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An evaluation of southern Africa's elephant sub-populations as a metapopulation

By

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An evaluation of southern Africa's elephant sub-populations as a metapopulation

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Abstract

Elephant management traditionally centers on reducing ecological impact and human-elephant conflict by controlling numbers. However, such an approach only deals with symptoms, and ignores the causes of the problem. Planning for cases when a species is a nuisance in some areas, but threatened in others, could benefit from the application of metapopulation theory. The theory offers a framework that is elegant, and have ecological as well as political appeal.

Applying classic metapopulation theory to long-lived species that are widely distributed in stochastic environments where they can resist extinctions is problematic. However, empirical evidence for metapopulation structure may exist when applying more lenient criteria. I examined the literature for empirical support of classic criteria set by Hanski (1999) and for a more lenient sub-set of criteria proposed by Elmhagen & Angerbjörn (2001) for specifically mammals. I propose that for small mammals (≤5kg) the full complement of classic criteria must be applied to yield perspectives on population regulation and conservation. However, for large (>100kg) and medium sized (>5≤100kg) mammals only habitat discreteness, potential of demographic asynchrony and the likelihood of dispersal among sub-populations must be evaluated. Metapopulation theory could then be useful when constructing conservation plans that ensure the persistence of a species and contribute to forces that stabilize populations regionally.

I evaluated the applicability of metapopulation theory to southern Africa's elephant sub-populations. I identified 51 discrete administrative sub-populations that occurred in six conservation clusters. Population growth rates varied across space and time within and among conservation clusters. Some sub-populations and conservation clusters increased or decreased while others remained stable. Therefore, elephant populations in southern Africa were in demographic asynchrony, both on a local and regional scale. I also suggest that dispersal may occur among sub-populations within clusters. Consequently, the regional population is stabilized by emigration to, or immigration from neighboring sub-populations as a result of demographic asynchrony across an ecological gradient. Elephant populations across southern Africa thus adhered to one and could possibly adhere to all metapopulation criteria.

Observed changes in elephant numbers could also be the result of survey error. To gain an understanding of how survey error could affect estimates, I used dung counts and measurements to estimate population size and construct an age structure for the elephants living in the Maputo Elephant Reserve in Mozambique. I suggest that dung surveys can yield population estimates with known precision and can be used in monitoring programmes aimed at assessing population trends - despite the fact that it can be affected by observer bias.

In this thesis I show that metapopulation theory provides the opportunity of applying a spatio-temporal approach to elephant conservation that is not obsessed with numbers. When implementing metapopulation theory, management no longer have to centre on elephants, but can focus on the landscape as a spatially and temporally dynamic area. Local fluctuations in elephant numbers could be construed within a regional context, rather than implementing management strategies on a local scale. Such an approach will focus on the causes rather than the symptoms of the elephant problem and may contribute to the persistence of elephants as well as other components of southern African biodiversity.

Opsomming

Die ekologiese impak van olifante en konflik tussen mense en olifante word tradisioneel hanteer deur olifant getalle te beheer. Ongelukkig los so ŉ benadering net die simptome en nie die oorsaak van die problem op nie. Gevalle waar ŉ spesie ŉ problem is in sommige areas maar bedreig is in ander, kan baat vind by die toepasing van die metabevolkings teorie. Die teorie bied ŉ elegante raamwerk wat op ekologiese en politieke gebiede aanklank vind.

Die toepasing van die klassieke metabevolkings teorie op lang lewende spesies wat wyd versprei voorkom in stochastiese omgewings waar hulle weerstand kan bied teen uitsterwings skep egter probleme. Emperiese bewyse vir ŉ metabevolkings struktuur kan egter voorkom waneer meer gematigde kriteria ondersoek word. Ek het die literatuur ondersoek vir emperiese ondersteuning vir die klassieke kriteria wat Hanski (1999) voorgestel het, asook vir ŉ meer gematigte sub-groep van kriteria wat deur Elmhagen & Angerbjörn (2001) vir spesifiek soogdiere voorgestel is. Ek stel voor dat die klassieke kriteria aangewend kan word om bevolkings van klein soogdiere (5≤kg) te reguleer, beter te kan verstaan en dan te bewaar. Vir groot (>100kg) en medium groot (>5≤100kg) soogdiere kan die metabevolkings teorie net gebruik word as die bestaan van aparte habitate, demografiese asinkronie en die potensiaal van verstrooing tussen tussen sub-bevolkings bewys kan word. Die metabevolkings toerie kan dan gebruik word om bewarings inisiatiewe in te stel wat spesies in staat sal stel om voort te bestaan en oor die streek te stabiliseer.

Ek het die toepasbaarheid van die metabevolkings teorie vir suidelike Afrika se olifant sub-bevolkings ondersoek. Ek het 51 aparte administratiewe sub-bevolkings

geidentifiseer wat in ses ‘bewaringsklosse’ voorkom. Bevolkings groeitempos het binne in en tussen bewaringsklosse gewissel. Sommige het of toegeneem of afgeneem terwyl ander stabiel gebly het. Olifant sub-bevolkings in Suider Afrika was dus in demografiese asinkronie, op ʼn lokale sowel as op ʼn streeks vlak. Ek het ook voorgestel dat verstrooing kan voorkom tussen sub-bevolkings binne in bewarings klosse. Die olifant bevolking van die streek word dus deur emigrasie na, of immigrasie van naburige sub-bevolkings as gevolg van demografiese asinkronie oor ʼn ekologiese gradient gestabiliseer. Olifant bevolkings in Suider Afrika het dus voldoen aan een, en kan potensieel voldoen aan alle metabevolkings kriteria.

Opmerklike veranderinge in olifant getalle kan ook wees as gevolg van foute wat tydens tellings gemaak word. Om beter te verstaan hoe sulke foute bevolking skattings affekteer, het ek olifant mis tellings en metings gebruik om ʼn bevolking skatting en ouderdomsstruktuur vir olifante in die Maputo Olifant Reservaat in Mosambiek saam te stel. Ek stel voor dat mis opnames bevolking skattings kan lewer wat bekende presiesie het en dat dit gebruik kan word in moniterings programme wat neigings in olifant bevolkings ondersoek - alhoewel sulke skattings beinvloed kan word deur die vooroordeel van waarnemers.

In hierdie tesis toon ek aan dat die metabevolkings teorie ʼn geleentheid skep vir ʼn ruimtelike-tydelike benadering in olifant bewaring wat nie net op getalle fokus nie. Wanneer die metabevolkings teorie toegepas word, kan bestuur op die landskap as ʼn ruimtelike en tydsgebonde dinamiese area fokus, in plaas van net op olifant getalle. Lokale wisselings in olifant getalle kan binne in ʼn streek konteks geinterpreteer word, eerder as om bestuurs inisiatiewe net op ʼn lokale vlak in te stel. So ʼn benadering sal

fokus op die oorsprong in plaas van die simptome van die olifant problem en mag bydra tot die voorbestaan van nie net olifante nie, maar ook tot die biologiese diversiteit van Suider Afrika.

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Disclaimer

This thesis includes three manuscripts, two that have been accepted for publication and one that will soon be submitted. Styles and formatting of the chapters follow the respective journal requirements. Chapters 1,2,3 and 5 follow the format requirements for the journal *Mammal Review*. I hereby declare all the work to be my own and that I have acknowledged all those who helped me and contributed to the production of this thesis.

Pieter I. Olivier

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For my parents

Chapter 1

GENERAL INTRODUCTION

Humans are changing ecosystems like never before (Myers & Knoll, 2001; Travis, 2003; Ehrlich & Pringle, 2008). Habitat destruction and landscape fragmentation are affecting plants (e.g. Young *et al.,* 1996; Helm *et al.,* 2006), insects (e.g. Didham *et al.,* 1996), birds (e.g. Adrén, 1994; Boulinier *et al.,* 2001), amphibians (e.g. Houlahan *et al.,* 2000; Cushman, 2006), reptiles (e.g. Driscoll, 2004) and mammals (e.g. Cardillo *et al.,* 2005). As a result, large numbers of species may go extinct (Ehrlich & Wilson, 1991; Pimm *et al.,* 1995).

For African elephants, habitat loss, fragmentation of their original distributional ranges (see Carrathurs *et al.,* 2008), and consequent confinement to protected areas have contributed to the so-called 'elephant problem' (Caughley, 1976). In some areas, range loss, and continued human prosecution have driven populations to the brink of extinction (see Blanc *et al.,* 2003; Blanc *et al.,* 2007). However, in others, increased protection, fences and artificial water provisioning have led to undesirably high numbers of elephants being confined in small areas (e.g. Skarpe *et al.,* 2004; Slotow *et al.,* 2005; van Aarde *et al.,* 2008). Here, they can have a detrimental impact on biodiversity (e.g. Cumming *et al.,* 1997; Guldemond & van Aarde, 2007, 2008; O'Conner *et al.,* 2007). Furthermore, elephants roaming across landscapes where people live may destroy crops or even be responsible for loss of life (e.g. Hoare, 1999; Walpole & Leader-Williams, 2002; Jackson *et al.,* 2008).

In recent years, the elephant problem has received increased attention from scientists and stakeholders interested in finding the best possible solution (Scholes & Mennell, 2008). In some areas where elephants were felt to be overabundant, culling was regarded as the standard tool to keep elephant numbers stable and at a desired level (Cumming & Jones, 2005). However, increased pressure from local and international animal rights groups, and the awareness that culling might actually enhance, instead of stabilize population growth rates, led to its cessation (see van Aarde *et al.,* 1999; van Aarde *et al.,* 2008).

Translocation of elephants into areas where elephant populations were absent or occurred in relatively low numbers, seemed a logical, and more ethical alternative to culling. For instance, in South Africa alone, 58 elephant populations were established from 1979-2001 (Garaï *et al.,* 2004). However, most of these newly established populations were in small, fenced reserves. Here, elephant populations showed unnaturally high growth rates (e.g. Slotow *et al.,* 2005). In addition, the lack of new areas to move elephants to, presents a major limitation to conservationists that wish to use translocation as a means of controlling elephant population size within reserves (van Aarde *et al.,* 2008). Alternatively, elephant immunocontraception has been suggested, and implemented to stabilize population growth rates. Its effects on elephant population and social dynamics are, however, still poorly understood (Pimm & van Aarde, 2001; Kerley & Shrader, 2007; Bertschinger *et al.,* 2008). Contraception may also not address impact as such and the effect that elephants may have on other species. Furthermore, contraception can currently only be regarded as a possible management tool in small confined populations, as the efforts needed to stabilize elephant numbers in large populations are impractical (Pimm & van Aarde, 2001).

Currently, all management actions that limit elephant numbers artificially suffer from potential shortcomings. They may, in some instances, have a desired short-term benefit, but unproven long term outcomes. Therefore, only the implementation of an alternative management strategy may solve the ‘elephant problem’. In this thesis, I investigate the applicability of the metapopulation concept as a more natural approach to manage elephant populations and their apparent impact on other species.

The metapopulation concept

In recent years the concept of a metapopulation has become a major paradigm in conservation biology and population ecology (Hanski, 1999; Grimm *et al.*, 2003; Hanski & Gaggiotti, 2004). The number of publications using the metapopulation concept has increased notably since the mid 1980’s (Hanski, 1999). The growing interest in the metapopulation concept indicates that the concept is considered useful for a wide range of systems, and problems, dealing with a variety of taxa (see Fig. 1). It also reflects on the most serious threats to biodiversity today, namely: loss, degradation and fragmentation of natural habitats (Pimm & Raven, 2000; Fisher & Lindenmayer, 2007).

Metapopulation theory originated from a framework laid out by Richard Levin in 1969 (Levin, 1969). From Levin’s relatively narrow, mathematically abstract concept, i.e. populations of populations that go locally extinct and recolonize unoccupied habitats, the present views of metapopulations have broadened and now include a variety of spatially structured population units (e.g. sources, sinks and pseudosinks) and metapopulation types (e.g. classical, mainland-island, source-sink, non-equilibrium and patchy metapopulations) (Harrison, 1994; Thomas & Kunin, 1999) (see Table 1). Classic metapopulation theory applies to situations where the habitat of individuals is not homogenous, but consists of discrete islands or patches. Due to isolation from other patches, the populations in individual patches have their own dynamics. However, these patches are not completely isolated because dispersers may occasionally cross the distances and barriers between patches. A patch that becomes empty due to local extinction may consequently be re-colonized by dispersers from occupied patches (see Hanski & Gilpin, 1991; Hanski, 1999; Hanski & Gaggiotti, 2004).

For a population to be considered as a metapopulation four criteria must be fulfilled (Hanski, 1999). There has to be discrete habitat patches which are, or can be, inhabited by breeding sub-populations (1), all sub-populations must have a risk of extinction (2) while empty habitat patches must be colonized by dispersing individuals (3) and the population dynamics of sub-populations have to be asynchronous (4).

However, as metapopulation studies became more frequent, biologists realized that very few natural populations strictly adhere to all four of these classic criteria, so more lenient definitions/criteria were developed (e.g. Hanski & Gilpin, 1991; Harrison & Taylor, 1997; Elmhagen & Angerbjörn, 2001; Pannell & Obbard, 2003). For instance, Hanski & Giplin (1991) define a metapopulation as ‘any assemblage of discrete local populations (sub-populations) with migration (dispersal) among them regardless of the rate of population turnover’. Elmhagen & Angerbjörn (2001), too, proposed two more lenient criteria based on the four original criteria from Hanski’s (1999) that should be used to classify populations of mammals as metapopulations. As a result, in some instances, these more lenient approaches have led to a loss in precision when applying the classic concept. Conversely, applying more lenient criteria has resulted in metapopulation theory being incorporated into more 'real world' conservation initiatives and strategies.

For metapopulations, regional persistence is possible despite local extinctions (Hanski, 1999). Individuals (sub-populations) die but are replaced by new ones, and the population (metapopulation) persists far longer than any of its individuals (sub-populations). Metapopulation theory has introduced the idea that the long term persistence of a metapopulation cannot be explained only by the persistence of the sub-populations that it consists of, but also depends on regional processes of colonization and extinction. Therefore, metapopulation dynamics depend on immigration and emigration. Sub-population dynamics depend on habitat patch size and quality, whereas regional dynamics depend on habitat patch position, connectivity, and environmental processes. The balance between these two levels of dynamics, local and regional is determined by various features of the patch network and of the species (see Hanski, 1999; Hanski & Simberloff, 1997; Hanski & Gaggiotti, 2004). Metapopulation theory is therefore particularly useful when constructing conservation plans based on the restoration of spatial axes to regain spatial-temporal dynamics that enhance persistence and overcome local impacts on other species (van Aarde & Jackson, 2007).

To present a holistic view of how metapopulation processes operate in space, Thomas & Kunin (1999) suggested that population units can be arranged along two axes that combine per capita birth (B), death (D), emigration (E) and immigration (I) rates. A diagonal line called the 'Compensation Axis' describes the source sink-component of population structure, with source populations exporting individuals (B>D, E>I) and sink and pseudosinks consuming individuals (B<D, E<I). Net demographic generators of individuals (sources) are situated on one side of the compensation axis and net consumers (sinks) on the other. The classical stable population where B=D and I=E is situated at the intersection of the B-D, I-E and compensation axes (see Fig. 2). The positions of sub-populations on the compensation axes may vary over time. However, the metapopulation should remain stationary with a growth rate that is less variable than those of the sub-populations. A classical metapopulation, with a growth rate that centres on zero, will be situated at the intersection of the B-D, I-E and compensation axes.

Metapopulation theory and elephants

Van Aarde & Jackson (2007) proposed that metapopulation theory might be 'a powerful ecological platform from which to manage elephant numbers and their impacts through southern Africa'. Local instabilities in numbers (low elephant numbers in sinks compared to high elephant numbers in sources or *vice versa*) could result in stable elephant numbers regionally by allowing for metapopulation processes, such as dispersal, to regulate populations and limit the impact of elephants on other species.

In southern Africa, elephant populations are spaced along an ecological gradient that range from the arid savannas of Namibia in the west to the mesic savannas of Mozambique in the east. Here, elephant populations are subjected to different rainfall, resource availability, landscape uses, management practices and human densities (Blanc *et al.,* 2007; Harris *et al.,* 2008; Young *et al.,* 2009). Therefore, studying elephant demography across southern Africa and applying the results in a regional metapopulation management framework rather than focusing on local sub-populations and site-specific objectives could potentially contribute to successful regional and local conservation outcomes (Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006).

In this thesis I argue that metapopulation theory can be applied to elephant conservation in southern Africa. The thesis comprises five chapters. In the first chapter, I provide a general introduction on the ecological theory and background underlying my study. The second chapter reviews the applicability of metapopulation theory to populations of mammals. Previous studies (e.g. Harrison, 1994; Elmhagen & Angerbjörn, 2001) suggest that mammals may not always adhere to classic metapopulation criteria. I investigate this and make recommendations of when metapopulation theory could be useful when applied to populations of mammals. In the third chapter, I investigate whether southern African elephants adhere to these recommended metapopulation criteria. I calculated the exponential growth rates in 51 administrative sub-populations of elephants and for six conservation clusters across southern Africa. I was interested in determining whether elephant population growth rates were asynchronous both within conservation clusters (on a local scale), and among conservation clusters (on a regional scale). Asynchronous population growth would indicate the possibility of metapopulation processes operating at local and regional scales. Chapter 4 comprise a case study that I conducted. I used dung surveys to determine the population size and age structure of the elephant population in the Maputo Elephant Reserve in Mozambique. Elephant population estimates are prone to errors associated with the methods used to obtain them. Survey errors could influence calculated population trends and therefore management decisions based upon them. I therefore evaluated the usefulness of a method that yields estimates with known precision and how it can be applied to designing monitoring programmes based on elephant population trends. In chapter five, I synthesize my findings and evaluate the management implications of metapopulation theory as an alternative conservation strategy for elephants in southern Africa.

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Table 1. Metapopulation terminology and population units (after Hanski & Gilpin, 1991; Thomas & Kunin, 1999; Leibold *et al.*, 2004).

Term	Definition
Sub-population or local population	All individuals of a single species within a habitat patch
Region	A large area of habitat containing multiple sub-populations and capable of supporting a metapopulation
Colonization	A mechanism for spatial dynamics in which populations become established at sites from which they were previously absent
Dispersal	Movement of individuals from a site (emigration) to another (immigration)
Population asynchrony	Spatial variation in population density and growth rate fluctuations
Occupied habitat	The area of space within which a sub-population live
Unoccupied habitat	An area of space within which a sub-population could live, but which is currently vacant
Source population	A population where the number of births and immigrations exceed the number of deaths and emigrations ($r > 0$)
Sink population	A population where the number of deaths and emigrations exceed the number of births and immigrations ($r < 0$)
Pseudo-sink	A viable population that appear as a sink as a result of dispersal into it ($r > 0$)
Mainland-island metapopulation	A system with variation in sub-population size, which influences the extinction probability of sub-populations. Usually consists of a extinction resistant mainland population and extinction prone island populations
Non-equilibrium metapopulation	A system where sub-population extinction rates exceeds sub-population colonization rates
Patchy metapopulation	A system where dispersal rates among sub-populations are so high that there are no distinct sub-populations
Classic metapopulation	A system where births equal deaths and immigration equals emigration. Usually the growth rate will centre on zero.

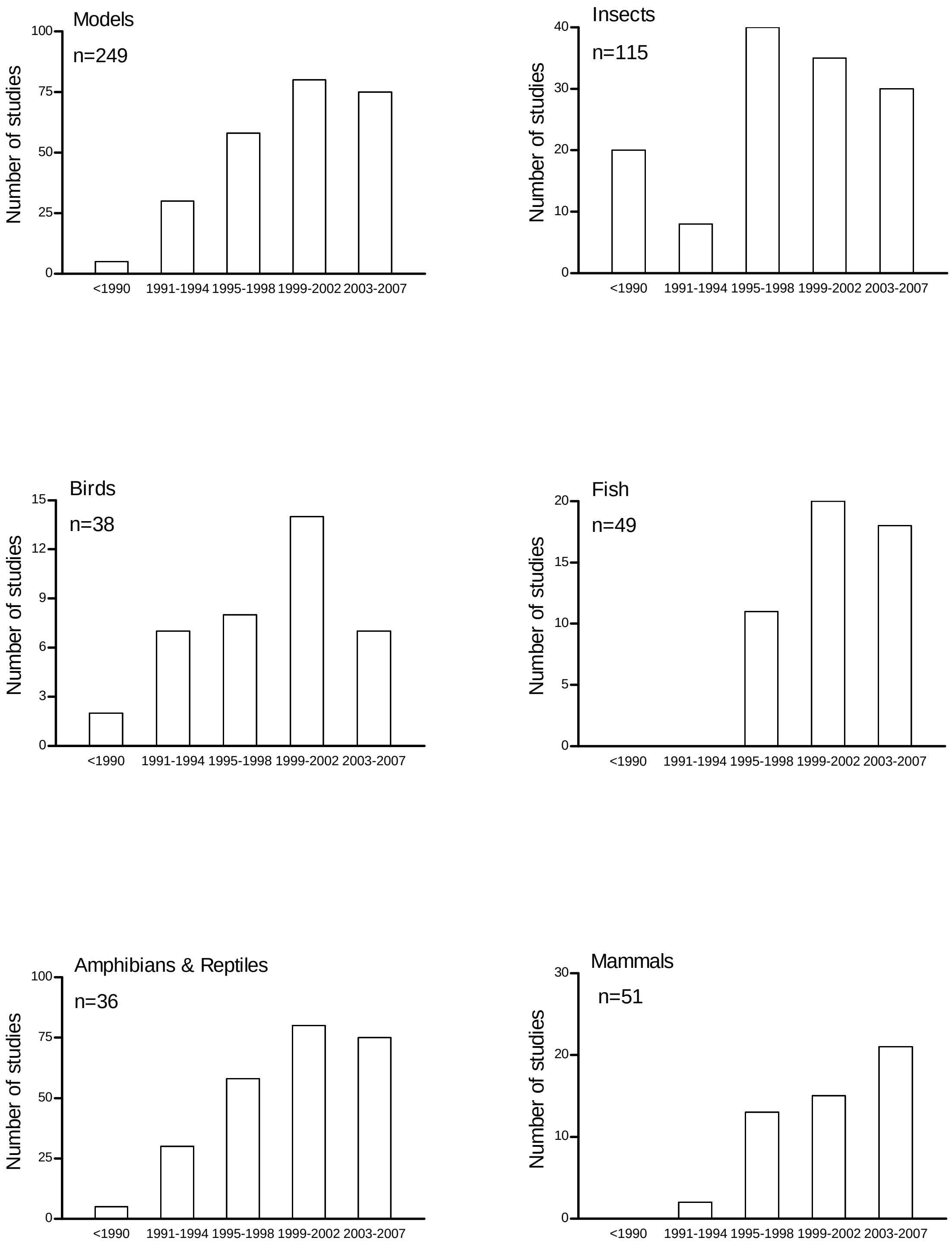

Figure 1. The number of publications in scientific journals that used metapopulation theory from 1991-2007. The figures are based on the results from the first 1000 'hits' in Google Scholar (http://scholar.google.co.za) using the keyword *metapopulation.

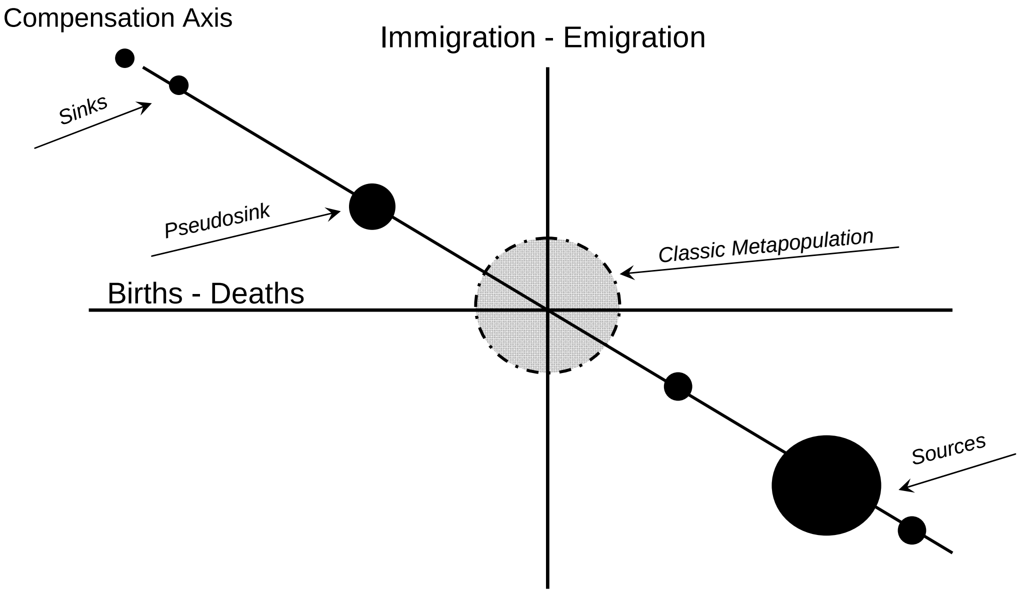

Figure 2. The arrangement of population units in demographic space. At equilibrium classical metapopulations fall at the intersection of the B-D, I-E and compensation axes (where birth equals deaths and immigration equals emigration), source populations sit in the lower right, and sink and pseudosink populations units are situated in the upper left of the compensation axis (Figure modified from Thomas & Kunin, 1999).

Chapter 2

Support for a metapopulation structure among mammals

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Running head: Metapopulation structure among mammals

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ABSTRACT

1. The metapopulation metaphor is increasingly used to explain the spatial dynamics of animal populations. However, metapopulation structure is difficult to identify in long-lived species that are widely distributed in stochastic environments where they can resist extinctions. The literature on mammals may not provide supporting evidence for classic metapopulation dynamics, which call for the availability of discrete habitat patches, asynchrony in local population dynamics, evidence for extinction and colonization processes, and dispersal between local[1] populations.
2. Empirical evidence for metapopulation structure among mammals may exist when applying more lenient criteria. To meet these criteria, mammals should live in landscapes as discrete local breeding populations, and their demography should be asynchronous.
3. We examined the literature for empirical evidence in support of the classical criteria set by Hanski (1999) and for the more lenient subset of criteria proposed by Elmhagen & Angerbjörn (2001). We suggest circumstances where metapopulation theory could be important in understanding population processes in mammals of different body sizes.
4. The patchy distribution of large (>100 kg) mammals and dispersal often motivate inferences in support of a metapopulation structure. Published studies seldom address the full suite of classical criteria. However, studies on small mammals are more likely to record classic metapopulation criteria than those on large mammals. The slow turnover rate that is typical for medium sized and large

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[1] At the request of the reviewer the term ‘sub-population’ was changed to ‘local population’ in this chapter and the subsequent published manuscript. There is no difference in the meaning of these two terms, except that personally I prefer to use the term ‘sub-population’.

mammals apparently makes it difficult to identify a metapopulation structure during studies of short duration.

5. To identify a metapopulation structure studies should combine the criteria set by Hanski (1999) and Elmhagen & Angerbjörn (2001). Mammals frequently live in fragmented landscapes and processes involved in the maintenance of a metapopulation structure should be considered in conservation planning and management.

Keywords: asynchrony, conservation, discrete local populations, dispersal, population turnover, vacant habitats

INTRODUCTION

Claims for the existence of metapopulations are dominated by descriptions of population networks of insects (e.g. Leisnham & Jamieson, 2002; Massonnet, Simon & Weisser, 2002; Caudill, 2003; Thomas & Hanski, 2004; Rabasa, Gutiérrez & Escudero, 2007), birds (e.g. Esler, 2000; Inchausti & Weimerskirch, 2002; Githiru & Lens, 2004), reptiles (e.g. Semlitsch & Bodie, 2003; Rodrigues, 2005), amphibians (e.g. Alford & Richards, 1999; Marsh & Trenham, 2001; Smith & Green, 2005; Werner *et al.,* 2007) and small mammals (e.g. Lima, Marquet & Jacksic, 1996; Lawes, Mealin & Piper, 2000). Few studies have addressed population networks in large mammals (>100 kg in body mass) and those that do, apparently provide little support for metapopulation structures (Elmhagen & Angerbjörn, 2001).

Habitat fragmentation and loss often reduce the distributional ranges of large mammal species (e.g. Brashares, 2003; Cardillo *et al.,* 2005). Anthropogenic alterations of landscapes for agricultural or conservation purposes fragmented many populations; some may even be confined to a fraction of their former ranges (Ceballos & Ehrlich, 2002). This may reduce individual survival and increase extinction risk (Cardillo *et al.,* 2006). The metapopulation concept caters for species that live in fragmented landscapes (Hanski, 1999). It focuses on populations that consist of local populations that exchange individuals through migration and dispersal, even when human-mediated (Hanski & Simberloff, 1997; Akçakaya, Mills & Doncaster, 2007). It also integrates extinction, dispersal and colonization in patchy environments. It thus has appeal when designing conservation networks to overcome the effects of fragmentation (Önal & Briers, 2005).

The detection of population networks as metapopulations requires that 1) dispersal occurs between local populations, 2) extinction and colonization take place, 3) the dynamics of local populations are in asynchrony, and 4) habitat patches support local breeding populations with colonisable vacant habitats (Hanski, 1999). Based on these criteria, Elmhagen & Angerbjörn (2001) found evidence for metapopulation dynamics among small mammals, but little support among large mammals. Based on Hanski's (1999) criteria, Elmhagen & Angerbjörn (2001) deduced two more lenient criteria for large mammals – first, breeding local populations should be discrete rather than inhabiting discrete habitat patches. Second, local populations should have dissimilar growth rates, i.e. some local populations may increase while, at the same time, others decrease. Such temporal fluctuations in growth rates imply demographic asynchrony among local populations (Elmhagen & Angerbjörn, 2001).

The use of the term 'metapopulation' has broadened substantially since it was proposed by Levins (1969). It now includes a variety of spatial population structures and definitions (see Hanski & Gilpin, 1991; Harrison, 1994; Pannell & Obbard, 2003; Akçakaya *et al*., 2007). However, this broadening of the original concept may detract from its meaning (Pannell & Obbard, 2003). As far as we are aware, only Hanski (1999) (for all species populations) and Elmhagen & Angerbjörn (2001) (for mammal species populations) recommended specific criteria that have to be met by a population to be classified as a metapopulation.

Here, we examine the empirical support for metapopulation dynamics among mammals. We determine the frequency of the application of the concept to mammal populations by searching literature published from 1991 to 2007 and recording proof for or against the classic criteria (Hanski, 1999), and the more lenient criteria proposed by Elmhagen & Angerbjörn (2001). We determine if body size influences the application of the criteria and speculate on the value of the concept. Our study adds to the contribution of the review by Elmhagen & Angerbjörn (2001) and may assist in the formulation of conservation plans based on the restoration of spatial axes to regain spatial-temporal dynamics (Thomas & Kunin, 1999) that enhance persistence and overcome local impacts on other species (e.g. van Aarde & Jackson, 2007). We appreciate that the metapopulation concept is based on mathematical abstraction rather than empirical observation, but argue that this abstraction has value when it describes population processes that can be manipulated to enhance conservation initiatives (van Aarde, Jackson & Ferreira, 2006).

MATERIAL AND METHODS

We collated empirical evidence for the existence of metapopulation dynamics among mammals by searching for relevant publications in the following electronic databases: Agricola, Biological Abstracts, Blackwell Synergy, Ecological Abstracts, Google Scholar (first 1000 ‘hits’ from http://www.google.com/scholar), JSTOR, Science Direct, Scirus, Scopus and Wildlife and Ecology Studies Worldwide. We based the search on the keywords “metapopulation and mammal*”. We recorded the number of studies that dealt with metapopulation dynamics in mammals for every year from 1991 to 2007. We included only papers in which the authors either described the metapopulation or stated that the population could potentially function as a metapopulation. We also included papers that did not explicitly test Hanski’s (1999) or Elmhagen & Angerbjörn’s (2001) criteria for metapopulations, but that casually may have deduced such dynamics. For instance, if authors stated that they classified their studied population based on evidence using the definition of Hanski & Gilpin (1991) that defines a metapopulation as 'a set of local populations which interact via individuals moving among populations', we assumed that the criteria of dispersal, discrete habitat patches or discrete local populations were met. We then recorded the specific criteria used by authors to infer a metapopulation structure for a species. For populations assessed more than once we used the most recent publications. We distinguished among studies based on the body weight of the species that were studied and noted whether the apparent metapopulation existed in a natural, or 'intact' landscape (e.g. rocky cliffs) or in an anthropomorphically altered, or 'disturbed' landscape (e.g. artificially fragmented forests).

For each study we recorded evidence for the populations meeting the criteria set by Hanski (1999) or the subset of criteria proposed by Elmhagen & Angerbjörn (2001). We noted whether the authors i) found evidence, ii) found no evidence, iii) did not asses the specific criteria and iv) stated or assumed that a condition could be fulfilled, but did not provide supportive evidence. We then recorded the number of criteria used in each study to describe metapopulations. Furthermore, we noted the incidence at which specific criteria were used to describe metapopulations.

We distinguished between small mammals (≤5kg), medium sized mammals (>5≤100kg) and large mammals (>100kg), and used contingency table analyses to test for the influence of body size on the frequencies at which criteria were met, as well as for the influence of the type of landscape in which the mammals were studied. Statistical significance was set at α =0.05.

RESULTS

The number of publications we found on metapopulation dynamics in mammals between 1991 and 2007 ranged from 1 to 9 per year. In total we included 63 studies representing 75 species. Studies by Lima *et al.* (1996) on five species and McShea *et al.* (2003) on nine species of small mammals were included as single studies and analyzed as each representing one ‘species’, as the authors did not consider metapopulation criteria separately for every species. Conversely, the study by Gerlach & Hoeck (2001) was included and analyzed as two studies, as the authors considered metapopulation criteria separately for two species. The studies included mammals ranging in body size from 0.002kg to 5000kg (see Appendix) and size classes were evenly distributed across intact and disturbed habitats ($\chi^2=5.12$, $df=2$, $P=0.077$). The three studies on mammals >500kg took place in landscapes fragmented by humans.

Not all the studies met the criteria recommended by Hanski (1999). In 90% of them ($n=57$) dispersal was recorded between local populations, 16 (25%) experienced extinction and colonization events, while 33 (52%) exhibited asynchrony in population dynamics. Thirty (48%) occurred as breeding local populations in discrete habitat patches with additional vacant habitats that could be colonized (Fig. 1). One of the criteria recommended by Elmhagen & Angerbjörn (2001) was met in 84% ($n=53$) of studies; species occurred as discrete breeding local populations. Thirty-three (52%) exhibited asynchrony in dynamics (Fig. 1). For 32% ($n=20$) of studies only one of Hanski’s (1999) criteria was used to describe a metapopulation structure, while 46% ($n=29$) of studies met one or the other of Elmhagen & Angerbjörn’s (2001) two criteria (Fig. 2). Both the criteria of Elmhagen & Angerbjörn (2001) were noted for 41% (*n*=26) of the studies, while 66% (*n*=42) met more than one of Hanski's (1999) criteria (Fig. 2).

Body size influenced the patterns noted above. For small (≤5kg), medium (>5≤100kg) and large (>100) species, dispersal was the condition most frequently assessed (Fig. 1). Dispersal between local populations was also assessed at similar frequencies among body size classes (χ^2=0.396, *df*=2, *P*=0.821). Population turnover was recorded for 14 of 30 studies on small mammals, but for only one of 15 on medium sized and one of 18 on large mammal species. The frequency of reporting asynchrony in population dynamics differed with body size (χ^2=8.476, *df*=2, *P*=0.014). The reporting of incidences of habitat patches that supported breeding local populations did not differ with body size (χ^2=5.670, *df*=2, *P*=0.059) (Table 1a). The occurrence of discrete breeding local populations was similar for small, medium sized and large mammals (χ^2=0.095, *df*=2, *P*=0.953) (Table 1b).

In most (60%) of the 63 studies published on metapopulation dynamics authors stated that they evaluated criteria before classifying the population as a metapopulation, while 15% (*n*=9) classified populations as metapopulations, but did not evaluate any criteria. In about 16% (*n*=10) of studies, authors suggested that the studied population would function as a metapopulation if suitable conservation measures were put into place, while a further 7% (*n*=4) of studies dealt with artificially created metapopulations where metapopulation processes and criteria were mimicked by management strategies. In two studies (3%) the population used to function as a metapopulation, but did not anymore. In one case the studied population was found not to be a metapopulation. For small mammals 9 out of 30 (30%) studies mentioned that metapopulation processes could contribute to the conservation of the studied species populations, while for large and medium sized mammals 22 out of 33 (67%) studies invoked metapopulation processes for conservation purposes.

DISCUSSION

Metapopulations are not always easy to identify (Hanski & Simberloff, 1997; Thomas & Kunin, 1999). Our analysis suggests that the use of the concept is not always supported by empirical information that may meet the criteria of Hanski (1999), or even the more lenient subset of criteria proposed by Elmhagen & Angerbjörn (2001). Most of the 63 studies that we assessed provide some evidence for a metapopulation structure and nearly all authors concluded that the population they studied functioned as a metapopulation. However, much of the evidence for metapopulations stems from the inconsistent application of the concept and the use of a range of definitions that ignores some of the original criteria. For instance, in only one (Hayward *et al.,* 2004) of the 29 studies published since 2001 is it stated explicitly that the criteria recommended by Elmhagen & Angerbjörn (2001) were evaluated.

The criteria of Elmhagen & Angerbjörn (2001) seem easier to apply than those of Hanski (1999). For example, in most (84%) of the 63 studies that we reviewed, the species comprised discrete breeding local populations and thus met one of the two criteria set by Elmhagen & Angerbjörn (2001), while in only half (48%) the studied species inhabited discrete habitat patches with additional vacant habitats that can be colonized, as expected by one of the four criteria of Hanski (1999). However, most (83%) of the studies that recognized discrete habitat patches, as recommended by Hanski (1999) or discrete breeding local populations as recommended by Elmhagen & Angerbjörn (2001), used dispersal to deduce metapopulation dynamics. Therefore, no matter the criteria, where species illustrate dispersal, studies deduced metapopulation structures.

Our analysis furthermore suggests that the size of mammals influence the criteria that may be used to support metapopulation dynamics. For instance, for small mammal species (≤5 kg) the criteria of Hanski (1999) were met with the same frequency as those of Elmhagen & Angerbjörn (2001). Small mammals were also more likely to adhere to the full set of criteria proposed by Hanski (1999). Extinction and colonization events were recorded in 46% of small mammal species populations compared to only 7% and 6% in medium sized and large mammals respectively.

Case studies that support the classical metapopulation structure are rare (Elmhagen & Angerbjörn, 2001). This is also supported by our review. Only five of 75 species populations adhered to classical metapopulation criteria – these are all small mammals and comprise the four-eyed opossum *Philander opossum*, American pika *Ochotona princeps*, black-tailed prairie dog *Cynomys ludovicianus*, field vole *Microtus agrestis* and the round-tailed muskrat *Neofiber alleni* (Adler & Seamon, 1996; Moilanen *et al.*, 1998; Roach *et al.*, 2001; Banks *et al.*, 2004; Schooley & Branch, 2007). Few studies thus provide support for the full set of criteria for the classical metapopulation. Meeting these criteria depends on case specific spatial conditions to which populations will respond. From the review of Krohne (1997) it is apparent that fragmentation, dispersal barriers, and dispersal corridors are all species population specific, and that species' responses to these depend on body size, habitat, physiological responses to stressful environments and social factors. We therefore agree with Clinchy, Haydon &

Smith (2002) that evidence of metapopulation processes rather than spatial occupancy should be used to provide evidence of metapopulation dynamics.

For studies on small mammals we propose that the full complement of metapopulation criteria (Hanski, 1999) can be applied to yield new perspectives on population regulation. Metapopulation processes could also be used to parameterize models that emphasize small mammal characteristics (see Lambin *et al.,* 2004). Furthermore, metapopulation processes can be incorporated into management and conservation paradigms. For instance, McShea *et al.* (2003) suggest that a timber harvest management paradigm based on metapopulation processes would conserve small mammal species populations more effectively than a traditional approach that only focused on the proportion of available habitat.

Our review suggests that the application of the metapopulation concept differs between small and other sized mammals, but is similar for medium and large mammals. Authors consider dispersal between discrete local populations of large mammals as the key condition for a metapopulation structure, and tend to ignore the other criteria. For instance, in 31 of the 33 studies on large mammal populations, all criteria except dispersal are ignored by authors labelling their studied population as a metapopulation. The limitations in evaluating the other criteria may induce this bias. Criteria associated with extinction and recolonization events may not be used because the time span of these events usually exceeds that of most studies, possibly due to the relatively long generation times and slow reproductive rates of large mammals (Murphy, Freas & Weiss, 1990). It may therefore prove futile for studies on larger mammals to focus on population turnover as a condition to be met for metapopulation dynamics. Even so, our results suggest that a metapopulation structure can exist in mammals, but that the longevity and slow turnover typical of medium and large sized mammals may make it difficult to find support for the full set of classical criteria for a metapopulation structure. Despite this detraction the metapopulation concept can be applied to large mammal species populations.

Our review suggests that most (31 of 33 studies, 94%) medium and large mammal species populations that occurred as discrete breeding local populations also dispersed between local populations. Furthermore, the dynamics of nearly half (15 of 31, 48%) of these populations were asynchronous. Such asynchrony could reflect on habitat heterogeneity, lack of dispersal between local populations, variation in community processes and trophic interactions, and environmental variation that can induce source-sink dynamics (Pulliam, 1988; Bjørnstad, Ims, & Lambin, 1999). Alternatively, synchrony in population dynamics can result from high dispersal rates or correlated changes in environmental conditions (Ranta, Kaitala & Lundberg, 1998).

Dispersal alone may not be a good indicator of metapopulation dynamics. We propose that both dispersal, the focus of much of the literature we reviewed, and asynchrony in dynamics between discrete local populations needs to be included in the evaluation. Because turnover is difficult to record in medium to large mammals the illustration of dispersal and asynchrony alone may serve as evidence for a metapopulation structure.

Determining the spatial structure of a population is essential when formulating conservation guidelines because it presents a conceptual tool for dealing with the interactions between, within and among populations (Githiru & Lens, 2004). The application of metapopulation theory may be more important for large than small mammals for the simple reason that large mammals usually operate at spatial scales at which they are exposed to landscape fragmentation. In other words, the large individual home ranges of large mammals relative to the scale of human activities constrain dispersal between populations as it approaches the scale of economic land use vs. conservation land use. Consequently large mammals are more frequently exposed to human induced disturbances than small mammals (Crooks, 2002; Cardillo *et al.,* 2005), and are often restricted to national parks and wildlife reserves (e.g. Brashares, 2003).

Spatial population patterns maintain processes that have implications for persistence (Thomas & Hanski, 2004). Emphasis therefore should shift from observing spatial patterns to recording spatial processes (e.g. Thomas & Kunin, 1999; Hanski & Giaglotti, 2004). We therefore suggest that metapopulation theory should be applied to populations of mammals when constructing conservation plans to ensure population persistence and to contribute to the forces that stabilise populations regionally.

Most (22 of 33, 67%) of the studies we included in our review which explicitly deal with medium and large mammals suggest that conservation will benefit from the inclusion of metapopulation processes. For instance, Singh & Kumara (2006) recognized that for a wide-ranging animal such as the Indian grey wolf *Canis lupus pallipes*, sanctuaries could only protect one or two wolf packs. They suggest that the conservation of forest patches of varying sizes in a landscape matrix could facilitate the dispersal of wolf packs that then may become part of a large metapopulation. Similarly, Sweanor, Logan & Hornocker (2000) and Hellgren, Onorato & Skiles (2005) showed that cougars *Puma concolor* and black bears *Ursus americanus* persist if conservation initiatives are implemented on a regional scale. The most artificial application of the metapopulation concept in conservation comes from the advocacy that removing individuals from one isolated population mimics dispersal. Translocations of wild dog *Lycanon pictus* and black rhino *Biceros dicornis* from one conservation area to another in Africa (Amin *et al.,* 2006; Akçakaya *et al.,* 2007) serve as good examples.

We caution against implementing conservation strategies based on metapopulation dynamics if habitat discreteness, likelihood of dispersal and potential of asynchrony have not been evaluated. The application of metapopulation theory to cases or species that do not meet the criteria to exist as a metapopulation may lead to conservation actions that neglect important life histories, with consequences for species persistence (see Grimm, Reise & Strasser, 2003). For instance, the metapopulation concept can motivate the development of movement corridors without evidence that corridors would be used, or forestall extinction (Biotani *et al.,* 2007). Such actions are expensive and could detract from efforts to protect particular populations that require specific refuges (Simberloff *et al.,* 1992; Biotani *et al.,* 2007). However, the correct and consistent application of metapopulation theory and the implementation of metapopulation processes in mammal populations may improve the persistence of mammals in fragmented habitats.

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Table 1a. An assessment of the classical criteria of metapopulations (Hanski, 1999) reported in studies on small (≤5kg) (*n*=30), medium (>5≤100kg) (*n*=15) and large (>100 kg) (*n*=18) mammal species (*n*=63).

Metapopulation criteria		Small mammals	Medium mammals	Large mammals
Individual dispersal	Yes	26	14	17
	No	3	1	1
	Not assessed	1	0	0
Population turnover	Yes	14	1	1
	No	0	0	0
	Not assessed	16	14	17
Asynchrony in dynamics	Yes	18	3	12
	No	0	0	0
	Not assessed	12	12	6
Habitat patches with breeding subpopulations	Yes	19	5	6
	No	0	0	0
	Not assessed	11	10	12

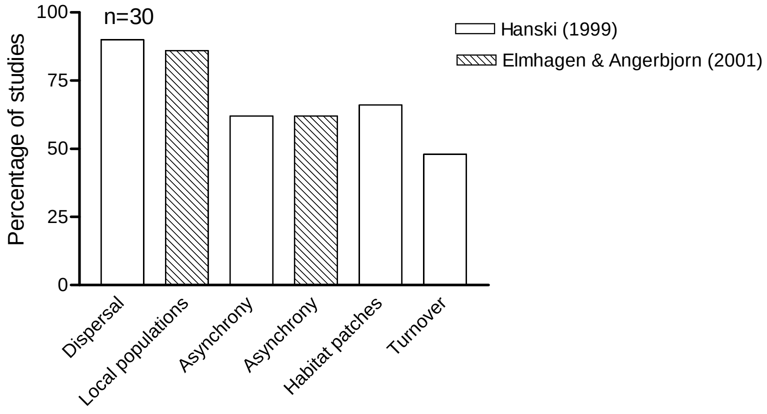
Table 1b. An assessment of the more lenient criteria of metapopulations (Elmhagen and Angerbjörn, 2001) reported in studies on small (<=5 kg) (*n*=30), medium (>5≤100kg) (*n*=15) and large (>100 kg) (*n*=18) mammal species (*n*=63).

Metapopulation criteria		Small mammals	Medium mammals	Large mammals
Breeding subpopulations are discrete	Yes	25	14	15
	No	0	0	0
	Not assessed	5	1	3
Asynchrony in dynamics	Yes	18	3	12
	No	0	0	0
	Not assessed	12	12	6

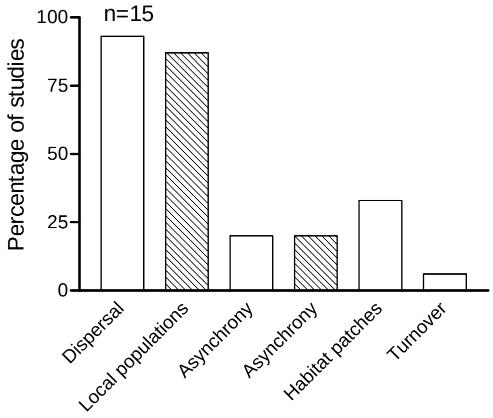
Figure 1: The percentage of (a) small, (b) medium sized and (c) large mammal species populations in which the criteria of Hanski (1999) and Elmhagen & Angerbjörn (2001) were used to describe metapopulation dynamics in mammals. Open bars indicate the classic criteria of Hanski (1999), shaded bars indicate the more lenient criteria described by Elmhagen & Angerbjörn (2001). Sample sizes are numbers of studies.

Figure 2: The number of criteria that researchers applied to describe (a) small, (b) medium sized and (c) large mammal species populations as metapopulations based on papers published from 1991 to 2007. Open bars indicate the classic criteria of Hanski (1999), shaded bars indicate the more lenient criteria described by Elmhagen & Angerbjörn (2001). Sample sizes are numbers of studies.

a) Small mammals



b) Medium sized mammals



c) Large mammals

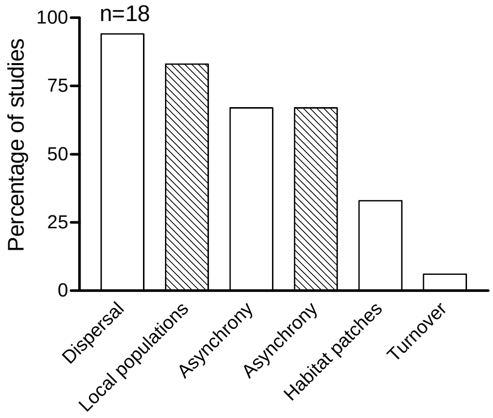
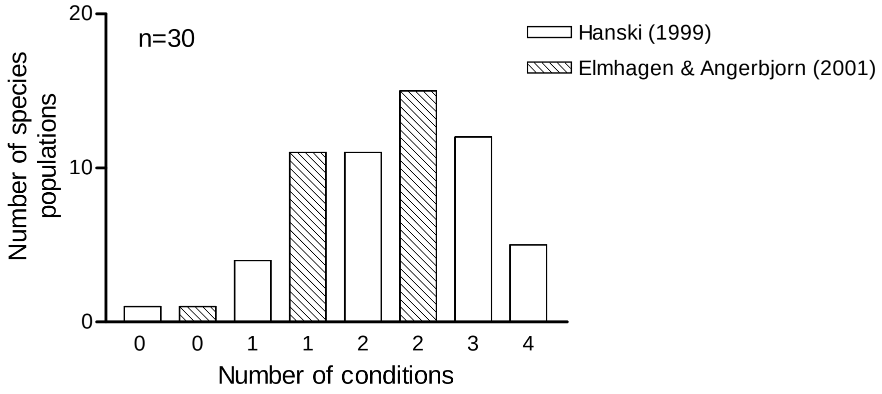
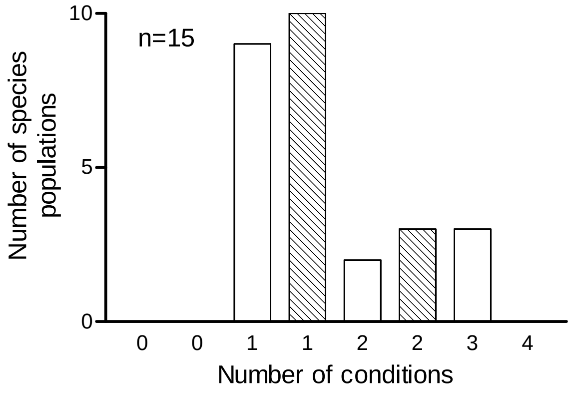


Figure. 1.

a) Small mammals



b) Medium sized mammals



c) Large mammals

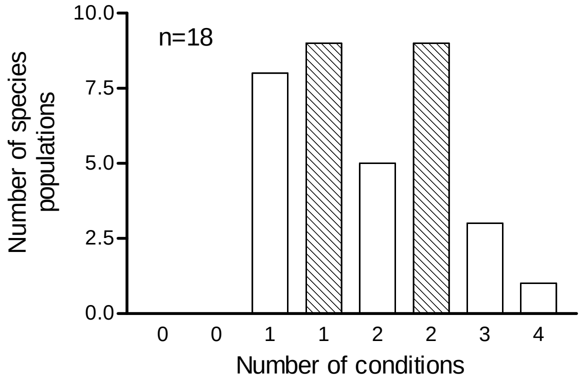


Figure 2.

Appendix. Studies in which mammals have been described as metapopulations or as possibly functioning as metapopulations. The empirical support for this classification or lack thereof, as described in the studies, is shown for each species. N.A. – Not Assessed.

Species population	Body Mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding subpopulations	Metapopulation Type	Reference
Bank vole *Clethrionomys glareolus*	0.002-0.003	Anthropogenic	Yes	Yes	Yes	N.A.	Yes	Source-sink	van Apeldoorn *et al.*, 1992
Euro *Macropus robustus*	90	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Arnold *et al.*, 1993
Greater glider *Petauroides volans*		Anthropogenic	Yes	Yes	N.A.	Yes	N.A.	Modelled	Possingham *et al.*, 1994
Pine vole *Microtus duodecimcostatus*	0.002-0.003	Natural	Yes	Yes	Potential	N.A.	Yes	Source-sink	Paradis, 1995
Four-eyed opossum *Philander opossum*	0.24-0.4	Natural	Yes	Yes	Yes	Yes	Yes	Boorman-Levitt	Adler & Seamon, 1996
Leadbeater's Possum *Gymnobelideus leadbeateri*	0.12-0.16	Anthropogenic	Possible	Yes	N.A.	Yes	Yes	Not described	Lindenmayer & Possingham, 1996
Vancouver island marmots *Marmota vancouverensis*	0.25	Natural	Yes	N.A.	N.A.	Yes	Yes	Not described	Bryant & Janz, 1996
Lower Keys marsh rabbit *Sylvilagus palustris hefneri*	2.5-3	Natural	Yes	Yes	Yes	N.A.	Yes	Not described	Forys & Humphrey, 1996
Leaf-eared mouse *Phyllotis darwini;* Olive grass mouse *Akodon olivaceus;* Elegant fat-tailed opossum *Thylamys elegans*; Degu *Octodon degus*; Long-tailed pygmy rice rat *Oligoryzomys longicaudatus*	0.005-0.01	Natural	N.A.	Yes	N.A.	N.A.	Yes	Not described	Lima *et al.*, 1996

Species population	Body Mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding subpopulations	Metapopulation Type	Reference
White-tailed deer *Odocoileus virginianus*	300-600	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Seagle & Close, 1996
Leaf-eared mouse *Phyllotis darwini*	0.007-0.01	Anthropogenic	Possible	Yes	Yes	N.A.	Yes	Partially coupled	Torres-Contreras *et al.*, 1997
Polar bear *Ursus maritimus*	300-600	Natural	Yes	N.A.	N.A.	N.A.	Yes	Not described	Ferguson *et al.*, 1998
Iberian lynx *Lynx pardinus*	13-25	Anthropogenic	Yes	Potential	N.A.	Yes	Yes	Source-sink	Gaona *et al.*, 1998
Puku *Kobus vardoni*	74-77	Natural	Yes	N.A.	N.A.	Yes	Yes	Not described	Goldspink *et al.*, 1998
American pika *Ochotona princeps*	0.5-1.0	Natural	Yes	Yes	Yes	Yes	Yes	Classical	Moilanen *et al.*, 1998
Woodland caribou *Rangifer tarandus caribou*	170-300	Anthropogenic	Possible	N.A.	Yes	N.A.	Yes	Not described	Rettie & Messier, 1998
Tiger *Panthera tigris*	205-227	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Smith *et al.*, 1998
Harbour seal *Phoca vitulina*	~130	Natural	Possible	N.A.	Potential	N.A.	Yes	Not described	Swinton *et al.*, 1998
White-footed mouse *Peromyscus leucopus*	0.023	Anthropogenic	Yes	N.A.	Yes	Yes	Yes	Not described[2]	Krohne & Hoch, 1999
Greater glider *Petauroides volans*	1.6-1.9	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	McCarthy & Lindenmayer, 1999
Nubian ibex *Capra ibex nubiana*	~50	Natural	Yes	N.A.	N.A.	N.A.	Yes	Not described	Shkedy & Saltz, 2000
Yellow-necked mice *Apodemus flavicollis*	0.016-0.032	Anthropogenic	Yes	N.A.	N.A.	Yes	N.A.	Patchy	Szacki, 1999
Long-furred woolly mouse opossum *Micoureus demerarae*	0.13	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Pires & Fernandez, 1999

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[2] Metapopulation described as 'type C' from Krohne (1997)

Species population	Body Mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding subpopulations	Metapopulation Type	Reference
San Joaquin kit foxes *Vulpes macrotus mutica*	7-8	Anthropogenic	Yes	N.A.	Yes	N.A.	Yes	Not described	Koopman *et al.*, 2000
Samango monkey *Ceropithecus mitis liabiatus*	7-9	Anthropogenic	No	N.A.	N.A.	N.A.	Yes	Transient non-equilibrium	Lawes *et al.*, 2000
Tree hyrax *Dendrohyrax arboreus*	~3	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Mainland-island	Lawes *et al.*, 2000
Blue duiker *Cephalophus monticola*	4-5	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Mainland-island	Lawes *et al.*, 2000
Bighorn sheep *Ovis Canadensis*	170-302	Natural	Yes	N.A.	Yes	Yes	Yes	Not described	Singer *et al.*, 2000
Cougar *Puma concolor*	~75	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Sweanor *et al.*, 2000
Silvery gibbon *Hylobates moloch*	~8	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Andayani *et al.*, 2001
Mountain pygmy possum *Burramys parvus*	0.045	Natural	Yes	N.A.	Yes	N.A.	Yes	Not described	Broome, 2001
Artic fox *Alopex lagopus*	3.1-3.8	Anthropogenic	Yes	N.A.	Yes	Yes	Yes	Not described	Elmhagen & Angerbjörn, 2001
Rock hyrax *Heterohyrax brucei*	~3	Natural	Yes	N.A.	Potential	Yes	Yes	Not described	Gerlach & Hoeck, 2001
Rock hyrax *Procavia johnstoni*	~3	Natural	No	N.A.	Potential	Yes	Yes	Not described	Gerlach & Hoeck, 2001
Black tailed prairie dog *Cynomys ludovicianus*	0.7-1.5	Anthropogenic	Yes	Yes	Potential	Potential	Yes	Not described	Roach *et al.*, 2001
Grey seal *Halichoerus grypus*	200-350	Natural	Yes	Yes	Yes	Yes	Yes	Not described	Gaggiotti *et al.*, 2002
Florida panther *Puma concolor corgi*	~75	Anthropogenic	Yes	N.A.	N.A.	N.A.	N.A.	Not described	Maehr *et al.*, 2002
Spanish ibex *Capra pyrenaica*	~50	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Pérez *et al.*, 2002

Species population	Body Mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding subpopulations	Metapopulation Type	Reference
Steller sea lion *Eumetopias jubatus*	~300	Natural	Yes	N.A.	Yes	N.A.	Yes	Not described	Ruam-Suryan *et al.*, 2002
Kodkod *Oncifelis guigna*	11-14	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Mainland-island	Acosta-Jamett *et al.*, 2003
White-footed mouse *Peromyscus leucopus*; Deer mouse *Peromyscus maniculatus*; Northern short-tailed shrew *Blarina brevicauda*; Eastern chipmunk *Tamias striatus*; Southern red-backed vole *Clethrionomys gapperi*; Woodland jumping mouse *Napaeozapus insignis*; Smoky shrew *Sorex fumeus*; Masked shrew *Sorex cinereus*; Pygmy shrew *Sorex hoyi*	0.01-0.05	Natural	Yes	Yes	Yes	Yes	N.A.	Not described	McShea *et al.*, 2003
Field vole *Microtus agrestis*	0.01-0.03	Natural	Possible	Yes	Potential	N.A.	Yes	Not described	Banks *et al.*, 2004
Water vole *Arvicola aphibius*	0.16-0.35	Natural	Yes	Yes	N.A.	Yes	Yes	Not described	Lambin *et al.*, 2004
Indus river dolphin *Platanista minor*	170-301	Natural	No	N.A.	N.A.	N.A.	Yes	Not described	Gachal & Slater, 2004
Tundra vole *Microtus oeconomus*	~0.05	Experimental population	Yes	N.A	Yes	Yes	Yes	Not described	Ims & Andreassen, 2005
Amur tiger *Panthera tigris altaica*	215-270	Anthropogenic	Yes	N.A.	Yes	N.A.	N.A.	Not described	Carroll & Miquelle, 2006
Quokka *Setonix brachyurus*	2.5-5.0	Anthropogenic	No	Yes	Yes	Yes	Yes	Not described	Hayward *et al.*, 2004

Species population	Body Mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding subpopulations	Metapopulation Type	Reference
European bison *Bison bonasus*	450-1000	Anthropogenic	Possible	N.A.	Potential	Yes	Yes	Not described	Perzanowski *et al.*, 2004
Ethiopian wolf *Canis simensis*	~20	Natural	Yes	N.A.	Potential	Yes	Yes	Not described	Sillero-Zubiri *et al.*, 2004
Fisher *Martes pennanti*	2.1-7.0	Natural	Possible	N.A.	N.A.	N.A.	N.A.	Not described	Wisely *et al.*, 2004
Black bear *Ursus americanus*	170-303	Natural	Yes	N.A.	Potential	Yes	Yes	Mainland-island	Hellgren *et al.*, 2005
Brown bear *Ursus arctos*	130-700	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Preatoni *et al.*, 2005
Gaint panda *Ailuropoda melanoleuca*	100-115	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Ran *et al.*, 2005
Ili pika *Ochotona iliensis*	0.5-1.0	Natural	No	N.A.	N.A.	N.A.	N.A.	Not described	Li & Smith, 2005
Amur tiger *Panthera tigris altaica*	215-270	Anthropogenic	Yes	N.A.	Yes	N.A.	N.A.	Not described	Carroll & Miquelle, 2006
Black rhino *Diceros bicornis*	~1000	Anthropogenic	Yes	N.A.	Potential	Yes	Yes	Not described	Amin *et al.*, 2006
Mountain caribou *Rangifer tarandus caribou*	170-300	Anthropogenic	Yes	N.A.	Yes	N.A.	Yes	Not described	Apps & McLellan, 2006
Indian gray wolf *Canis lupus pallipes*	18-27	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Singh & Kumara, 2006
Mountain vizcacha *Lagidium peruanum*	~3	Natural	Possible	N.A.	N.A.	Yes	Yes	Not described	Werner *et al.*, 2006
European hare *Lepus europaeus*	2.5-6.5	Anthropogenic	Yes	N.A.	Potential	N.A.	N.A.	Not described	Bray *et al.*, 2007
Wild dog *Lycanon pictus*	24-28	Anthropogenic	Yes	N.A.	Potential	Yes	Yes	Not described	Akçakaya *et al.*, 2007
Peccary *Tayassu pecari*	20-40	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Mendes Pontes & Chivers, 2007
Elephant *Loxodonta Africana*	5500-6000	Anthropogenic	Yes	N.A.	Yes	N.A.	N.A.	Source-sink	van Aarde & Jackson, 2007
Round-tailed muskrat *Neofiber alleni*		Natural	Yes	Yes	Potential	Yes	Yes	Source-sink	Schooley & Branch, 2007

Chapter 3

Demographic asynchrony among southern African elephant *Loxodonta africana* populations

ABSTRACT

Elephant conservation management is controversial. Where elephants occur at high densities they may threaten biodiversity and the livelihoods of people. Where they live at low densities they may face extinction with adverse consequences for ecosystems. Metapopulation theory provides an attractive management platform for elephants living under diverse conditions because it may induce regional stability in numbers, despite local instabilities. Here I investigate whether elephant sub-populations[1] in southern Africa are in demographic asynchrony and therefore adhere to one of the criteria required for metapopulation dynamics. I found spatial and temporal asynchrony among populations at both local and regional scales. Regionally elephant numbers remained relatively stable and had low variance as some sub-populations increased while others decreased or remained stable. I suggest that metapopulation processes, operating across a spatial gradient may stabilize elephant numbers on the sub-continent. My results highlight the importance of space for elephant management.

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[1] The term 'local population' has been changed to 'sub-population' in this chapter as well as in the rest of the thesis (except Chapter 2). There is no difference in the meaning of these two terms, except that personally I prefer to use the term 'sub-population'.

INTRODUCTION

Nearly 60% of an estimated 470 000 of Africa's savanna elephants *Loxodonta africana* live in southern Africa (Blanc *et al.*, 2007), a region that stretches across ten countries and that covers some 5.9 million km^2, an area roughly half of that of the USA. Recent estimates suggest that many elephant populations in the region are increasing (Blanc *et al.*, 2005; van Aarde *et al.,* 2008), while others, notably those in Zambia, are declining (e.g. Guldemond *et al.,* 2005; Ferreira *et al.*, 2009a). At the same time the populations across north-western Zimbabwe and northern Botswana seem stable (Chamaillé-Jammes *et al.,* 2007; Junker *et al.,* 2008). This apparent variability in trends and the range of densities (0.001 to 2.4 n.km^{-2}) at which elephants live across a gradient of environmental conditions have conservation management implications, some of which may be more costly than others (see Owen-Smith *et al.*, 2006; van Aarde & Jackson, 2007; Scholes & Mennell, 2008).

Apparent local high abundances of elephants may threaten other species and their habitats (e.g. Cumming *et al.*, 1997; Birkett, 2002; Owen-Smith *et al.,* 2006; Guldemond & van Aarde, 2007; O'Connor *et al.,* 2007), while elephants that roam beyond conservation areas may come into conflict with people (e.g. Hoare, 1999; Sitati *et al.*, 2003; Jackson *et al.*, 2008). High elephant numbers may be considered undesirable (Laws, 1970; Caughley, 1976; Skarpe *et al.,* 2004) and instigate management actions such as culling, contraception and translocation to control population growth (van Aarde *et al.,* 1999; Pimm & van Aarde, 2001; van Aarde & Jackson 2007; Kerley & Shrader, 2008; van Aarde *et al.,* 2008). High elephant numbers and the consequent management actions may also impinge on tourism and the generation of revenue (Leader-Williams *et al.,* 2001; Walpole & Leader-Williams, 2002).

Wildlife management in southern Africa traditionally focused on manipulating population numbers to achieve park-specific objectives (Owen-Smith *et al.,* 2006; van Aarde *et al.,* 2006). However, many biological processes that limit populations, and thus conservation decisions, operate at regional or even global scales (e.g. Bjørnstad *et al.,* 1999; Gering *et al.,* 2003) and therefore needs to be incorporated in conservation management (Armbruster & Lande 1993; Harris *et al.,* 2008; van Aarde & Ferreira, 2009). Studying elephant demography across southern Africa and applying the results in a regional management framework rather than focusing on local populations and site-specific objectives could potentially contribute to successful regional and local conservation outcomes (Hanks, 2001; Owen-Smith *et al.,* 2006; van Aarde *et al.,* 2006). Van Aarde & Jackson (2007) therefore recognized and advocated the potential of the metapopulation paradigm as a powerful spatial and dynamic platform to develop a regional management program for elephants that also can mitigate their impact on vegetation and conflict with people.

Metapopulation theory can explain the dynamics of populations exposed to heterogeneous landscapes where different individuals are exposed to varying habitat quality in response to the existence of discrete habitat islands or patches of different quality. Some patches may serve as source habitats where sub-populations normally have positive growth rates, while other patches may consist of so-called sink habitats where sub-population growth rates are consistently negative (see Puliam, 1988; Thomas & Kunin, 1999). Sources can turn into sinks and *vice versa* due to random variations in their environment and demographic processes induced by natural or anthropogenic factors. All local populations face the risk of extinction, but dispersers from sources may re-colonize empty patches or immigrate into sinks. A metapopulation therefore can bring about regional persistence, despite local extinctions, while local instability in numbers can be associated with relative regional stability (Hanski, 1999; Thomas & Kunin, 1999; Grimm *et al.,* 2003).

Three other conditions have to be met to fulfil the needs of classical metapopulation models (Hanski, 1999): (1) there has to be discrete habitat patches which are, or can be, inhabited by breeding sub-populations, (2) all sub-populations must have a risk of extinction, and (3) empty habitats must be colonized as a result of dispersal between sub-populations. The application of metapopulation models in conservation management, however, may be problematic. Populations of large mammals rarely meet all four the conditions required by classical metapopulation models (Elmhagen & Angerbjörn, 2001; Olivier *et al*., 2009). Because of relatively low population turnover, low growth rates and relatively low densities (Murphy *et al*. 1990; Sinclair, 2003) large mammals are less likely to be affected by local environmental and weather conditions that often cause asynchronous dynamics and extinctions between sub-populations of insects (Gaggiotti & Hanski, 2004). It might therefore be difficult to find empirical support for classical metapopulation existence among large mammals (Olivier *et al.,* 2009).

In spite of this, reviews by Elmhagen & Angerbjörn (2001) and Olivier *et al*., (2009) suggest that the metapopulation metaphor may be applicable to large mammals. Elmhagen & Angerbjörn (2001) proposed that such populations should adhere to two more lenient conditions deduced from the four originally proposed by Hanski (1999). First, breeding sub-populations should be discrete rather than inhabiting discrete habitat patches. Secondly, sub-populations should have different growth rates, i.e. some populations may increase while, at the same time, others decrease or remain stable. Such temporal differences in growth rates imply demographic asynchrony among sub-populations (Elmhagen & Angerbjörn, 2001). Elephant populations therefore must meet these criteria before the metapopulation metaphor can be used to develop a regional management plan as proposed by van Aarde & Jackson (2007) and by van Aarde & Ferreira (2009).

In this chapter I focus on one of the lenient criteria and investigate if the population growth rates of elephant populations in southern Africa are asynchronous. For my analysis, I considered six of the eight potential conservation clusters in southern Africa where more than one sub-population of elephants exists and where individuals can potentially disperse between sub-populations (see van Aarde & Ferreira, 2009). Fences and international borders separated some of these sub-populations from others, but in most instances elephants could roam between sub-populations, albeit across landscapes where people live at varying densities. For my study, I used time series of population estimates to calculate growth rates and compared these for sub-populations within conservation clusters (local growth rates) as well as for populations of the conservation clusters (regional growth rates) and compared these between clusters. I used this information to evaluate the applicability of metapopulation theory to the conservation management of elephants across southern Africa.

To meet one of the criteria for a metapopulation I expected local growth rates (growth rates of sub-populations within conservation clusters) to differ from each other - during the same time period some sub-populations may increase while others decrease or remain stable and consequently the growth rate for the metapopulation may centre around zero. The asynchrony in growth rates implies asynchrony in demography and therefore that the elephants of a specific conservation cluster meet one of the criteria for metapopulation dynamics. I expected similar differences and consequences when scaling to the regional level and when comparing conservation clusters. The assessment of demographic asynchrony at both the local and the regional scales allow for inferences on how metapopulation processes may regulate or limit elephant numbers, both locally and regionally.

MATERIALS AND METHODS

Population estimates

I used African Elephant Status Reports (Blanc *et al*., 2003; Blanc *et al*., 2007) to distinguish administrative elephant populations as sub-populations in each of the six conservation clusters recognized by van Aarde & Ferreira (2009) across southern Africa (Fig. 1). A cluster comprised of any number of open or fenced conservation areas that supported discrete sub-populations of elephants, some of which may disperse between sub-populations or even between conservation clusters (see van Aarde & Ferreira, 2009). Published and unpublished estimates for 51 populations were extracted from a database that the Conservation Ecology Research Unit (CERU) compiled from information in the *Pachyderm* series (volumes 1 to 41), the African Elephant Databases (Said *et al*., 1995;

Barnes *et al*., 1998) and the African Elephant Status Reports (Blanc *et al*., 2003; Blanc *et al*., 2007) as well as other published papers and unpublished reports (see Junker, 2008).

I included all estimates that covered the same approximate area for each sub-population for the period 1980 to 2006. However, where a discrete sub-population was counted in its entirety for successive surveys, the estimates were regarded as comparable even if the total survey areas were somewhat different. Estimates were based on direct surveys, either from the ground or the air, or indirect surveys based on structured dung counts. I also included estimates based on informed and other guesses.

Defining elephant population trends

I constructed time series for each of the sub-populations for the period 1980 to 2006. Each of the time series included at least four estimates. The natural logarithms of estimates plus 1 (to compensate for estimates where the population was zero) linearly regressed against time yielded estimates of percentage exponential growth (slope of line x 100), their 95% confidence intervals and standard errors (Caughley, 1977). I distinguished between declining, increasing and stable populations within each conservation cluster. I considered a sub-population as stable when the exponential growth rate was ≥-1% and ≤1%, rather than when the 95% confidence intervals of the regression analysis included zero.

To calculate the growth rate for a conservation cluster (the change in the total number of elephants in the cluster over time) I had to determine the number of elephants present in each year for every sub-population. Because estimates were not available for the same years for all sub-populations within a cluster, I interpolated estimates for a given year using the exponential growth rate between the last estimate before and the first estimate after missing values using $N_t = N_0e^{rt}$, where N_t = the first population estimate after missing values, N_0 = the last population estimate before missing values, r = the exponential growth rate, and t = the time between estimates (Caughley, 1977). The sum of estimates for all the sub-populations within a cluster for a given year then yielded the total number of elephants for that year. These values were $\log_e$ transformed and exponential growth rates and 95% confidence intervals were calculated as described before. I used piecewise linear regression with a single breakpoint (see Toms & Lesperance, 2003) to determine when a significant change in population growth occurred in a cluster.

The sum of the number of elephants for a given year for each of the six conservation clusters yielded my estimate of the total number of elephants in southern Africa for that year. These values were also used to calculate growth rates as described above for each of the time series identified by piecewise linear regression.

I used contingency table analyses to determine if there was a significant difference between the total number of elephant sub-populations that increased, decreased or remained stable before and after the breakpoint in the growth rate of the southern African region.

RESULTS

Population estimates

I used 568 population estimates to calculate growth rates for 51 sub-populations in six conservation clusters. Within most of the clusters sub-populations increased, decreased, or remained stable, suggesting demographic asynchrony (see Table 1). The number of increasing, decreasing and stable populations differed between clusters, as did the position (thus timing) of breakpoints for each of the time series (see Table 1). The time series for five of the six clusters had breakpoints, suggesting that population trends changed over time.

The number of sub-populations across the region that increased, decreased or remained stable for the time series before and after the calculated breakpoints for each cluster differed significantly (χ^2=6.06; *df*=2; *P*=0.05). The Chobe cluster had no breakpoint and the highest incidence of increasing sub-populations (11 of 13). For the Limpopo cluster that comprised 12 sub-populations three increased prior to the breakpoint (1995) and seven thereafter. For the Luangwa cluster three of 11 sub-populations increased before the breakpoint (1993) and four thereafter. For the Zambezi cluster one, and five of seven sub-populations increased before and after the breakpoint (1984) respectively, while for the Kafue cluster only one, of six sub-populations increased before the breakpoint (2001). For the Etosha cluster, that comprised only two sub-populations, one increased after the breakpoint (1995).

Luangwa was the cluster with the highest incidence of decreasing sub-populations – three subpopulations decreased before and three sub-populations decreased after the breakpoint. For the Kafue cluster four sub-populations decreased before the breakpoint. For the Zambezi cluster, four sub-populations decreased before the breakpoint and one thereafter. For the Limpopo cluster two sub-populations decreased before and two sub-populations decreased after the breakpoint respectively. For the Etosha cluster one sub-population decreased before and one after the breakpoint. Within the Chobe cluster two sub-populations decreased.

Sub-population growth rates within clusters ranged from -8 to 75% in Chobe, 1 to 3% in Etosha, -30 to 11% in Kafue, -19 to 16% in Limpopo, -30 to 6% in Luangwa and -6 to 5% in Zambezi (see Appendix I). Asynchronous changes in elephant numbers for sub-populations within clusters were thus apparent among all the clusters. In addition, 12 of the 51 sub-populations increased at growth rates beyond the estimated theoretical or observed maximum for elephant populations calculated from birth and survival rates (see Hanks & McIntosh, 1973; Calef, 1988; and Moss, 2001).

Piecewise linear regression analysis identified breakpoints in population trends in 1995, 2001, 1995, 1993 and 1984 for the Etosha, Kafue, Limpopo, Luangwa and Zambezi clusters respectively (Fig. 2). No breakpoint could be identified for the Chobe cluster. These analyses suggest that conservation clusters (with the exception of Chobe) experienced marked changes in elephant numbers during the time span of the 26 years of my time series. Etosha were relatively stable since 1995, after an earlier decline of -4.2% per year. Kafue declined at varying rates for the last two decades. In the Limpopo cluster elephant numbers increased at 3.4% per annum after the cessation of culling in the Kruger National Park in 1995 – prior to 1995 the cluster was stable and changed at -0.2% per year. The Luangwa cluster stabilized at -0.4% per year since 1992 after suffering an annual decline of -6.8%. There was also an apparent declined in the Zambezi cluster before 1983. More recently the population of this cluster increased at a rate of 3.2% annually. These differences in trends and growth rates suggest temporal and spatial asynchrony in the population dynamics of elephants.

Piecewise regression further support the notion of spatial asynchrony across the region – a breakpoint in the regional trend occurred in 1987 (Fig. 3). Before 1987 the regional population declined at -2.8% annually. From 1980 to 1987 four clusters of populations declined (Etosha, Kafue, Luangwa and Zambezi), one was stable (Limpopo), and one increased (Chobe). However, since 1987 the regional population increased at 3.1% annually, with four clusters of populations increasing (Chobe, Etosha, Limpopo and Zambezi), one stabilizing (Luangwa) and one decreasing (Kafue).

DISCUSSION

The temporal and spatial asynchrony in population growth, as is apparent for elephants across the southern African sub-continent, implies temporal and spatial asynchrony in the forces affecting birth-, death-, immigration- and emigration rates. These drivers of population growth do respond to varying environmental conditions. For instance, both Wittemyer *et al.* (2007) and Trimble *et al,* (2009) illustrated that reproductive variables underlying birth rates vary with rainfall, pending on conception rate, prenatal survival, first year survival and cumulative juvenile survivorship. In elephants, mortality is also affected by rainfall and in drought years a disproportionate fraction of young elephants die (Jachmann, 1986; Moss, 2001; Loveridge *et al.,* 2006; Foley *et al.,* 2008). Rainfall, or the lack thereof, also induces immigration and emigration (Beuchner *et al.,* 1963; van Aarde *et al.,* 2008; Young, 2009b) as do primary productivity, albeit best known for seasonal patterns in movements (Harris *et al.,* 2008; Young *et al.,* 2009a, 2009b). Given that my analyses incorporated elephant sub-populations across a gradient of rainfall and resource availability, it is not surprising that I recorded varying growth rates across both temporal and spatial gradients.

The trends I have recorded, or at least some of these, may also have been induced by survey error (see Barnes, 2002; Ferreira *et al.,* 2009b; Junker, 2008; Olivier *et al.,* 2009) and the interpolations that I had to rely on. Survey data is often limited and of poor quality (Junker, 2008) and direct and indirect estimates are obtained from, amongst others, aerial surveys, dung surveys or even guesses. For some populations different methods were also used between survey dates which could lead to spurious changes in population sizes. Estimating demographic rates such as age of first calving, calving intervals and age specific survival rates (as suggested by Ferreira *et al.,* 2009a; van Aarde & Ferreira, 2009) could allow scientists to predict population trends, which will overcome the effects of survey errors and aid analyses that seek to determine the relative contributions of metapopulation processes in population changes. This also should overcome the limitations of interpolating population estimates from population growth rates.

In southern Africa, elephants occur across a rainfall gradient that spans from the western arid savannas of Namibia to the eastern mesic savannas of Mozambique (see Sankaran *et al.,* 2005). Here, the arrangement and distribution of protected areas, as well as the different land uses elephants may encounter in a matrix of human-dominated landscapes, give rise to discontinuities in elephant distribution and densities. Admittedly, the existence of elephants as apparent discrete sub-populations may be a mere reality of the distribution of protected areas across southern Africa. It thus may be argued that the apparent asynchrony in population growth merely reflects a response to anthropogenic forces that fragmented a once continuous population into several sub-populations. Varying conditions of protection, water availability and densities driven by the space set aside for the conservation of elephants, rather than 'natural forces' therefore may be driving the asynchrony in dynamics.

Because the demography of elephants are affected by site specific differences in environmental stressors such as climatic conditions, rainfall and resource quality (e.g. Dudley *et al.,* 2001; Foley *et al.,* 2001; Wittemyer *et al.,* 2007; Foley *et al.,* 2008; Trimble *et al.,* 2009; Young *et al.,* 2009a, 2009b), management practices such as culling, fences and water provision (e.g. van Aarde *et al.,* 1999; Slotow *et al.,* 2005; Chamaillè-Jammes *et al.,* 2007; Loarie *et al.,* 2009), human-elephant conflict and poaching incidences (e.g. Hoare & du Toit, 1999; O'Connell-Rodwell *et al.,* 2000; Aleper & Moe, 2006; Wasser *et al.,* 2007; Gobush *et al.,* 2008; Ferreira *et al.,* 2009a), as well as through density-dependent processes (e.g. Laws, 1975; van Aarde *et al.,* 1999; Chamaillè-Jammes *et al.,* 2008) the growth rates of sub-populations may differ, but the regional population may fortuitously remain less variable or even stable. Despite the artificiality of the regional elephant population now being structured into units of near independent sub-populations, I argue that it is this structure that lends itself to the application of the metapopulation metaphor in conservation management.

One of the prerequisites for a metapopulation is that the dynamics of the sub-populations of which it comprised should be in asynchrony. I showed that population growth rates and trends differed between sub-populations and that these changed over time, both within and between conservation clusters. This suggest asynchrony in the dynamics of populations and therefore that the regions elephant populations collectively may operate as a metapopulation, albeit within clusters rather than across clusters.

Further support for a metapopulation structure comes from my observation that almost a quarter (12 out of 51) of sub-populations within clusters increased at rates higher than the expected theoretical rates of 7% calculated by Calef (1988;) or the 11.2% recorded by Moss (2001). This implies that that dispersal from neighbouring sub-populations may be driving growth rates for these populations.

Local differences in growth rates that may indicate demographic asynchrony and the possibility of dispersal are both criteria that have to be met by sub-populations across a region before accepting that the species follows a metapopulation structure. Therefore, I suggest that populations within conservation clusters should be viewed as part of a linked system with the potential to be driven, and limited, by metapopulation dynamics. In addition the subsequent variability in growth rates among clusters, and between time periods, imply that clusters themselves across the sub-continent could also potentially function as sub-populations within a regional southern African metapopulation. This suggestion, however, may only hold if elephants can move between clusters.

My assessment shows that collective growth rates for conservation clusters were positive, negative or stable. Although metapopulation dynamics imply that these differences, as well as the differences between sub-populations within clusters, may be driven by demographic variables, additional anthropogenic forces that influence population growth rates cannot be ignored. For instance, demographic asynchrony may be the outcome of management actions. Fences that inhibit dispersal may enhance growth rates (Owen-Smith *et al.,* 2006; Junker, 2008; van Aarde *et al.,* 2006; van Aarde *et al.,* 2008), while water provisioning may attract elephants by inducing dispersal (Chamaillé-Jammes *et al.,* 2007; van Aarde & Jackson, 2007; Junker, 2008). This may explain the positive growth rates observed for some clusters, and notably that of the Limpopo cluster, which are dominated by the Kruger National Park population. This population had an extended history of management interferences (see Whyte *et al.,* 2003) that consistently boosted population growth (van Aarde *et al.,* 1999; van Aarde *et al.,* 2008). This may have interfered with demographics and explain the positive, rather than stable growth for the cluster.

The same management interferences may also explain sub-population growth rates for the Etosha and Chobe clusters, and their deviation from the expected outcomes of metapopulation dynamics. For instance, water provisioning and fences boasted the populations of Etosha National Park, and Hwange National Park as well as the Khaudum Game Reserve (Chamaillé-Jammes *et al.,* 2007; van Aarde & Jackson, 2007; de Beer & van Aarde, 2008). However, annual outbreaks of anthrax in the Etosha National Park may have stabilized population growth in the Etosha cluster.

Poaching is another factor that could affect elephant population growth rates (Foley, 2002; Blake *et al.,* 2007; Gobush *et al.,* 2008). Wasser *et al.* (2007) found that illegal ivory seized could be traced back to central Zambia, which imply that the Kafue National Park may be a poaching hotspot. In addition Ferreira *et al.,* (2009a) suggested that continued ivory poaching disrupts the population age structure of Zambian elephant populations. These findings are also reflected in my results as the Kafue cluster in Zambia was decreasing at 26% per annum since 2001. However, during the same period, the Luangwa cluster seemed stable after years of decline. The stabilization of this cluster may be in response to increased protection and anti-poaching campaigns implemented within and around the Luangwa Valley (see Jachmann & Billiouw, 1997; Owens & Owens, 2009).

My findings may have consequences for elephant management in southern Africa. I caution against only interpreting local fluctuations and the subsequent implementation of managing practices as my results highlight the importance of interpreting local changes within a regional context. For instance, the development of transfrontier conservation areas (TFCAs) across southern Africa provide opportunities for so called ‘megaparks’ (van Aarde & Jackson, 2007) where the conservation landscape are joined by incorporating a mosaic of different land use scenarios, even across international borders. Here, the restoration of spatial-temporal axes that recover spatio-temporal dynamics may stabilize elephant populations regionally and mitigate the local impacts on other species, including humans (van Aarde & Jackson, 2007). My results indicate that sub-populations in the Etosha, Chobe, Kafue, Luangwa and Zambezi clusters could be part of a potential regional metapopulation that spans the borders of at least five countries (see van Aarde *et al.,* 2006; van Aarde & Ferreira, 2009). The application of metapopulation theory here could provide the opportunity for a spatial-temporal approach that does not focus only on elephant numbers. Recognizing the sub-continent’s conservation clusters as biological and spatial entities could also aid law enforcement and CITES decision-making (see van Aarde & Ferreira, 2009). Furthermore, a regional conservation strategy may negate the impact that global climate change may have on elephant populations and on co-occurring species.

Ultimately my study illustrates that elephant populations within and among conservation clusters adhere to one, and most likely, to the other criteria of a metapopulation as proposed in the literature (Elmhagen & Angerbjörn, 2001; Olivier *et al.,* 2009). Furthermore, it highlights the potential that metapopulation processes may have in maintaining elephant numbers across southern Africa. The importance of space and the interpretation of local population trends within a regional context, rather than just within political units dictated by artificial boundaries, cannot be overemphasized (as also been advocated by van Aarde & Jackson, 2007; van Aarde & Ferreira, 2009).

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Table 1. The number of sub-populations that increased decreased or remained stable within conservation clusters, before and after calculated breakpoints.

Conservation cluster	Number of sub-populations	Time series (years)	Growth rate (%) (95% Confidence intervals)	Number of sub-populations			Time series (years)	Growth rate (%) (95% Confidence intervals)	Number of sub-populations		
				Increase	Decrease	Stable			Increase	Decrease	Stable
Etosha	2	1980-1994 (15)	-3.3 (-5.1 – 0)	0	1	1	1995-2006 (12)	5.3 (1.1 – 9.1)	1	1	0
Chobe	13	1980-2006 (27)	3.3 (3.1 - 3.6)	11	2	0	[1]-	-	-	-	-
Kafue	6	1980-2000 (21)	-2.0 (-5.1 – 0)	1	4	1	2001-2006 (6)	-26.0 (-36.0 – 0)	-[2]	-	-
Limpopo	12	1980-1994 (15)	-0.2 (-1.2 – 0)	3	2	1	1995-2006 (12)	3.4 (2.7 – 3.9)	7	2	0
Luangwa	11	1980-1992 (13)	-6.8 (-9.1 – -5.1)	3	3	0	1993-2006 (14)	-0.4 (-1.1 – 0.3)	4	3	0
Zambezi	7	1980-1983 (4)	-5.6 (-8.1 – -3.1)	1	4	0	1984-2006 (23)	3.2 (2.3 – 3.4)	5	1	0
Total[3]	51	1980-2006 (27)	-	20	15	3	1980-2006 (27)	-	27	8	0

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[1] No breakpoint was indentified for the Chobe cluster

[2] The lack of sub-population estimates for this time series (2001-2006) did not allow the calculation of growth rates here.

[3] The sum of sub-populations that increased decreased or remained stable before and after breakpoints calculated for each conservation cluster.

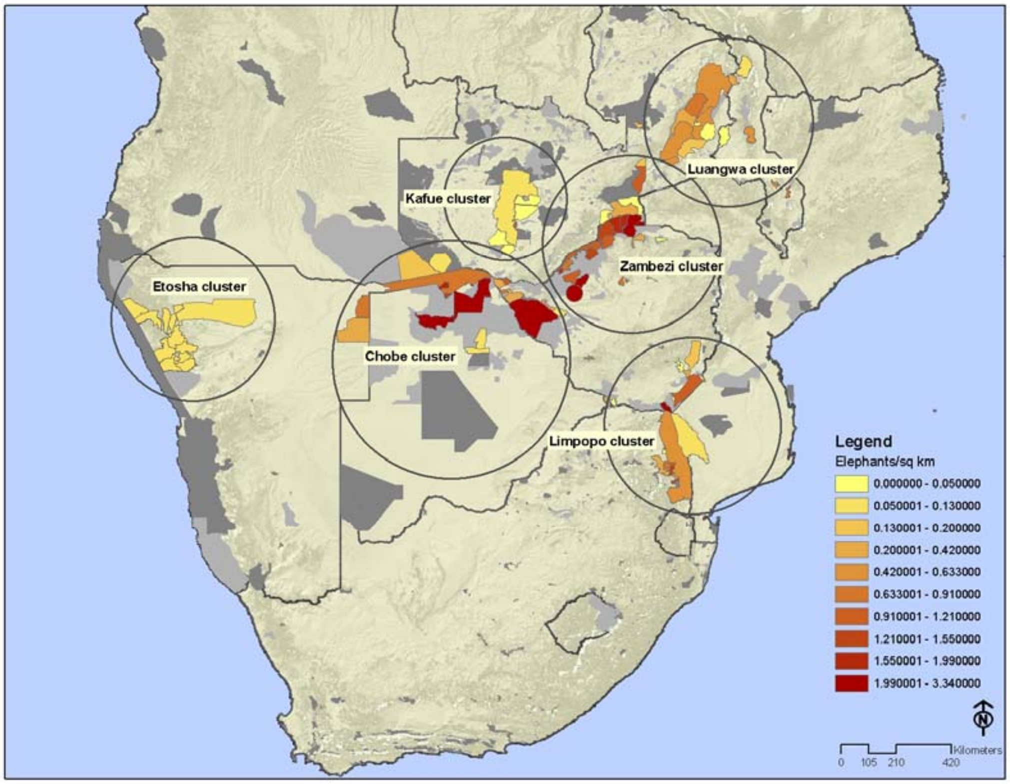

Figure 1: The southern African sub-continent showing six conservation clusters across eight countries where elephants occur. Each cluster represents a potential metapopulation. In addition, the southern African sub-continent also represents a potential metapopulation. Within and among clusters elephant densities and numbers vary considerably. From CERU unpublished data, Blanc *et al*, (2007) and van Aarde & Ferreira (2009). [The map is based on a model developed by van Aarde (in litt.) and composed by Theresia Ott (CERU). The base layer of conservation areas is courtesy from the Peace Parks Foundation (PPF) and elephant density data are from Junker (2008)].

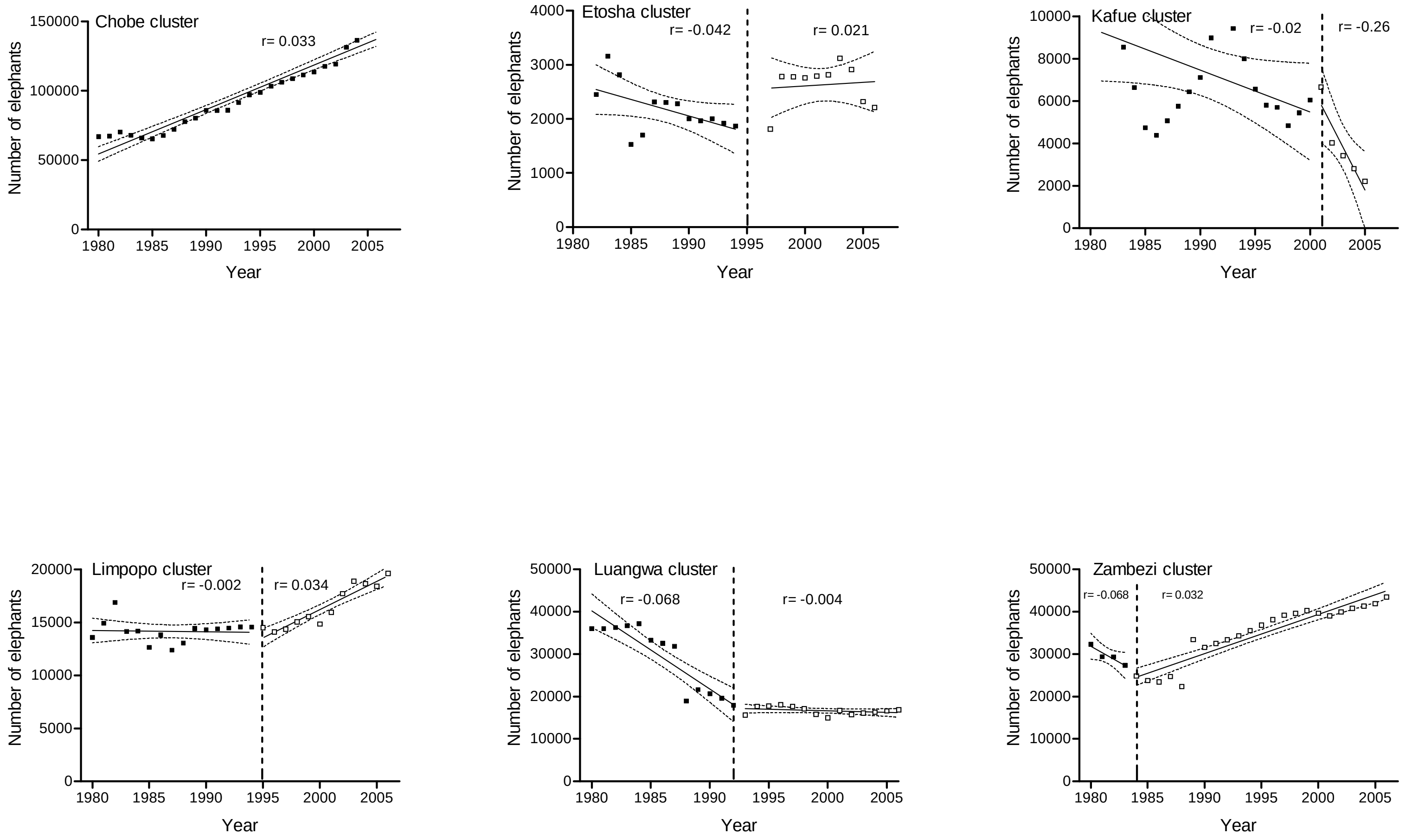

Figure 2. Population growth rates calculated for elephant conservation clusters proposed for southern Africa. The dotted line indicates the breakpoints identified by piecewise linear regression. Growth rates for the period before and after breakpoints are illustrated.

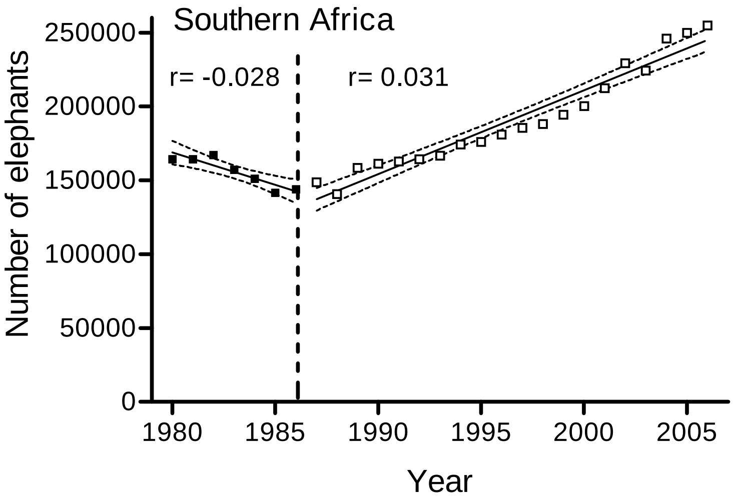

Figure 3. Temporal trend in elephant numbers calculated for the southern African region. The broken line indicate the breakpoint identified by piece-wise linear regression. Growth rates for the period before and after the breakpoint are also presented.

Appendix I. Growth rates and 95% confidence intervals calculated for local populations within conservation clusters, before and after breakpoints estimated in the time series for conservation clusters. The F- and P- values indicate when the slope of the regression line (which represents intrinsic growth rate) differs significantly from zero.

Table 1. Sub-population growth rates, for and within, the Etosha conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
Pre-Breakpoint						
Etosha National Park	8	1980-1990 (11)	-0.04 (-0.10 - 0.03)	0.22	1.68	0.24
Kunene Damaraland District	5	1982-1990 (9)	-0.05 (-0.10 - 0)	0.71	7.34	0.07
Cluster	11	1980-1990 (11)	-0.04 (-0.10 – 0.02)	0.25	2.34	0.18
Post-Breakpoint						
Etosha National Park	6	1998-2004 (7)	0.0005 (-0.05 – 0.05)	0.0004	0.001	0.98
Kunene Damaraland District	6	1992-2005 (14)	-.0.019 (-0.15 – 0.11)	0.07	0.21	0.67
Cluster	15	1991-2005 (15)	0.02 (0 – 0.04)	0.58	13.61	0.004**

Table 2. Sub-population growth rates, for and within, the Chobe conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
Caprivi Region	9	1980-2005 (26)	0.06 (0.001 - 0.12)	0.45	5.84	0.05*
Chobe National Park	11	1981-2006 (26)	0.02 (-0.002 - 0.03)	0.32	4.25	0.07
Hwange National Park	15	1980-2001 (22)	0.04 (0.02 - 0.05)	0.72	34.11	<0.001**
Khaudum Game Reserve	11	1984-2004 (12)	0.18 (0.08 - 0.29)	0.63	15.35	0.004**
Mamili National Park	12	1980-2005 (26)	0.11 (0.05 - 0.16)	0.65	18.29	0.002**
Matetsi Safari Complex	13	1980-2001 (22)	-0.08 (-0.16 - 0.01)	0.24	3.50	0.09
Mudumu National Park	11	1980-2005 (26)	0.13 (-0.005 - 0.27)	0.36	5.00	0.05*
Mgadigadi National Park	6	1996-2004 (9)	0.75 (0.33 - 1.17)	0.86	25.28	0.007**
Naye-Naye Conservancy	9	1984-2004 (25)	0.06 (0.02 - 0.10)	0.67	14.25	0.007**
Rest of Northern Botswana	7	1980-2006 (27)	0.02 (0 - 0.05)	0.52	5.40	0.07
Nxai Pan National Park	6	1996-2004 (9)	0.57 (0 – 1.6)	0.37	2.30	0.20
Okavango Delta	9	1980-2006 (27)	0.07 (0.02 - 0.12)	0.60	10.39	0.015
Sioma Ngwezi National Park	6	1984-2005 (22)	-0.08 (-0.19 – 0.03)	0.50	3.95	0.12
Cluster	27	1980-2006 (27)	0.033 (0.031 - 0.036)	0.97	731.20	<0.001**

Table 3. Sub-population growth rates, for and within, the Kafue conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
Pre-Breakpoint						
Kafue National Park	8	1980-1996 (17)	0.01 (-0.02 - 0.05)	0.095	0.63	0.45
Lunga-Luswishi Game Management Area	4	1989-1997 (9)	-0.51 (-1.12 - 0.14)	0.84	11.23	0.078
Mulobezi Game Management Area	3	1984-1997 (14)	-0.47 (-0.66 - 0.27)	0.99	940.31	0.02*
Mumbwa Game Management Area	6	1984-2000 (17)	0.09 (-0.17 - 0.36)	0.18	0.91	0.39
Namwala Game Management Area	3	1989-2000 (12)	-0.02 (-4.8 – 4.8)	0.002	0.002	0.97
Sichifulo Game Management Area	4	1984-1997 (14)	-0.09 (-0.45 – 0.42)	0.02	0.34	0.87
Cluster	21	1980-2000 (21)	-0.02 (-0.05 – 0.005)	0.13	2.90	0.11
Post-Breakpoint						
Kafue National Park	2	2001-2005 (5)	-	-	-	-
Lunga-Luswishi Game Management Area	1	2001-2005 (5)	-	-	-	-
Mulobezi Game Management Area	1	2001-2005 (5)	-	-	-	-
Mumbwa Game Management Area	2	2001-2005 (5)	-	-	-	-
Namwala Game Management Area	1	2001-2005 (5)	-	-	-	-
Sichifulo Game Management Area	2	2001-2005 (5)	-	-	-	-
Cluster	5	2001-2005 (5)	-0.25 (-0.36 - -0.15)	0.95	59	0.005**

Table 4. Sub-population growth rates, for and within, the Limpopo conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
Pre-Breakpoint						
Banhine National Park	2	1980-1994 (15)	-	-	-	-
Gonarezhou National Park	8	1981-1989 (9)	-0.04 (-0.12 – 0.046)	0.16	1.20	0.31
Klaserie Private Nature Reserve	8	1980-1990 (11)	0.05 (-0.03 – 0.14)	0.28	2.34	0.17
Kruger National Park	14	1981-1994 (14)	-0.002 (-0.01 – 0.007)	0.025	0.30	0.59
Letaba Game Ranch	3	1989-1994 (6)	-0.13 (-1.4 – 1.4)	0.62	1.67	0.42
Makuya Nature Reserve	1	1980-1994 (15)	-	-	-	-
Manyeleti Game Reserve	1	1980-1994 (15)	-	-	-	-
Phalaborwa Mining Company	2	1980-1994 (15)	-	-	-	-
Sabi Sands Game Reserve	3	1981-1993 (13)	0.05 (-0.28 – 0.38)	0.65	3.87	0.29
Save Valley Conservancy	1	1980-1994 (15)	-	-	-	-
Timbavati Private Nature Reserve	6	1980-1994 (15)	0.08 (-0.001 – 0.16)	0.62	7.45	0.05*
Umbabat Private Nature Reserve	1	1980-1994 (15)	-	-	-	-
Cluster	15	1980-1994 (15)	-.0.002 (-0.01 – 0.01)	0.045	0.61	0.45
Post-Breakpoint						
Banhine National Park	2	2002-2005 (4)	-	-	-	-
Gonarezhou National Park	3	1995-2001 (7)	0.024 (-0.37 – 0.42)	0.37	0.61	0.58
Klaserie Private Nature Reserve	2	1996-2006 (11)	-	-	-	-
Kruger National Park	10	1995-2006 (12)	0.04 (0.03 – 0.05)	0.89	65.40	<0.001**
Letaba Game Ranch	2	1997-2006 (10)	-	-	-	-
Makuya Nature Reserve	3	1997-2006 (10)	0.20 (0 – 0.41)	0.99	149.60	0.05*
Manyeleti Game Reserve	3	1997-2006 (10)	0.11 (-1.9 – 1.3)	0.56	1.28	0.46
Phalaborwa Mining Company	5	1995-2006 (12)	-0.07 (-0.33 – 0.19)	0.18	0.66	0.47
Sabi Sands Game Reserve	6	1996-2006 (11)	0.13 (0.05 – 0.21)	0.83	19.95	0.01*
Save Valley Conservancy	3	1996-2003 (8)	-0.04 (-0.17 – 0.08)	0.95	17.62	0.15
Timbavati Private Nature Reserve	5	1996-2006 (11)	0.11 (0.06 – 0.15)	0.95	60.70	0.004**
Umbabat Private Nature Reserve	4	1996-2006 (11)	0.11 (0 – 0.52)	0.41	1.40	0.36
Cluster	324	1995-2006 (12)	0.03 (0.027 – 0.039)	0.94	166	<0.001**

Table 5. Sub-population growth rates, for and within, the Luangwa conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
<u>Pre-Breakpoint</u>						
Chisomo & Sandwe Game Management Areas	1	1980-1992 (13)	-	-	-	-
Kasungu National Park	5	1980-1992 (13)	-0.03 (-0.15 – 0.09)	0.16	0.56	0.51
Luano Game Management Area	3	1981-1985 (5)	0.98 (-4.28 – 6.25)	0.84	5.63	0.25
Lukukuzi National Park	3	1980-1989 (10)	-0.16 (-1.23 – 0.89)	0.83	4.08	0.29
Lupande Game Management Area	2	1980-1992 (13)	-	-	-	-
Musalungu Game Management Area	4	1984-1991 (7)	0.04 (-0.35 – 0.46)	0.06	0.13	0.75
North Luangwa National Park	2	1980-1992 (13)	-	-	-	-
Nyika National Park	2	1980-1992 (13)	-	-	-	-
South Langwa National Park	5	1985-1990 (6)	-0.26 (-0.83 – 0.31)	0.41	2.08	0.25
Vwaza Marsh Wildlife Reserve	3	1984-1992 (9)	0.03 (-0.43 – 0.51)	0.42	0.74	0.55
West Petauke Game Management Area	1	1980-1992 (13)	-	-	-	-
Cluster	13	1980-1992 (13)	-0.068 (-0.09 - -0.05)	0.81	46.41	<0.001**
<u>Post-Breakpoint</u>						
Chisomo & Sandwe Game Management Areas	4	1994-2006 (13)	0.09 (-0.38 – 0.56)	0.24	0.65	0.50
Kasungu National Park	4	1995-2005 (11)	-0.19 (-0.25 - -0.14)	0.99	208.71	0.005**
Luano Game Management Area	1	1993-2006 (14)	-	-	-	-
Lukukuzi National Park	2	1993-2006 (14)	-	-	-	-
Lupande Game Management Area	5	1993-2002 (10)	0.05 (-0.20 – 0.31)	0.13	0.43	0.56
Musalungu Game Management Area	3	1996-2004 (9)	0.16 (-0.83 – 1.15)	0.81	4.25	0.29
North Luangwa National Park	5	1993-2003 (11)	0.03 (-011 – 0.17)	0.12	0.41	0.56
Nyika National Park	2	1993-2006 (14)	-	-	-	-
South Langwa National Park	7	1993-2002 (10)	-0.03 (-0.12 – 0.05)	0.16	0.98	0.37
Vwaza Marsh Wildlife Reserve	2	1993-2006 (14)	-	-	-	-
West Petauke Game Management Area	3	1994-1999 (6)	-0.16 (-1.79 – 1.47)	0.61	1.54	0.43
Cluster	24	1993-2006 (24)	-0.004 (-0.01 – 0.003)	0.10	1.41	0.26

Table 6. Sub-population growth rates, for and within, the Zambezi conservation cluster

Cluster population	Number of data points in time series	Length of time series (years)	Intrinsic *r* (95% Confidence Intervals)	Co-efficient of determination (r^2)	F-value for slope of regression	*P*
<u>Pre-Breakpoint</u>						
Binga Communal Lands	0	1980-1983 (4)	-	-	-	-
Chete Safari Area	4	1980-1983 (4)	0.12 (-0.20 – 0.48)	0.55	2.51	0.25
Chirisa Safari Area	4	1980-1983 (4)	-0.14 (-0.41 – 0.12)	0.73	5.49	014
Sebungwe Region	3	1980-1983 (4)	-0.05 (-0.79 – 0.69)	0.41	0.69	0.55
Sengwa Communal Land	3	1980-1983 (4)	-0.30 (-1.76 – 1.15)	0.88	7.02	0.23
Mutusadona National Park	3	1981-1983 (4)	-0.04 (-1.32 – 1.24)	0.11	0.13	0.78
Zambezi Valley	2	1980-1983 (4)	-	-	-	-
Cluster	4	1980-1983 (4)	-0.05 (-0.10 – 0)	0.87	13.33	0.068
<u>Post-Breakpoint</u>						
Binga Communal Lands	5	1989-2006 (18)	-0.05 (-0.12 – 0.01)	0.70	6.98	0.08
Chete Safari Area	9	1984-2006 (23)	0.03 (-0.12 – 0.06)	0.26	2.48	0.16
Chirisa Safari Area	9	1984-2006 (23)	0.03 (-0.03 – 0.10)	0.17	1.40	0.28
Sebungwe Region	7	1985-2006 (22)	0.03 (0 – 0.05)	0.52	5.69	0.06
Sengwa Communal Land	8	1984-2001 (18)	0.06 (0.03 – 0.09)	0.79	21.09	0.004**
Mutusadona National Park	10	1984-2006 (23)	0.04 (0 – 0.07)	0.45	6.57	0.03*
Zambezi Valley	7	1984-2003 (20)	0.05 (0.03 – 0.06)	0.91	54.19	0.001**
Cluster	23	1984-2006 (23)	0.03 (0.02 – 0.03)	0.83	100.50	<0.001**

Chapter 4

Dung survey bias and elephant population estimates in southern Mozambique

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Running head: Dung counts estimate elephant population size

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Abstract

We used dung surveys to estimate population size and extracted an age structure from boli diameters for the elephants living in the Maputo Elephant Reserve. Our estimate was based on published defecation rates, dung decay rates, distance-sampling techniques and 1672 dung piles encountered on 204 line-transects. The Reserve had at least 311 (95% CI: 198 – 490) elephants at a density of 0.60 (95% CI: 0.38 – 0.94) per km^2. However, observer bias reduced effective strip widths and inflated estimates and their confidence limits. The age structure extrapolated from dung measurements indicated few newborn calves compared to other populations. To detect population changes of 2-5% at 80% power, dung surveys should be carried out every second year for the next 20 years using 100 transects of at least 500m each. Comparison with a 1995 dung survey suggests that the population is stable and that previous fears of a major population decline during the civil war have no foundation.

Introduction

Several different survey techniques provide information that forms the basis of population estimates for African elephants (*Loxodonta africana* Blumenbach) (Douglas-Hamilton, 1996). For elephants that live in dense woodlands and forests, scientists often use dung surveys. Such surveys apparently provide estimates of abundance that are comparable with those that count elephants directly (Barnes, 2001) and as precise as estimates derived from aerial surveys (Barnes, 2002).

Population estimates based on dung counts require estimates of the number of dung piles per km², the number of piles produced by an elephant in a day and the rate at which dung piles decay (Barnes & Jensen, 1987). Dung surveys can also provide additional population information. For instance, dung boli diameters allow for the assignment of ages to elephants (Morrison *et al*., 2005) that may be converted to population age structures (Jachmann & Bell, 1984; Reilly, 2002). Such age structures and independent estimates of fecundity can be used to calculate intrinsic population growth rates using the procedures suggested by Udevitz & Ballachey (1998).

A key to the success of dung surveys is the level of precision that may be required to deduce population growth rates. Narrower confidence intervals imply greater precision of estimates. From published information we know that sampling intensity and observer bias can influence estimates of dung pile density (Jachmann & Bell, 1984). We also know that habitat types and boli sizes affect decay rates (Barnes *et al*., 2006) and that limited visibility in forests makes it difficult to observe elephants defecating to estimate defecation rates (Barnes, 2001). In addition, the presumed lower detectability and faster decay rate of small boli could skew age frequencies. Dung surveys therefore may be of limited use unless designed to meet criteria that will return reliable demographic profiles without challenging the practicalities of undertaking such surveys.

We investigated the reliability and practicality of dung surveys based on a case study in the Maputo Elephant Reserve (MER) in southern Mozambique. We estimated the size of the elephant population, derived an age structure and addressed some sources of error associated with dung surveys. We also reviewed the literature on defecation and dung decay rates, and then estimated habitat-specific decay rates and dung pile densities in the MER. We evaluated the effect of sampling intensity on our estimates and used a power analysis to determine the frequency of surveys required to detect population changes.

Material and Methods

Study area

The MER covered an area of 800 km² in southern Mozambique (26º25'S, 32º45'E, Fig. 1). The reserve was unfenced but for an electric fence of about 30 km along the western boundary that may have protected farmers from elephant raids (de Boer & Ntumi, 2001). Here summers (October – March) were hot and wet and winters (April – September) were relatively cool and wet. Annual rainfall varied from 690 to 1000 mm (Direccao Nacional de Florestas e Fauna Bravia [DNFFB], 1997). The reserve is located in a biodiversity hotspot (Küper *et al*., 2004) and the vegetation include sand-, swamp- and coastal dune forests, open and closed woodlands, grasslands as well as reed beds. Sand forests are endemic to the region (van Wyk & Smith, 2001) and may be threatened by elephant activities (Guldemond & van Aarde, 2007). The woodlands had a closed and layered canopy with dense undergrowth. Sparsely spaced mature trees and a prominent grass sward dominated the open woodlands.

The elephants of the MER are secretive and spend most of their time in the sand forests (Ntumi *et al.,* 2005; de Boer *et al.,* 2000), either foraging to accommodate the lower quality of browse, or to seek refuge following the historic poaching pressures (de Boer *et al.,* 2000), or to escape from the high direct solar radiation typical of the region (Kinahan, Pimm & van Aarde, 2007). These elephants seldom forage on the grass and flood plains during the day and apparently do so mostly at night (de Boer *et al*. 2000). They are therefore not frequently encountered.

Data collection and analysis

For our analysis we relied on published defecation rates that we collated along with decay rates noted elsewhere in Africa (Table 1). Fresh dung placed in sand forests (*n* = 59 dung piles spaced five meters apart in three quadrants), open woodlands (*n* = 51, three quadrants) and grasslands (*n* = 36, two quadrants) during April 2006 allowed us to estimate habitat-specific dung decay rates. For this, we collected fresh Stage A dung piles (following the classification of Barnes & Jensen, 1987) throughout the MER. We used a tape measure to determine the circumference of boli in these piles and moved them to the different quadrants where stages of decay as described by Barnes & Jensen (1987) were recorded at irregular intervals over a period of 147 days.

We used the models of Laing *et al.,* (2003) to estimate dung decay rates. To determine whether large and small boli decayed differently we separated dung piles of adults (≥ 42 cm in circumference) from those of sub-adults (< 42 cm) (Jachmann & Bell, 1984). We compared the number of days that it took for large boli ($n = 23$) to reach Stage E (Barns & Jensen, 1987) or be absent, with those of small boli ($n = 38$) using a *t*–test (Sokal & Rohlf, 1995).

We estimated decay rates for all boli combined and defined dung piles ranging from Stage A to Stage D of decomposition (Barnes & Jensen, 1987) as surviving and present, while those at Stage E or completely gone, were considered absent and not surviving. The decay quadrants were inspected during April, June, July and August. For analytical purposes surviving dung piles were recorded as 1 and absent piles as 0. We fitted three logistic decay models (Laing *et al.,* 2003) through maximum likelihood (Edwards 1972; Microsoft Excel macro from Hood, 2005) to these data and used R^2-values to choose the model that best represent the habitat-specific dung decay at our study site. These models allowed us to estimate the average time to decay, *i.e.* when 50% of the dung piles have disappeared (Laing *et al.,* 2003). Variances in habitat-specific decay rates were calculated through Monte Carlo simulation (Gentle, 1943) using the error structure of coefficients in the models already obtained through maximum likelihood.

To estimate dung density, three counting teams counted dung piles while on foot during September 2006 along 98 km of line-transects ($n = 204$), each with a maximum length of 500 meters (Fig. 1). Each survey team comprised two observers. A cluster of four transects (at least 250 m apart in a square design) were placed at equal intervals along the existing road network of the MER. Our unpublished satellite tracking data suggest that elephants in the MER did not avoid roads. We used a GPS (Garmin Etrex, manufactured by GARMIN International Inc. 1200 E 151st Street, Kansas, 66062-3426) to mark the beginning and end of each transect. Observers noted every dung pile that they encountered and measured the perpendicular distance to the transect using either a rangefinder (Impulse, manufactured by Laser Tech Inc. 7070 South Tucson Way, Engelwood, CO 80112) or tape measure. As the MER comprises a mosaic of different landscape types, a homogenous transect was seldom encountered. We thus recorded the GPS positions of changes in the vegetation along a transect. This allowed us to estimate transect length within a vegetation type as well as habitat-specific dung densities.

We evaluated three potential sources of survey error. We first evaluated if detection differed between counting teams by calculating the effective strip widths covered by each team using DISTANCE 5.0 *Release 2* (Thomas *et al.,* 2005), hereafter referred to as DISTANCE. We then used DISTANCE to estimate population sizes using published defecation rate, estimated decay rate and dung density for each counting team.

We investigated sampling intensity as a second source of error by assessing how an increase in transect length would change the total number and the 95% confidence intervals of estimates. To evaluate boli size as a source of error, we measured boli circumferences while walking line transects and calculated a detection function for these different sizes of boli using DISTANCE.

To compare our estimate with previous estimates and guesses, we collated published and unpublished estimates of the same population.

Estimating individual ages

We searched the MER for fresh signs of elephants and followed these until we found intact boli. We then measured the circumference of a minimum of 2 and a maximum of 4 boli per dung pile and used the average to estimate the age of an individual elephant based on the model of Morrison *et al.* (2005).

Dung pile density, elephant density and population estimate

We estimated dung pile densities and 95% confidence intervals for the sand forests, open woodlands and grasslands respectively using DISTANCE. DISTANCE combined habitat-specific density estimates to calculate a total density and its 95% confidence interval. We used the average wet season defecation rate that we collated from published studies and our own habitat-specific decay rates to estimate elephant densities and abundance within the three landscape types following the model of Laing *et al,* (2003). DISTANCE allowed these rates and their variances as input variables. In the same way separate estimates were calculated for each different counting team in each different habitat. To evaluate the effect of effective strip widths (and therefore observer bias) on our estimates we calculated ten separate estimates for strip widths ranging from one meter to more than ten meters. For instance, the first estimate only included dung piles recorded within 1 m of the transect, the second only recorded dung piles within 2 m of the transect and so on (1-9 m), until the final estimate which was made up of all recorded dung piles irrespective of strip width. In addition we calculated the width of the 95% confidence interval for each of these estimates and compared the width of the 95% confidence intervals to the effective strip widths.

We also evaluated the effect of sampling intensity on our estimates by performing 100 separate analyses using DISTANCE as described above. These analyses were performed on randomly selected transects that made up distances that ranged from 13 000

– 96 000 m covered throughout the MER and included transects conducted by the three counting teams and transects within the different vegetation types. This yielded 100 population estimates with 95% confidence intervals (CI) that were then related to transect lengths.

Earlier estimates of the MER's elephant population are not comparable with ours except for a dung density estimate obtained in 1995 by de Boer *et al.* (2000). We used the defecation rate and habitat specific decay rates of our study and applied it to the dung pile densities recorded by de Boer *et al.* (2000) to obtain a population estimate and its confidence interval for 1995. An estimate of exponential growth rate and its variance followed Caughley (1977) by applying a Monte Carlo simulation (Gentle, 1943) using the estimates and their 95% confidence intervals for 1995 and 2006.

We defined the sampling (intervals and period) needed to detect future upward (2-5 %) or downward (2-5 %) trends in elephant numbers within the MER using TRENDS (Gerrodette, 1993). We assumed a linear decline or increase and set the coefficient of variation (CV) at 46.95% based on the results from our estimates (the standard error was calculated as SE = CL/2, and coefficient of variation as CV = SE/estimate). The power tests were one tailed and we set α =0.02 (Barnes, 2002;Gibbs, Droege & Eagle, 1998)]. We defined a Power of >80% as sufficient to detect 2-5% changes in population growth (Gerrodette, 1993).

Age structure

Following the assignment of ages from boli diameters (Morrison *et al.,* 2005) estimated from our measured circumferences, we grouped elephants into one-year age classes up to

15 years of age, with all individuals above 15 years of age in one age class. We could not distinguish sexes from boli features and assumed an equal sex ratio up to 15 years of age (Moss, 2001). In this analysis we only included dung boli measured for breeding herds and excluded boli deposited by lone bulls.

Results

Defecation rates

Based on our literature review elephants across Africa defecated 16.6 to 37.7 times per day during the wet season, but only 12.0 to 16.6 times per day in the dry season (Table 1). In the MER, rainfall is relatively high throughout the year and defecation rates here may therefore be typical of that noted for wet seasons elsewhere. We calculated an average defecation rate of 25.3 (±SD 8.5, n=17 studies) based on the published wet season rates and used this value to estimate population density.

Dung decay rates

Our estimates of decay rates varied between the landscape types, with the fastest rate in the open woodlands (115 days, 95% CI: 91 – 139), followed by the grasslands (124 days, 95% CI: 91 – 155) and the Sand forests (148 days, 95% CI: 111 – 184). These were thus similar to those noted (43 – 167 days) for other study sites (see Table 1). The decay rates of small and large boli were similar (t = 0.18; df = 59; p = 0.43).

Dung pile densities

We covered 36, 29 and 33 km of transects in sand forests, open woodlands and grasslands respectively, and found the highest dung pile density in sand forests (3629 piles per km², 95% CI: 2381 – 5529). The open woodland had 1111 (95% CI: 654 – 1886) and the grassland 148 (95% CI: 68 – 312) piles of dung per km² respectively (Table 2).

A half normal cosine detection model was selected for the sand forests (AIC = 4875) and grasslands (AIC = 413), while a half normal cosine detection model with two adjustment factors was selected for the open woodlands (AIC = 2195).

The survey teams, landscape types and the size of the dung boli influenced detectability. Team 1's survey yielded an estimate of 298 (95% CI: 188-475) elephants while team 2 and team 3's surveys gave estimates of 578 (95% CI: 336-1026) and 374 (95% CI: 226-640) elephants respectively (Table 3). Survey teams missed 11, 19 and 3% of all dung piles encountered on the 13, 15 and 16 sub-sample transects that were conducted while being accompanied by an independent observer. Population estimates and estimates of confidence limits were sensitive to effective strip widths - narrow effective strip widths yielded high estimates with wide confidence intervals, while wide effective strip widths yielded lower estimates with narrower confidence intervals (Fig. 2). We prefer the estimate with the widest effective strip width as an indicator of population size because it was based on our complete data set.

Total transect length had no effect on our estimates. Estimates ranged from 194 to 667 elephants, with 92% of the randomly calculated estimates falling within the 95% CI of our total estimate (Fig. 3a). In our study, increased survey intensity did not affect estimates. However, the percentage confidence interval calculated for different transect lengths reached an asymptote at 51000 m of transects (Fig. 3b).

Detection probability was not a function of boli size and a half-normal cosine model was most appropriate for both small (AIC = 632) and large (AIC = 1165) boli - the model parameters were similar.

Elephant density and numbers

Elephants occurred at a density of 0.60 (95% CI: 0.38 – 0.94) elephants per km² across the 518 km² of the MER that we sampled. The highest elephant density (0.97 elephants per km², 95% CI: 0.63 – 1.49) occurred in the sand forests. Densities in open woodlands were 0.38 (95% CI: 0.23 – 0.63) and in the grasslands 0.05 (95% CI: 0.02 – 0.10) elephants per km². When corrected for area these results yielded 234 (95% CI: 152 – 360) elephants in the sand forests, 73 (95% CI: 44 – 121) in the open woodlands and 4 (95% CI: 2 - 9) in the grasslands. The total population thus was estimated at 311 (95% CI: 198 – 490) elephants (Table 2). When the variables used in our study (decay and defecation rates) were integrated with the dung pile densities obtained by de Boer *et al.* (2000), elephant densities of 1.23 (95% CI: 0.80 – 1.88), 0.48 (0.29 – 0.79) and 0.44 (0.18 – 0.88) elephants per km^2 were calculated for the sand forests, open woodlands and grasslands respectively (Table 2). These amounted to a total population estimate of 425 (95% CI: 264 – 679).

The confidence intervals for our estimate represented a coefficient of variation of 46.95%. Inclusion of this value into a power analysis suggests that yearly elephant dung surveys for 10 years will only detect relative large changes (*e.g.* 5% annual increase or decrease) with high power (>80%). Surveys every second year for 10 years will only detect relatively large declines (*e.g.* 5% annual decrease). By doubling the monitoring period to 20 years, annual surveys will detect a 2% yearly increase in population size, where as surveys every second year may detect annual declines of 2%. Monitoring programmes that last 30 or 40 years may detect such changes with surveys at 5-year intervals (Fig. 5).

Age structure

Only one of the four surveys yielded a sample size (*n*=159) that was large enough for analysis (see Caughley, 1977). Relatively few elephants less than three years of age were noted and the age structure seemed uneven (Fig. 6).

Discussion

The small elephant population of the Maputo Elephant Reserve and their secretive nature hinder attempts to estimate population size and structure. We estimated that 311 elephants lived in the MER during 2006. Twelve previous estimates of elephant population size in the Reserve varied from 80 to 350 individuals (Morley, 2006). The population was estimated at 350 elephants in 1970 (Tello, 1973), 269 in 1972 (Tinley & Dutton, 1973) and 80 in 1979 (Klingelhoefer, 1987). The onset of the Mozambique civil war in 1979 prohibited surveys during this period (but one guess by Tello, 1986) and raised fears that the population would be influenced. Since 1995 four surveys reported estimates that ranged from 100 to 300 elephants, suggesting that elephant numbers increased since 1979 (Morley, 2006). However, none of these estimates had measures of precision and were either based on total counts during aerial surveys, or educated guesses.

Given the limitations of the historical data, we opted to estimate the number of elephants using indirect surveys. We do concede, however, that the use of an indirect method such as a dung count has sources of error other than that related to elephant behaviour or small populations. Therefore, we evaluated these and determined what their effect would be on our estimates.

The first thereof is the assumption that the elephants of the MER defecate at the mean wet season rate noted for other regions in Africa. Defecation rate is determined by the quality and quantity of food consumed (Coe, 1974) which differs from season to season. As the MER does not experience seasonal changes in rainfall that relate to vegetation changes (van Wyk & Smith, 2001) we assumed that a mean wet season defecation rate for the elephants here were the same as elsewhere.

A second source of error is dung decay, a process influenced by a variety of factors, principally dung beetle activity and precipitation (Jachmann & Bell, 1984; Barnes & Barnes, 1992). Decay rates also vary typically according to season, weather, habitat, diet, canopy cover and time of day of defecation (Laing *et al.,* 2003; Nchanji & Plumptre, 2001). We monitored dung piles for a period of 148 days under conditions prevailing in the park – more than half of the dung piles then decayed to an unrecognizable state.

For practical reasons we could not sample reed beds. Therefore the exclusion of reed beds from our analysis could be a further source of error to our estimate. However, space and habitat use of five elephants based on locations through satellite tracking showed that they spent <3% of their time in the reed beds that make up one third of the MER (Harris *et al*., 2008). Consequently we assumed that our estimate would not be affected by us not having sampled the reed beds.

Boli size, observer bias, and sampling intensity may induce errors that will influence estimates based on dung surveys. We showed that detectability of small and large boli were similar, but our observers missed 3 to 19% of dung piles. The effective strip width also differed between observers – narrow strip widths inflated estimates and *vice versa*. Strip widths also influenced confidence intervals. Consequently we consider observer bias as a major source of error in our study. Training local field rangers to conduct future surveys could result in the same observers conducting successive surveys and may reduce the effect of observer bias.

In our study the level of precision did not improve with survey intensity once the total transect length exceeded ~51 km. Future dung surveys in the MER may therefore be based on about 50 km of line transects comprising 100 transects of 500 meters each.

Considering the potential caveats of our approach, our estimate had a defined precision that lacked in earlier total counts and guesses. Our estimate exceeded most other recent estimates. The previous estimates may be correct, suggesting that elephant numbers did reach low levels then. People abandoned the area during the war years (Soto, Munthali & Breen, 2001) so that less than 1000 people lived in the MER during the mid-1990s compared to 10 000 before the war (Ogelthorpe, 1997; Morley, 2006). Such a decline could have facilitated the recovery of the elephant population.

Alternatively, the difference in estimates may not reflect on real changes in population size, but may be due to different survey methodologies returning different estimates. The dung survey by de Boer *et al.* (2000) in 1995 yielded data comparable with ours, even though they focused on roads rather than randomly placed transects. As in our study they found that the sand forest had the highest dung pile density, followed by the open woodlands and grasslands. Applying the defecation and decay rates from our study to the dung densities of de Boer *et al.* (2000) gave an estimate of 425 elephants living in the MER during 1995. This could suggest a recent decline in elephant numbers. However, due to wide confidence the change in numbers from 1995 to 2006 was not significant. The population therefore may be stable, as supported by the few infant dung boli noted during our survey.

In addition, retrospective modelling by Morley (2006) suggested that the earlier estimates of Klingelhoefer (1987) and Matthews (2000) were incorrect. The population may have declined during the period of civil unrest in Mozambique, but it may not have been as threatened as was feared at the time (Klingelhoeffer, 1987; Hall-Martin, 1988; Ostrosky, 1989; Morley, 2006).

When we examined the age structure of the MER we noticed few individuals in the 1, 2 and 3-year age classes when compared to the rest. Age structures that have been constructed by measuring dung boli are prone to errors presented by the method. The age structure constructed for the elephant population by Jachmann & Bell (1984) in Kasungu National Park in Malawi also lacked young calves. They proposed three explanations. First, newborn calves could have a lower defecation rate than the older individuals – the published literature does not support this notion (Coe, 1974). Second, small boli decay faster than larger boli – we found no difference in the decay rates at the MER. We could not analyze very small boli (<20cm) separately as our sample did not include enough very small boli. Third, the droppings of newborn calves are small and are therefore not detected by the counting teams – we found no difference in detection rates in our study. Nevertheless, the dung boli of very young elephants (<1 year of age) may be softer and more dispersed as a result of their partial milk diet and softer forage than older animals and could therefore have been more readily overlooked by observers. When grouped into broader age classes (following Jachmann & Bell, 1984) there are still a significant shortcoming of younger individuals. We thus suggest that the marked under-representation of young calves in our sample could be exaggerated by sampling error – but that there are still fewer than expected juvenile elephants aged 1-3 years in the population.

The uneven age structure for the elephants in the MER may be a result of a population that experienced some or other form of disturbance and this apparent unstable age structure prohibits estimates of survival rate (Udevitz & Ballachey, 1998) and hence modelling of intrinsic growth using demographic variables and procedures proposed by Ferreira & van Aarde (2008).

The precision of population estimates in a time series determines the ability to detect trends (Gerrodette, 1987). Our power analyses aimed to direct the intensity of future survey efforts and we recommend that a dung survey be carried out every other year for a 20-year time period. This approach will enable us to confidently detect 2% per year changes in population growth rates and therefore can facilitate the development of management strategies.

Precision is only one of the criteria to be considered when developing survey procedures as survey intensity may be limited by budgetary and logistical constraints. An aerial survey of the MER would require observers to cover the entire reserve simply because it is small (*e.g.* Douglas-Hamilton, 1996; Ntumi *et al.*, 2005) and because the population is relatively small. What is more, estimates of small populations have a low level of precision (Gerrodette, 1987) best addressed for elephants using dung surveys (Barnes, 2002). Like aerial surveys, registration studies (*e.g.* Moss 2001, Whitehouse & Hall-Martin, 2000) and mark-recapture techniques (*e.g.* Morley & van Aarde, 2007) through observation are limited by the secretive habit of these elephants. Individual identification of dung through genetic techniques (*e.g.* Eggert, Eggert & Woodruff, 2003) may enable the application of mark-recapture models to improve the precision of estimates.

In addition to cost-efficiency, easily applied techniques also carry the potential to build capacity at a local scale. For instance, our recommendation of repeated surveys over an extended period can include local field rangers participating in surveys. Supplementary data (*e.g.* age structures) obtained during dung surveys combined with field observations of activities such as poaching (Walsh & White, 1999) could tilt the cost-benefit of surveys in favour of indirect methods.

Conclusion

Dung surveys yield population estimates with known precision that could be used in monitoring programs aimed at assessing population trends. However, these estimates can be affected by observer bias. The similar dung pile densities found by de Boer *et al.*, (2000) and our own in 2006 suggest that the elephant population of the MER is most likely stable. Furthermore, the age structure derived from dung boli circumference compares well with age structures of other known age elephant populations bar the lack of 1-3 year old elephants. Future dung pile surveys at two-year intervals may shed further light on the dynamics of this relatively small and secretive elephant population.

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Table 1. Wet and dry season defecation rate (dung piles per day) and decay rates collated for 17 study areas across Africa. ± Denotes error and *n* = sample size.

Study Area	**Defecation rates**			**Days to decay to level E**			**Reference**
	Dry	**Wet**	**Unknown**	**Dry**	**Wet**	**Unknown**	
Queen Elizabeth National Park	-	-	17.0	-	-	160	Wing & Buss (1970)
Tsavo National Park	-	37.7	-	-	-	-	Coe (1974)[4]
Rua National Park	12.0	32.0	-	-	-	-	Barnes (1982)[5]
Bia National Park	-	-	-	-	-	80	Short (1983)[6]
Kasungu National Park	15.7	-	-	-	-	-	Jachmann & Bell (1984)[7]
Tai National Park	-	-	18.0	-	-	80	Mertz (1986)
Santchou Reserve	-	-	20.0	-	-	-	Tchamba (1992)[8]
Nazinga Game Ranch	14.1	27.2	-	-	-	165	Jachmann (1991)
Lope Reserve	-	-	-	-	-	81	White (1995)
Gabon	-	-	19.7	-	-	44	Barnes *et al.*, (1997)[9]
Kahuzi-Biega National Park	-	-	19.8	-	-	43	Jefferson *et al.*, (1997)[10]
Manovo-Gounda St Floris National Park	12.2	16.6					Ruggiero (1992)[11]
Maputo Elephant Reserve	14.0	20.0					De Boer *et al*., (2000)
Bossematiė Forest Reserve	16.6	18.1					Theuerkauf & Ellenberg (2000)
Banyang-Mbo Wildlife Sanctuary	-	-	-	123±30 *n*=318	89±25 *n*=552	-	Nchanji & Plumptre (2001)[12]
Parc National des Virunga				90.9	100.8	55±12 *n*=75	Mubalama & Sikubwabo (2002)
Shimba Hills National Park	-	-	19.0	-	-	125	Litorho (2003)

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[4] No day-night or age differences

[5] Bulls only

[6] Used Wing & Buss (1970) estimate of defecation rate, decay only observed for max 80 days

[7] No significant difference between sexes

[8] No significant defecation difference between seasons

[9] Used estimates obtained from bootstrapping Tchamba's (1990) defecation rates and Barnes & Barnes (1992) decay rates

[10] Used Tchamba's (1990) defecation rates, the decay rate includes 2 wet seasons and 1 dry season decay sample

[11] No significant differences between sexes, significant difference between seasons

[12] Dry and Wet season decay rates differ significantly (Nchanji & Plumtre 2001)

Table 2.Dung pile densities and population estimates (95% confidence intervals) derived from the line transect survey conducted during August 2006 and dung pile densities and population estimates (95% confidence intervals) recalculated from de Boer *et al*. (2000) for a survey conducted in 1995.

	Sand forest		Open woodland		Grassland	
	1995	2006	1995	2006	1995	2006
Area (km²)	241		190		87	
Days to decay	148 (111-184)		115 (91-139)		124 (91-155)	
Transect length (km)	4.6	36	9.4	29	4.6	33
Dung pile density per km²	4600 (3100-6600)	3629 (2381-5529)	1400 (800-2500)	1111 (654-1886)	1300 (600-2900)	148 (68-312)
Population estimate	296 (193-453)	234 (152-360)	91 (55-150)	73 (44-121)	38 (16-76)	4 (2-9)
Total population estimate (1995)	425 (264-679)					
Total population estimate (2006)	311 (198-490)					

Table 3. Observer and landscape specific survey variables and population estimates, where ESW = effective strip width. The 95% confidence intervals are presented in brackets.

Landscape type	Team 1			Team 2			Team 3		
	Estimate	Transect length (m)	ESW	Estimate	Transect length (m)	ESW	Estimate	Transect length (m)	ESW
Sand forest	212 (136- 330)	13134	4.06 (3.66-4.51)	429 (264-697)	8760	2.84 (2.67-3.03)	263 (173-401)	12146	5.07 (4.82-5.34)
Open woodland	79 (49-127)	10630	6.90 (6.15-7.75)	139 (70-278)	12548	3.17 (2.83-3.56)	104 (51-212)	7433	4.19 (3.45-5.09)
Grassland	7 (3-18)	10035	8.33 (6.54-10.62)	10 (2-51)	10061	2.17 (1.39-3.41)	7 (2-27)	13601	2.97 (2.48-3.57)
MER	298 (188-475)	33799	6.43 (5.45-7.63)	57 (336-1026)	31369	2.76 (2.30-3.33)	374 (226-640)	33380	4.08 (3.58-4.67)

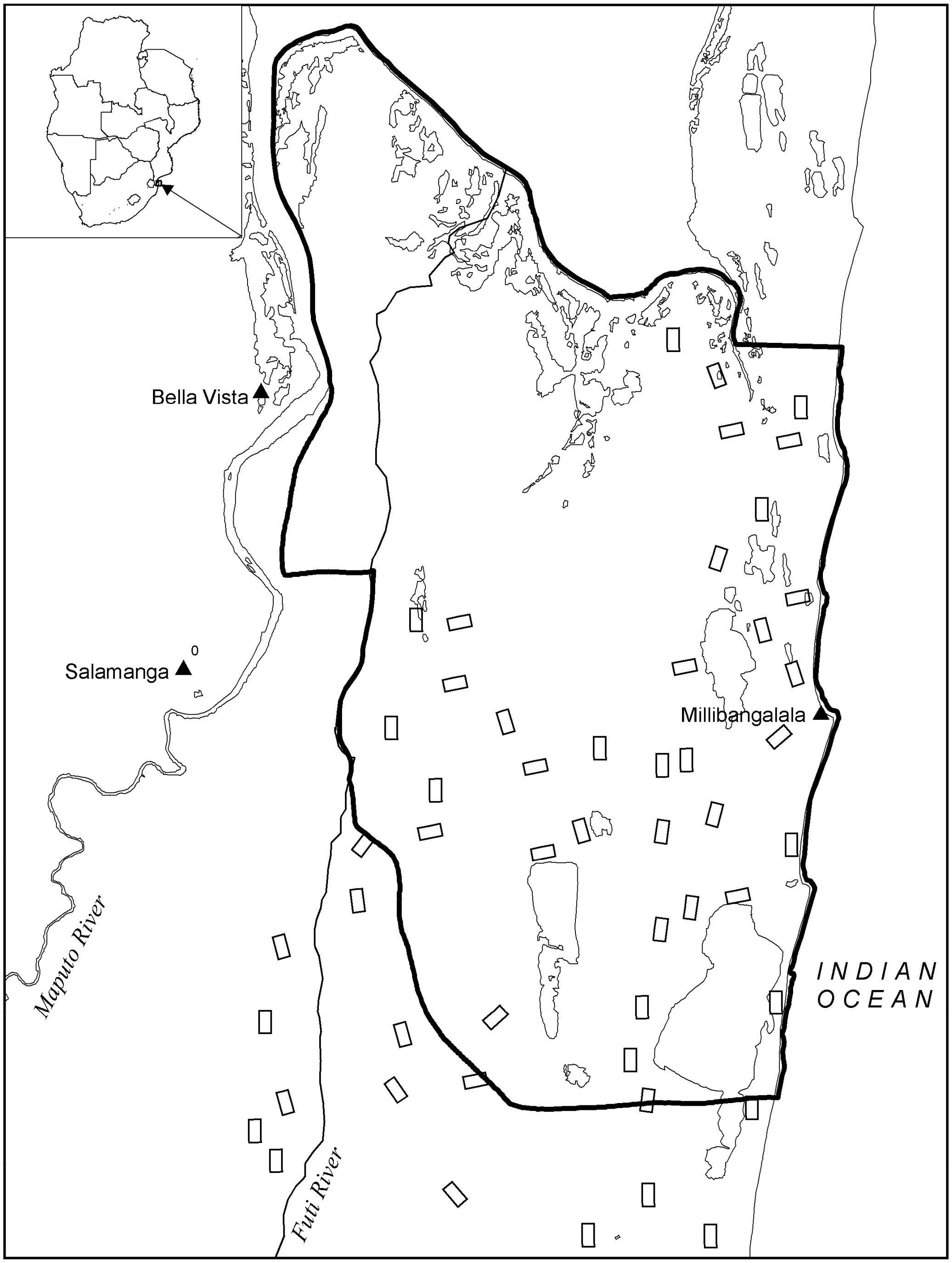

Figure 1. Map of the Maputo Elephant Reserve showing the park boundary (thick black line), rivers and lakes as well as the line transects used in the survey (squares) throughout the MER and adjacent areas.

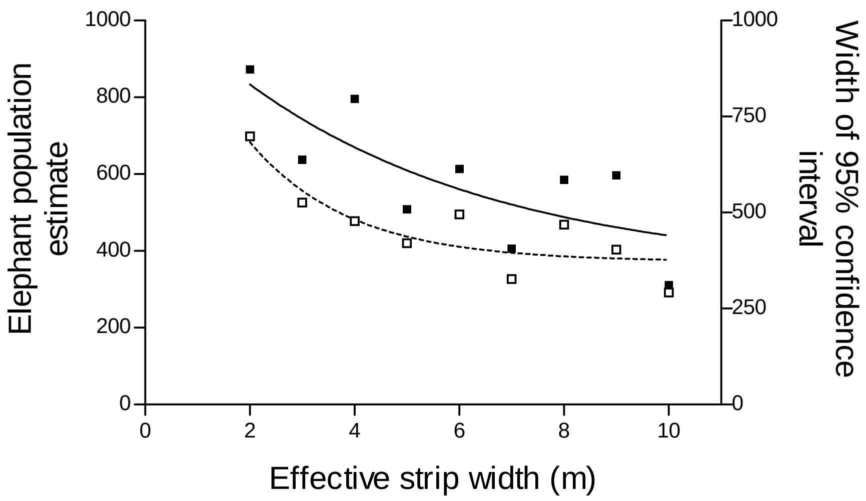

Figure 2. Population estimates (filled squares and solid line) and their 95% confidence intervals (open squares and stippled line) as a function of effective strip widths. The lines were fitted for illustrative purposes using non-linear regression analyses.

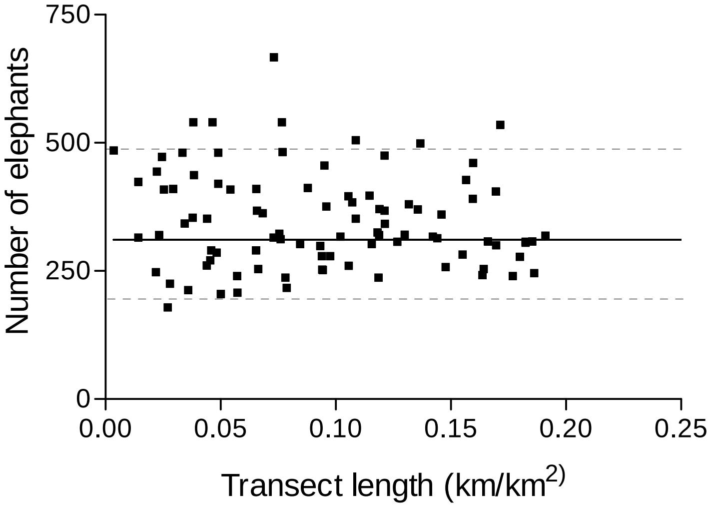

Figure 3a. Relationship between sampling intensity (transect length) and the number of elephants estimated in the Maputo Elephant Reserve. The solid line indicates our total estimate of 311 and the stippled lines indicate the 95% confidence intervals (198-490).

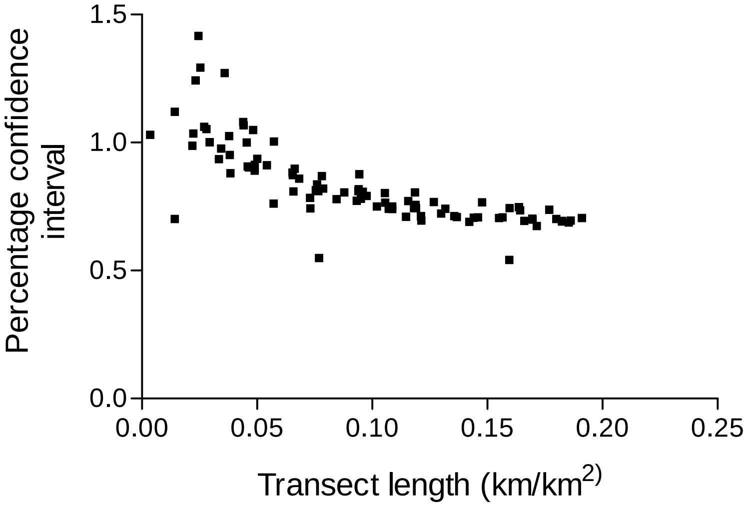

Figure 3b. Relationship between sampling intensity (transect length) and the percentage confidence levels for 100 randomly selected analyses and estimates performed by DISTANCE.

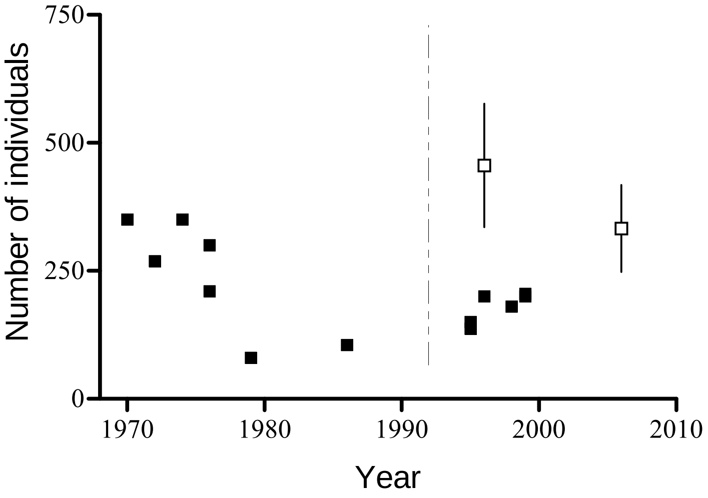

Figure 4. The number of elephants living in the Maputo Elephant Reserve. Solid squares indicate estimates from aerial counts and educated guesses. No confidence intervals were reported for these estimates. The stippled vertical line indicates the end of the Mozambican civil war in the early 1990s. To the left of the stippled line the squares indicate a population decline during and preceding the Mozambique civil war. The squares to right suggest a population recovery after that disturbance. Open squares indicate estimates with 95% confidence intervals derived from our own dung survey (2006) and the 1995 study by De Boer *et al.*, (2000). [Information from de Boer *et al.*, (2000), Ntumi (2002) and Morley (2006)].

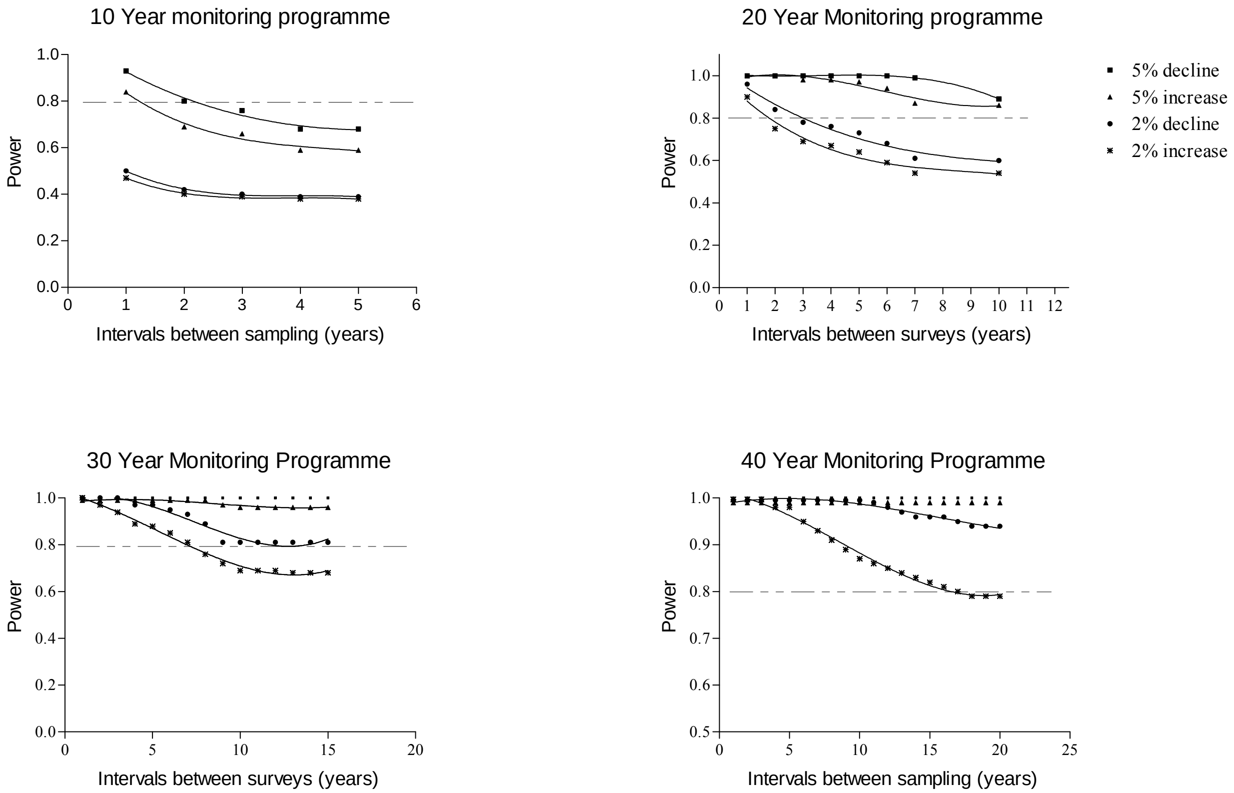

Figure 5. The ability to detect a 2 and 5% annual increase or decrease in population size as a function of the frequency of surveys. The stippled line indicates 80% power (1-β) and the curves were based on the linear model with CV=46.95% and α =0.2.

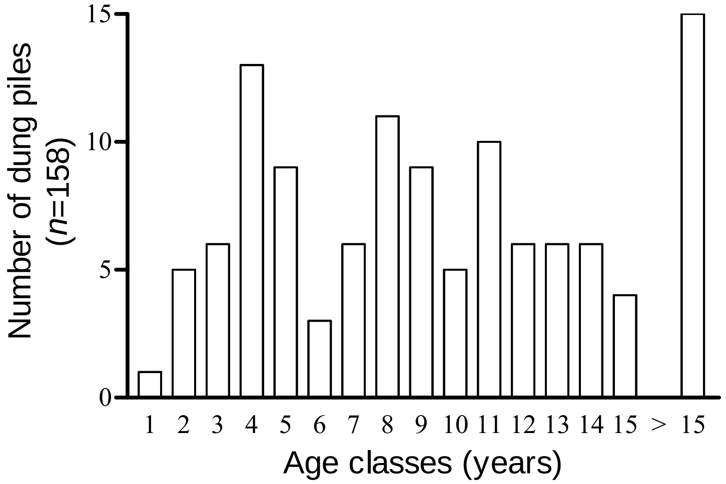

Figure 6. The age distribution for the elephant population in the Maputo Elephant Reserve based on measurements of dung boli circumference. The value in brackets indicates the number of dung piles found during a survey in August 2006.

Chapter 5

SYNTHESIS

In many protected areas in southern Africa the apparent high elephant numbers cause concern – they influence other species (Guldemond & van Aarde, 2007; 2008; Kerley *et al.,* 2009) and disrupt the livelihoods of rural people (Lee & Graham, 2006; Jackson *et al.,* 2008). Yet the problem is more complicated than it appears. Many populations in southern Africa are experiencing substantial poaching related declines (Wasser *et al.,* 2007; Wasser *et al.,* 2008) that may have lasting ecological and economic effects. Furthermore, most of the protected areas where elephants impact on other species are fenced or provided with artificial watering points. These restrict elephant movements (van Aarde *et al.,* 2006; Harris *et al.,* 2008) and may impair population regulation (van Aarde *et al.* 2008). Providing elephants with more space that will allow them to roam along seasonal and ecological gradients could be a solution to the impact that they may have on other species and humans (Owen-Smith *et al.,* 2006; van Aarde *et al.,* 2006).

The metapopulation metaphor may provide a solution for those that wish to ameliorate impact and that can allow for the demography of elephants to be limited by intrinsic and extrinsic factors rather than those enforced by management (van Aarde & Jackson, 2007). Metapopulation theory gives a key role to space in the dynamics of populations, as it explores demographic responses to spatial scale (Thomas & Kunin, 1999; Schtickzelle & Quinn, 2007) and landscape heterogeneity (Hanski, 1999). Under these conditions sub-populations can fluctuate in numbers, while the sum of total numbers across the region may remain relatively stable (i.e. birth rates equals death rates and immigration rates equals emigration rates) and less variable – an attractive scenario for ecologists interested in elephant conservation and management (van Aarde & Jackson, 2007).

My thesis evaluates the applicability of the metapopulation concept to elephant conservation management. Based on the work of others (e.g. Hanski, 1999; Elmhagen & Angerbjörn, 2001) and my own assessment (Chapter 2) I proposed that elephants and other populations of large mammals should fulfil three criteria before they are classified as metapopulations. First, the populations should comprise discrete breeding sub-populations, second, the dynamics of sub-populations have to be asynchronous, and thirdly, dispersal should occur among sub-populations. I also suggested that metapopulation theory could be useful when applied to populations of mammals when developing conservation plans to ensure population persistence and regional stability (Chapter 2).

At the time of my study most southern African elephants lived within eight potential conservation clusters (of which I considered six) and populations existed as administrative units that could be considered as sub-populations, some of which were maintained. I showed temporal and spatial asynchrony in dynamics, which implied demographic asynchrony among sub-populations as well as clusters. In addition, higher than theoretically possible growth rates for a quarter of the sub-populations suggest that dispersal took place between neighbouring sub-populations. I therefore concluded that elephant populations in southern Africa adhered to one, and possibly all metapopulation criteria.

The attractiveness of metapopulation theory for elephant conservation results from the hypothesis that, within metapopulations, local instability in growth rates can give rise to a less variable or even stable regional growth rate (see Hanski, 1999; Thomas & Kuinin, 1999). To test this hypothesis, I arranged sub-populations within each conservation cluster along two axes that combine per capita birth (B), death (D), emigration (E), and immigration (I) rates (as suggested by Thomas & Kunin, 1999; Chapter 1). Consequently each conservation cluster and its sub- populations could be represented as a metapopulation. Based on Thomas & Kunin (1999) I expected each cluster would support both source and sink sub-populations and that the growth rate for the cluster of sub-populations (metapopulation) would be less variable in time than the growth rates of sub-populations. A classic metapopulation, with a growth rate that centres on zero, will sit at the intersection of the Birth-Death, Immigration-Emigration and compensation axes (see Figure 2 in Chapter 1). To visualise each of the clusters of conservation areas as representing a metapopulation, I modified the presentation of Thomas & Kunin (1999) to reflect on the empirical status of each cluster. For this I arranged sub-populations along the compensation axes based on their growth rates as described in Chapter 3 (see Appendix I in Chapter 3).

Based on this presentation, the Chobe, Limpopo, and Zambezi conservation clusters (Figs. 1a-c) comprised mostly source sub-populations with occasional sinks. These metapopulations increased in numbers at rates ranging from 3.2 to 3.4% compared to sub-populations that varied from –8.0 to 75% here. The Etosha metapopulation (Fig. 1d) comprised one large stable and one smaller sink population. The Kafue conservation cluster (Fig. 1e) apparently comprised mainly sink populations, but for one apparent source and was decreasing in numbers, probably due to poaching as discussed in Chapter 3. The Luangwa conservation cluster (Fig. 1f) had three sources and three sinks and the metapopulation growth rate was stable after constantly decreasing before 1993 (see Chapter 3). Sub-population growth rates varied considerably more than those of metapopulations, suggesting that adherence to the metapopulation structure begets stability in growth rates – albeit not always on zero (see Fig. 2).

The southern African metapopulation (comprised of the six conservation clusters) increased at a rate of 3.1% per year since 1987 (Fig. 3). The positive growth interpolated for southern Africa's elephants as a single entity is considerably lower than the values derived by Cumming & Jones (2005) and Blanc *et al.* (2005), possibly as a result of my analysis that used the sum of interpolated estimates to calculate the regional growth rate. The continued increase is driven by trends noted for the larger conservation clusters, notably the Chobe cluster that grew at 3.3% per year and that in 2006 consisted of about 207 000 (73%) of the southern African elephants. Positive growth rates recorded for other clusters, notably the Limpopo cluster may be driven by management actions that interfere with dispersal and natural mortalities (Chapter 3). In addition, increased protection in some areas may have stabilized previously declining populations (Chapter 3).

Even though sub-populations within conservation clusters, as well as conservation clusters across the southern African region followed a metapopulation structure, metapopulation growth rates did not always centre on zero. This could be as a result of a number of factors. Firstly, the size and ratio of sources and sinks influence metapopulation growth rates (see Pullliam, 1988; Thomas & Kunin, 1999). For instance, Pulliam's (1996) review indicated that, on average, only 10% of source areas could lead to stable populations, while Novaro *et al.* (2005) recommended that more than 30% of source areas are needed to stabilize culpeo *Pseudalopex calpaeus* populations in Argentina. The different levels of rainfall and management practices as well as the variable sizes of sub-populations within conservation clusters make it difficult to predict the amount of source and sink areas needed that will lead to stable elephant populations.

Secondly, anthropogenic influences could prevent a metapopulation from stabilizing. Management action such as artificial water supplementation and fences could cause unnaturally high growth rates by preventing dispersal and natural mortalities (see Chapter 3). Conversely, high levels of poaching may cause negative rates of growth. As a result, it may be unrealistic to expect conservation clusters to always function as classical metapopulations – rather; they may alternate between existing as classic, non-equilibrium, mainland-island or patchy metapopulations. In my study, the Luangwa cluster was the only cluster that had a stable metapopulation growth rate of zero, which could indicate classic metapopulation dynamics. Increased protection was implemented during the early nineties, but sub-populations here were not fenced or provided with artificial water supplementation. The observed stable growth rate for the cluster may thus be as a result of the lack of artificial management. I therefore suggest that if management abandon actions that interfere with demographic variables such as birth and survival rates and dispersal, it might create the opportunity for metapopulation processes to drive elephant dynamics, growth and density in a way that may limit effects on other species and humans.

Elephant metapopulation dynamics have implications for conservation strategies and the management of natural resources. In more natural situations, management no longer have to centre on elephants, but could rather view the landscape as a spatially and temporally dynamic area that may not always be at equilibrium. Climate, rainfall, and forage abundance vary over time scales that range from years to decades (Barrett & Arcese, 1998; van Aarde *et al.,* 2008). Ecosystems may occupy several 'multiple stable states' at any given point in time or may be in transition from one state to another (see Bulte *et al.,* 2004). As a result, elephant population sizes and distributions may vary over time and space. Sources may turn into sinks and *vice versa*. It might thus be misleading to expect elephant populations to reach, and remain, at an idealized 'carrying capacity' as often proposed (e.g. Ben-Shahar, 1997; Hambler *et al.,* 2005).

The idea that more space will contribute to the persistence of elephant populations is not new. In order to ameliorate the effect of habitat fragmentation the concept of habitat corridors have been introduced first in Sri Lanka (Anon, 1959). Since then, the use of corridors to link isolated populations of elephants have been advocated with varying degrees of success in Africa and Asia (e.g. Johnsingh & Williams, 1999; Mpanduji *et al.,* 2002; Osborn & Parker, 2003; Sebogo & Barnes, 2003). Furthermore, the growth and decline of populations through dispersal have been illustrated by a recent study on the elephant population of Hwange National Park (Chamaillé-Jammes *et al.,* 2008). My study also support the views expressed by van Aarde & Jackson (2007) that advocated the implementation of the metapopulation metaphor to manage elephant numbers and impact through southern Africa. It is, however, the first study that I am aware of that shows elephant sub-populations within southern Africa follows a metapopulation structure, irrespective of the drivers of such dynamics.

At present the potential development of megaparks across southern Africa allow for the application of metapopulation theory to elephant conservation. In creating megaparks, conservation space that transcends international boundaries are defragmented and elephant populations can become connected across space and time in order to operate as a metapopulation where numbers can be limited through natural processes. For instance, the proposed Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) involves five countries and incorporates 36 national parks, game reserves and wildlife management areas (van Aarde *et al.,* 2006). It will eventually extend over an area of more than 300 000km^2 and support more than 200 000 elephants. In addition the Kruger National Park presently covers less than one-fifth of the 100 000km over which the Greater Limpopo TFCA eventually will stretch (van Aarde *et al.,* 2006; van Aarde & Jackson, 2007). As I have shown in this thesis, in practice, such megaparks could provide the opportunity for elephant populations to be limited more naturally through metapopulation processes.

I do not suggest that providing more space will be the solution to high elephant numbers, and the intensity with which they use areas everywhere. Elephant populations confined to small isolated areas will invariably require intensive management. However, the expansion and connection of protected areas, combined with the application of metapopulation theory to southern African elephant conservation may provide an opportunity for a spatial-temporal approach that does not focus only on numbers. Such an approach will deal with the causes rather than the symptoms of the elephant problem and may contribute to the persistence of not only elephant populations, but also biological diversity as a whole. Restoring natural processes may therefore present the future of elephant management that will focus on spatial rather than numerical aspects.

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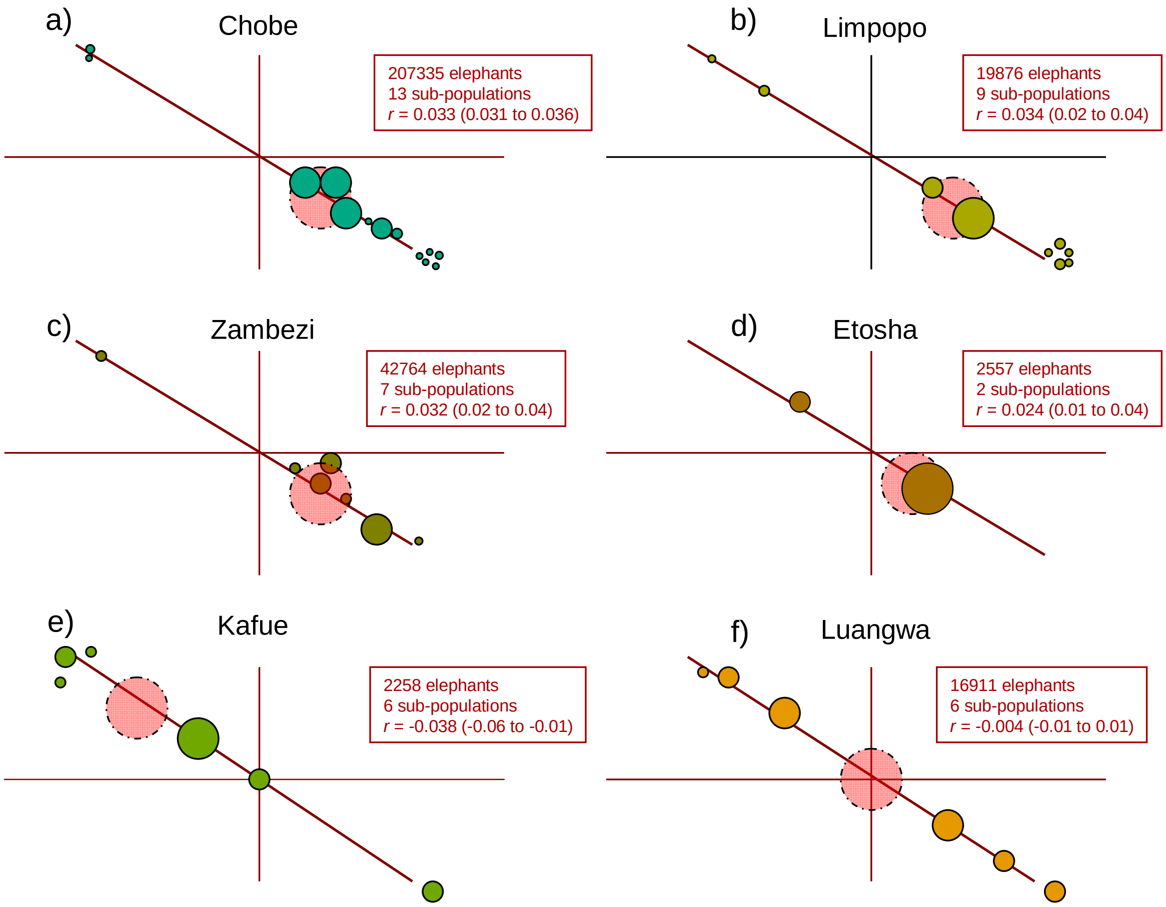

Figure 1 (a-f). A schematic representation of the six hypothetical southern African metapopulations and the distribution of sub-population units that comprise them on B-D, I-E, and compensation axes. Source populations sit in the lower right, and sink population units are situated in the upper left of the compensation axis. Population units are weighted by size; larger circles represent larger populations, at one snapshot in time. Over time, each sub-population unit will move around in demographic space, the amount of movement depending on stochastic environmental events, density dependence and anthropogenic influences such as management actions or high poaching incidences. However, the metapopulation may remain stationary in time, despite the movements of sub-populations along the compensation axis. All six metapopulations was made up of source and sink sub-populations. The Chobe, Limpopo and Zambezi metapopulations comprised mostly sources with occasional small sinks. The Etosha cluster comprised one large source population and a smaller sink. This cluster may represent an example of a mainland-island metapopulation that is driven by the Etosha National Park. The Kafue cluster may represent a potential non-equilibrium metapopulation where sub-population extinction rate may in time exceed sub-population colonization rates, possible as a result of high poaching incidences. The Luangwa cluster exhibited classic metapopulation dynamics. The figures are based on the schematic representation of demographic space as proposed by Thomas & Kunin, (1999).

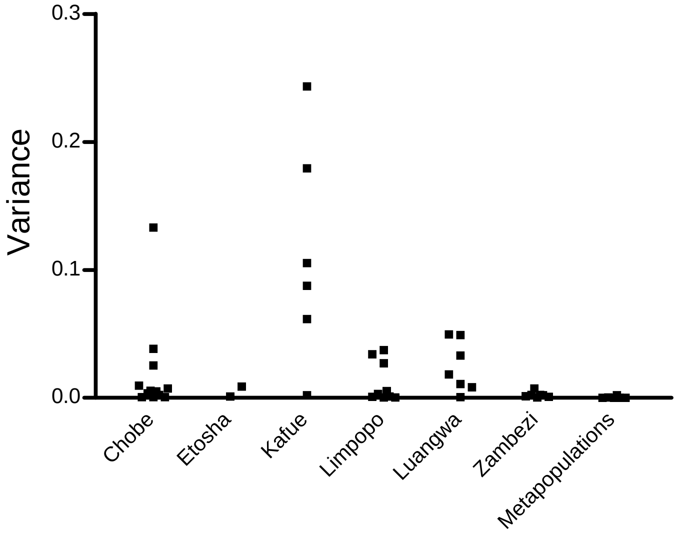

Figure 2. Variance calculated for sub-populations within conservation clusters and the variance calculated for conservation clusters (metapopulations). Sub-population growth rates varied considerably more than those of metapopulations, suggesting that adherence to a metapopulation structure may lead to stability in growth rates.

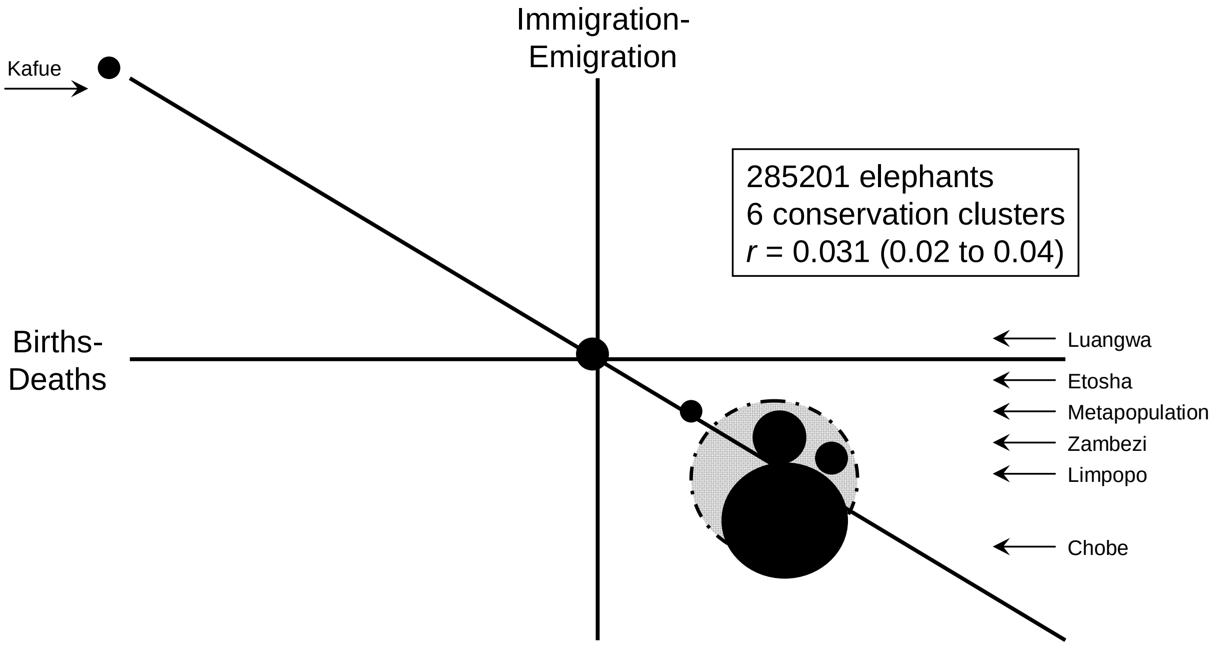

Figure 3. A schematic presentation of the southern African region as a metapopulation that shows the arrangement of conservation clusters in demographic space as implied by population growth rates calculated from population estimates from 1984-2006. The relative sizes of the shaded circles denote the number of elephants present in each cluster. The Etosha, Chobe, Zambezi and Limopopo clusters functioned as sources within the region, while the Kafue cluster was a sink. The Luangwa cluster was the only stable cluster. The broken circle indicates the relative size of the metapopulation and its location is based on the estimated intrinsic growth rate of the metapopulation. Here, the regional 'southern African metapopulation' was increasing at 3.1% annually since 1987.