabel model.

The Poisson, Robust and negative binomial and Schnabel models are designed for open populations. Of these models only the Poisson assumes equal catchability. As could be expected the least applicable model for this closed population was the Jolly-Seber. The Jolly-Seber model is specifically designed for open populations and is highly sensitive to violations of the assumption of equal catchability. Although the estimate of population size (63 bulls) was within the range of other models tested

(Petersen = 38 bulls to negative binomial = 87 bulls), model evaluation using AIC_c showed it to be an unsuitable model. The negative binomial model was the only model that did not show an improved 'match' to the registration count with increased effort.

Previous estimates of population size for elephants in the TEP using aerial survey methods yielded under estimates. As a result of small population size too few observations were obtained to allow the calculation of confidence intervals (Matthews 2000). Aerial survey methods are relatively expensive and reliant on specialist staff. Mark-resight surveys also are expensive and time intensive to initiate but once the initial survey has been conducted subsequent estimates can be more cost effective (Minta & Mangel 1989). Conservation organizations in Africa have to compete for funding with other agencies and financial resources are limited so cost efficient methods are vital.

I show that for small, closed elephant populations such as that of TEP estimates of population size based on mark-resight estimates are valid with confidence intervals narrower than those reported for dung counts elsewhere. Where population estimates have been determined from dung counts investigators often failed to calculate mean decay rate or mean defecation rate, therefore their estimates are unreliable (Nchanji & Plumptre 2001; Barnes 2002). Where defecation and decay rates were determined, confidence intervals are wide (see Barnes & Dunn 2002).

Population counts based on the individual identification of elephants have assumed all elephants in the populations are known (Whitehouse & Hall-Martin 2000; Moss 2001) and no confidence intervals are obtained. These estimates are based on long-term studies conducted over about 30 years (Moss 2001) and 70 years (Whitehouse & Hall-Martin 2000), and therefore not applicable to most populations.

It has recently been proposed that the monitoring of vocal communication between elephants is a potential method of estimating population size (McComb *et al*. 2003; Payne, Thompson & Kramer 2003). At present, however, these methods work over short distances and do not reliably identify individuals (McComb *et al*. 2003). Currently methods based on vocal communication are experimental and are not yet suitable for estimating population size for elephants (see Payne *et al*. 2003).

Aerial surveys are widely used to estimate elephant populations (see Blanc *et al*. 2003), although shortcomings have been identified (see Caughley 1974; Pollock & Kendall 1987; Jachmann 2002; Khaemba & Stein 2002). Aerial surveys of small populations living in forests or thickets yield questionable estimates of population size (Whitehouse *et al*. 2001; Barnes 2002).

Few aerial surveys conducted in central, southern and east Africa report confidence intervals. Even in the Kruger National Park, where aerial surveys have been conducted yearly since 1967, confidence intervals are not derived for population estimates.

Repeated mark-resight surveys can yield population trends for closed populations. A complete mark-resight survey for reserves similar in size to TEP could be completed in eight to ten days. Once established, three to four resight surveys per year would be sufficient to monitor population size and could be maintained by non-specialist technical staff.

The population estimates I derived from Bowden's estimator (N=179, 95% CI=136-233), show that given the difficulties associated with alternative methods of estimating abundance for savanna elephant populations under conditions such as those prevailing in the TEP, mark-resight methods are an alternative to methods of enumeration more commonly used.

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 ($0\leq4$, $>4\leq8$, $>8\leq12$, $>12\leq16$) 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_{0-1}, s_{1-4}, s_{5-16}, $s_{>16}$) 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
$0-\leq 1$	0.00	0.00
$>1-\leq 4$	0.00	0.00
$>4-\leq 8$	0.00	0.00
$>8-\leq 12$	0.096	0.11
$>12-\leq 16$	0.11	0.17
$>16-\leq 20$	0.10	0.22
$>20-\leq 24$	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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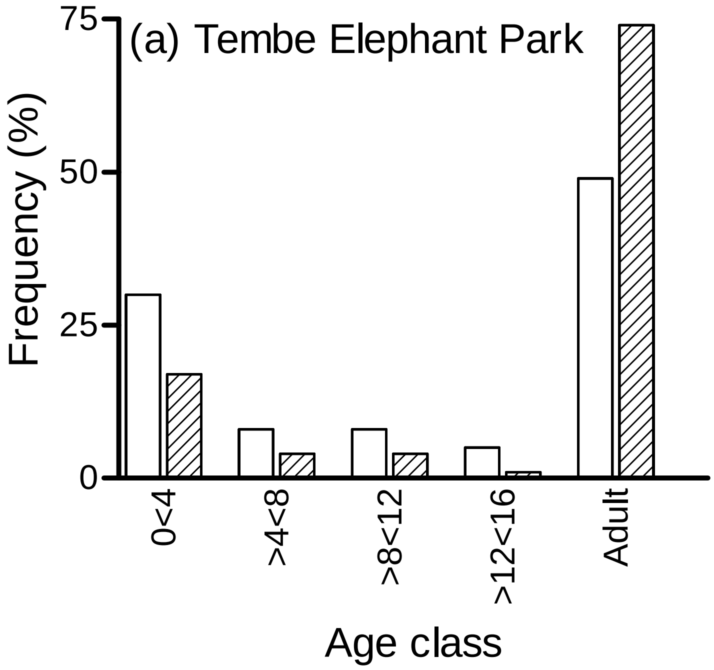
[15] The demographic assessment in MER is constrained by sample size (<100 individuals for which age was estimated and included in the analysis) and therefore must be considered with caution. Studies on the population are continuing.



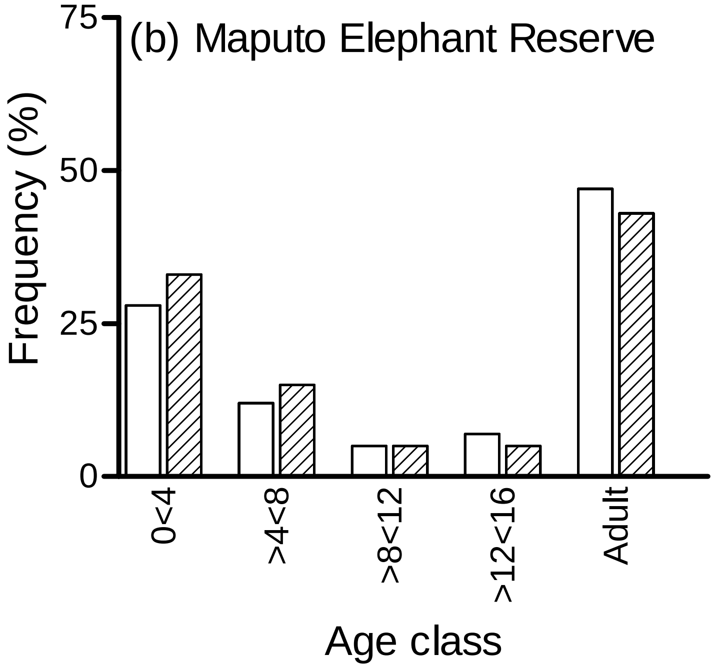


Figure 5.1. Sex specific age distribution of elephants in (a) the Tembe Elephant Park (n=163) and (b) the Maputo Elephant Reserve (n=131). Males are indicated by shaded bars and females by open bars. For Tembe Elephant Park estimates were derived from ground-based observations and for Maputo Elephant 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-≤4 years $t_{98} = 14.40$, $P<0.001$, >4-≤12 years ($t_{98} = 13.94$, $P<0.001$, >12-≤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.

Time (years)	**Predicted Population size (x)** **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.

Time (years)	**Predicted Population size (x)** **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

Chapter 6

Landscape use by elephants in the Tembe Elephant Park

Introduction

The quantity and quality of resources such as food, water and shelter are unevenly distributed across landscapes (Johst & Schoeps 2003; Koops & Abrahams 2003; Silver *et al*. 2000). Animals that depend on these resources should therefore be distributed unevenly (Verlinden & Gavor 1998). Consequently natural selection may favour individuals that have access to superior resources (Boyce 1979; Basolo 1998). Individuals may opt, therefore, to use those landscapes within their range that will enable them to optimize resource extraction. Under favourable and unrestricted conditions it is expected that individuals will select for landscapes that are superior in providing resource requirements and will avoid sub-optimal or marginal landscapes.

Landscapes incorporated into fenced-off protected conservation areas, such as the Tembe Elephant Park (TEP), some 300km^2, may not contain all landscape types or landscapes at the ratios, or of the quality, typical of unconfined ranges. Elephants fenced into TEP since 1989, may, therefore, be restricted in the landscapes they can select compared to those individuals that roamed over a much larger area (see Chapters 1 & 3). From studies elsewhere (e.g. Hall-Martin 1992; Armbruster & Lande 1993; Seydack, Vermeulen & Huisamen 2000; Whitehouse & Harley 2001; Whyte 2001; Osborn & Parker 2003) it is apparent that confinement prevents traditional movement patterns, thus supporting the notion that elephants living in the TEP may have limited opportunities to exercise landscape selection. The elephant population of TEP has been increasing in size over a number of years (see Chapter 3), and at current densities elephants may have less opportunity to select landscape types than when densities were lower. High local densities may also challenge opportunities for landscape selection. Here I aim to define the distribution of elephants across the TEP, and to determine if their distribution can be ascribed to them no longer having the opportunity to selectively use certain landscapes. This study is based on individual sightings made during repetitive surveys over a nine month period across all landscapes within TEP. It assumes that sightings (and therefore occurrence) proportional to the area of each of the landscapes signifies a lack of selection. Such a lack of selection may then be considered as a response to restrictions imposed upon individuals, either through social factors or through spatial limitations, or both.

Elephants occur across a wide range of landscapes in southern African savannas (Blanc *et al*. 2003). They are, however, unevenly distributed across these landscapes and when they are not confined prefer certain landscapes above others (see Caughley & Goddard 1975; Jachmann 1983; Viljoen 1989; Lindeque & Lindeque 1991; Dublin 1996; de Villiers & Kok 1997; Thouless 1998; Verlinden & Gavor 1998; Seydack *et al*. 2000; Stokke & du Toit 2002; Leggett *et al*. 2003; Osborn & Parker 2003). During the dry season elephants browse on woody species and use landscapes where water and other resources are available (Jachmann 1983; Ruggiero & Fay 1994; Dublin 1996; Thouless 1996; de Villiers & Kok 1997; Whyte 2001; Stokke & du Toit 2002; Osborn & Parker 2003).

Landscape selection is usually modelled under the assumption that a species will select and use habitats best suited to their life requirements. Consequently higher-quality habitat will be used more often than other habitats (Schamberger & O'Neil 1986). The use of habitat will then be directly proportional to its availability (Mysterud & Ims 1998). Landscape has been defined as 'a mosaic of habitat patches across which organisms move, settle, reproduce, and eventually die' (Forman &

Godron 1986). Habitats are those elements of a landscape in which a species is spatially and temporally distributed. I simplified landscape categories to address ambiguities in determining specific vegetation types (see Fairall & van Aarde 2004a).

Materials & Methods

Study Design

Data on elephant locations were collected from March to December 2001 during a mark-resight programme (see Chapter 4). Sampling took place from an existing road network divided into fixed non-overlapping transects which traversed all the landscape types of the Park (Fig. 6.1). I surveyed these transects on 14 occasions and recorded the position of all elephant sightings. Positions were plotted onto a landscape map of the Park on which transects (the road network) were superimposed (see Fig. 6.1).

I determined the proportion of each landscape type available to elephants from the proportional transect length in each landscape type. A landscape map constructed using Idrisi software and a LANDSAT 5 TM satellite image (ID 167-79 of 30 August 1999) purchased from the CSIR Satellite Applications Centre (PO Box 395, Pretoria, South Africa) was used to distinguish and outline open woodland, closed woodland, sand forest, reedbed and hygrophilous grassland as landscape types (Fairall & van Aarde 2004a). Hygrophilous grassland covers <1% of the Park and was therefore combined with the reedbed category (see Fairall & van Aarde 2004b).

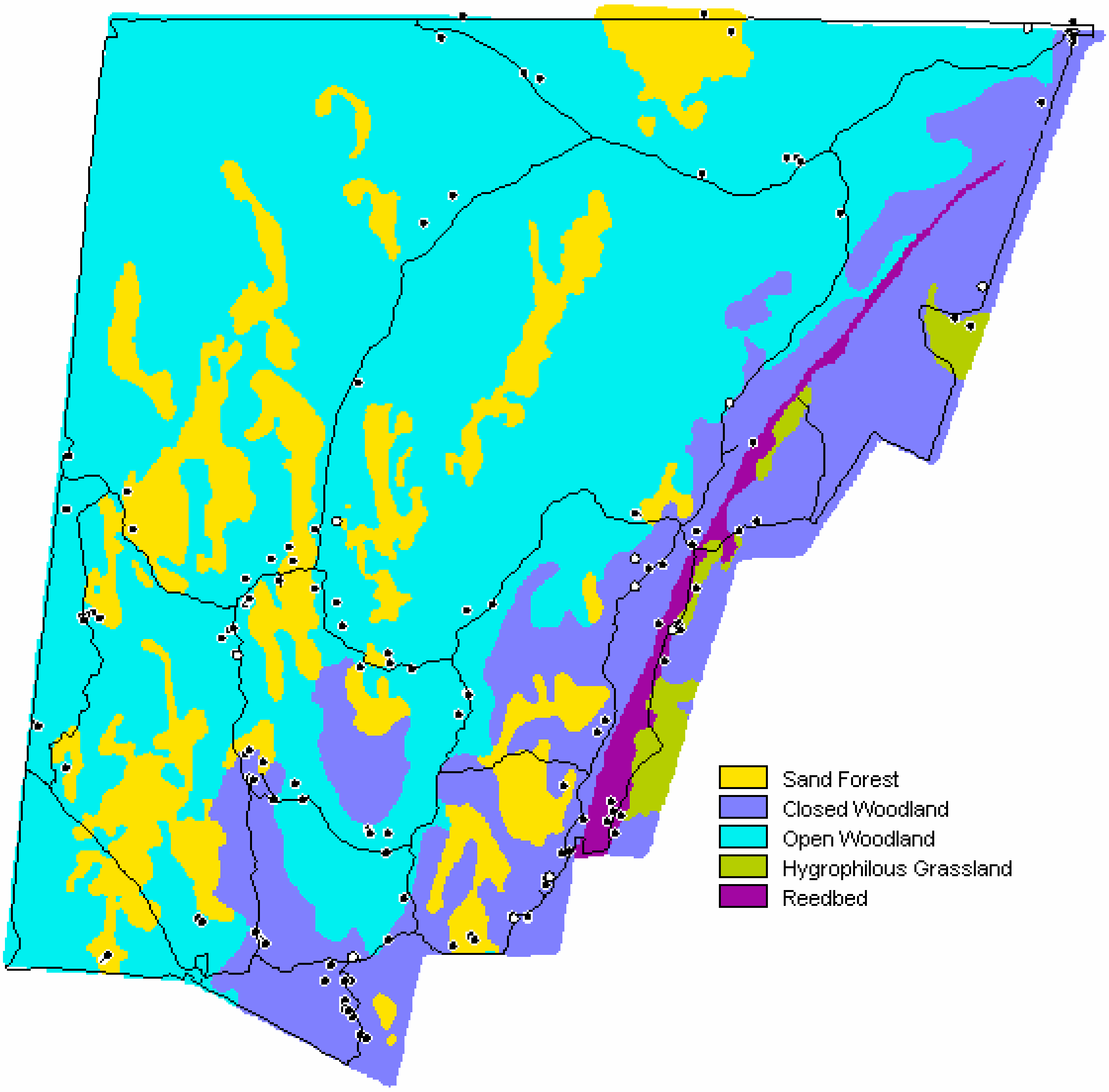

Figure 6.1. The landscape types of Tembe Elephant Park and elephant distribution. Black points indicate sightings of males and white points indicate sightings of breeding herds. The reedbed coloured purple represents the Muzi swamp. The black lines represent the survey routes.

Observations of elephants

Between March and December 2001 I observed elephants on 136 occasions in all available landscape types, during transect surveys. The sightings comprised 123 observations of bulls and 13 observations of breeding herds. The observations were used to calculate expected levels of use and actual use (Table 6.1). The potential consequences of landscape type for sightability have not been incorporated in the present study[17].

Data analysis

Landscape use at the population level

I used a Design I approach (Thomas & Taylor 1990) to evaluate landscape selection at the population level. Here the availability and use of landscape types is considered in terms of the entire study area and collectively for all individuals. The Design I protocol used a selection index following Neu, Byers & Peek (1974), and assumed that observations were independent within and between animals, and that all habitat types were equally available to all animals (McClean *et al*. 1998). The design II approach (Thomas & Taylor 1990) I used differed from the design I as individuals were recognised as separate entities.

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[17] A more recent landscape study based on satilite tracking of elephants in Tembe (R.A.R. Guldemond PhD thesis 2005 in review) suggests that elephants in the park avoided reedbeds in the dry season but did not show landscape preference in the wet season. It is therefore unlikely that my observations were biased by sightability.

Table 6.1. Utilisation-availability data for landscape types in the Tembe Elephant Park. Utilisation is based on 123 observations of males and 13 observations of breeding herds. Proportion of available habitat type indicates availability. Proportion of observations in a landscape type indicates utilisation.

Landscape Type	**Proportion of available landscape** ***(p_i)***	**Number of observations in landscape** ***(u_i)***			**Proportion of observations in landscape** ***(o_i)***		
		Bulls	Breeding herds	Bulls & Breeding herds	Bulls	Breeding herds	Bulls & Breeding herds
Open Woodland	0.52	54	5	59	0.439	0.382	0.434
Closed Woodland	0.32	44	6	50	0.358	0.458	0.368
Sand Forest	0.09	15	0	15	0.122	0.008	0.110
Reedbed	0.07	10	2	12	0.081	0.153	0.088
Total	1.00	123	13	136	1.00	1.00	1.00

Observations were considered independent as they were logged along systematic sighting routes and an elephant could not be sighted twice in a single day. TEP is relatively small (300 km^2, Matthews *et al.* 2001) and elephants have the ability to use the entire area, so all landscape types were assumed equally available to all elephants.

To obtain a simple measure of selection I used the forage ratio (Savage 1931 and Williams & Marshall 1938 cited in Krebs 1999), now commonly referred to as the selection index (Manly, MacDonald & Thomas 1993), and calculated as:

$$\hat{w}_i = \frac{o_i}{p_i},$$

where $\hat{w}_i$ is the forage ratio for species i, o_i the proportion or percentage of habitat used and p_i the proportion or percentage of habitat available. To allow comparison of ratios between sexes and for the combined observations I calculated standardised selection indices as standardised ratios (Manly *et al.* 1993) that sum to 1.0 for all resource types:

$$B_i = \frac{\hat{w}_i}{\sum_{i-1}^{n} \hat{w}_i},$$

where B_i is the standardised selection index for habitat i and $\hat{w}_i$ the forage ratio for habitat i. I used a G-test goodness-of-fit to test the null hypothesis that elephants use habitats in proportion to their availability (Manly *et al.* 1993):

$$G = 2\sum_{i=1}^{n} \left[u_i \ln\left(\frac{u_i}{Up_i} \right) \right],$$

where u_i is the number of observations using habitat i, U the total number of observations of use equals $\sum u_i$,G is the G value with (n – 1) degrees of freedom (H_o: random selection) and n is the number of habitat categories.

Landscape use at the individual level

To determine if landscape use differed from random for individual elephants I used a Design II protocol, compositional analysis (Aebischer, Robertson & Kenward 1993). Aebischer *et al.* (1993) identify four problems in analysing data of habitat use. Problem 1 is an inappropriate level of sampling and sample size, problem 2 is non-independence of proportions where the proportions that describe habitat composition sum to 1 over all habitat types, (unit-sum constraint), problem 3 is differential habitat use by groups of individuals and problem 4 is the arbitrary definition of habitat availability. To overcome these problems Aebischer *et al.* (1993) recommend a compositional analysis method which is statistically robust and handles the unit sum constraint for habitat use and availability using individuals as sample points (Aebischer *et al*. 1993; McClean *et al*. 1998). This analysis assumes independence between animals but not within the observations of each animal (McClean *et al*. 1998). The assumption of independence of observations and availability of habitats was met as shown for the Neu *et al*. (1974) method. I pooled data using sightings of individual animals as sample units (see Aebischer *et al*. 1993). All observations of bulls (n=123) were pooled. I then made "packages" of observations, using a table of random numbers to select individual sightings randomly and without replacement, and used these packages to represent 17 individual bulls. Breeding herds were observed on too few occasions to allow Design II (landscape use by individuals) protocols to be applied (see Aebischer *et al*. 1993; Arthur *et al*. 1996).

For the simple measure of preference in the selection index comparing use and availability (Krebs 1999) values above 1.0 indicate preference, while values below 1.0 indicate avoidance. Selection indices are awkward to interpret as values cannot be directly compared between bulls and breeding herds. I therefore standardised the selection indices as ratios (Manly *et al*. 1993). I simplified the ranking matrices for the 17 bulls (Table 6.5) by replacing elements in the matrix with + where the selection value is >0 and – where selection value is <0 and triple signs indicate significant difference from random at $p = 0.05$. I used the number of positive signs to assign rank habitat preference from 0 (lowest) to 3 (highest) following Aebischer *et al*. (1993).

Results

Landscape use at the population level

In relation to availability all elephants avoided open woodland and all preferred closed woodland and reedbed (Table 6.2). Bulls show preference for sand forest in relation to its availability while no breeding herds were encountered in this landscape type (Table 6.2). From the standardised indices, where values greater than 0.25 indicate preference and values below 0.25 indicate avoidance, it is apparent that both bulls and breeding herds avoid open woodland in relation to its availability (Table 6.3). For closed woodlands bulls use this habitat in relation to its abundance, not preferring or avoiding it, but breeding herds highly prefer these woodlands. Sand forest appears to be favoured by bulls but no breeding herds were recorded in sand forest suggesting that they avoid this landscape type. The reedbed landscape is not preferred or avoided by bulls, but is preferred by breeding herds (Table 6.3). Based on this analysis the most preferred habitat for bulls is sand forest, while breeding herds preferred reedbeds. When analysed with G-test's, however, the landscape preferences of male elephants are not statistically significant (G_3=3.633, P=0.304) (Table 6.2). Breeding herds also did not select significantly for landscape type (G_3=3.836, P=0.208).

Table 6.2. Selection indices for landscapes for elephants in Tembe Elephant Park. Values above 1.0 indicate preference, values below 1.0 indicate avoidance. Values are not directly comparable between bulls and breeding herds.

Landscape type	Bulls n = 123	Breeding herds n = 13
Open Woodland	0.844	0.735
Closed Woodland	1.118	1.431
Sand Forest	1.355	0.000
Reedbed	1.161	2.186

Table 6.3. Standardised selection indices for landscape selection of elephants in Tembe Elephant Park. Values above 0.25 indicate preference, values below 0.25 indicate avoidance. Values are comparable between bulls and breeding herds.

Landscape type	Bulls n = 123	Breeding herds n = 13
Open Woodland	0.189	0.169
Closed Woodland	0.250	0.328
Sand Forest	0.303	0.00
Reedbed	0.259	0.502
Total	1.00	1.00

Landscape use at the individual level

I constructed a ranking matrix of landscape use by calculating the log-ratio mean values (±95% CI) of landscape use for 17 bulls (Table 6.4) derived from the randomly created packages of observations. To determine if the landscape use values are significant I added and subtracted the 95% confidence limit values and if the resultant value included a zero value it was not considered significant (see Aebischer *et al.* 1993). For individuals the between-rank differences in landscape use are not significant. Landscapes are, therefore, used at random and use did not differ significantly from their occurrence. When landscape preference is ranked for individuals, closed woodland was the landscape most selected for, followed by open woodland and then sand forest. The least selected for landscape was reedbed.

Table 6.4. Ranking matrix values (mean±SE) based on a comparison of proportional landscape use and proportional landscape availability for 17 bulls in Tembe Elephant Park.

Landscape type	**Open Woodland**	**Closed Woodland**	**Sand Forest**	**Reedbed**
Open Woodland	0	-0.185 ± 0.308	0.169 ± 0.403	0.338 ± 0.368
Closed Woodland	0.185 ± 0.308	0	0.354 ± 0.520	0.563 ± 0.466
Sand Forest	-0.169± 0.403	-0.354± 0.520	0	0.209 ± 0.552
Reedbed	-0.338± 0.369	-0.562± 0.466	-0.209± 0.552	0

Table 6.5. Simplified ranking matrix in descending order of landscape preference based on comparing proportional habitat use with proportional habitat availability for 17 bulls in Tembe Elephant Park.

Landscape type	**Open Woodland**	**Closed Woodland**	**Sand Forest**	**Reedbed**	**Rank***
Closed Woodland	+		+	+	3
Open Woodland		-	+	+	2
Sand Forest	-	-		+	1
Reedbed	-	-	-		0

*Results for Aebischer's (1993) model ranks are not significant

Discussion

The TEP was established to conserve elephants and protect the endemic sand forest vegetation type (Sandwith 1997). There is concern that these two conservation goals are mutually exclusive as elephants may threaten this forest type (Matthews *et al.* 2001). I have attempted to ascertain if elephants showed preference for landscape types as any preference for sand forest may influence future management decisions.

At the population level a Design I (Manly *et al.* 1993) approach yielded an outcome that suggests that there are inter-sexual differences in landscape selection. In proportion to availability sand forest was the most preferred landscape for bulls but for breeding herds it was the least preferred landscape type (Table 6.3). Bulls neither avoided nor preferred closed woodlands while for breeding herds it was a preferred landscape type. For breeding herds reedbed was the most preferred landscape type while bulls used this landscape type in proportion to its availability. This implies that the conditions prevailing in TEP at the time of the study were still permitting elephants to selectively use certain landscapes.

In TEP bulls use all available landscape types while breeding herds may be more selective. Stokke & du Toit (2002) found that, in the dry season in northern Botswana, elephant bulls use all habitat types with the exception of one (used less than expected), in proportion to their occurrence. In their study females used five out of seven habitat types in proportion to availability. An earlier study, however, showed significant selection for three vegetation types (from 20 identified) for elephants in the same region (Verlinden & Gavor 1998), when using a simple method of frequency of observations in vegetation type *i* divided by the percentage elephant range covered by vegetation type *i*. Their vegetation types were, however, based on species compositions that may not reflect actual habitat types, and used fewer animals (18 collared elephants) than vegetation types.

Using different landscape classifications and more landscape types and monitoring four females elephants and one male, Ntumi (2002) determined that, at least during the wet season, elephants preferred the Futi floodplains and hygrophilous grasslands. These landscape types are the ones that most closely conform to the reedbed classification for TEP indicating that both sub-populations prefer the same landscape types. The elephant sub-population of Maputo Elephant Reserve (MER) appears to shows a higher affinity for forested landscapes than the TEP sub-population and this may be attributed to human disturbance in the MER (de Boer *et al*. 2000; Ntumi 2002).

When landscape preference is ranked for individuals the Design II approach of Thomas & Taylor (1990), based on the compositional analysis method of Aebischer *et al*. (1993), suggests that landscape preferences exercised by bulls differ from that of the Design I approach of landscape preferences at the population level. At the population level closed woodland is the most preferred landscape type followed by open woodland, then sand forest, with reedbed the least preferred. The ranks assigned to the landscape types in simplified ranking matrix indicate preference but are not statistically significant (Table 6.5). At this level I was, therefore, unable to reject the hypothesis of equal use of landscape types in proportion to their occurrence. That the two different approaches (Design I & Design II) give different results is not unusual even when the null hypothesis of equal use is rejected (Johnson 1980; Alldredge & Ratti 1986, 1992; Manly *et al.* 1993; McClean 1998), and may not represent real differences in landscape use (Bender, Roloff & Haufler 1996).

In northern Botswana, during the dry season, elephants concentrate in woodland habitats that are close to permanent water (Ben-Shahar 1996; Verlinden & Gavor 1998; Stokke & du Toit 2002). The preference shown by breeding herds for reedbeds in TEP may reflect the close association of this landscape with permanent water (Matthews *et al*. 2001). The reedbeds are situated in, or adjacent to, the Muzi drainage line (see Fig. 6.1) and the three females in the Park fitted with radio collars showed spatial affinity with the Muzi drainage line (Fairall & van Aarde 2004b). The sand forests of the TEP are dominated by large trees (Matthews *et al*. 2001). Elsewhere elephant bulls use woody vegetation types that are less available to elephants in breeding herds due to stem size, height or tolerance of variation in diet quality (Stokke & du Toit 2000). In addition sand forests are further from permanent water than reedbed or closed woodland forest types and selection may, therefore, favour the use of closed woodlands by breeding herds. In Tembe all landscapes are within 10 kilometres from water and so available to bulls, which can range further from perennial water than breeding herds (Knight, Hitchins & Erb 1994; Stokke & du Toit 2002). Based on dung counts de Boer *et al*. (2000) reported that elephants in the nearby MER in southern Mozambique preferred sand forest and other forest types over more open habitat types in the mid-1990s but previously preferred open habitats. They postulated that this was a behavioural change due to human persecution.

Elephants are generalists and bulk feeders (Owen-Smith 1988) it is, therefore, likely that they use resources such as habitats in proportion to occurrence. In the wet season when grasses are abundant and of high forage quality elephants are predominantly grazers, in the dry season elephants browse woody vegetation when it provides higher quality forage than grasses (Field 1971; Field & Ross 1976; Guy 1976; Barnes 1982).

Although I was unable to show that individual bulls significantly select for sand forest environments, at the population level this was the landscape type most favoured by bulls in the TEP. Elephants may modify landscapes (e.g. Laws 1970; Barnes 1983; Owen-Smith 1988; Dublin 1995; Cumming *et al*. 1997) and with further increases in population density and the high ratio of bulls to breeding herd members (see Chapter 4), elephants in TEP may have an impact on this landscape type. This will have conservation implications (see Sandwith 1997; Matthews *et al*. 2001). If elephants are using landscape types in proportion to their availability, and elephant density is high, additional habitat availability should alleviate pressure on habitats of conservation concern. Proposals for the development of a transfrontier reserve that will link the TEP and the MER through the Futi Corridor would add habitat types suitable for elephants and increase the area of each landscape type available to the TEP elephant population. While the MER and the Futi Corridor currently support elephants population density there is much lower than for the TEP (see Chapter 3). The successful establishment of a Transfrontier Conservation Area including the TEP, Futi Corridor and Maputo Elephant Reserve would reunite the Maputaland elephant population and may negate the impact of elephants on local stands of sand forests in the TEP.

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 2500km^2 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 km^2 and an additional 24 to areas <2 000 km^2. Some 54% of populations (n=107) therefore occur in areas <2 000 km^2. Only a quarter of elephant populations (n=48) live in areas >5 000 km^2 (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 it roams. Key management issues here relate to perceived overabundance (Whyte, van Aarde & Pimm 1998, 2003; van Aarde *et al*. 1999; Whyte 2001, 2004).

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, Hluhuwe-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 103km^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 it 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. Guldemond & 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 then 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.

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