An analysis of numerical trends in African elephant populations

by

Jessica Junker

Submitted in partial fulfilment of the requirements for the degree

Magister Scientiae (Zoology)

In the Faculty of Natural and Agricultural Science

University of Pretoria

Pretoria

July 2008

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

An analysis of numerical trends in African elephant populations

I had seen a herd of elephant travelling through dense native forest, pacing along as if they had an appointment at the end of the world.

Isac Dinesen, *Out of Africa*

Student: Jessica Junker

Supervisor: Professor Rudi J. van Aarde
Conservation Ecology Research Unit
Department of Zoology and Entomology
University of Pretoria
Pretoria, 0001
South Africa

Co-supervisor: Dr Sam M. Ferreira
Conservation Ecology Research Unit
Department of Zoology and Entomology
University of Pretoria
Pretoria, 0001
South Africa

Abstract

The elephant debate deals largely with population size, how elephant numbers change over time, how they may affect vegetation, and how their populations should be managed. Trends in elephant numbers frequently motivate management decisions, and past efforts to alleviate elephant impact aimed at controlling population size. However, methodological and statistical constraints may influence interpretation of trends and lead to incorrect management decisions. Furthermore, inferences about the response of elephant populations to specific management actions are seldom based on scientific evidence.

In this thesis I assess the consequences of survey design and monitoring features on the interpretation and statistical reliability of population trends as well as the effect of population management on elephant densities and population growth rates. To do this, I collated information on elephant population estimates and past management actions across Africa.

I used information from the northern Botswana elephant population to clarify temporal trends in elephant densities and numbers. Elephant numbers in northern Botswana increased from 1973 to 1993 while densities remained relatively stable. This difference in trends is due to an associated increase in survey area during the same time. In contrast, from 1996 to 2004 surveyed areas remained constant in size and neither elephant numbers, nor densities changed significantly during this time. This apparent stabilisation in numbers may have resulted from density-related elephant dispersal. This case study suggests that in open populations movements may complicate the interpretation of trends, and that differences in the rates of change in numbers and densities may have different management implications.

The precision of population estimates, sample size, population size, and the magnitude of the annual rate of population change to be detected, affect power to identify trends. Two-thirds of the 156 time series that I assembled apparently were stable, and only 30 % of these had sufficient statistical power to detect population changes. These apparent stable trends without sufficient statistical power are inconclusive and should not be used to inform management decisions.

Past elephant population management practices may have increased densities and growth rates in African elephant populations. Case studies of populations that were exposed to different management actions indicated that fencing of populations and water supplementation may have enhanced growth rates probably by influencing dispersal patterns. Thus, past management practices may have contributed to the ‘elephant problem’ by enhancing local elephant densities and population growth rates.

In this thesis, I showed that trends based on elephant numbers may be misleading when the area over which elephants were counted, increased in size. Second, despite much effort and resources devoted to the monitoring of elephant populations for more than 50 years, population estimates and time series including such estimates had low quality, thereby reducing statistical power to detect trends in population change. Third, population growth rates were associated with management, where elephant population densities grew at faster rates when managed. Future conservation efforts should take into account the methodological and statistical constraints that may influence trend analyses of elephant populations and take cognizance of the fact that management decisions need to be evaluated against expected outcomes.

Acknowledgements

First, I would like to thank my supervisor, Professor Rudi van Aarde for his guidance, intellectual input and continued support. I learned so much during my time at CERU and I feel well prepared to take on the challenges that are waiting for me in the world. Rudi, I thank you for your trust in me. I admire you as a scientist and your passion and enthusiasm, which continued to inspire me throughout my study. You have built my confidence and certainly contributed to who I am today. I will never forget you and the great time I had at CERU - I hope that my work will stand to make a difference in the way that people think about elephants and approach future conservation management decisions.

Dr Sam Ferreira as my co-supervisor as well as friend – thank you for your guidance and support regarding methodological and conceptual issues. I would also like to say thank-you to my colleagues from the ‘CERU-team’ for their friendship, support and motivation. I am especially grateful to the following people for their advice and assistance: Dr Rob Guldemond, Yolandi Ernst, Zvikomborero Tangawamira, Morgan Trimble and Kim Young. I would also like to thank Daleen Funston and Lilian Scholtz for administrative assistance and Hannetjie Boshoff and Annemarie Bezuidenhout from the library of the University of Pretoria for their remarkable efforts to retrieve documents including information on elephant population estimates. I thank John Halley for his comments regarding an earlier draft of the power-analysis paper and Louwtjie du Toit and Paul Putter for writing the software for the analysis.

This project would not have been possible without the financial support by the International Fund for Animal Welfare (IFAW), the Mozal Community Development Trust, the Peace Parks Foundation (PPF), the Conservation Foundation, Zambia and the University of Pretoria. I also want to thank the following people and organisations for allowing me to use some of their data in my thesis: the Department of Wildlife and National Parks, Botswana (DWNP), the Food and Agriculture Organisation of the United States (FAO), The World Wide Fund for Nature (WWF), the Peace Park Foundation (PPF), the Zambian Wildlife Authority, Julian Blanc and co-authors from the IUCN African Elephant Specialist Group, David Cumming, Kevin Dunham, Rowan Martin, and Neil Fairall.

Last, I would like to thank my mum and my granny for their love and their financial support throughout my many years of studying.

Disclaimer

This thesis includes three manuscripts, one which has been published, another which is in review and one which I prepared for publication. One additional manuscript, which is not part of my thesis, but of which I am co-author, has been attached as an appendix. Styles and formatting of the chapters follow the respective journal requirements. This results in some duplication in methods between chapters. Chapters 1 and 5 and the appendices follow the format requirements for the journal *Oryx* and I compiled a single reference list for these chapters. 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.

Jessica Junker

Table of contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

List of appendices

Appendix 1. Ivory poaching disrupts Zambian savanna elephant populations. Sam M. Ferreira, Rudi J. van Aarde & Jessi Junker.

Appendix 2. Reference list of documents from which I extracted information on elephant population estimates and management.

Appendix 3. List of websites that I searched to obtain both published and unpublished documents with information on elephant population estimates and management.

Appendix 4. List of areas, the region and the country in Africa (in alphabetical order) for which I collated information on elephant population estimates.

Chapter 1

General introduction

High elephant (*Loxodonta africana* Blumenbach, 1979) numbers and their apparent impact on the environment have fuelled debate about their management for more than 40 years (van Aarde & Jackson, 2007). Population trends based on numbers frequently motivated management decisions to control population size to alleviate the impact that elephants may have on other species (Owen-Smith *et al*. 2006; van Aarde *et al*., 2006; van Aarde & Jackson, 2007). Such management may ignore the factors that cause impact and large local populations in the first place. Besides, inferences about how elephant populations will respond to such management are often based on personal opinion (see Pienaar *et al*., 1966; Bell, 1983; Child, 2004) rather than scientific evidence.

This approach to management may be flawed. First, population trends based on elephant numbers and densities may differ when the size of the area over which elephants are counted changed over time. Additionally, shortcomings in survey design and monitoring features may compromise statistical power to detect trends in population change (e.g. Barnes, 2002). Ignoring such concerns could lead to the implementation of management actions that may not achieve the desired outcomes. Moreover, management that interferes with the ecological mechanisms that may limit populations, such as density dependent dispersal (see Chamaillé-Jammes *et al*., 2008) and decreased survival through drought events (see Walker & Goodman, 1983; Dudley et al., 2001) may in part be responsible for the relatively high elephant numbers and population growth rates in some areas in southern Africa (Blanc *et al*., 2005), thereby counteracting conservation efforts to reduce impact.

Notwithstanding, methodological and statistical constraints are frequently ignored in the analysis and interpretation of elephant population trends (but see Barnes, 2002). Furthermore, few studies have collated empirical evidence to assess the consequences that management practices may have for elephant populations (e.g. van Aarde *et al.*, 1999). My thesis deals specifically with these concerns.

This study addressed methodological and statistical constraints in trend analyses of African elephant populations. In addition, I investigate the effect of past management practices on elephant densities and population growth rates across Africa. The thesis comprises five chapters. In the first chapter, I provide a general introduction and I briefly describe the study area and the methods and results of my literature search. The second chapter is a case study of trends in elephant numbers and densities in northern Botswana, followed by a statistical power analysis of trends in elephant numbers across Africa (Chapter 3). The fourth chapter compares elephant densities and population growth rates between managed and unmanaged elephant populations across Africa. In chapter 5, I synthesise my findings and evaluate the relevance thereof for future population monitoring and conservation efforts. I also make recommendations with regard to the conservation management of southern Africa's elephant populations.

Study area

This study is based on a comparative approach at a continental scale. The study area therefore included the 37 range countries in sub-Saharan Africa (Fig. 1). West Africa is the region with the lowest number of elephants (12,035) and here, individual populations are relatively small (< 3,000; with the exception of Burkina Faso, which is estimated to have >

6,000 elephants). Southern Africa holds the largest number of elephants (325,345), as well as the largest population of African elephants (156,024 in northern Botswana). East- and central Africa follow with 213,393 and 113,247 elephants, respectively.

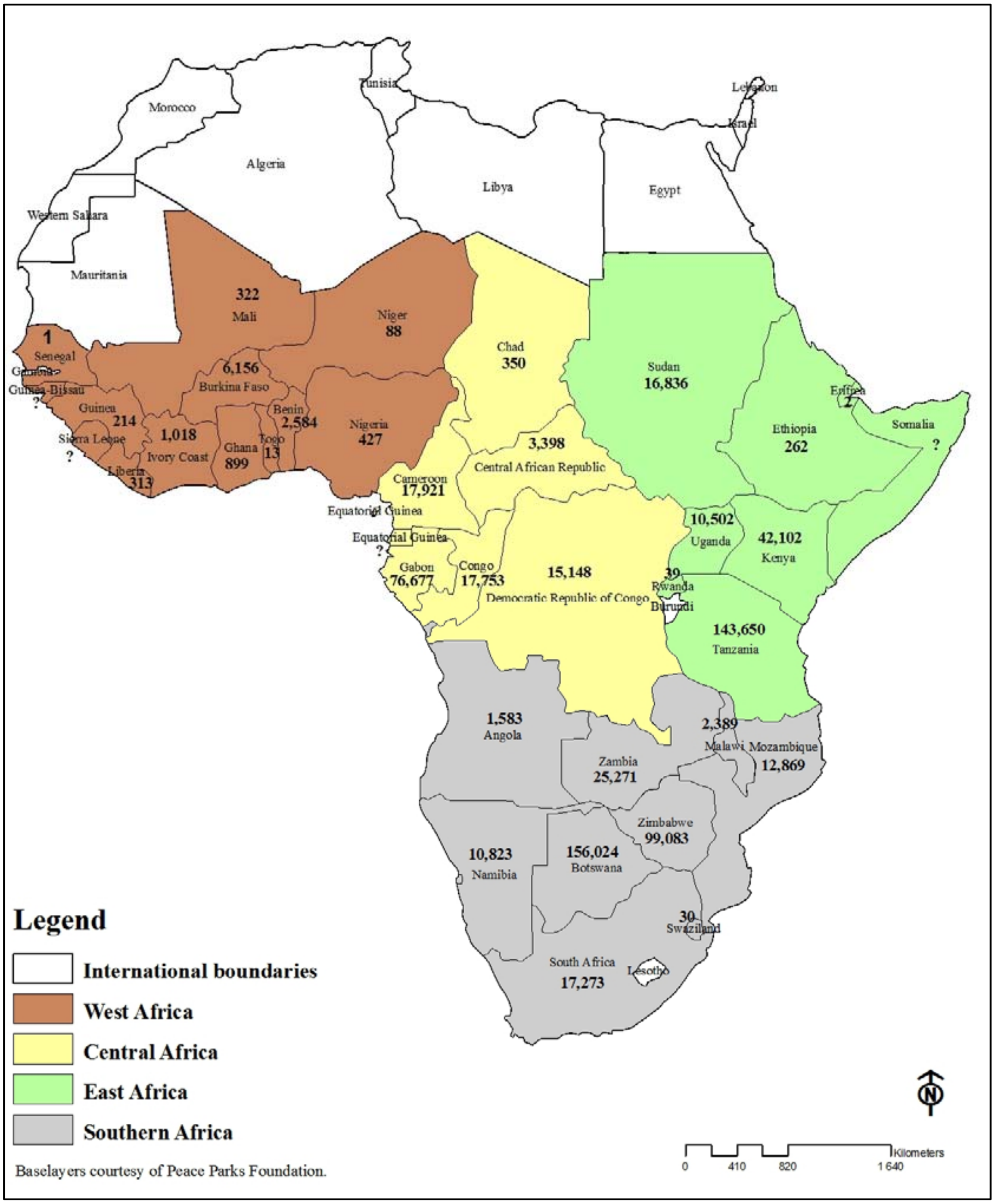


Fig. 1 Elephant range countries in Africa and their total number of elephants based on the most recent population estimates extracted from published and unpublished documents.

Countries were grouped into four regions (see Blanc *et al*., 2003), namely West, central, East- and southern Africa (indicated by different colours). The question mark indicates that elephants are believed to occur here, but that their status is uncertain.

Much of the distributional range of elephants falls beyond formal conservation areas (Blanc *et al*., 2003; Blanc *et al*., 2007). The distribution of elephants varies across the continent. In West Africa, populations are relatively small and fragmented, while elephants occur in vast and relatively undisturbed tracts of land in southern and central Africa (Blanc *et al*., 2007). East Africa ranks third in terms of range extend – behind central and southern Africa - and human population growth and associated habitat loss and fragmentation are presently threatening the long-term viability of elephant populations in this region (Blanc *et al*., 2007).

Methods and results of literature search

For this thesis I collated data on African elephant population estimates and management practices from published and unpublished documents (Appendix 2). I searched electronic databases and websites (Appendix 3), the complete *Pachyderm* series (volumes 1-41), as well as the African Elephant Databases (Said *et al*., 1995; Barnes *et al*., 1998) and Status Reports (Blanc *et al*., 2003; Blanc *et al.*, 2007). I also conducted hand searches through the reference lists of the retrieved documents. I excluded guesses from all of my analyses.

I used predetermined search criteria limited to a number of keyword combinations when searching the electronic databases (Table 1). I searched each database three times (three of the searched databases allowed me to use all combinations at once) and I used different keyword combinations for each of the three searches. To reduce bias, I exposed each database to the same three sets of keyword combinations. I constructed an accumulation curve (e.g. Srivastava, 1999; Thompson & Withers, 2003) to model search effort. Here, I plotted the number of new documents found as a function of the number of searches conducted. I stopped searching when the curve reached an asymptote.

I collated 2 494 elephant population estimates (for 862 of these, I could obtain information on population management) across 661 different areas in Africa (Appendix 4). These data were extracted from 277 documents of a total of 630 documents found during the literature search. When I plotted the number of documents against the number of database searches, the initial increase in the slope of the curve stabilized with an increase in search effort (Boltzmann sigmoid curve: $y = -173.7(323.9+173.7)/(1+\exp((0.41-x)/4.47)$; df = 17; $R^2 = 0.98$; Fig. 2a). The graph approached an asymptote after I searched 19 databases at which stage I had attained 323 documents. I pursued another two databases to find three additional documents. I then discontinued the electronic literature search. An additional 304 documents, not found previously, were retrieved from websites ($n = 55$) and searches through the relevant reference lists of documents ($n = 249$). Of all the documents, 503 were published documents, 94 were unpublished documents, and 33 were PhD ($n = 18$), MSc ($n = 14$) and Honours ($n = 1$) theses.

The earliest population estimate that I found from my literature search was for elephants in the Okavango/Caprivi region for the year 1931 (Wilhelm, 1931). The number of documents published on elephant population estimates increased over time, where most documents ($n = 162$) were published between 2000 and 2005 (Fig. 2b). The majority of documents ($n = 228$) included survey information on elephant populations in southern

Africa, followed by East- (*n* = 141), West- (*n* = 63), and central Africa (*n* = 55) (Fig. 2c). An additional 143 documents were grouped into the "General" category, which included documents that at first sight could not be grouped into a specific region or country, or that referred to more than one survey site.

Table 1 Keywords used during the literature search. Each electronic database was searched three times. Each time, I used the same string of keywords (or words contained in the title), which referred to the study animal, and a different string of keywords for each of the three searches linked by Boolean logic (here I used the conjunction "AND").

Searches 1, 2, 3	**Search 1**	**Search 2**	**Search 3**
= Keyword OR title	*= Title*	*= Title*	*= Title*
Elephant	Status	Population	Decline
"Large herbivore"	Trend	Count	Incline
"Large mammal"	Growth	Survey	Decrease
Herbivore	Dynamics	Estimate	Increase
Mammal	Demography	Rate	Survival
	Number		Age
	Distribution		Fecundity
			Structure
			Regulation
			Control
			Mortality
			Management

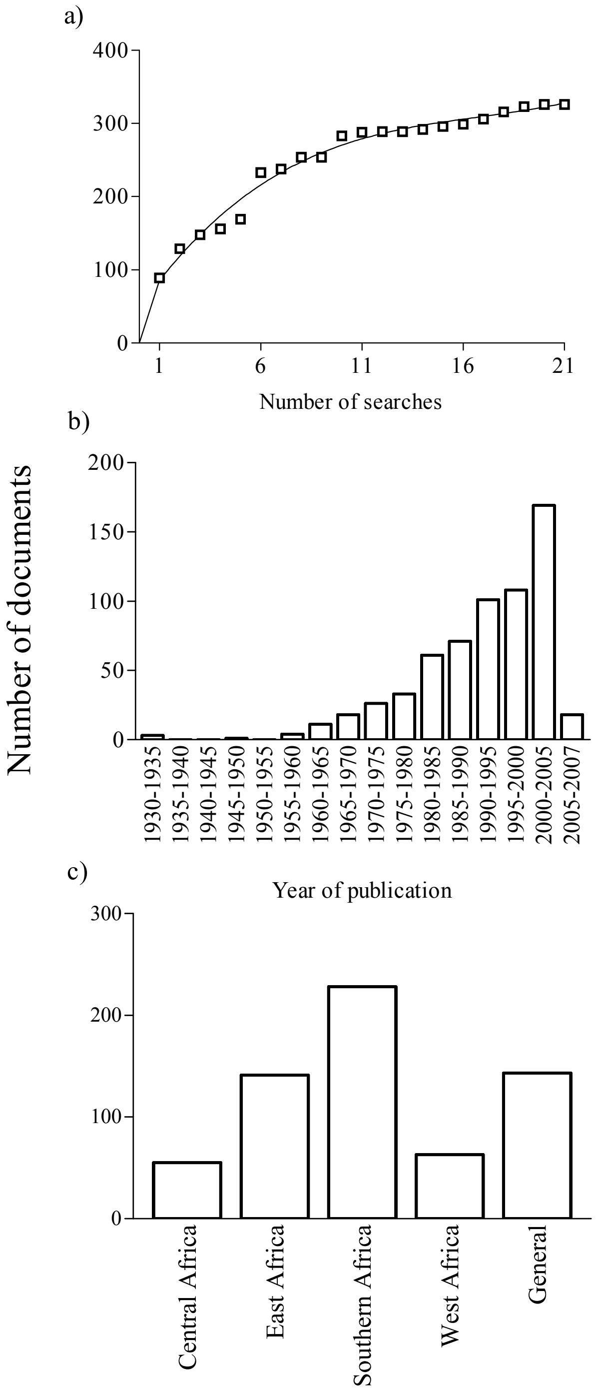


Fig. 2 Number of documents retrieved during the literature search, plotted as a function of a) the number of searches conducted, b) the year of publication, and c) the region in Africa that the document referred to.

Chapter 2

Temporal trends in elephant *Loxodonta africana* numbers and densities in northern Botswana: is the population really increasing?

Jessica Junker, Rudi J. van Aarde and Sam M. Ferreira

Jessica Junker, **Rudi J. van Aarde and Sam M. Ferreira**

Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa. E-mail rjvanaarde@zoology.up.ac.za

Running title: Elephants in northern Botswana

Oryx, Received 4 Oct 2006. Revision requested 14 Nov 2006. Accepted 21 Dec 2006. Published February 2008 (Formatted accordingly)

Abstract

The apparent increase in elephant *Loxodonta africana* numbers in northern Botswana is of concern because it may affect other species. We compared changes in population growth rates based on elephant numbers and densities over 1973-2004. Population estimates and survey details extracted from published and unpublished sources allowed us to calculate growth rates. From 1973 to 1993 growth rate was positive when based on elephant numbers but did not differ from zero when calculated for densities. This discrepancy may be because of the significant increase in survey area during the same period. In contrast, none of the growth rates differed from zero for time series between 1996 and 2004, when the size of the survey area varied little. We propose two explanations for these results. The first suggests that the population did not grow, while the second proposes that the population expanded its range and increased in size. Notwithstanding, an equilibrium model best explained the variance in dry season estimates of elephant numbers for the complete time series. Such apparent density-dependence could be disrupted by any artificial reduction of numbers through culling as a management option in northern Botswana.

Keywords: Botswana, density, elephant, intrinsic growth rate, *Loxodonta africana*, number.

Introduction

Botswana supports the largest population of African elephant *Loxodonta africana* in any country (Cumming & Jones, 2005), and numbers are apparently increasing (Gibson, *et al*., 1998; Spinage, 1990; Blanc *et al*., 2003; Cumming & Jones, 2005). This has generated concern about potential adverse effects on vegetation and on co-occurring species (Sommerlatte, 1976; Colegrave *et al*., 1992; Ben-Shahar, 1997; Skarpe *et al*., 2004) and the likely increase in human conflict (Bengis, 1996). In such cases population management is often mooted as a precaution.

There is a general assumption that elephant numbers and impact are directly related (van Aarde *et al*., 2006; van Aarde & Jackson, 2007). This may not necessarily be the case because density and, more specifically, the intensity of land use, may dictate impact. For instance, elephants in areas with a high density of water sources have smaller home ranges than those in areas with a low density of water sources (Grainger *et al*., 2005). In small home ranges elephants may use specific parts of their ranges more intensely than in large home ranges and therefore impact may be more intense. Thus, it may be more appropriate to define elephant impact in terms of range utilization functions or densities rather than population numbers per se. This is particularly important for open populations where movement is not restricted by fences. In such cases, elephant movements may complicate the interpretation of trends in population size because an increase in number may not equate to an increase in density if the population expands its range. The northern Botswana elephant population may represent such a case.

Growth rates based on time series data may serve as a first estimate of population trends but the interpretation of these trends may be constrained by methodological aspects. For instance, an expansion of survey area over time could return an increase in number while density remains the same. Differences in the rates of change in numbers and densities may have different management implications and it is therefore important to address temporal trends in both.

Here we collated information on elephant population estimates and survey areas for northern Botswana, from which we calculated densities and intrinsic growth rates. We compare changes in these parameters over 1973-2004 to clarify temporal trends. Identification of any trends may guide future management actions to control the assumed impact that elephants may have on other species and on the livelihoods of people that live in areas onto which elephants are apparently expanding (Chafota & Owen-Smith, 1996).

Methods

As most of Botswana's elephants occur in the northern parts of the country (Gibson *et al*., 1998), we extracted population estimates and survey details for elephants in northern Botswana from published (Melton, 1985; Gibson *et al*., 1998) and unpublished (Sommerlatte, 1976; DWNP, 1996, 1999a,b, 2001, 2002, 2003, 2004) sources. For all surveys, Method II of Jolly (1969) provided population estimates from fixed-width transects of unequal size sampled without replacement. Surveys were conducted during both dry and wet seasons. We excluded a 1985 survey (Spinage, 1990) for which the methodology was unknown. We also omitted estimates based on partial surveys conducted in 1983, 1984 and 1995 (Gibson *et al*., 1998) and the 2005 survey conducted by the Department of Wildlife and National Parks (DWNP). In each case the survey area was that area for which the authors estimated population size. We calculated crude density (Gaston *et al*., 1999) as the number of elephants per km^2 survey area.

From 1996 to 2004 surveys were countrywide, used standardized methods, and covered areas of 425,694 - 578,364 km^2. For these surveys the DWNP divided the population estimate by the total area covered represented by all transects, irrespective of whether elephants occurred there or not. Because much of the survey area stretched beyond the known elephant range in northern Botswana, we opted to calculate ecological densities (Gaston *et al*., 1999) for each of these years by dividing the population estimate by the sum of transect areas along which elephants were counted. The 1994 survey covered all of Botswana but we excluded these data from our analysis of trends in numbers and densities because Gibson *et al*. (1998) did not provide information that could be used to calculate the area over which elephants were encountered.

Following our filtering, the database represented two time periods: the first (1973-1993) comprised population estimates and crude densities and the second (1996-2004) population estimates and ecological densities. We used least squares regression analysis to test whether the natural logarithm of population estimates (expressed as elephant numbers) and elephant densities increased with time during each of these periods. The slopes and variances yielded estimates of exponential growth and their variances (Caughley, 1977). To accommodate the variances of population estimates in our calculation of population growth rates, we used Monte Carlo simulations (Manly, 1991). This allowed us to estimate growth rates and their variance alternatively. We randomly drew population sizes from normal distributions defined for each population estimate and then recalculated exponential growth as the slope of the linear regression. We repeated this to find 2,000 estimates of population growth from which we calculated variance (Legendre & Legendre, 1998). From these we could define standard errors for both methods of estimating population growth rate. We also used regression analysis to examine temporal trends in survey areas during each of the time periods.

In our final analyses we fitted two models to the complete time series of population estimates. We fitted an equilibrium model (Boltzman sigmoidal model $y = a + (b-a) / \left[1 + e^{((v_{50} - x)c} \right]$, where a = lower asymptote, b = equilibrium population size or density, v_{50} = the population estimate halfway between the lower asymptote and equilibrium, and c = growth when population size or densities are near a), and a non-equilibrium model (exponential model, $y = a\,e^{bx}$, were a = population size at time zero and b = the growth rate) using *GraphPad Prism v. 3* (GraphPad Software, San Diego, USA). We relied on the F-test in *GraphPad Prism* to choose the best model.

Results

Differences in sampling procedures that affected density estimates required us to analyse the data for the two time periods separately. The first period included eight estimates for dry and wet seasons but not all estimates were for the same years. As we had only one wet season estimate for the second time period, we excluded this period from the analysis of wet season data (Table 1).

Seasonal differences in estimates were not consistent (paired t-test $t = 0.39$, df = 7, P = 0.71). From 1973 to 1993 elephant numbers and densities were 8,542-79,033 and

0.34-0.98 km^{-2}, respectively. From 1996 to 2004 elephant numbers were 100,538-151,000 and densities 0.73 -1.06 km^{-2}. Variances of population estimates for 1973-1993 differed for both the dry (F_{max} = 168.55, df = 5, P <0.05) and wet seasons (F_{max} = 8.76, df = 4, P <0.05). However, variances for population estimates over 1996-2004 were similar (F_{max}= 1.61, df = 4, P = 0.15).

Population growth rates calculated by regression analysis from population estimates for 1973-1993 were 11.2 ± SE 0.53% and 9.6 ± SE 1.11% (Fig. 1a,b, Table 2) for the dry and wet seasons, respectively. Monte Carlo simulations predicted growth rates of 11.1 ± SE 0.51% during the dry and 9.5 ± SE 0.54% during the wet season (Table 2). In contrast, growth rates in elephant densities for the same time period did not differ significantly from zero (Fig. 1a,b, Table 2). Growth rates for population estimates and densities differed significantly (F_{dry} = 34.0, df = 1,6, P_{dry} <0.0001; F_{wet} = 60.52, df = 1,6, P_{wet} <0.0001).

From 1996 to 2004 neither elephant numbers nor densities changed significantly (Fig. 1c, Table 2). Estimated population size averaged 120,292 ± SE 13,990 and mean elephant density was 0.91 ± SE 0.06 km^{-2}.

From 1973 to 1993 the size of the survey area increased significantly over time during both the dry and wet seasons (F_{dry} = 15.10, df = 1,6, P_{dry} <0.01; F_{wet} = 205.30, df = 1,6, P_{wet} <0.0001; Fig. 2a,b). However, since 1996 the size of the area over which elephants were encountered during surveys (averaging 134,800 ± SE 9,513 km^2) did not change significantly (F = 4.94, df = 1,4, P = 0.09; Fig. 2c). However, statistical power for this regression is relatively low ($1-\beta = 0.37$), resulting in an increased probability of making a Type 2 error, i.e. falsely accepting that the size of the area over which elephants were encountered during surveys did not change.

The time series combining dry season elephant numbers from both periods were best described by an equilibrium model (Boltzman sigmoidal; $F = 4.50$, df = 11, $P < 0.05$, $R^2 = 0.97$; Fig. 3). This suggests that, as elephant numbers increased over time, population growth rate declined until it did not differ significantly from zero.

Discussion

Between 200,000 and 400,000 elephants may have lived in Botswana at the beginning of the 19th century (Campbell, 1990), mostly in the north. In the 80 years that followed, uncontrolled commercial hunting for ivory exterminated elephants from southern Botswana and reduced their population to a mere remnant in the far north (Campbell, 1990). The reinvasion of the region by the tsetse fly, the subsequent collapse of the cattle population, and improved protection (Melton, 1985) caused elephants to reappear along the Chobe River by the late 1940s (Sommerlatte, 1976). Hearsay, suggesting that numbers increased, was supported by spoor and direct ground surveys carried out over 1963-1970 (Sommerlatte, 1976; Campbell, 1990).

The first aerial counts in 1973-1975 were motivated by concerns that elephants may become overabundant in this region (Sommerlatte, 1976). Since then, elephants in northern Botswana have been counted repeatedly, albeit at varying time intervals and survey intensities (Melton, 1985; Gibson *et al*., 1998 and sources therein, including KCS, 1984, 1985; Work, 1986; Gavor, 1987; Calef, 1988, 1990; Craig, 1991, 1996; Bonifica, 1992; DWNP, 1993, 1995; ULG, 1993, 1994). However, survey methods were standardized in the mid 1990s (DWNP, 1996, 1999a,b, 2001, 2002, 2003, 2004).

The census data from 1973 to 1993 revealed a significant increase in elephant numbers in northern Botswana. During this period mean annual growth rate exceeded the maximum 7% estimated for elephants (Calef, 1988). This may have been because of elephants dispersing from Zimbabwe, Zambia, Angola and Namibia (Campbell, 1990; Gibson *et al*., 1998). In contrast, the growth rate for elephant densities during the same time did not differ from zero. How can this anomaly be explained?

A key constraint in the analysis of these temporal trends is that the surveys were carried out in areas that differ in size (surveyed areas increased from 1973 to 1993 but remained relatively constant afterwards). There are two possible explanations for the different trends in numbers and densities recorded before 1993. The first is that both the range of the population and the population size were stable over time and that we recorded an increase in numbers while densities remained constant; the initial surveys focused on only a fraction of the area in which elephants occur, and later survey areas increased until the entire range of the population was included (Fig. 4a). The second explanation is that both the range of the population and elephant numbers increased over time and surveys focused on those areas in which elephants were relatively abundant. Surveys thus covered larger areas over time in response to the expansion of elephant range and, as a result, more elephants were counted in larger areas, resulting in an increase in estimates of elephant numbers while densities remained relatively stable (Fig. 4b). We cannot unequivocally distinguish between the two explanations. However, given the historical accounts of the distribution of elephants in Botswana (Sommerlatte, 1976; Campbell, 1990) it seems likely that this population increased and expanded its range from 1973 to 1993, i.e. in recovery following a precipitous decline.

Changes in surveyed areas do not constrain the trends recorded from 1996 to 2004 because the DWNP conducted countrywide surveys that included the entire range of Botswana's elephants. Elephant numbers for this period were therefore comparable between years, and neither the number of elephants nor densities changed significantly. This is in contrast to some earlier reports and deductions that implied a continuing increase of the northern Botswana population (Blanc *et al*., 2003, 2005; Cumming & Jones, 2005).

If the first explanation is correct, then the stabilization of numbers could be the result of surveys having reached the periphery of the range of the population. However, if the second explanation is correct, then the onset of density-dependence (Sinclair, 2003; Owen-Smith *et al*., 2006; Chamaillé-Jammes, *et al*., 2007) could be responsible for the apparent stabilization in numbers. The underlying mechanisms for any such stabilization are not yet clear but may result from density-dependent dispersal. Dispersal may also explain the abrupt increase in numbers from 2003 to 2004 (Fig. 3, Table 1). During this period surveys used standardized methods, yielding estimates with similar levels of precision. Therefore, the differences in population size may be the result of movements by elephants across national boundaries rather than variation in census error or population increase through reproduction. These matters need further investigation, most importantly by making use of synchronized counts across countries and population boundaries. Density-dependent stabilization, if it occurs, would be of particular importance for conservation management. For instance, should the levelling off in population size be induced by density, a reduction in numbers would merely be followed by an increase in growth rate.

Irrespective of which of the two explanations is correct, it appears that elephant numbers in northern Botswana have begun to stabilize despite a high growth rate noted previously (Gibson *et al*., 1998). Our results support this notion. An equilibrium model best described the trend in dry season elephant numbers over time, suggesting that population growth decreased with an increase in population size. Analyses of changes in elephant distribution and seasonal variability in densities calculated from survey data may identify areas where elephant impact and conflict is most intense. In addition, analyses that compare count-based growth rates and demographically derived growth rates may clarify the contribution of emigration and immigration to local population sizes.

Trends aside, the expansion of the elephant population onto its traditional distributional range (Campbell, 1990; Gibson *et al*., 1998), now inhabited by people, is a matter of concern because the livelihoods of people are influenced by the presence of elephants (Jackson *et al*., 2007). However, the expansion of the range has the benefit of ameliorating impact on vegetation by allowing seasonal changes in habitat utilization through the restoration of traditional migratory patterns (van Aarde *et al.,* 2006), and also helps maintain metapopulation dynamics and caters for local instabilities (van Aarde & Jackson, 2007). The regional management of landscapes and spatial utilization could therefore replace the need for the local management of numbers. The DWNP has expressed concern about the possible impact that elephants may have on biodiversity and included this as a criterion for management action in Botswana's Elephant Management Plan (DWNP, 1991 in Herremans, 1995). However, no culling of elephants has taken place in Botswana to date and the management plan is currently under review. Based on our recent satellite tracking studies and on the work of Verlinden & Gavor (1998) we know that northern Botswana's elephants are part of a much larger regional population. Any efforts to reduce Botswana's elephants to ameliorate local impacts may therefore have regional effects on dispersal and hence on apparent local population trends, as has been illustrated for elephants in the Kruger National Park (van Aarde *et al.*, 1999). This may nullify efforts to lower impact on local vegetation and other species.

References

Bengis, R.G. (1996) Elephant population control in African national parks. *Pachyderm*, **22**, 83-86.

Ben-Shahar, R. (1997) Elephants and woodlands in northern Botswana: how many elephants should be there? *Pachyderm,* **23**, 41-43.

Blanc, J.J., Barnes, R.F.W., Craig, C.G., Douglas-Hamilton, I., Dublin, H.T., Hart, J.A. & Thouless, C.R. (2005) Changes in elephant numbers in major savanna populations in eastern and southern Africa. *Pachyderm*, **38**, 19-28.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, C.G. & Barnes, R.F.W. (2003) *African Elephant Status Report 2002. An Update from the African Elephant Database.* IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Calef, G.W. (1988) Maximum rate of increase in the African elephant. *African Journal of Ecology*, **26**, 323-328.

Campbell, A.C. (1990) History of elephants in Botswana. In *The Future of Botswana's Elephants*. *Proceedings of Kalahari Conservation Society Symposium, 1990* (eds P. Hancock, M. Cantrell & S. Hughes), pp. 5-15. The Kalahari Conservation Society/Department of Wildlife and National Parks, Gaborone, Botswana.

Caughley, G. (1977) *Analysis of Vertebrate Populations*. John Wiley & Sons, New York, USA.

Chafota, J. & Owen-Smith, N. (1996) Options for the management of elephants in northern Botswana. *Pachyderm*, **22**, 67-73.

Chamaillé-Jammes, S., Valeix, M. & Hervé, F. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, **44**, 625-633.

Colegrave, R.K., Lungu, E.M. & Muwezwa, M.E. (1992) What is happening to the elephants in Botswana? *Revue de Bio Matematique*, **30**, 49-55.

Cumming, D. & Jones, B. (2005) *Elephants in Southern Africa: Management Issues and Options*. WWF–SARPO Occasional Paper No. 11. WWF–SARPO, Harare, Zimbabwe.

DWNP (Department of Wildlife and National Parks) (1996) *Aerial Census of Wildlife and some Domestic Animals in Botswana. Dry Season 1996.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (1999a) *Aerial Census of Wildlife and some Domestic Animals in Botswana. Dry Season 1999.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (1999b) *Aerial Census of Wildlife and some Domestic Animals in Botswana. Wet Season 1999.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (2001) *Aerial Census of Animals in Botswana. Dry Season 2001.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (2002) *Aerial Census of Animals in Botswana. Dry Season 2002.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (2003) *Aerial Census of Animals in Botswana. Dry Season 2003.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

DWNP (Department of Wildlife and National Parks) (2004) *Aerial Census of Animals in Botswana. Dry Season 2004.* Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Gaston, K.J., Blackburn, T.M. & Gregory, R.D. (1999) Does variation in census area confound density comparisons*? Journal of Applied Ecology*, **36**, 191-204.

Gibson, D.S., Craig, G.C. & Masogo, R.M. (1998) Trends of the elephant population in northern Botswana from aerial survey data. *Pachyderm*, **25,** 14-27.

Grainger, M., van Aarde, R.J. & Whyte, I. (2005) Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology*, **43**, 369–375.

Herremans, M. (1995) Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. *Ecography*, **18**, 440-454.

Jackson, T.P., Mosojane, S., Ferreira, S. & van Aarde, R.J. (2008) Solutions for elephant crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx*, **42**, 83-91.

Jolly, J.M. (1969) Sampling methods for aerial censuses of wildlife populations. *East African Agriculture and Forestry Journal*, **34**, 46-49.

Legendre, L. & Legendre, P. (1998) *Numerical Ecology*, 2nd edition. Elsevier, Amsterdam, The Netherlands.

Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, London, UK.

Melton, D.A. (1985) The status of elephants in northern Botswana. *Biological Conservation*, **31**, 317-333.

Owen-Smith, N., Kerley, G.I.H., Page, B., Slotow, R. & van Aarde, R.J. (2006) A scientific perspective on the management of elephants in Kruger National Park and elsewhere. *South African Journal of Science,* **102**, 389-394.

Sinclair, A.R.E. (2003) Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society London B*, **358**, 1729-1740.

Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., Du Toit, J.T. *et al*. (2004) The return of the giants: ecological effects of an increasing elephant population. *Journal of the Royal Swedish Academy of Sciences*, **33**, 276-282.

Sommerlatte, M.W. (1976) *A Survey of Elephant Populations in North-eastern Botswana.* Department of Wildlife and National Parks, UNDP/ FAO Project

72/020, Wildlife Management and Utilisation in Botswana. Government Printer, Gaborone, Botswana.

Spinage, C.A. (1990) Botswana's problem elephants. *Pachyderm*, **13**, 14-20.

Van Aarde, R.J. & Jackson, T.P. (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation,* **134**, 289-297.

Van Aarde, R.J., Jackson, T.P. & Ferreira, S.M. (2006) Conservation science and elephant management in southern Africa. *South African Journal of Science,* **102**, 385-388.

Van Aarde, R., Whyte, I. & Pimm, S. (1999) Culling and dynamics of the Kruger National Park African elephant population. *Animal Conservation*, **2**, 287-294.

Verlinden, A. & Gavor, I.K.N. (1998) Satellite tracking of elephants in northern Botswana. *African Journal of Ecology*, **36**, 105-116.

Table 1 Population estimates (with 95% confidence limits where available), size of the areas for which the estimates were extrapolated, and elephant densities (with 95% confidence limits) for both wet and dry seasons, and the source reference. All densities are rounded to the second decimal place.

Year	Wet season			Dry season			Reference
	Population estimate	Survey area (km^{2})	Density (km^{-2})	Population estimate	Survey area (km^{2})	Density (km^{-2})	
1973	11,205	20,034	0.56	8,671 (7,120-10,227)	16,782	0.52 (0.40-0.61)	Sommerlatte, 1976
1974	11,027	23,365	0.47	8,542 (6,465-10,619)	19,752	0.43 (0.33-0.54)	Sommerlatte, 1976
1975				13,520	23,389	0.58	Sommerlatte, 1976
1981	39,511	93,400	0.42				Melton, 1985
1987	50,440 (40,352-60,528)	119,774	0.42 (0.34-0.51)	40,530 (26,750-54,310)	119,774	0.34 (0.22-0.45)	Gibson *et al.*, 1998
1989	66,051 (45,554-86,548)	132,016	0.50 (0.35-0.66)	59,896 (42,806-76,987)	60,878	0.98 (0.70-1.26)	Gibson *et al.,* 1998
1990	49,064 (37,276-60,878)	140,387	0.35 (0.27-0.43)	55,835 (35,635-76,036)	67,206	0.83 (0.53-1.13)	Gibson *et al.*, 1998
1991	64,916 (44,864-84,968)	150,448	0.43 (0.30-0.56)	68,771 (50,571-86,971)	154,919	0.44 (0.33-0.56)	Gibson *et al.*, 1998

1993	73,901 (44,052-103,751)	143,943	0.51 (0.31-0.72)	79,033 (65,364-92,701)	166,236	0.48 (0.39-0.56)	Gibson *et al.*, 1998
1994	54,927 (41,082-68,772)	573,694[1]		78,304 (61,477-95,131)	579,049[1]		Gibson *et al.*, 1998
1996				100,538 (80,452-120,624)	94,554[2]	1.06 (0.85-1.27)	DWNP, 1996
1999	106,494 (84,898-128,090)	109,284[2]	0.97 (0.78-1.16)	120,603 (98,934-142,274)	150,646[2]	0.80 (0.66-0.94)	DWNP, 1999a,b
2001				116,987 (95,196-138,779)	118,257[2]	0.99 (0.80-1.17)	DWNP, 2001
2002				123,152 (106,000-140,304)	146,059[2]	0.84 (0.73-0.96)	DWNP, 2002
2003				109,472 (91,028-127,914)	151,054[2]	0.73 (0.60-0.85)	DWNP, 2003
2004				151,000 (130,995-171,004)	148,202[2]	1.02 (0.88-1.15)	DWNP, 2004

---

[1] Countrywide surveys; survey area is the entire area over which the survey was conducted.

[2] Countrywide surveys; survey area is the area over which elephants were encountered.

Table 2 Linear regression analysis and Monte Carlo simulations used to calculate intrinsic growth rates (*r)*, expressed as a percentage. The slopes of the regression lines represent *r*. Growth rates in elephant numbers and densities are calculated separately for wet and dry season and for 1973-1993 and 1996-2004. Both numbers and densities were $\log_e$ transformed for the linear regression analyses. Significant regressions are in bold.

	Years	Simulation	Wet season					Dry season				
			r (%)	SE	***F***	df	P	*r* (%)	SE	***F***	df	P
Numbers	1973-1993	Linear	9.6	1.11	73.94	1,6	**<0.0001**	11.2	0.53	435.7	1,6	**<0.0001**
		Monte Carlo	9.5	0.54				11.1	0.51			
	1996-2004	Linear						3.27	1.7	3.83	1,4	0.12
		Monte Carlo						3.37	1.4			
Densities	1973-1993	Linear	-0.72	0.7	1.00	1,6	0.36	0.75	1.7	0.20	1,6	0.67
		Monte Carlo	-0.81	0.6				0.72	0.5			
	1996-2004	Linear						-0.17	2.47	0.47	1,4	0.53
		Monte Carlo						-1.63	1.38			

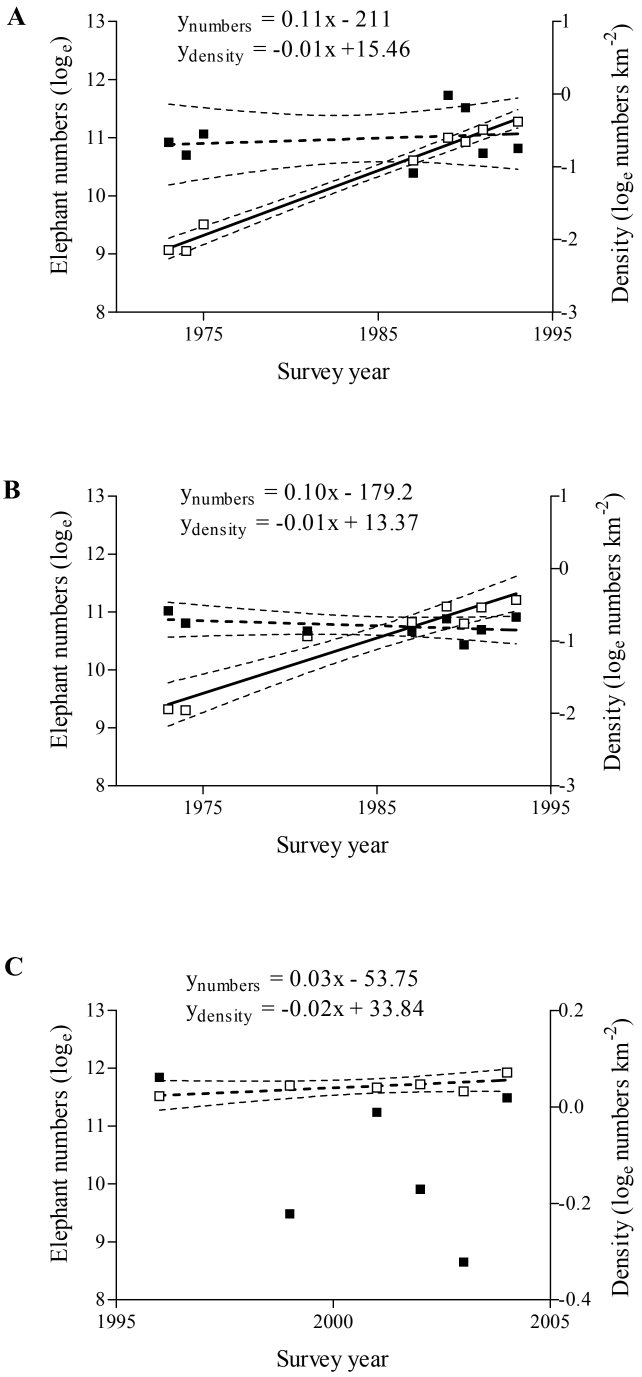


Fig. 1 Linear regressions (with 95% confidence limits) of the natural logarithm of (a) dry season and (b) wet season elephant numbers (open squares) and densities (solid squares) for 1973-1993, and (c) dry season elephant numbers and densities for 1996-2004. The regression line of density for 1996-2004 had wide confidence limits and is not shown. The slopes of the linear regressions represent intrinsic annual growth rates (*r*). Solid and stippled regression lines indicate significant and non-significant slopes, respectively. Note the different scaling of the vertical axis.

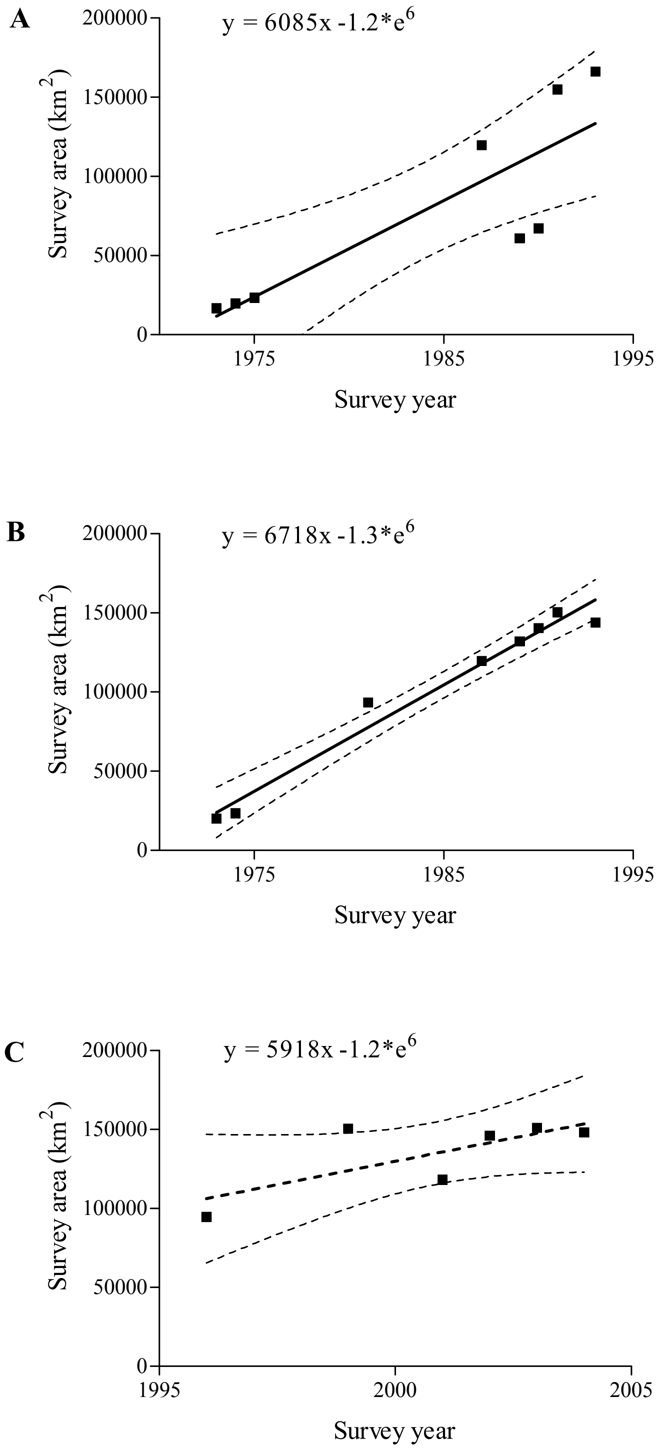


Fig. 2 Linear regressions (with 95% confidence limits) of (a) dry and (b) wet season survey area sizes for 1973-1993, and (c) dry season survey area sizes for 1996-2004. Solid and stippled regression lines indicate significant and non-significant slopes, respectively.

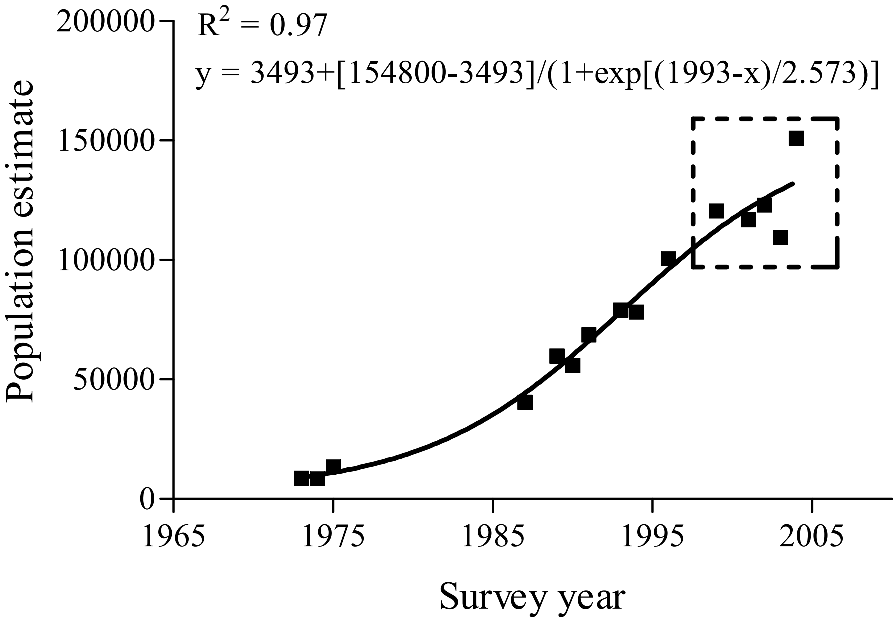


Fig. 3 Dry season elephant numbers for 1973-2004. The data converged best to a Boltzman sigmoidal curve, suggesting that numbers are currently stabilizing.

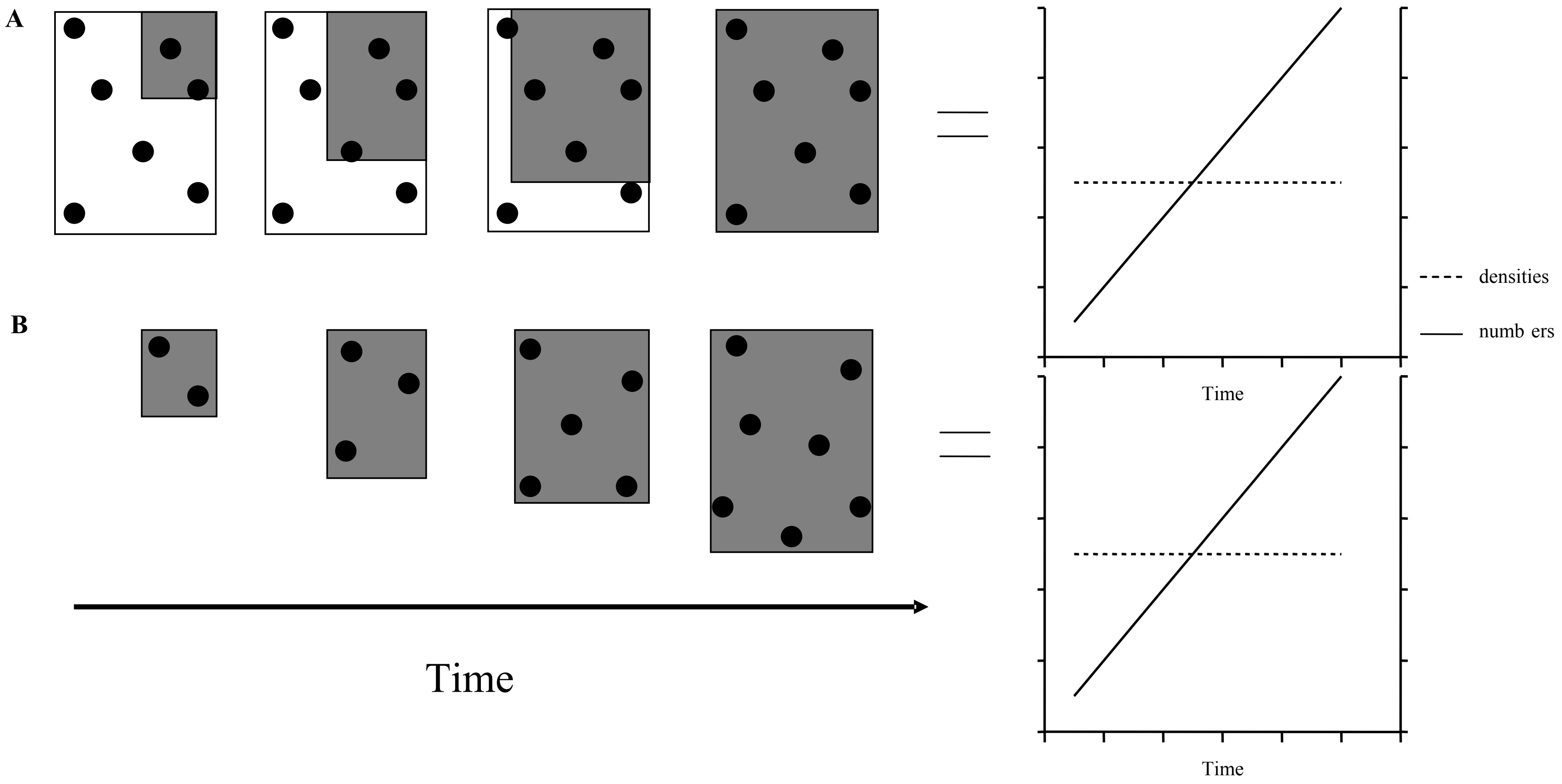


Fig. 4 Simplified illustration of the two possible explanations for the trends in numbers and densities over time observed for the northern Botswana elephant population. Solid dots depict individuals and grey shading survey areas. The explanations differ in that the first (a) proposes a stable range and population size over time, whereas the second (b) suggests that the population increased in size and expanded its range over time (see text for further details).

Chapter 3

Detecting population trends in African elephants

Jessica Junker[*], Rudi van Aarde[*], Sam Ferreira[*□]

[*] Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

[□] Scientific Services, South African National Parks, Skukuza, South Africa

Correspondence: Rudi van Aarde, Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa. E-mail: rjvaarde@zoology.up.ac.za, Telephone: +27 12 420-2753, Cell: +27 82 908-7313, Fax: +27 12 420-4523

Running title: Trends in African elephants

Submitted to *Animal Conservation, 5 February 2008. Revision requested 6 June 2008.*

(Formatted according to *Animal Conservation*)

Abstract

Temporal trends in population size are calculated from time series that are based on population estimates and frequently form the basis for management decisions. However, survey design and monitoring features may negatively influence the reliability of such trends, which could lead to the implementation of inappropriate management actions. For instance, one may conclude that population size is not changing when in fact it is, which is termed a Type 2 error. We tested the probability of making this error when calculating population trends for African elephants *Loxodonta africana*. We collated data on elephant population estimates in Africa, evaluated their quality, and determined how differences in data quality affected statistical power to detect a trend in elephant numbers. Precision of population estimates, sample size, population size, and the magnitude of the annual rate of population change to be detected, affected power to identify trends. Two-thirds of the 156 time series we assembled were stable. However, only 30 % of these had sufficient power. Failure to detect a trend in numbers may have consequences for the conservation and management of elephant populations. Small populations in decline that are thought to be stable may become extinct and increasing populations considered stable may impact on other species. Consequently, such stable trends need to be treated with caution, particularly when they form the basis for decision-making processes. These findings highlight the importance of statistical power analysis to increase confidence in non-significant trend results. *A priori* power analysis also represents an important planning tool for reliable and cost-effective monitoring programs.

Keywords: *Loxodonta africana*; management; monitoring; power analysis; trends; Type 2 error

Introduction

Monitoring of population trends is fundamental to evaluating the effectiveness of management plans (Gibbs, 2000). Population trends are difficult to assess because they require precise information that demands considerable effort and resources (Gibbs, Droege & Eagle, 1998). This also holds for elephants – their management is controversial (see van Aarde, Jackson & Ferreira 2006; van Aarde & Jackson, 2007) and costly efforts continue to be made to determine elephant population sizes and the rates at which these change over time (see Blanc *et al.,* 2007).

Estimates of total population size typically form the basis of monitoring programs (Jachmann, 2001). Individual registrations, aerial and ground total surveys yield reliable estimates with high levels of precision (Morley & van Aarde, 2006). However, counting all individuals in a population is not always possible, due to financial and logistic constraints. Consequently, authorities frequently use sample surveys to estimate population size (see Olivier, Ferreira & van Aarde, 2008 and references therein).

Survey design may influence the precision of the population estimate (Seber, 1986). For example, surveys that use few samples to calculate total numbers may produce estimates with low precision (e.g. Ogutu *et al.,* 2006). This affects the reliability of population trends calculated from time series that include such estimates (Barnes, 2002). Furthermore, time series may suffer from small sample sizes, large time increments between survey events, and short monitoring periods.

A population trend represents either an increase or a decrease in population size over time and occurs when the slope of the line regressing elephant numbers against time, differs significantly from zero. There are two types of statistical errors that may arise in the analysis of temporal trends. First, one might conclude, that a change in population size over time is occurring, when it is not, thereby falsely rejecting a true null-hypothesis (a Type 1 error) (Steidl, Hayes & Schauber, 1997). The probability at which Type 1 errors will be accepted (α) is typically set at 0.05. Second, concluding that no trend in numbers is occurring, when in fact it is, is termed a Type 2 error. The probability of making this error is denoted as β. Statistical power ($1-\beta$) is the probability of correctly rejecting a false null-hypothesis (Gerrodette, 1987).

Most analyses of population trends test hypotheses that assess statistical significance. When the statistical test produces a significant *P*-value (i.e. $P < \alpha$), the null-hypothesis is rejected and the population is considered to be changing over time (e.g. Junker, van Aarde & Ferreira, 2008). This frequently leads to the assumption that failure to detect statistical significance supports the null-hypothesis (e.g. Ottichilo *et al.,* 2000). This approach is flawed and implies that the consequences of Type 2 errors are accepted over those of Type 1 errors. For example, one may conclude that a population is not changing significantly over time, when in fact it is decreasing in size – a supposition that may ultimately lead to population extinction. Survey design and monitoring features may influence the probability of conducting a Type 2 error, because power is a function of the precision of estimates, sample size, sampling intensity, and the rate of change to be detected (Gerrodette, 1987).

Power is seldom considered in trend analyses (but see Taylor & Gerrodette, 1993; Lesica & Steele, 1996; Hayes & Steidl, 1997; Lougheed, Breault & Lank, 1999; Barnes, 2002; Crouch & Paton, 2002). Barnes (2002) seems the only published account investigating statistical power to detect elephant population trends.

The present paper evaluates the quality of African elephant population estimates and population trends derived from these. We tested how the precision of estimates, the number of estimates in time series, survey frequency, population size, and the rate of population change to be detected, affected power to detect population trends. We also determined the probability that time series with no apparent trend were in fact stable.

Methods

Data sources and data quality evaluation

We searched 21 electronic databases and 28 websites for published and unpublished information on population estimates for African elephants (Appendix 1). We also searched through the complete *Pachyderm* series (volumes 1 to 41), the African Elephant Databases (Said *et al.,* 1995; Barnes *et al.,* 1998), Status Reports (Blanc *et al.,* 2003; Blanc *et al.,* 2007) and relevant references from the documents we found.

Authors noted whether elephant populations were surveyed directly (individuals) or indirectly (dung counts) from the air or from the ground, using either total or sample surveys. However, some population estimates were guesses and we distinguished educated guesses from other guesses. Estimates for which information on survey methodology was not provided or where such information was incomplete, were educated guesses. Opinion-based estimates were other guesses.

We followed Blanc *et al.* (2003) to assess data quality. Accordingly, population estimates were assigned to one of three categories where Category 1, 2 and 3 represented highest, intermediate and lowest quality of information, respectively. Estimates from ground- and aerial sample surveys were categorised according to the percentage of area (survey intensity) covered per survey. Estimates from aerial total surveys were categorised in terms the area covered in an hour (searching rates) while estimates from genetic surveys (Eggert, Eggert & Woodruff, 2003) were categorised in terms of the number of unique genotypes identified. Barnes *et al.* (2003) provide details on all these categories.

For each time series, we recorded one population estimate per year. We excluded wet season counts, gave preference to estimates from primary data sources (original publication of survey results) over secondary data sources (e.g. reviews) and when estimates were attained from the same data source, we selected for data quality as defined by Blanc *et al.* (2003). When these criteria could not be applied, we opted to use the estimate that was published most recently.

To illustrate trends in estimate precision, we excluded zero-estimates and plotted the number of estimates from aerial and ground sample surveys as a function of their 95 % CL (SE*1.96; see Jachmann, 2001). We also plotted the number of time series (defined as having three or more estimates) as a function of the number of estimates within the time series (N), the length of the time series in years (L), and the average time interval between survey events in years (i) for population estimates from both sample and total counts.

Power analysis

We regressed the coefficient of variation (*CV*) (a measure of precision) of the estimate against the inverse of the square root of the population estimate to test for the dependence of the precision of the estimate on population size (Gerrodette, 1987). We calculated *CV* as *CV* = SE / Estimate. We separated all estimates from aerial and ground sample surveys into one of the three quality categories to test whether survey effort (and thus data quality) affected the precision of population estimates.

We calculated mean *CV*, mean *i* (the average time interval between survey events in years) and mean *N* (the number of estimates in a time series in years) for time series of population estimates from sample surveys and with 95 % CL's. To explore how *CV*, *i*, and *N,* affected power, we allowed each variable to vary while the other two were kept constant at their mean values. Based on these data, we determined cut-off points for sufficient power ($1-\beta = 0.8$) to detect population trends.

We used Gerrodette's (1987) inequality $\left([\ln(1+r)]^2 N(N-1)(N+1) \geq 12\left(z_{\alpha/2} + z_\beta\right)^2 \left\{\frac{1}{N}\sum^{N} \ln\left[\frac{cv_i^{\,2}}{(1+r)^{i-1}} + 1\right]\right\}\right)$ and the programming language C#.Net (Microsoft Visual Studio.Net 2005) to estimate statistical power for time series of estimates with 95 % CL's as a function of *CV*, *i*, and *N*. We solved for z_β, found β and then computed power as $1-\beta$. True power is unknown and statistical power (Gerrodette's, 1987) can only be estimated by finding approximate solutions. Such *a posteriori* power analysis is only meaningful for a pre-determined effect size (i.e. the rate of population change over time) but not for the observed effect size calculated from the data available (Hayes & Steidl, 1997). We estimated power for four different exponential rates of population change ($r = 0.05$; $r = 0.02$; $r = -0.02$; and $r = -0.05$) and assumed that CV is proportional to the inverse of the square root of the population estimate. We set α at 0.05 and β at 0.2 (Cohen, 1988).

Our calculation of trends in elephant numbers was for time series of estimates with 95 % CL's and estimates from total counts, which were assigned a CV of 0.0001. We calculated the natural logarithms of estimates, after the addition of the constant 0.1 (because some surveys had counts of zero), and regressed these against time. The slopes and variances thereof yielded estimates of exponential growth and their variances (Caughley, 1977). We distinguished between populations that declined (negative trend), those that increased (positive trend), and those that appeared stable (no trend). We followed Blanc *et al.* (2003) to group time series into four regions in Africa (central, East-, southern-, and West Africa).

We then estimated power for those time series of population estimates that showed no significant trend in numbers (each one with individual CV-, i-, and N-values), using the methods described earlier.

Results

Data quantity and quality

We collected 2 494 (central Africa: 214; East Africa: 688; southern Africa: 1201; West Africa: 391) elephant population estimates across 661 areas in Africa (Table 1; and see Supplementary table 1). Of these, 906 (36 %) were from sample surveys, 711 (29 %) from total surveys, and 900 (36 %) were informed and other guesses.

Eight percent (69) of estimates from sample surveys and 42 % (300) of those from total surveys fell into the high quality category 1. Intermediate quality category 2 included 42 % (382) of estimates from sample surveys and 16 % (114) from total surveys. Fifty percent (455) of estimates from sample surveys and 42 % (297) of estimates from total surveys fell into the low quality category 3 (Table 1). Furthermore, only 66 % (596) of estimates from sample surveys had 95 % CL's reported for them.

The 95 % CL's ranged from 0 to 391 % of the estimate for aerial sample surveys (mean 77 %, $n = 514$ estimates; Figure 1a) and from 3.8 to 363 % of the estimate for ground sample surveys (mean 63 %, $n = 82$ estimates). The frequency distributions of 95 % CL's for estimates from aerial and ground sample surveys did not differ (Kolmogorov-Smirnov two-sample test: $n_{\text{aerial}} = 430$ estimates, $n_{\text{ground}} = 82$ estimates, $D = 0.084$, $P > 0.1$). When we excluded guesses, our dataset included 184 time series that comprised at least three estimates. The number of estimates in time series (N) ranged from 3 to 70 estimates (mean 6.9 estimates, $n = 184$ time series; Figure 1b), time series length (L) from 1 to 74 years (mean 20.1 years, $n = 184$ time series; Figure 1c), and the average time interval between surveys (i) from 1 to 15 years (mean 4.5 years, $n = 184$ time series; Figure 1d).

Power analysis

Gerrodette's (1987) assumption that CV is proportional to the inverse of the square root of the population estimate held for both aerial and ground survey estimates in our study. The inverse relationship between CV and the inverse of the square root of the population estimate confirmed that precision of elephant population estimates declined with declining population size ($F_{\text{aerial}} = 272.9$, d.f. = 511, $P < 0.001$; $F_{\text{ground}} = 21.4$, d.f.= 80, $P < 0.001$).

The slopes of the linear regression lines, based on estimates of varying quality (data quality category 1 – 3), differed significantly ($F_{2,508} = 3.89$, $P < 0.05$). However, precision of estimates did not increase with an increase in data quality (i.e. slopes of the regression lines did not consistently decrease with an increase in data quality; $y_{<5\%} = 5.14x + 0.22$, $y_{5\text{-}20\%} = 4.39x + 0.22$, $y_{>20\%} = 5.9x + 0.07$) suggesting that population size dominated the precision of estimates. Because of too few data we did not compare the slopes of the linear regression lines for ground sample estimates of varying quality.

Means for the variables *CV*, *i*, and *N*, which we calculated from estimates with 95 % CL's, were 0.38 ($n = 596$), 4.17 years ($n = 85$), and 4.78 estimates ($n = 85$), respectively. Power to detect a trend decreased rapidly with the precision of estimates (Figure 2a). Time series of estimates with *CV*'s of less than 0.06 yielded sufficient power to detect a trend in population growth of 5 % per year. Less than 2 % (9/596) of estimates obtained from sample surveys had *CV*'s low enough to achieve acceptable power ($1\text{-}\beta = 0.8$) at the mean *N* (the number of estimates in time series) and the mean *i* (the average time interval between survey events in years). Power also increased with the rate of population change to be detected (*r*).

The average time interval between surveys (*i*) had little effect on power (Figure 2b). Power increased slightly with an increase in *i* at $r = 0.05$. Furthermore, there was a positive relationship between *i* and *L* ($F = 37.6$, d.f. = 83, $P < 0.001$), indicating that time series with greater time intervals between surveys were also longer, thus resulting in a greater power to detect trends over time (Taylor & Gerrodette, 1993).

Power also increased rapidly with the number of estimates in time series (*N*) (Figure 2c). Time series needed at least 17 estimates to yield sufficient power to detect a population trend of 5 % per year. Only one of the 85 time series based on sample surveys with 95 % CL's had sufficient estimates to achieve acceptable power at the mean *CV* and the mean *i*. Again, power increased with *r*.

Of the 156 time series based on total- and sample surveys with 95 % CL's, 6 % showed a decreasing trend, 25 % an increasing trend, and 69 % showed no trend in numbers over time. West Africa had the highest percentage of time series showing no population trends (95 %, 19/20). East, central, and southern Africa followed with 76 % (32/42), 67 % (2/3), and 60 % (55/91), respectively.

Between 23 % and 30 % of the stable trends yielded acceptable power to detect changes in population size from -5 % to 5 % per year (exponential growth $r = 0.02$: 27/108; $r = -0.02$: 25/108; $r = 0.05$: 32/108; $r = -0.05$: 27/108; Figure 3). Between 27 % and 36 % of southern African, and 31 % and 38 % of East African time series had sufficient power to detect population changes of -5 % to 5 % per year (southern Africa: $r = 0.02$: 16/55; $r = -0.02$: 15/55; $r = 0.05$: 20/55; $r = -0.05$: 16/55; East Africa: $r = 0.02$: 11/32; $r = -0.02$: 10/32; $r = 0.05$: 12/32; $r = -0.05$: 11/32). None of the time series from central and West Africa had sufficient power to detect population trends.

Discussion

As expected from published information (Gerrodette, 1987; Steidl *et al.*, 1997; Barnes, 2002) our analysis showed that precision of population estimates, sample size, population size, and the magnitude of the rate of change to be detected, affected power to detect trends in elephant numbers over time. This was particularly important for time series with no apparent trends in population size – only 30 % of these had sufficient power. This has consequences for interpreting such trends and the planning and evaluation of elephant monitoring and management programs.

For elephants, different survey methods yield population estimates of varying quality (Jachmann, 2001; 2002) and thus influence trends derived from these. Nearly half (47 %) of the elephant population estimates from across Africa were of low quality (data quality category 3) due to low survey intensities, high aircraft speeds, and failure to report confidence limits for estimates obtained from sample surveys. Population size also affected the precision of estimates, where large populations yielded estimates with higher precision than small populations.

Power to detect population trends was affected by the precision of estimates and the number of estimates in time series. Time series of estimates with 95 % CL's of less than 12 % of the estimate (*CV*'s < 6 %) yielded sufficient power to detect a 5 % yearly change in population size. Only nine of the 596 estimates from sample surveys with 95 % CL's reported for African elephants over the past 40 years (1966 to 2006) had confidence limits of less than 12 %.

Time series with few estimates had low power, and only those with at least 17 estimates achieved acceptable power to detect a 5 % annual rate of change in population size. Only one out of the 85 time series that could be constructed from sample survey estimates with 95 % CL's contained sufficient estimates to detect a population trend. Thus, for elephants, the low precision of estimates and the limited number of estimates per time series rendered most census information from sample surveys insufficient for the detection of trends.

Failure to detect a trend in elephant numbers may influence conservation and management decisions. First, small populations in decline that are considered stable may become extinct (Barnes, 2002). Second, increasing populations that are thought to be stable may adversely affect co-occurring species. Confidence in non-significant results, and thus correctly concluding that a population shows no change over time, increases with an increase in power (Cohen, 1988).

While elephant censuses are costly and few conservation bodies can afford annual surveys to ensure sufficient estimates with high levels of precision, the challenge is to develop a monitoring program that produces results that are statistically robust, while minimising the limitations of logistical and financial constraints. For instance, it may be more cost-efficient to improve precision of estimates by increasing survey intensities or decreasing aircraft speed, rather than increasing the number of surveys. Furthermore, power to detect trends increases with the length of time series (Gibbs *et al.,* 1998). Thus, when monitoring spans longer time periods, fewer estimates may yield sufficient information on population trends at a set level of precision.

We could not detect trends in 108 (69 %) of the 156 time series that we assembled of elephant population estimates from sample surveys with 95 % CL’s and total surveys (see Supplementary Table 1). It is tempting to infer that these populations are stable. However, such inference is only justified where time series have high statistical power – only 30 % of these time series had sufficient power to deduce that populations were stable (mostly from southern and East Africa).

The apparently high incidence of population stability suggested here might be due to between-survey variation in population estimates. Such variation may stem from large-scale movements of elephants in and out of specific survey areas (e.g. Verlinden & Gavor, 1998; Chamaillé-Jammes *et al.,* 2008). However, as estimates obtained from sample surveys had low precision and wide confidence limits, measurement error is more likely to be the primary source of variation. Consequently, 70 % of these time series is inconclusive and should not inform decision-making processes for elephant management.

None of the time series for elephants from central and West Africa had sufficient power to conclude that populations are not changing over time. West Africa also had the highest percentage (95 %) of time series showing apparent population stability. While our sample size for central Africa was too small to draw any conclusions, there are several reasons for the lack of significant trend results and the low power associated with time series form West Africa. First, nearly two thirds of the estimates from West Africa comprise guesses (Blanc *et al.,* 2007) and here, analyses of time series suffer from small sample sizes. Second, elephant populations in West Africa are relatively small, resulting in population estimates with low levels of precision. Thus, in the case of West African elephant populations, spending time and money on successive surveys would be a waste of resources if the only objective were to detect a change in numbers over time. Here, it may be more feasible to monitor sex and age distributions, carcass density, law enforcement and indices of illegal activity to determine trends in elephant mortality and their causes (Barnes, 2002).

Another analytical constraint is that the theoretical maximum annual rate of increase for the African elephant is relatively low (between 5.5 % and 7 %; see Hanks & McIntosh, 1973; Calef, 1988) compared to other animal taxa. The lower the rate of change to be detected, the lower the power. However, as we cannot control growth rate, ecologists must address what magnitude of change is meaningful to detect, given specific management objectives. Therefore, if the management objective was to detect a high rate of population change over a particular period of time, this would require less intensive sampling than if one sought to detect a much weaker or an initial population change.

Fifty percent of the population estimates for African elephants obtained from sample counts were of low quality. This limits our ability to detect trends in elephant numbers calculated from time series including such estimates. We thus encourage survey teams to consider statistical power in the planning of monitoring programs to ensure reliable outcomes and cost-effective implementation and evaluation of management actions. In addition, *a posteriori* power analysis increases objectivity in interpreting non-significant results and can also be used to identify shortcomings in monitoring programs presently employed. In the case of small populations, effort should be directed at monitoring size and age distributions rather than trying to detect changes in numbers where analyses are based on population estimates with low levels of precision.

To conclude, elephant populations in Africa may be increasing, decreasing, or be stable in size over time. The majority (69 %) of populations showed no significant change over time. Of these, only 30 % had sufficient statistical power to detect trends in population change. Therefore, 70 % of the time series of elephant population estimates that showed no population trends are inconclusive and should thus not motivate management decisions.

References

Barnes, R.F.W. (2002). The problem of trend detection posed by small elephant populations in West Africa. *Afr. J. Ecol.* **40**, 179-185.

Barnes, R.F.W., Craig, G.C., Dublin H.T., Overton, G., Simons, W. & Thouless, C.R. (1998). *African Elephant Database 1998.* IUCN/SSC African Elephant Specialist Group. Gland: IUCN.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, C.G. & Barnes, R.F.W. (2003). *African Elephant Status Report 2002. An update from the African Elephant Database.* IUCN/SSC African Elephant Specialist Group. Gland: IUCN.

Blanc, J.J., Barnes, R.F.W., Craig, C.G., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. & Hart, J.A. (2007). *African Elephant Status Report 2007. An update from the African Elephant Database.* IUCN/SSC African Elephant Specialist Group. Gland: IUCN.

Calef, G.W. (1988). Maximum rate of increase in the African elephant. *Afr. J. Ecol.* **26**, 323-328.

Caughley, G. (1977). *Analysis of vertebrate populations*. New York: John Wiley & Sons.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. & Clobert, J. (2008). Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *J. Anim. Ecol.* **77**, 135-144.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. 2nd edn. Hillside: Lawrence Erlbaum.

Crouch, W.B. & Paton, P.W.C. (2002). Assessing the use of call surveys to monitor breeding anurans in Rhode Island. *J. Herpetol.* **36**, 185-192.

Eggert, L.S., Eggert, J.A. & Woodruff, D.S. (2003). Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Mol. Ecol.* **12**, 1389-1402.

Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology,* **68**, 1364-1372.

Gibbs, J.P. (2000). Monitoring populations. In *Research techniques in animal ecology – controversies and consequences*: 213-252. Boitani L. & Fuller T.K. (Eds.). New York: Columbia University Press.

Gibbs, J.P., Droege, S. & Eagle, P. (1998). Monitoring populations of plants and animals. *Bioscience,* **48**, 935-940.

Hanks, J. & McIntosh, J.E.A. (1973). Population dynamics of the African elephant (*Loxodonta africana*). *J. Zool. (Lond.)* **169**, 29-38.

Hayes, J.P. & Steidl, R.J. (1997). Statistical power analysis and amphibian population trends. *Conserv. Biol.* **11**, 273-275.

Jachmann, H. (2001). *Estimating abundance of African wildlife: an aid to adaptive management.* Boston: Kluwer.

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *J. Appl. Ecol.* **39**, 841-852.

Junker, J., van Aarde, R.J. & Ferreira, S.M. (2008). Temporal trends in elephant *Loxodonta africana* numbers and densities in northern Botswana: is the population really increasing? *Oryx,* in press.

Lesica, P. & Steele, B.M. (1996). A method for monitoring long-term population trends: an example using rare arctic-alpine plants. *Ecol Appl.* **6**, 879-887.

Lougheed, L.W., Breault, A. & Lank, D.B. (1999). Estimating statistical power to evaluate ongoing waterfowl population monitoring. *J. Wildl. Mgmt.* **63**, 1359-1369.

Morley, R.C. & van Aarde, R.J. (2006). Estimating abundance for a savanna elephant population using mark-resight methods: a case study for the Tembe Elephant Park, South Africa. *J. Zool. (Lond.)* **271**, 418-427.

Ogutu, J.O., Bhola, N., Piepho, H.P. & Reid, R. (2006). Efficiency of strip- and line-transect surveys of African savanna mammals. *J. Zool. (Lond.)* **269**, 149-160.

Olivier P.I., Ferreira, S.M. & van Aarde, R.J. (2008). Dung counts and measurements to estimate population sizes and extract age structures: a case study on elephants in the Maputo Elephant Reserve, Mozambique. *Afr. J. Ecol.* in press.

Ottichilo, W.K., De Leeuw, J., Skidmore, A.K., Prins, H.H.T. & Said, M.Y. (2000). Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *Afr. J. Ecol.* **38**, 202-216.

Said, M.Y., Chunge, R.N., Craig, G.C., Thouless, C.R., Barnes, R.F.W. & Dublin, H.T. (1995). *African Elephant Database 1995*. IUCN/SSC African Elephant Specialist Group. Gland: IUCN.

Seber, G.A.F. (1986). A review of estimating animal abundance. *Biometrics,* **42**, 267-292.

Steidl, R.J., Hayes, J.P. & Schauber, E. (1997). Statistical power analysis in wildlife research. *J. Wildl. Mgmt.* **61**, 270-279.

Taylor, B.L. & Gerrodette, T. (1993). The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conserv. Biol.* **7**, 489-500.

van Aarde, R.J., Jackson, T.P. & Ferreira, S.M. (2006). Conservation science and elephant management in southern Africa. *S. Afr. J. Sci.* **102**, 385-388.

van Aarde, R.J. & Jackson, T.P. (2007). Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biol. Conserv.* **134**, 289-297.

Verlinden, A. & Gavor, I.K.N. (1998). Satellite tracking of elephants in northern Botswana. *Afr. J. Ecol.* **36**, 105-116.

Table 1 The number of estimates extracted from published and unpublished documents for central -, East-, southern-, and West Africa. Estimates were obtained from different survey methods and assigned to one of three data quality categories (1 - 3, highest to lowest quality of information).

Survey type	Data quality category	Number of estimates				
		Total	Central Africa	East Africa	Southern Africa	West Africa
Individual Registration	1	**206**	3	19	183	1
Aerial total count	1	**56**	-	3	52	1
	2	**114**	3	48	33	30
	3	**297**	1	115	171	10
Aerial sample count	1	**56**	-	4	51	1
	2	**289**	9	46	200	34
	3	**422**	20	165	205	32
Ground total count	1	**38**	-	16	17	5
Ground sample count	1	**1**	-	1	-	-
	2	**6**	-	2	3	1
	3	**31**	1	3	11	16
Dung count	1	**12**	1	4	3	4
	2	**86**	40	22	9	15
Genetic dung count	2	**1**	-	-	-	1
	3	**2**	-	-	-	2
Informed guess	3	**636**	98	184	183	171
Other guess	3	**241**	38	56	80	67
Total		**2494**	**214**	**688**	**1201**	**391**

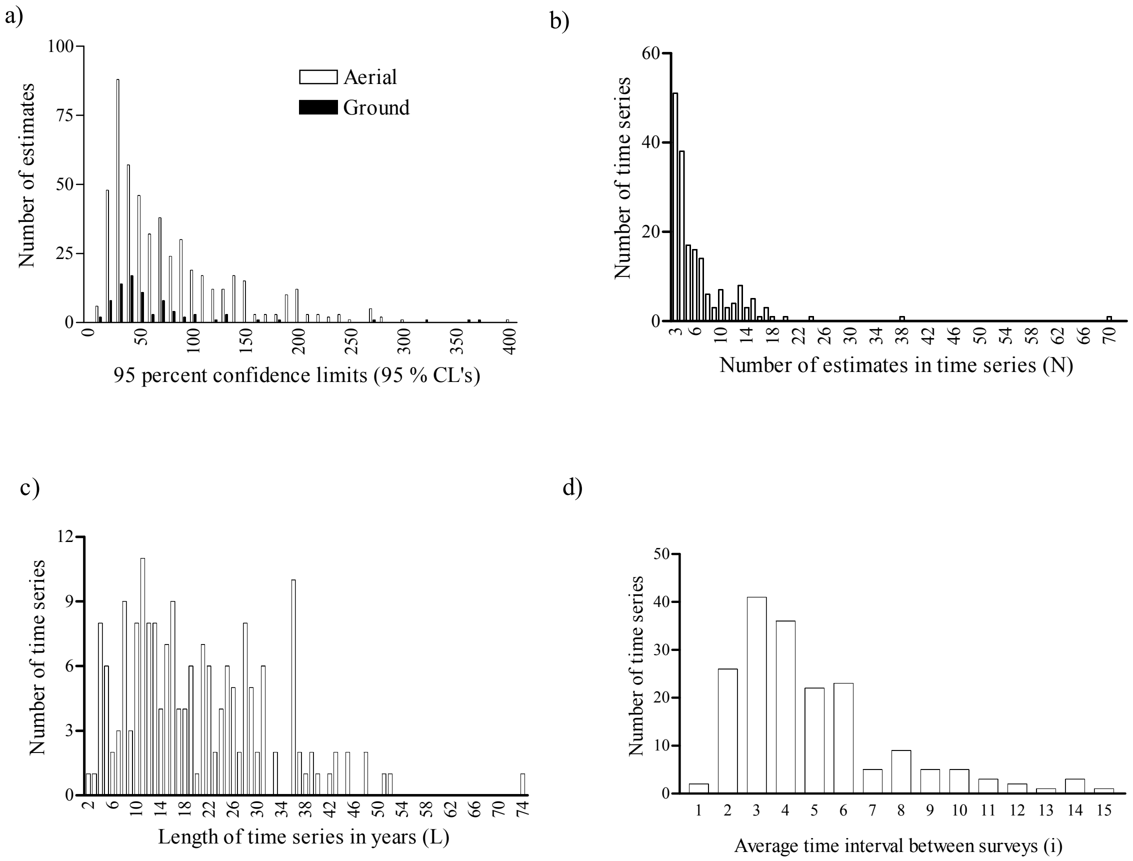


Fig. 1 Quality of time series (≥ 3 estimates) of African elephant population estimates, excluding guesses. a) The number of population estimates obtained from aerial- and ground-based sample surveys against their respective 95 % CL's. b) The number of time series against the number of estimates in time series (*N*). Note the large number of time series with few estimates. c) The number of time series against the length of time series (*L*). d) The number of time series against the average time interval between surveys (*i*).

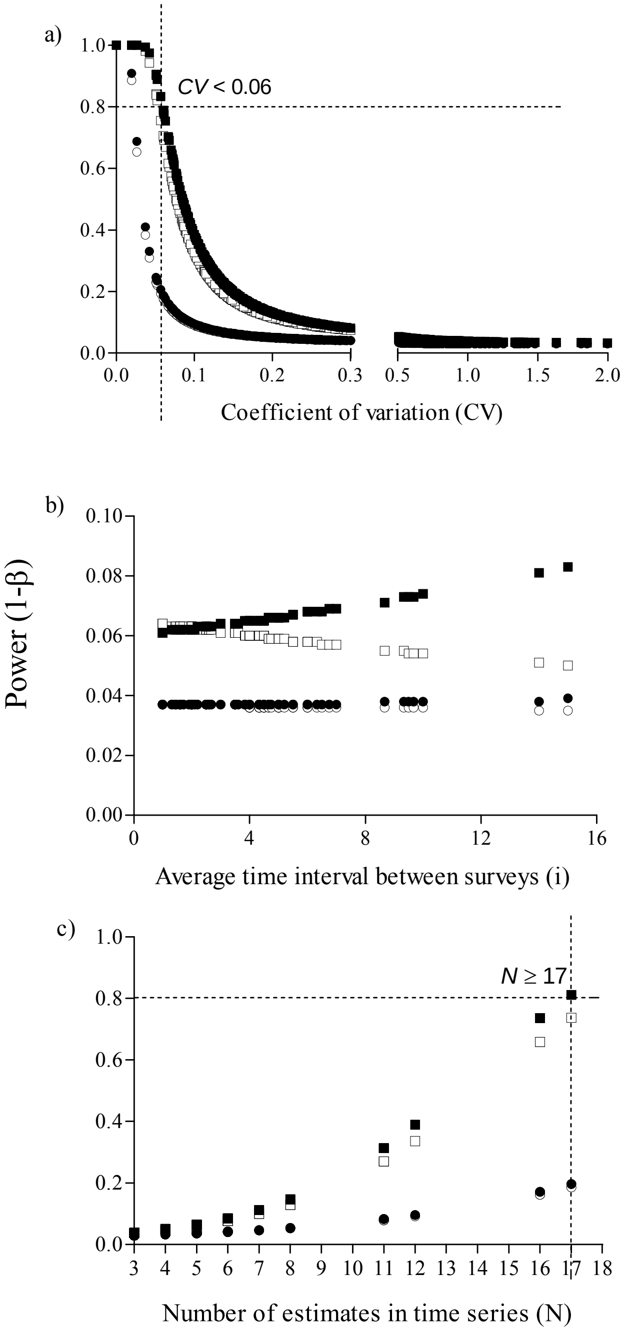


Fig. 2 Power (1-*ß*) calculated for different rates of change *r* = 0.05 (solid squares), *r* = -0.05 (open squares), *r* = 0.02 (solid circles), and *r* = -0.02 (open circles). a) Power as a function of the coefficient of variation (*CV*). Power decreases with estimate precision and the numbers of estimates in time series. Time series must include estimates with *CV*'s

smaller than 0.06 (vertical stippled line) to achieve acceptable power (horizontal stippled line) to detect an annual 5 % rate of population change. b) Power as a function of the average time interval between surveys (*i*). The average time interval between surveys had little effect on power. c) Power as a function of the number of estimates in a time series (*N*). Power increases as *N* increases. To yield acceptable power (horizontal stippled line) to detect an annual 5 % rate of population change, time series must have at least 17 estimates (vertical stippled line).

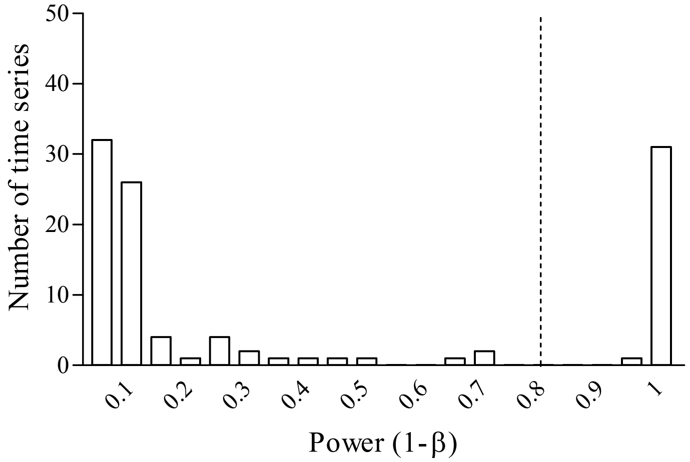


Fig. 3 The number of time series of elephant population estimates that showed no trend in population size over time, as a function of power (1-*ß*) to detect an annual 5 % rate of population change. These include data from sample and total aerial and ground-based surveys, where estimates from sample surveys had 95 % CL's reported for them. The vertical stippled line indicates acceptable power.

Supplementary table 1

Elephant populations in Africa for which we assembled time series of population estimates from published and unpublished sources of information. Populations were named according to the area where elephants were surveyed. We also show the region in Africa that the area belongs to, the number of estimates in the time series, and the trend in elephant numbers over time.

Area	Region	Sample size	Trend in elephant numbers over time
Dzangha-Sangha & Dzangha-Ndoki National Parks	Central Africa	3	negative 1985-2004
Garamba National Park	Central Africa	5	stable 1984-2004
Okapi National Park	Central Africa	3	stable 1995-2006
Amboseli Ecosystem	East Africa	12	positive 1969-2005
Katavi National Park	East Africa	3	stable 1995-2006
Kerio Valley Conservation & Dispersal Areas	East Africa	4	stable * 1992-2002
Kidepo Valley National Park	East Africa	12	stable * 1967-2005
Kilifi & Kwale Districts	East Africa	3	stable 1977-1981
Kilifi District	East Africa	4	stable 1978-1993
Kilombero Game Controlled Area	East Africa	4	stable 1976-2002
Kitui District	East Africa	5	stable 1977-1993
Laikipia District	East Africa	10	stable 1977-2005
Lake Manyara National Park	East Africa	13	negative 1966-2006
Lamu District	East Africa	6	negative 1977-2000
Loliondo Game Controlled Area	East Africa	5	negative 1967-1984
Marsabit National Reserve	East Africa	3	stable 1977-1981
Masai Mara National Reserve	East Africa	7	positive 1961-1998
Masai Mara surrounds	East Africa	3	stable* 1983-1998
Maswa-Ngorongoro	East Africa	6	stable* 1965-1992
Meru Conservation Area	East Africa	10	negative 1977-2002
Meru National Park	East Africa	3	stable* 1965-1976
Mkomazi Game Reserve	East Africa	5	negative 1978-2005
Moyowosi-Kigosi Game Reserve	East Africa	3	stable 1994-2006
Mt Kenya National Park & Forest Reserve	East Africa	3	stable 1991-2001
Murchison Falls National Park	East Africa	13	negative 1957-2002
Murchison North	East Africa	3	stable* 1964-1982
Ngorongoro Crater Conservation Area	East Africa	14	stable* 1964-1992
Nguruman Hills	East Africa	3	stable* 1967-1984
Queen Elizabeth Conservation Area	East Africa	17	stable* 1963-2006
Ruaha National Park	East Africa	4	stable1972-2002
Ruaha-Rungwa Ecosystem	East Africa	4	stable1977-2006
Rukingwa Wildlife Sanctuary & Taita Ranch	East Africa	5	stable* 1988-2001
Samburu District	East Africa	4	stable 1977-1996
Samburu-Laikipia Districts	East Africa	3	stable* 1992-2002
Selous Ecosystem	East Africa	5	stable 1986-2006
Selous Game Reserve	East Africa	6	stable 1976-2002

Area	Region	Sample size	Trend in elephant numbers over time
Serengeti National Park	East Africa	12	positive 1961-2006
Shimba Hills Nature Reserve & Forest Reserves	East Africa	5	stable 1992-2002
Tana River Delta	East Africa	3	stable 1977-1981
Tarangire National Park	East Africa	3	stable 1998-2006
Tarangire surrounds	East Africa	3	stable 1998-2006
Tsavo Ecosystem	East Africa	6	stable 1974-2005
Tsavo National Park	East Africa	9	stable* 1962-2005
Turkana District	East Africa	3	stable 1977-1981
Ugalla River Game Reserve	East Africa	5	positive 1979-2006
Addo Elephant Park	Southern Africa	70	positive 1931-2005
Atherstone Nature Reserve	Southern Africa	4	stable* 1994-2005
Binga Communal Lands	Southern Africa	3	stable 1997-2006
Caprivi region	Southern Africa	5	stable 1995-2005
Chete Safari Area	Southern Africa	4	stable 1993-2006
Chewore Safari Area	Southern Africa	7	positive 1967-2003
Chiawa Game Management Area	Southern Africa	3	stable 1991-2003
Chirisa Safari Area	Southern Africa	4	stable 1993-2006
Chisomo Game Management Area	Southern Africa	3	stable 1994-1999
Chizarira National Park	Southern Africa	4	stable 1993-2006
Chobe National Park	Southern Africa	12	positive 1970-2006
East Caprivi Forestry Area	Southern Africa	9	negative 1980-2004
Caprivi - East Core Area (Susuwe)	Southern Africa	3	stable 1994-2005
Caprivi - Eastern Floodplains (Salambala)	Southern Africa	8	stable* 1980-2004
Etosha National Park	Southern Africa	10	stable* 1973-2004
Gonarhezou National Park	Southern Africa	13	stable* 1970-2001
Greater St. Lucia Wetland Park	Southern Africa	3	stable* 2002-2005
Hlane Royal National Park	Southern Africa	4	stable* 1994-2005
Hluhluwe-Umfolozi Game Reserve	Southern Africa	12	positive 1981-2001
Hurungwe Safari Area	Southern Africa	7	positive 1967-2003
Hwange National Park	Southern Africa	16	positive 1979-2001
Ihtala Game Reserve	Southern Africa	5	positive 1990-2005
Kafue National Park	Southern Africa	4	stable 1991-2004
Kariba Communal Lands	Southern Africa	8	positive 1967-2006
Kasungu National Park	Southern Africa	4	negative 1977-2005
Khaudom & Nyae Nyae Conservancy	Southern Africa	3	stable 1990-2000
Klaserie Private Game Reserve	Southern Africa	10	positive 1978-2006
Kruger National Park	Southern Africa	38	positive 1964-2006
Kunene-Damaraland	Southern Africa	3	stable 1983-2005
Letaba Ranch	Southern Africa	4	stable* 1990-2006
Liwonde National Park	Southern Africa	9	positive 1977-1995
Lower Zambezi National Park	Southern Africa	3	stable 1991-2003
Lumimba Game Management Area	Southern Africa	3	stable 1994-1999
Lunga-Luswishi Game Management Area	Southern Africa	3	stable 1991-2004
Lupande Game Management Area	Southern Africa	6	stable 1989-2002
Mabula Game Lodge	Southern Africa	4	stable* 1989-2004
Madikwe Nature Reserve	Southern Africa	4	positive 1995-2005
Magoe District	Southern Africa	3	stable 1995-2003
Makalali Private Game Reserve	Southern Africa	4	stable* 1994-2005
Makuya National Park	Southern Africa	4	stable* 1990-2006

Area	Region	Sample size	Trend in elephant numbers over time
Mamili National Park	Southern Africa	12	positive 1980-2005
Mana Pools National Park	Southern Africa	7	positive 1967-2003
Manyeleti Game Reserve	Southern Africa	3	stable* 1990-2006
Maputo Elephant Reserve (& Futi River)	Southern Africa	4	positive 1998-2006
Marakele National Park	Southern Africa	4	positive 1996-2005
Matabeleland Forest Area	Southern Africa	3	stable 1996-2001
Matetsi Complex	Southern Africa	12	positive 1980-2001
Matusadona National Park	Southern Africa	22	positive 1967-2006
Makgadikgadi Pans	Southern Africa	6	positive 1996-2004
Mkhaya Nature Reserve	Southern Africa	4	stable* 1989-2005
Mkuzi Game Reserve	Southern Africa	4	stable* 1994-2005
Moremi Game Reserve	Southern Africa	6	stable 1996-2004
Mthethomusha Game Reserve	Southern Africa	3	stable* 1990-2005
Mudumu National Park	Southern Africa	11	stable* 1980-2005
Mulobezi Game Management Area	Southern Africa	3	stable 1997-2004
Mumbwa Game Management Area	Southern Africa	5	stable 1991-2004
Munyamadzi Game Management Area	Southern Africa	3	stable 1994-1999
Musalungu Game Management Area	Southern Africa	4	stable 1991-2004
Niassa & surrounds	Southern Africa	4	stable 1998-2004
North Gokwe Communal Lands	Southern Africa	3	stable 1997-2006
North Luangwa National Park	Southern Africa	6	stable 1985-2003
Northern Botswana elephant range	Southern Africa	16	positive 1973-2006
Northern Tuli Game Reserve	Southern Africa	6	stable 1994-2006
North-West Matabeleland	Southern Africa	17	positive 1980-2001
Nxai-Pan National Park	Southern Africa	4	stable 1999-2004
Okavango Delta	Southern Africa	8	stable 1996-2006
Phalaborwa Mining Co.	Southern Africa	6	stable* 1990-2006
Phinda Resource Reserve	Southern Africa	4	stable* 1990-2004
Pilanesberg National Park	Southern Africa	9	positive 1980-2005
Pongola Game Reserve	Southern Africa	4	positive 1997-2005
Pongolapoort Game Reserve	Southern Africa	5	positive 1997-2005
Sabi Sand Game Reserve	Southern Africa	6	positive 1990-2006
Sapi Safari Area	Southern Africa	7	positive 1967-2003
Sebungwe region	Southern Africa	8	stable* 1979-2006
Sengwa Wildlife Research Area	Southern Africa	15	positive 1965-2001
Shamwari Game Reserve	Southern Africa	4	positive 1994-2005
Sichifula Game Management Area	Southern Africa	3	stable 1997-2004
Sijarira Forest Area	Southern Africa	3	stable 1997-2006
Sioma Ngwezi National Park	Southern Africa	4	stable 1991-2005
Songimvelo Game Reserve	Southern Africa	4	stable* 1992-2002
South Luangwa National Park	Southern Africa	8	stable 1990-2002
Tembe Elephant Park	Southern Africa	17	positive 1974-2005
Timbavati Game Reserve	Southern Africa	10	positive 1985-2006
Umbabat Game Reserve	Southern Africa	5	stable* 1994-2006
Venetia Limpopo Nature Reserve	Southern Africa	6	positive 1990-2005
Welgevonden Private Game Reserve	Southern Africa	4	positive 1995-2005
West Caprivi Game Reserve	Southern Africa	5	positive 1993-2005
West Petauke	Southern Africa	3	stable 1994-1999
Zambezi Valley	Southern Africa	12	positive 1967-2003

Area	Region	Sample size	Trend in elephant numbers over time
Zambezi Valley Communal Lands	Southern Africa	3	stable 1995-2003
Zimbabwe-Botswana Border	Southern Africa	6	stable 1996-2004
Arly National Park	West Africa	7	positive 1981-2005
Atakora Hunting Zone	West Africa	3	stable 1981-2003
Bia National Park & Resource Reserve	West Africa	3	stable 1976-2004
Djona Hunting Zone	West Africa	4	stable 1981-2003
Kakum Conservation Area	West Africa	3	stable 1997-2004
Konkombouri Hunting Zone	West Africa	4	stable 1998-2003
Mole National Park	West Africa	3	stable 1993-2004
Nazinga Game Ranch	West Africa	10	stable 1982-2003
Oumou Hunting Reserve	West Africa	4	stable 1992-2003
Pagou-Tondougou Hunting Zone	West Africa	3	stable 1998-2000
Pama Centre Sud	West Africa	4	stable 1998-2003
Pama Partial Faunal Reserve	West Africa	4	stable 1992-2003
Pama, Singou & Arly combined	West Africa	3	stable 1999-2003
Pendjari Biosphere Reserve	West Africa	3	stable 1981-2006
Pendjari National Park	West Africa	5	stable 2000-2004
Remainder of Pama Partial Faunal Reserve	West Africa	4	stable 1981-2003
Singou Partial Faunal Reserve	West Africa	4	stable 1992-2000
W du Benin National Park	West Africa	3	stable 1981-2003
W du Burkina National Park & Kourtiagou Partial Faunal Reserve	West Africa	3	stable 1992-2003
Yankari National Park	West Africa	4	stable 1977-2006

Chapter 4

Management may inflate densities and population growth rates in African elephants

(Format according to the *South African Journal of Wildlife Management*)

Abstract

Elephant population management may have implications for their demography and dispersal. Direct management, such as culling may increase population growth rate by lowering elephant density and by releasing vital rates from limitations induced by density dependent forces. Indirect management, including the construction of fences and the provisioning of additional water may disrupt dispersal and reduce drought related mortalities, therefore enhancing local densities and population growth rates. In this chapter, I collated information on elephant population estimates and management actions across Africa to compare elephant densities and population growth rates for unmanaged and managed populations. I also used case studies to investigate how populations responded to specific management regimes. The analysis showed that population growth rates were associated with management, where elephant densities of populations that were managed grew at faster rates than those of populations that were unmanaged. The so-called ‘elephant problem’, which has its origin in the locally high elephant densities in conservation areas and their perceived impact on vegetation, may be resolved by reducing management intensity and providing for spatial heterogeneity that induces variable demographic responses and asynchrony in local population growth rates.

Introduction

Elephant numbers and population growth rates vary in response to changing environmental conditions that influence the availability of food and water resources. However, human interventions, such as poaching, excessive hunting, and changing land-use practices may reduce elephant populations (Viljoen 1988, Campbell 1990, Hall-Martin 1992, Gillson & Lindsay 2003, Stiles 2004, Wasser *et al*. 2007), while the construction of fences around conservation areas and the provisioning of additional water may explain the high local elephant numbers in some parts of southern Africa (Owen-Smith *et al*. 2006, van Aarde *et al*. 2006, van Aarde & Jackson 2007, van Aarde *et al*. 2008). Such apparent overabundances and positive population growth rates raise concern about the negative impact elephants may have on other species and their habitats (MacGregor & O'Connor 2004, Wiseman *et al*. 2004, de Beer *et al*. 2006, van Aarde *et al*. 2006, Guldemond & van Aarde 2008).

Most conservation management actions are experience-based rather than evidence-based (Pullin *et al*. 2004, Pullin & Knight 2005) and this is no different for elephants. In the past, elephant management focused on stabilising numbers and their resources, assuming that elephant numbers and impact are directly related (van Aarde *et al*. 2006, van Aarde & Jackson 2007). For instance, in the Kruger National Park (South Africa), the original decision to cull elephants was motivated by the concern about their apparent impact on vegetation without illustrating that such impact occurred (see Pienaar *et al*. 1966). In Hwange National Park (Zimbabwe), culling was initiated in 1966 and in 1974, based on a policy of maintaining the population at 13 000 elephants (Chamaillé-Jammes *et al*. 2007). The decision to increase the yearly culling quota in Zimbabwe after 1971 was based on an "estimate from the air that elephant had knocked down over 60% of the large Mopane trees within half a mile of the river and there was extensive raw gully erosion due to elephant paths" (Child 2004). Thus, culling targets had no scientific basis (see Caughley 1983, Owen-Smith 1983, van Aarde *et al*. 2006, van Aarde & Jackson 2007) and were supported by the concept of a stable carrying capacity, which was set arbitrarily (Owen-Smith *et al*. 2006).

The management of elephant populations may have implications for their demography and dispersal (van Aarde *et al*. 1999, van Aarde *et al*. 2006, van Aarde & Jackson 2007). Direct elephant population management, such as culling aims at controlling population size by increasing death rates, while populations are managed indirectly by the construction of fences and the provisioning of additional water. By lowering elephant density and releasing vital rates from limitations induced by density dependent forces, culling may effectively increase population growth rate (van Aarde *et al*. 2008). Fencing as a management action that protects conservation areas from people and people from wildlife also may enhance elephant population growth by inhibiting dispersal (Owen-Smith 1996, Whyte *et al*. 2003). Other management, such as water provisioning may reduce drought related mortalities and dispersal, thus enhancing local densities and population growth rates (Walker *et al.* 1987). All of this may contribute to the impact of elephants on other species and may be counteractive to conservation actions that aim to maintain biological diversity.

I am aware of only one published study (van Aarde *et al*. 1999) that collated empirical evidence to evaluate the consequences that such management actions may have had for elephant populations. The present study thus uses a comparative approach to investigate the effect of past management on elephant densities and population growth rates. I collated information on elephant population estimates and management actions across their range in Africa and compared elephant densities and population growth rates for unmanaged and managed populations. I also used case studies to investigate the consequences that different management regimes may have had for elephant populations and based on these, made recommendations for future conservation efforts.

Methods

I searched 21 electronic databases and 28 websites for published and unpublished information on population estimates for African elephants. I also searched through the complete *Pachyderm* series (volumes 1 to 41), the African Elephant Databases (Said *et al*. 1995, Barnes *et al*. 1998), Status Reports (Blanc *et al*. 2003, Blanc *et al*. 2007) and relevant references from the documents we found.

To compile time series (≥ 3 population estimates), I recorded one population estimate per year. I excluded wet season counts, gave preference to estimates from primary data sources (original publication of survey results) over secondary data sources (e.g. reviews) and when estimates were attained from the same data source, I selected for data quality as defined by Blanc *et al*. (2003). When these criteria could not be applied, I opted to use the estimate that was published most recently. I excluded guesses from all the analyses.

For each population estimate, I noted management actions. Here, I distinguished between populations that were not managed (unmanaged) and those that lived in fenced protected areas (fence), those that were culled (cull), or those that were provided with additional water sources (water), such as dams and waterholes maintained by boreholes. Populations that were partially fenced, where few elephants had been killed through sports hunting or control shooting, were regarded as unmanaged populations. I excluded populations where elephants may have utilised waterholes provided for people and their livestock (such as in communal lands). I established eight ‘management categories’, these included ‘unmanaged’ populations and populations exposed to different management practices: “fence”, “cull”, and “water”, and any combinations of these (‘fence+water+cull’; ‘fence+water’; ‘fence+cull’; ‘water+cull’). Each time series was then grouped into either one of these categories.

I calculated elephant densities by converting population estimates to number of elephants/km^2 (survey area) and estimated exponential rate of population change (r) as the slope of the linear regression of the natural logarithm of elephant densities over time. The variances of the slopes yielded estimates of the variances in growth rates (see Caughley 1977). For each time series I used only the most recent density estimate to compare unmanaged and managed populations and excluded all surveys during which no elephants were counted (n = 13). I used the Kolmogorov-Smirnov two-sample test (Sokal & Rohlf 1995) in *STATISTICA 6.0* (StatSoft, Inc. 2001) to compare frequency distributions of elephant densities and population growth rates of unmanaged and managed populations. I used the Mann-Whitney-*U* test to test for differences in elephant densities and population growth rates between unmanaged and managed populations. I also used the Chi-square test in *GRAPHPAD PRISM V. 3* (GraphPad Software, San Diego, USA) to determine whether there was an association between frequencies of positive-, stable, and negative population growth rates and management.

Populations that had been exposed to two or more different management regimes (i.e. different management categories) were treated separately as case studies. For these, I plotted elephant densities within each management category over time and fitted linear regression lines and their 95 % confidence intervals to the density estimates within each management category to determine how populations changed during and after exposure to specific management conditions.

Results

I constructed 151 time series from 862 elephant population estimates for which I had information on management. These were grouped into one of eight management categories (unmanaged: 83, fence+water+cull: 2, fence+water: 14, fence+cull: 0; fence: 3, water+cull: 10, water: 17, cull: 8), or were treated separately as case studies ($n = 14$).

Elephant densities ranged from 0.01 to 3.34 elephants per km^2 and managed populations had higher densities than unmanaged populations (mean ± SD: unmanaged = 0.53 ± 0.57; managed = 0.76 ± 0.76). However, elephant densities did not differ significantly between unmanaged and managed populations (Mann-Whitney-*U* test: $U_{83,54} = 1849$, $P = 0.08$). Frequency distributions of elephant densities were also similar (Kolmogorov-Smirnov two-sample test: $n_{\text{unmanaged}} = 83$ time series, $n_{\text{managed}} = 54$ time series, $P > 0.1$; Figs. 1A&B).

Frequency distributions of yearly growth rates based on estimates of elephant densities for unmanaged and managed populations differed significantly (Kolmogorov-Smirnov two-sample test: $n_{\text{unmanaged}} = 83$ time series, $n_{\text{managed}} = 54$ time series, $P > 0.005$; Figs. 1C&D). While yearly growth rates of unmanaged populations centred on zero, those of managed populations were shifted to the right and were significantly higher (Mann-Whitney-U test: $U_{83,54} = 1688$, $P < 0.05$) than those of unmanaged populations (mean ± SD: unmanaged = 0.01 ± 0.14; managed = 0.04 ± 0.08). Elephant population growth rates ranged from -60 % to 39 % per year.

Population change was associated with management ($\chi^2_2 = 10.59$, $P < 0.01$; Table 1, Fig 2), but not so with specific management actions (i.e. different management categories) ($\chi^2_{10} = 14.08$, $P = 0.18$).

Population's responses to culling varied and were site-specific. Elephant populations in Chete Safari Area and Sengwa Wildlife Research Area showed no trends during and after culling. In South Luangwa National Park, elephant densities decreased 14 - 31 years after culling ceased ($F_{1,8} = 11.26$, $P < 0.05$). In the Zambezi valley, elephant densities increased during years of culling ($F_{1,10} = 66.06$, $P \leq 0.0001$), but did not change after culling ceased (Fig. 3).

Four of seven populations increased in densities during culling and when provided with additional water (North-West Matabeleland: $F_{1,10} = 18.52$, $P < 0.01$, Matusadona National Park: $F_{1,19} = 12.51$, $P < 0.01$, Sebungwe region: $F_{1,7} = 6.96$, $P < 0.05$; Hwange National Park: $F_{1,15} = 50.71$, $P < 0.0001$; Fig. 4). Elephant densities continued to increase in two of the four populations after culling ceased and when additional water was still available (North-West Matabeleland: $F_{1,3} = 41.56$, $P < 0.01$, Hwange National Park: $F_{1,1} = 1682$, $P < 0.05$; Fig. 4). Three populations (Chirisa and Chizarira Safari Areas, Gonarezhou National Park) did not change significantly while culled and provided with additional water (Chirisa Safari Area: $F_{1,7} = 1.12$, $P = 0.32$; Chizarira Safari Area: $F_{1,7} = 1.26$, $P = 0.3$; Gonarezhou National Park: $F_{1,10} = 2.43$, $P = 0.15$) and the same populations also did not change after culling ceased, but when additional water was still available (Chirisa Safari Area: $F_{1,2} = 2.27$, $P = 0.27$; Chizarira Safari Area: $F_{1,2} = 0$, $P = 0.98$; Gonarezhou National Park: $F_{1,1} = 0.73$, $P = 0.55$; Fig. 4).

When populations were fenced and provided with additional water, elephant densities increased over time (Tembe Elephant Park: $F_{1,7} = 35.83$, $P < 0.001$, Addo Elephant National Park: $F_{1,45} = 276.9$, $P < 0.0001$; Fig. 5). Densities in Kruger National Park did not change significantly when elephants were culled and provided with water ($F_{1,7} = 0.08$, $P = 0.79$) or when culled, provided with water and fenced ($F_{1,16} = 0$, $P = 0.97$), but increased when culling ceased ($F_{1,6} = 22.62$, $P < 0.01$).

Discussion

Elephant populations in this study had densities and growth rates that varied greatly and in some cases the latter exceeded the theoretical maximum annual rate of increase for the African elephant, which is between 5.5 % and 7 % (see Hanks & McIntosh 1973, Calef 1988). This may be due to extensive movements of elephants within and between populations, synchronised breeding in small populations with skewed age structures (e.g. Moss 2001) and different survey methods that yield estimates that vary in accuracy and precision (Seber 1986, Lehmann 2005). The effect of poaching on populations can be severe (e.g. Douglas-Hamilton 1987) and may have resulted in the low population growth rates of some populations in this study.

Furthermore, there was a high frequency of stable trends for both managed (59%) and unmanaged (82%) populations. This may in part be due to small sample sizes, irregular sampling intervals and low precision of estimates in time series, hence reducing statistical power (Gerrodette 1987).

Despite these influences, this study showed that management was associated with population change and that elephant populations that were managed grew at faster rates than populations that were unmanaged. It is possible that management actions were taken because of such high population growth rates and that these do not represent a response to management as such. However, the case studies suggest that management actions, such as the fencing of populations and supplementing them with water may enhance growth rates.

For instance, all populations that were fenced and provided with additional water increased during this type of management. Furthermore, four out of seven populations that were culled and provided with additional water increased in densities, and in two of the four populations, densities continued to increase after culling ceased. Their increased growth rates may be ascribed to dispersal as has been noted for sub-populations in Kruger National Park (see van Aarde *et al*. 1999), but may also be due to increased birth and/or survival rates induced by water supplementation as a management action (Whyte *et al*., 1998), or a combination of these factors.

Resource availability and quality may influence the age at sexual maturity in large herbivores (Owen-Smith 1990), and also in elephants (Trimble *et al*. in review). Thus, elephant populations that have additional water may have access to better resources and consequently females may mature at an earlier age. This could boost population growth. This also could be due to improved foraging opportunities during dry spells due to artificial waterholes and dams that provide water in otherwise inaccessible areas. Density related increases in calving intervals noted for elephants in Uganda (Laws *et al*. 1975) and

Zambia (Dunham 1988) may also be masked by improved resource availability reducing the effect of density on calving intervals.

Several of the managed populations in South Africa included in this analysis were newly established populations (Garaï *et al*. 2004, Slotow *et al*. 2005). The relatively high growth rates among these may be explained by eruptive dynamics, which have been well documented in herbivore populations following the introduction of individuals to new ranges, or after the release from harvesting (Forsyth & Caley 2006). This suggests that the high population growth rates noted for managed populations despite relatively high densities could be due to eruptive population dynamics. Additionally, synchronised breeding in small populations with skewed age structures that often comprise only one or two breeding herds may explain high growth rates in some of these populations (Moss 2001).

Competition for resources (Fritz *et al*. 2002, Chamaillé-Jammes *et al*. 2008), disease (Hedger *et al*. 1972, Prins & Weyerhaeuser 1987, Turnbull *et al*. 1991) and predation (Ruggiero 1991, Brain *et al*. 1998, Moss 2001, Loveridge *et al*. 2006) may affect elephant survival. Generally, too few elephants are killed by disease and predation (Woolley *et al*. 2008) to reduce survival rates at the population level (Lindeque & Turnbull 1994). Conversely, drought, which limits both food and water resources, may increase death rates (Ottichilo 1987, Walker *et al*. 1987), particularly among calves and sub-adult elephants (Dudley *et al*. 2001). Thus, supplying elephants with additional water, which reduces the effects of resource limitation on survival, may enhance densities and result in an increase in population growth rate.

Water provisioning may also influence elephant distribution and immigration rates by attracting elephants to previously less favoured habitats. Recent work in the Hwange National Park in Zimbabwe suggests that density tends to increase with the increase in artificial waterhole densities (Chaímmale-Jammes *et al*. 2007). Distance to water is also a determinant of the densities at which elephants occur (Western 1975, Stokke & du Toit 2002, Redfern *et al*. 2003, Grainger *et al*. 2005).

Elephant numbers in Etosha National Park and the Khaudum Game Reserve in Namibia increased from 50 individuals in 1950, to 2000 individuals in 1980, and from 80 individuals in 1976 to 3400 individuals in 2004, respectively (van Aarde & Jackson 2007). Such population explosions exceed the reproductive capacity of elephants (calculated at a maximum of 5.5 – 7% per annum, see Hanks & McIntosh 1973, Calef 1988) and may be ascribed to large-scale movements of animals into areas where surface water is no longer limiting, albeit seasonally.

Dispersal is a mechanism that can adjust population densities of long-lived animals to short-term fluctuations in resources (e.g. Chafota & Owen-Smith 1996), thereby influencing population growth rates. The construction of fences around conservation areas therefore may negate the role of dispersal to reduce elephant densities. For instance, half of the newly established South African elephant populations in small fenced reserves increased at over 7.5 % per year since their initial introduction (Slotow *et al*. 2005), Here, the restriction of movements may have accelerated population growth. However, other factors such as eruptive population dynamics, skewed age structures and synchronised breeding, as discussed earlier, may also have contributed to the high densities and population growth rates.

Since the mid-1960s, culling has been promoted as a management tool to reduce elephant numbers in southern- and East Africa (e.g. Laws *et al*. 1970, Field 1971, Sherry 1975, Cumming 1981, de Vos *et al*. 1982, Walker *et al*. 1987, Chambal 1993, Martin *et al*. 1995, Martin 2005). However, van Aarde *et al.* (1999) suggested that culling might stimulate local immigration of elephants into culled areas where competition for resources may have been reduced. Moreover, by lowering elephant density and releasing vital rates from limitations induced by density dependent forces, culling may effectively increase population growth rate (van Aarde *et al*. 2008).

The case studies did not provide conclusive evidence that culling positively influenced population growth rates. However, some populations showed increases in elephant densities during culling. For instance, densities in the Zambezi valley (Zimbabwe) increased during culling and in North-West Matabeleland, Sebungwe region, and Matusadona and Hwange National Parks (Zimbabwe), densities increased while elephants were culled and provided with additional water. It is possible that in these populations, the culling of elephants, especially when this was in combination with water supplementation, may have lead to increased elephant densities, albeit through dispersal from elsewhere since none of these populations lived as fenced-off units. Following the cessation of culling in North-West Matabeleland and Kruger and Hwange National Parks, elephant densities increased dramatically. Here, culling may have limited densities and population growth, albeit temporarily.

To conclude, elephant population management, more specifically the fencing of populations and the provisioning of additional water supplies may enhance elephant densities and population growth rates, probably by influencing dispersal patterns. High densities and growth rates are the base of the so-called 'elephant problem' and may be resolved by reducing management intensity and by providing for a spatial matrix that allows for dispersal and consequently for the variability in population growth across both space and time. Thus, the regional management of landscapes and spatial utilization could replace the need for the intensive local management of elephant numbers. This would alleviate the likelihood of elephants becoming so-called overabundant at a given locality, and at the same time, ensure their persistence in the future. However, I acknowledge that in the case of small and geographically isolated populations, this approach may not be viable and intense management may be necessary to control population growth and maintain populations at a desired size.

References

BARNES, R.F.W., CRAIG, G.C., DUBLIN, H.T., OVERTON, G., SIMONS, W. & THOULESS, C.R. 1998. African Elephant Database 1998. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

BLANC, J.J., THOULESS, C.R., HART, J.A., DUBLIN, H.T., DOUGLAS-HAMILTON, I., CRAIG, C.G. & BARNES, R.F.W. 2003. African Elephant Status Report 2002. An update from the African Elephant Database. IUCN/ SSC African Elephant Specialist Group, Gland, Switzerland.

BLANC, J.J., BARNES, R.F.W., CRAIG, G.C., DUBLIN, H.T., THOULESS, C.R., DOUGLAS-HAMILTON, I. & HART, J.A. 2007. African Elephant Status Report 2007: an update from the African Elephant Database. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

BRAIN, C., FORGE, O. & ERB, P. 1998. Lion predation on black rhinoceros (*Diceros bicornis*) in Etosha National Park. *Afr. J. Ecol.* 37: 107-109.

CALEF, G.W. 1988. Maximum rate of increase in the African elephant. *Afr. J. Ecol.* 26: 323-327.

CAMPBELL, A.C. 1990. History of elephants in Botswana. In: P. Hancock, M. Cantrell & S. Hughes (Eds.), The future of Botswana's elephants. Proceedings of Kalahari Conservation Society Symposium, 1990. The Kalahari Conservation Society/ Department of Wildlife and National Parks, Gaborone, Botswana.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, USA.

CAUGHLEY, G. 1983. Dynamics of large mammals and their relevance to culling. In: N. Owen-Smith (Ed.), Management of large mammals in African conservation areas. HAUM Educational Publishers, Pretoria, South Africa.

CHAFOTA, J. & OWEN-SMITH, N. 1996. Options for the management of elephants in northern Botswana. *Pachyderm* 22: 67-72.

CHAMAILLÉ-JAMMES, S., VALEIX, M. & FRITZ, H. 2007. Managing heterogeneity in elephant distribution: between elephant population density and surface-water availability. *J. Appl. Ecol.* 44: 625-633.

CHAMAILLÉ-JAMMES, S., FRITZ, H., VALEIX, M., MURINDAGOMO, F. & CLOBERT, J. 2008. Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *J. Anim. Ecol.* 77: 135-144.

CHAMBAL, M. 1993. Current elephant range and status in Mozambique. *Pachyderm* 16: 44-47.

CHILD, G. 2004. Elephant culling in Zimbabwe. *ZimConservation Opinion* 1: 1-6.

CUMMING, D.H.M. 1981. The management of elephant and other mammals in Zimbabwe. In: P.A. Jewell & S. Holt (Eds.), Problems in management of locally abundant wild mammals. Academic Press, New York, USA.

DE BEER, Y., KILIAN, W., VERSVELD, W. & VAN AARDE, R.J. 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *J. Arid Environ.* 64: 412-421.

DE VOS, V., BENGIS, R.G. & COETZEE, H.J. 1982. Population control of large mammals in the Kruger National Park. In: N. Owen-Smith (Ed.), Management of large mammals in African conservation areas. HAUM Educational Publishers, Pretoria, South Africa.

DOUGLAS-HAMILTON, I. 1987. African elephants: population trends and their causes. *Oryx* 21: 11-24.

DUDLEY, J.P., CRAIG, G.C., GIBSON, D.S., HAYNES, G. & KLIMOWICZ, J. 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *Afr. J. Ecol.* 39: 187-194.

DUNHAM, K.M. 1988. Demographic changes in the Zambezi Valley elephants (*Loxodonta africana*). *J. Zool.* 56: 382-388.

FIELD, C.R. 1971. Elephant ecology in the Queen Elisabeth National Park, Uganda. *Afr. J. Ecol.* 9: 99-123.

FORSYTH, D.M & CALEY, P. 2006. Testing the irruptive paradigm of large-herbivore dynamics. *Ecology* 87: 297-303.

FRITZ, H., DUNCAN, P., GORDON, I.J. & ILLIUS, A.W. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620–625.

GARAÏ, M.E, SLOTOW, R., CARR, R.D. & REILLY, B. 2004. Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm* 37: 28-36.

GERRODETTE, T. 1987. A power analysis for detecting trends. *Ecology* 68: 1364-1372.

GILLSON, L. & LINDSAY, K. 2003. Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environ. Sci. Policy* 6: 411-419.

GRAINGER, M., VAN AARDE, R. & WHYTE, I. 2005. Landscape heterogeneity and the use of space by elephants in Kruger National Park, South Africa. *Afr. J. Ecol.* 43: 369-375.

GULDEMOND, R. & VAN AARDE, R. 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *J. Wildlife Manage.* 72: 892–899.

HALL-MARTIN, A.J. 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe* 35: 65-80.

HANKS, J. & MCINTOSH, J.E.A. 1973. Population dynamics of the African elephant (*Loxodonta africana*). *J. Zool.* 169: 29-38.

HEDGER, R.S., CONDY, J.B. & GOLDING, S.M. 1972. Infection of some species of African wild life with foot-and-mouth disease virus. *J. Comp. Pathol.* 82: 455-461.

LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.C.B. 1970. Elephants and their habitats in North Bunyoro, Uganda. *Afr. J. Ecol.* 8: 163-180.

LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.C.B. 1975. Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda. Clarendon Press, Oxford, UK.

LEHMAN, E. 2005. Survey efforts to estimate population size for African elephant conservation. MSc Thesis, University of Pretoria, Pretoria, South Africa.

LINDEQUE, P.M. & TURNBULL, P.C. 1994. Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. *Onderstepoort J. Vet. Res.* 61: 71-83.

LOVERIDGE, A.J., HUNT, J.E., MURINDAGOMO, F. & MACDONALD, D.W. 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool.* 270: 523-530.

MACGREGOR, S.D. & O'CONNOR, G.O. 2004. Response of *Acacia tortilis* to utilization by elephants in a semi-arid African savanna. *South Afr. J. Wildl. Res.* 34: 55-66.

MARTIN, R.B. 2005. Transboundary Species Project. Background study. Elephants. The Transboundary Mammal Project, Ministry of Environment and Tourism/ The Namibia Nature Foundation, Windhoek, Namibia.

MARTIN, R.B., CRAIG, G.C. & BOOTH, V.R. (re-edited, R.B MARTIN and A.M.G. CONYBEARE). 1995. Elephant management in Zimbabwe. Department of National Parks and Wild Life Management, Harare, Zimbabwe.

MOSS, C.J. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool.* 255: 145-156.

OTTICHILO, W.K. 1987. The causes of the recent heavy elephant mortality in the Tsavo ecosystem, Kenya, 1975-80. *Biol. Conserv.* 41: 279-289.

OWEN-SMITH, N. 1983. Management of large mammals in African conservation areas. Proceedings of a symposium held in Pretoria. South Africa, April, 1982. HAUM Educational Publishers, Pretoria, South Africa.

OWEN-SMITH, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J. Anim. Ecol.* 59: 893-913.

OWEN-SMITH, R.N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South Afr. J. Wildl. Res.* 26: 107–112.

OWEN-SMITH, N., KERLEY, G.I.H., PAGE, B., SLOTOW, R. & VAN AARDE, R.J. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *S. Afr. J. Sci.* 102: 389-394.

PIENAAR, U. DE V., VAN WYK, P. & FAIRALL, N. 1966. An aerial census of elephant and buffalo in Kruger National Park, and the implications thereof on intended management schemes. *Koedoe* 9: 40-107.

PRINS, H.H.T. & WEYERHAEUSER, F.J. 1987. Epidemics in populations of wild ruminants: anthrax and impala, rinderpest and buffalo in Lake Manyara National Park, Tanzania. *Oikos* 49: 28-38.

PULLIN, A.S., KNIGHT, T.M., STONE, D.A. & CHARMAN, K. 2004. Do conservation managers use scientific evidence to support their decision-making? *Biol. Conserv.* 119: 245-252.

PULLIN, A.S. & KNIGHT, T.M. 2005. Assessing conservation management evidence base: a survey of management-plan compilers in the United Kingdom and Australia. *Conserv. Biol.* 19: 1989-1996.

REDFERN, J.V., GRANT, R., BIGGS, H. & GETZ, W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84: 2092-2107.

RUGGIERO, R.G. 1991. Opportunistic predation on elephant calves. *Afr. J. Ecol.* 29: 86-89.

SAID, M.Y., CHUNGE, R.N., CRAIG, G.C., THOULESS, C.R., BARNES, R.F.W. & DUBLIN, H.T. 1995. African Elephant Database 1995. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

SEBER, G.A.F. 1986 A review of estimating animal abundance. *Biometrics* 42: 267-292.

SHERRY, B.Y. 1975. Reproduction of elephant in Gonarezhou, south-eastern Rhodesia. *Arnoldia* 7: 1-13.

SLOTOW, R., GARAÏ, M.E., REILLY, B., PAGE, B. & CARR, R.D. 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South Afr. J. Wildl. Res.* 35: 23-32.

SOKAL, R.R. & ROHLF, F.J. 1995. Biometry. W. H. Freeman and Company, New York, USA.

STILES, D. 2004. The ivory trade and elephant conservation. *Environ. Conserv.* 31: 309-321.

STOKKE, S. & DU TOIT, J.T. 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *Afr. J. Ecol.* 40: 360-371.

TRIMBLE, M.J., FERREIRA, S.M. & VAN AARDE, R.J. Drivers of megaherbivore demographic fluctuations: inference from elephants. *J. Zool.*, in review.

TURNBULL, P.C., BELL, R.H., SAIGAWA, K., MUNYENYEMBE, F.E., MULENGA, C.K. & MAKALA, L.H. 1991. Anthrax in wildlife in the Luangwa Valley, Zambia. *Vet. Rec.* 128: 399-403.

VAN AARDE, R., WHYTE, I. & PIMM, S. 1999. Culling and dynamics of the Kruger National Park African elephant population. *Anim. Conserv.* 2: 287-294.

VAN AARDE, R.J., JACKSON, T.P. & FERREIRA, S.M. 2006. Conservation science and elephant management in southern Africa. *S. Afr. J. Sci.* 102: 385-388.

VAN AARDE, R.J. & JACKSON, T. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in South Africa. *Biol. Conserv.* 134: 289-297.

VAN AARDE, R., FERREIRA, S., PAGE, B., JACKSON, T., JUNKER, J., GOUGH, K., OTT, T., TRIMBLE, M., OLIVIER, P., GULDEMOND, R. & DE BEER, Y. 2008. Elephant population biology and ecology. Chapter 2. In: B. Scholes (Ed.), South African elephant assessment. Wits University Press, Johannesburg, South Africa.

VILJOEN, P.J. 1988. The ecology of the desert-dwelling elephants *Loxodonta africana* (Blumenbach, 1797) of western Damaraland and Kaokoland. PhD thesis, University of Pretoria, Pretoria, South Africa.

WALKER, B.H., EMSLIE, R.N., OWEN-SMITH, R.N. & SCHOLES, R.J. 1987. To cull or not to cull: lessons from a southern African drought. *J. Appl. Ecol.* 24: 381-401.

WASSER, S.K.C., MAILAND, R., BOOTH, B., MUTAYOBA, E., KISAMO, B., CLARK, B. & STEPHENS, M. 2007. Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proc. Natl. Acad. Sci. U. S. A.* 104: 4228-4233.

WESTERN, D. 1975. Water availability and its influence on the structure and dynamics of large mammal community. *Afr. J. Ecol.* 13: 265-286.

WHYTE, I.J., VAN AARDE, R.J. & PIMM, S.L. 1998. Managing the elephants of Kruger National Park. *Anim. Conserv.* 1: 77-83.

WHYTE, I.J., VAN AARDE, R.J. & PIMM, S.L. 2003. Kruger's elephant population: its size and consequences for ecosystem heterogeneity. In: J.T. du Toit, K.H. Rogers & H.C. Biggs, (Eds.), The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington, DC, U.S.A.

WISEMAN, R., PAGE, B.R. & O'CONNOR, T.G. 2004. Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. South Afr. J. Wildl. Res. 34: 25-37.

WOOLLEY, L., MACKEY, R.L., PAGE, B.R. & SLOTOW, R. 2008. Modelling the effect of age-specific mortality on elephant *Loxodonta africana* populations: can natural mortality provide regulation? *Oryx*: 42: 49-57.

Table 1 The frequency of positive-, stable-, and negative trends in elephant densities over time for unmanaged populations and for populations during management (also given as %). Populations in the "managed" category are also listed separately as part of the different management categories.

Management category	Positive trend	Stable trend	Negative trend
Unmanaged	10 (12%)	68 (82%)	5 (6%)
Managed (all categories combined)	19 (35%)	32 (59%)	3 (6%)
Fence+water+cull	0	2	0
Fence+water	6	8	0
Fence	1	2	0
Water+cull	6	4	0
Water	2	12	3
Cull	4	4	0

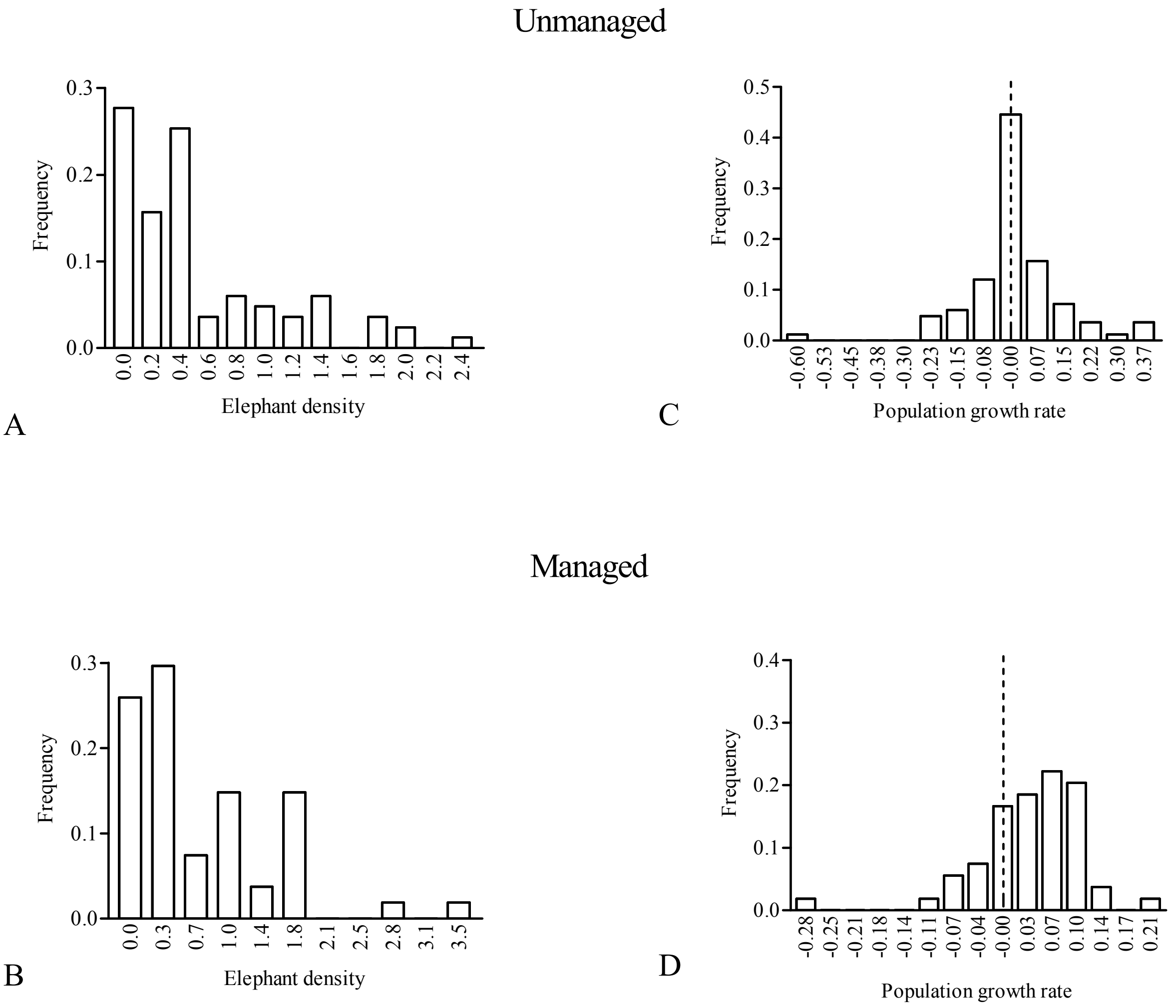


Fig. 1 Frequency distributions of elephant densities and yearly population growth rates for unmanaged populations and for populations during management. The stippled line indicates zero population growth. Frequency distributions of elephant densities for unmanaged and managed populations were similar. More populations that were managed grew at faster rates than when compared to unmanaged populations.

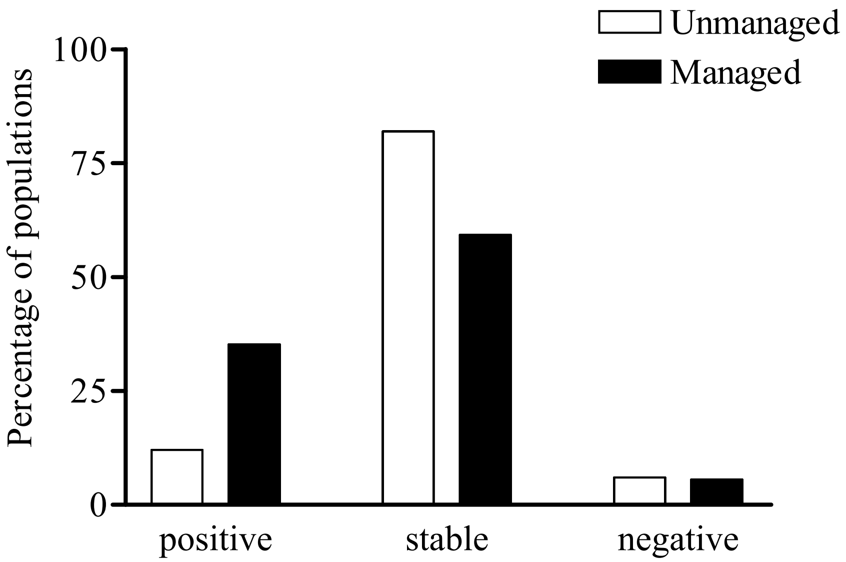


Fig. 2 The frequency distribution of unmanaged populations and populations during management that showed positive-, stable-, and negative trends in elephant densities over time. Population change was associated with management.

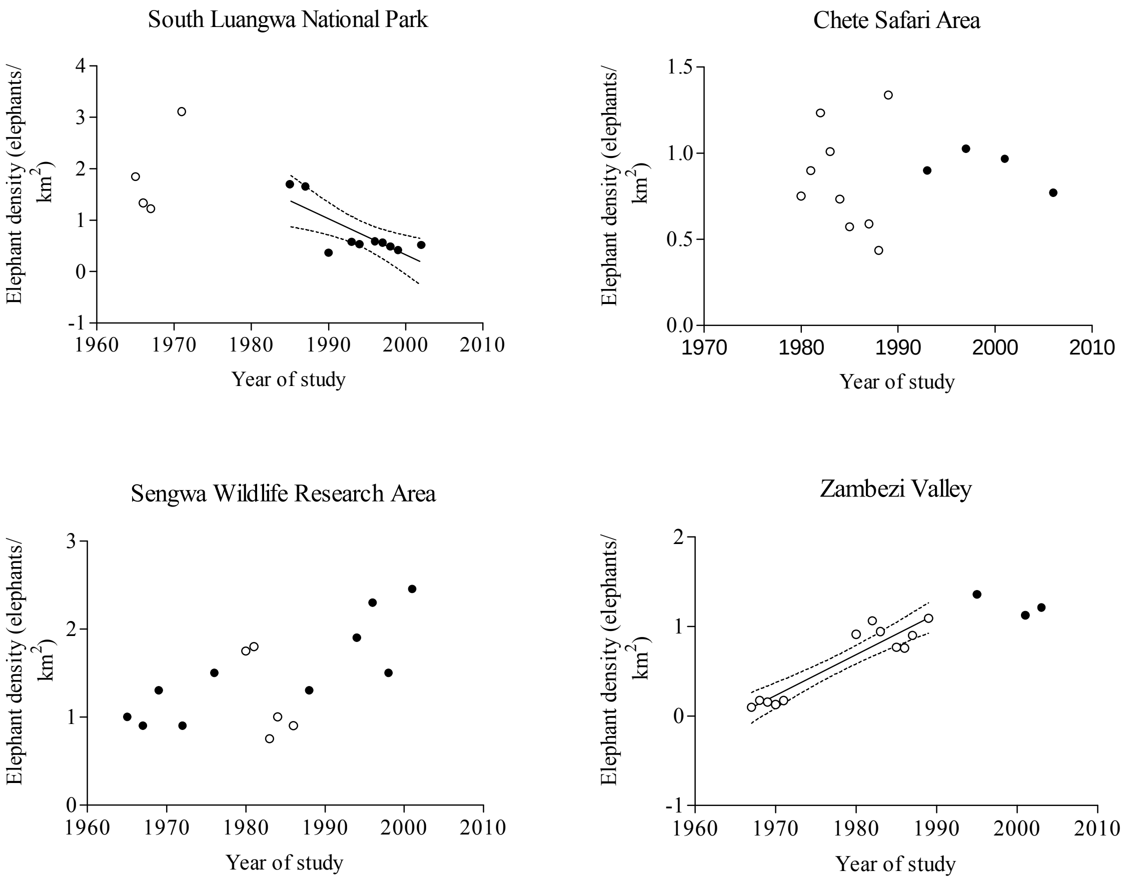
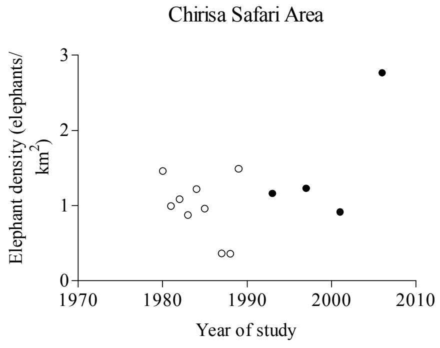
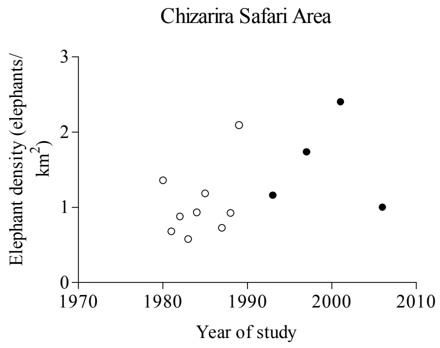
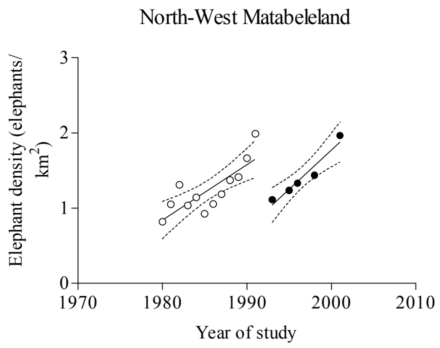
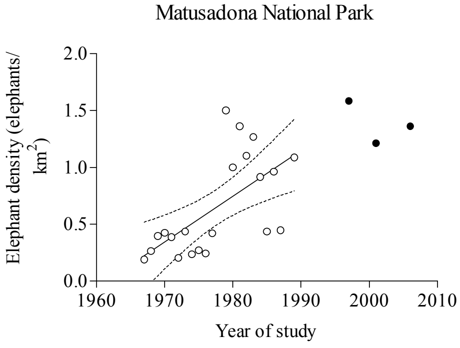


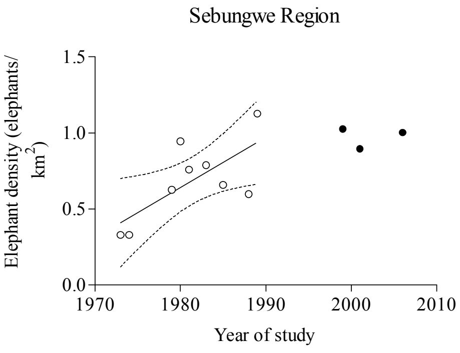
Fig. 3 Time series of elephant densities of four African elephant populations. Each time series had at least three density estimates in the management categories: “cull” (○) and “unmanaged” (●). Solid and stippled lines represent significant linear regression slopes and their 95 % confidence intervals, respectively.

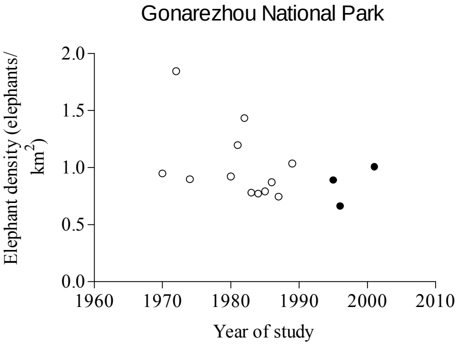

Chirisa Safari Area


Chizarira Safari Area


North-West Matabeleland


Matusadona National Park


Sebungwe Region


Gonarezhou National Park

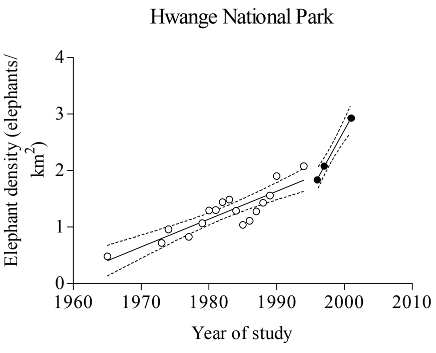

Hwange National Park

Fig. 4 Time series of elephant densities of seven African elephant populations. Each time series had at least three density estimates in the management categories: “water+cull” (○) and “water” (●). Solid and stippled lines represent significant linear regression slopes and their 95 % confidence intervals, respectively.

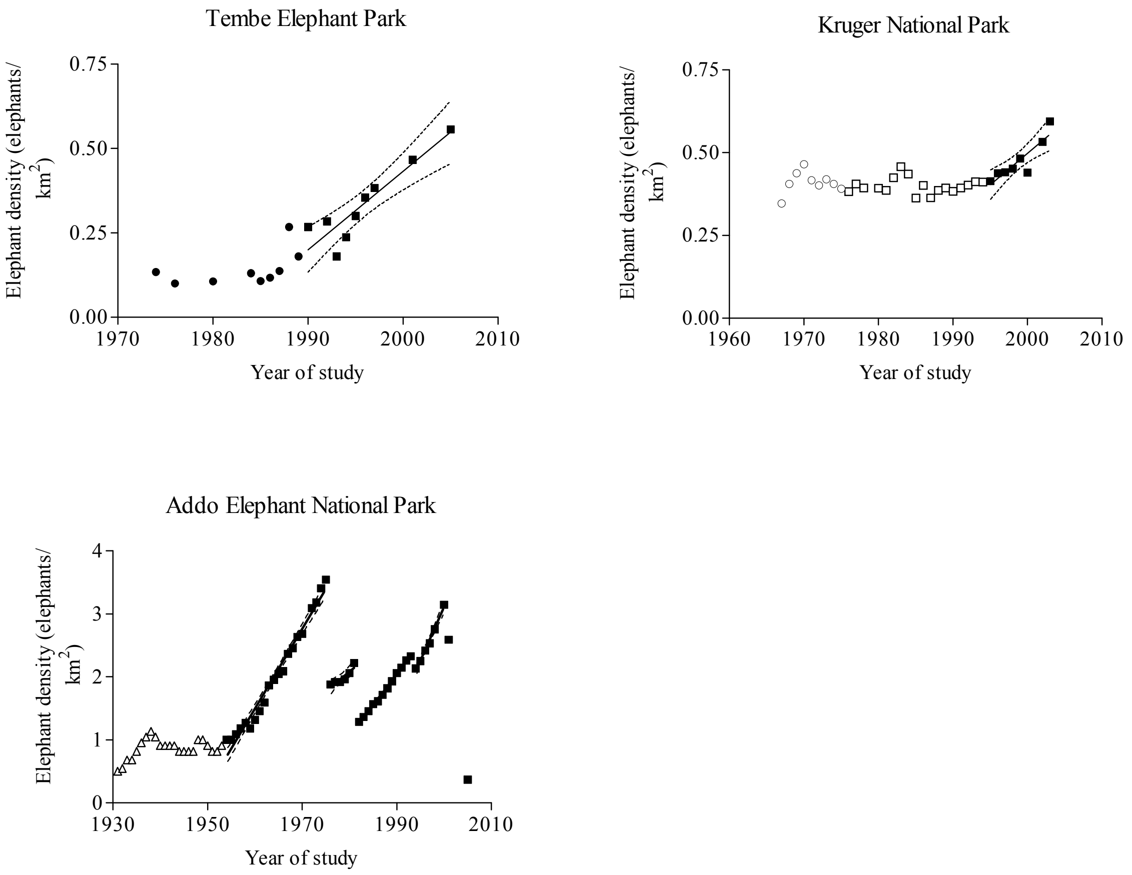


Fig. 5 Time series of elephant densities of three African elephant populations. Each time series had at least three density estimates in the management categories: “water” (●), “water+cull” (○), “fence+water+cull” (□) “fence+water” (■) and “unmanaged” (Δ). Solid and stippled lines represent significant linear regression slopes and their 95 % confidence intervals, respectively. In Addo Elephant National Park, the area available to elephants was enlarged five times (1976, 1982, 1994, 2001, and 2005).

Chapter 5

Synthesis

For more than 100 years, ecologists have estimated populations of animals to describe their status and trends (Krebs, 2003). African elephants were no exception and over the past 50 years, much effort and resources have been devoted to the monitoring of their populations. Population growth rate, which is the summary parameter of trends in population density or size, indicates whether the population is increasing, stable or decreasing, and how fast it is changing (Sibly *et al*., 2003). Trends in elephant numbers have frequently formed the basis for management decisions, where past efforts to control populations aimed at decreasing or maintaining population size (van Aarde *et al.*, 2006; van Aarde & Jackson, 2007).

There are two problems associated with this approach. First, survey design and monitoring features may influence the reliability of population trends (Seber, 1986; Barnes, 2002), which could lead to the implementation of inappropriate management actions. Second, past management that focused on controlling elephant numbers to reduce their impact on other species, may have effectively enhanced population growth rates, either by releasing vital rates from limitations induced by density dependent forces (van Aarde *et al*., 1999) or by interfering with dispersal. This study addressed these concerns.

The issue that fuels the elephant debate is the prevailing increase in elephant numbers across areas in southern Africa and the concern that they may reduce biological diversity. One such area is northern Botswana (Sommerlatte, 1976; Colegrave *et al*., 1992; Ben-Shahar, 1997; Skarpe *et al*., 2004), which supports the largest elephant population in Africa (Cumming & Jones, 2005). I used this population as a case study to illustrate just how misleading population trends may be (Chapter 2). Here, I focused on elephant numbers and densities and the area over which elephants were counted. From 1973 to

1993, elephant numbers in northern Botswana increased significantly, while elephant densities remained relatively stable. This difference in trends could be explained by the increase in survey area over the same time period. Given historical accounts of elephant distribution in Botswana, it seems likely that this population expanded its range onto their traditional distributional range. If surveys focused on areas where elephants were relatively abundant, then they covered larger areas over time in response to the expansion of elephant range and, as a result, more elephants were counted in larger areas, resulting in an increase in estimates of elephant numbers while densities remained relatively stable. From 1996 to 2004, surveyed areas were similar in size and elephant numbers for this period were therefore comparable between years. In contrast to some reports that implied a continuing increase of the northern Botswana population (Blanc *et al*., 2005; Cumming & Jones, 2005), neither elephant numbers, nor densities changed significantly during this time. Here, density related forces may have caused the leveling-off of population size, resulting in the apparent stabilisation in elephant numbers.

The take-home message is clear. One needs to be cautious about drawing conclusions from trends that are based on numbers when the area over which elephants were counted, differed in size. This is especially important for populations that are not fenced and are part of a much larger regional population, such as in northern Botswana. Second, a reduction in numbers through culling, as suggested by the Department of Wildlife and National Parks Botswana, may not yield the desired reduction in population size, where elephants may immigrate from populations in neighbouring countries, thereby nullifying efforts to reduce elephant impact on other species. As an alternative to culling, the northern Botswana elephant population could effectively be managed as part of a metapopulation, spanning Botswana, Namibia, Zambia, Zimbabwe, and Angola, as has been suggested by van Aarde & Jackson (2007).

The first systematic surveys (aerial- and ground surveys) of elephant populations began in Zambia, Uganda and Tanzania and date back to the early 1950s (Lamprey, 1964; Buss, 1990; Astle, 1999). Authorities frequently used sample counts to estimate population size where financial and logistic constraints did not allow for the counting of all individuals in the population (see Olivier *et al*., 2008 and references therein). Despite all effort and resources invested into the monitoring of African elephant populations for more than 50 years, nearly half of all population estimates available from the literature were of low quality, due to low survey intensities, high aircraft speeds and failure to report confidence limits. A power analysis (Chapter 3) of trends in elephant numbers across Africa revealed that two-thirds of populations were stable and only 30 % had sufficient statistical power. As low statistical power limits our ability to detect and interpret population changes, these trends are inconclusive and should not inform management decisions.

Failure to detect a population trend may influence conservation and management decisions. For instance, small populations in decline that are considered stable may become extinct (Barnes, 2002). Here, effort should be directed at monitoring size and age distributions as proposed by Ferreira & van Aarde (2008), rather than trying to detect changes in numbers where analyses are based on population estimates with low levels of precision.

Yet changes in elephant numbers and poaching data continue to inform ivory trade decisions by the Convention on the International Trade of Endangered Species of Wild Flora and Fauna (CITES) (Hunter & Milliken, 2004). For instance, at the 2002 Conference of the Parties, CITES allowed some southern African countries (Namibia, South Africa and Botswana) to sell their ivory stockpile on condition that a system for monitoring the illegal killing of elephants was in place (Gillson & Lindsay, 2003). A comparative assessment of elephant demography in southern Africa (Ferreira *et al*. in review, see Appendix 1) showed that populations in Zambia had few large and old elephants, herds were small and individuals were often tuskless, supporting the renewed concern about the effect of illegal ivory trade on elephant populations (see Wasser *et al*., 2007). However, Zambian authorities only noted 135 such killings between 1992 and 2001 (Wasser *et al*., 2007). This disparity in findings may be due to inefficient survey methods to monitor the effect of poaching on elephant populations. Here, evaluating size and age distributions to assess the consequences that poaching may have for the demographic profiles of populations may provide more precise information than aerial censuses.

While elephant populations in Zambia may be either stable or declining (Guldemond *et al*., 2005), those in some areas in Zimbabwe (Cumming *et al*., 1997), Namibia (Lindeque, 1991) and South Africa (van Aarde *et al*., 1999; Gough & Kerley, 2006) are increasing. Here, conservation authorities are trying to solve the apparent problem of overpopulation and their threat to human livelihoods and biological diversity. Culling has been promoted as a management tool to reduce or maintain the sizes of local populations since the mid 1960s (e.g. Laws *et al*., 1970; Field, 1971; Sherry, 1975; Cumming, 1981). Few studies, however have collated empirical data to measure the effect that culling and other past management practices may have had on elephant populations (e.g. van Aarde *et al*., 1999).

An analysis of managed and unmanaged elephant populations across Africa (Chapter 4) suggests that population growth rates were associated with management and that populations that were managed grew at faster rates than those that were unmanaged. Although it is possible that management actions were taken because of such high population growth rates, case studies of populations that were exposed to different management practices suggest that the fencing of populations and water supplementation in particular, may have enhanced their densities and growth rates, probably by influencing dispersal patterns.

To summarise, elephant population trends may be misleading when these are based on elephant numbers where the area over which elephants were counted, differed in size. Furthermore, nearly half of all elephant population estimates collected during surveys over the past 50 years had low quality, thereby compromising the reliability of population trends including such estimates. Low confidence in trend data could lead to the implementation of management actions that may not achieve the desired outcomes.

For instance, in view of the low numbers of illegal killings noted by Zambian authorities between 1992 and 2001, Zambia applied to CITES for a one-off sell of their ivory stockpiles at the 12th Meeting of the Parties in Chile in 2002. The application was followed by an ivory seizure of > 6.6 tons of contraband elephant ivory that was shown to have originated from Zambia (Wasser *et al*., 2007), which resulted in the rejection of Zambia's application to sell their ivory. This highlights the importance of credible and robust information on which authorities can provide decisions.

Furthermore, for conservation management actions to have the desired long-term effects, it is crucial to evaluate the consequences that past management practices may have had for elephant populations. For instance, the fencing of populations and the provisioning of additional water may have caused elephant densities to increase, thereby contributing to the impact of elephants on other species and counteracting conservation efforts that aim at maintaining biological diversity.

Perhaps, elephant management is in need for a paradigm shift. Instead of intensively managing local elephant numbers, management should focus on the landscape as a spatially and temporally dynamic entity, allowing elephant populations to be stabilised regionally by large-scale processes (e.g. density-dependent decrease in birth rate, decreased survival through drought events, and dispersal) and structure (van Aarde & Jackson, 2007). Finally, I would like to ask 'Should we not learn from our previous mistakes and look for innovative solutions that address the *cause* of the 'elephant problem' instead of arguing about management options that clearly did not achieve the desired outcomes in the first place?' I contend that the metapopulation approach to the conservation management of southern Africa's elephants may represent just *that* solution.

References

Astle, W.L. (1999) *A History of Wildlife Conservation and Management in the Mid-Luangwa Valley, Zambia*. Research Paper Number 3. British Empire & Commonwealth Museum, Bristol, UK.

Barnes, R.F.W. (2002) The problem of trend detection posed by small elephant populations in West Africa. *African Journal of Ecology,* **40**, 179-185.

Barnes R.F.W., Blom, A., Alers, M.P.T. & Barnes, K.L. (1995) An estimate of the numbers of forest elephants in Gabon. *Journal of Tropical Ecology*, **11,** 27-37.

Barnes, R.F.W., Craig, G.C., Dublin H.T., Overton, G., Simons, W. and Thouless, C.R. (1998) *African Elephant Database 1998*. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Bell, R.H.V. (1983) Decision making in wildlife management with reference to problems of overpopulation. In *Management of Large Mammals in African Conservation Areas* (ed N. Owen-Smith), pp. 145-171. Haum Educational Publishers, Pretoria, South Africa.

Ben-Shahar, R. (1997) Elephants and woodlands in northern Botswana: how many elephants should be there? *Pachyderm,* **23**, 41-43.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, C.G. *et al.* (2003) *African Elephant Status Report 2002. An Update from the African Elephant Database.* IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Blanc, J.J., Barnes, R.F.W., Craig, C.G., Douglas-Hamilton, I., Dublin, H.T., Hart, J.A. *et al.* (2005) Changes in elephant numbers in major savanna populations in eastern and southern Africa. *Pachyderm*, **38**, 19-28.

Blanc, J.J., Barnes, R.F.W. Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, *et al*. (2007) *African Elephant Status Report 2007: an Update from the African Elephant Database.* IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Buss, I.O. (1990) *Elephant Life. Fifteen Years of High Population Density*. Iowa State University Press, Ames, USA.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. & Clobert, J. (2008) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology,* **77**, 135-144.

Child, G. (2004) Elephant culling in Zimbabwe. *ZimConservation Opinion,* **1**, 1-6.

Colegrave, R.K., Lungu, E.M. & Muwezwa, M.E. (1992) What is happening to the elephants in Botswana? *Revue de Bio Matematique*, **30**, 49-55.

Cumming, D.H.M. (1981) The management of elephant and other mammals in Zimbabwe. In *Problems in Management of Locally Abundant Wild Mammals* (eds. P.A. Jewell and S. Holt), pp. 91-118. Academic Press, New York, USA.

Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., *et al.* (1997) Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science,* **93**, 231-236.

Cumming, D. & Jones, B. (2005) *Elephants in Southern Africa: Management Issues and Options*. WWF–SARPO Occasional Paper No. 11. WWF–SARPO, Harare, Zimbabwe.

Dudley, J.P., Craig, G.C., Gibson, D.S., Haynes, G. & Klimowicz, J. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology,* **39**, 187-194.

Ferreira, S.M. & van Aarde, R.J. (2008) A rapid method to estimate population variables for African elephants. *Journal of Wildlife Management*, **72**, 822-829.

Field, C.R. (1971) Elephant ecology in the Queen Elisabeth National Park, Uganda. *East African Wildlife Journal*, **9**, 99-123.

Gillson, L. & Lindsay, K. (2003) Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environmental Science and Policy*, **6**, 411-419.

Gough, K. & Kerley, G.I.H. (2006) Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? *Oryx,* **40**, 434-441.

Guldemond, R., Lehman, E., Ferreira S. & van Aarde R. (2005) Elephant numbers in Kafue National Park, Zambia. *Pachyderm,* **39**, 50-56.

Hunter, N & T. Milliken. 2004. Clarifying MIKE and ETIS. *Pachyderm*, **36**, 129-132.

Krebs, C.J. (2003) Two complementary paradigms for analysisng population dynamics. In *Wildlife Population Growth Rates* (eds R.M. Sibly, J. Hone & T.H. Clutton-Brock), pp. 110-126. Cambridge University Press, Cambridge, UK.

Lamprey, H.F. (1964) Estimation of the large mammal densities, biomass and energy exchange in the Tarangire game reserve and the Masai Steppe in Tanagnyika. *African Journal of Ecology*, **2**, 1-46.

Laws, R.M., Parker, I.S.C., Johnstone, R.C.B. (1970) Elephants and their habitats in North Bunyoro, Uganda. *East African Wildlife Journal*, **8**, 163-180.

Lindeque, M. (1991) Age structure of the elephant population in the Etosha National Park, Namibia. *Madoqua,* **18,** 27-32.

Olivier P.I., Ferreira, S.M. & van Aarde, R.J. (2008) Dung counts and measurements to estimate population sizes and extract age structures: a case study on elephants in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology, in press*.

Pienaar, U. de V., van Wyk, P. & Fairall, N. (1966) An aerial census of elephant and buffalo in Kruger National Park, and the implications thereof on intended management schemes. *Koedoe*, **9**, 40-107.

Said, M.Y., Chunge, R.N., Craig, G.C., Thouless, C.R., Barnes, R.F.W. & Dublin, H.T. (1995) *African Elephant Database 1995*. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Seber, G.A.F. (1986) A review of estimating animal abundance. *Biometrics,* **42**, 267-292.

Sherry, B.Y. (1975) Reproduction of elephant in Gonarezhou, south-eastern Rhodesia. *Arnoldia*, **7**, 1-13.

Sibly, R.M., Hone, J. & Clutton-Brock, T.H. (2003) Introduction to wildlife population growth rates. In *Wildlife Population Growth Rates* (eds R.M. Sibly, J. Hone & T.H. Clutton-Brock), pp. 1-10. Cambridge University Press, Cambridge, UK.

Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., du Toit, J.T. *et al*. (2004) The return of the giants: ecological effects of an increasing elephant population. *Journal of the Royal Swedish Academy of Sciences*, **33**, 276-282.

Sommerlatte, M.W. (1976) *A Survey of Elephant Populations in North-Eastern Botswana.*

Department of Wildlife and National Parks, UNDP/ FAO Project 72/020, Wildlife Management and Utilisation in Botswana. Government Printer, Gaborone, Botswana.

Srivastava, D.S. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology,* **68**, 1-16.

Thompson, G.G. & Withers, P.C. (2003) Effect of species richness and relative abundance on the shape of the species accumulation curve. *Austral Ecology,* **28**, 355-360.

van Aarde, R., Whyte, I. & Pimm, S. (1999) Culling and dynamics of the Kruger National Park African elephant population. *Animal Conservation*, **2**, 287-294.

van Aarde, R.J., Jackson, T.P. & Ferreira, S.M. (2006) Conservation science and elephant management in southern Africa. *South African Journal of Science,* **102**, 385-388.

van Aarde, R.J. & Jackson, T.P. (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation,* **134**, 289-297.

Walker, P.S. & Goodman P.S. (1983) Some implications of ecosystem properties for wildlife management. In *Management of Large Mammals in African Conservation Areas* (ed R.N. Owen-Smith), pp. 79-91. Haum Educational Publishers, Pretoria, South Africa.

Wasser, S.K.C., Mailand, R., Booth, B., Mutayoba, E., Kisamo, B., Clark, B. *et al*. (2007) Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proceedings of the National Academy of Science,* **104**, 4228-4233.

Wilhelm, J.H. (1931) Das Wild des Okavangogebietes und des Caprivizipfels. *Journal SWA/ Scientific Society* **7**, 1-71.

Appendix 1

Ivory poaching disrupts Zambian savanna elephant populations. Sam M. Ferreira, Rudi J. van Aarde & Jessi Junker.

Ivory poaching disrupts Zambian savanna elephant populations

Sam M. FERREIRA*, Rudi J. VAN AARDE* & Jessi JUNKER*

*Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

Correspondence should be addressed to Rudi J. van Aarde. Department of Zoology & Entomology, University of Pretoria, Pretoria 0002, South Africa, E-mail: rjvaarde@zoology.up.ac.za, Telephone: +27 12 420-2753, Cell: +27 82 908-7313, Fax: +27 12 420-4523

(Format according to the journal *Biological Conservation*)

Abstract: Although the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) banned trade in 1989, trafficking of contraband ivory continues. The demand for ivory maintains poaching and recent ivory seizures suggest that poachers may kill between 800 and 6 000 elephants (*Loxodonta africana*) each year in a poaching hotspot that centres on Zambia in central southern Africa. Zambian authorities, however, reported only 135 illegal killings over ten years. These findings challenge the success of the Ivory Ban and the methods employed by CITES to monitor elephant populations. Such irregularities may persist because of inefficient monitoring and the high costs of intensive censusses. We surveyed ten populations across southern Africa and digitally recorded the size of individual elephants as well as the size of herds they live in. We also collated data on population estimates and the incidence of tusklessness. Our comparative assessment of elephant demography in southern Africa shows that populations in Zambia have few large and old elephants, herds are small and individuals are often tuskless. These results provide supporting evidence for the continuing decline in numbers after the Ivory Ban came into effect. Monitoring the size and age distribution of elephant populations is less costly and may be more precise than aerial censusses. It also compliments the existing information base of trends in numbers and illegal killing of elephants on which CITES' decision-making processes are put forward. This serves to illustrate the importance of robust and credible information used by international agreements to curb environmental degradation globally.

Keywords: African elephant, CITES, poaching, age distribution, rapid population assessment

Introduction

The success of international environmental agreements depends on enforcement through political and diplomatic processes (e.g. Caplan and Silva, 2007; Kampragou et al., 2007; Lange et al., 2007; Weston, 2007), quality information and honesty. These may not be easy to achieve in complex political and socio-economic settings (e.g. Walther et al., 2005; Reeve, 2006; Rubio & Ulph, 2006; Weikard, 2006; Kolstad, 2007; McGinty, 2007). An example of the difficulties that may be encountered include the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) that since 1975 aims to control international trade in wildlife products (IUCN, 1976). Different to more recent multilateral environmental agreements, CITES is a particularly challenging case because it does not have a treaty article to mandate compliance procedures (Reeve, 2006). It relies on resolutions until repealed, and decisions stay in effect from one Conference of the Parties to the next, three years later (Reeve, 2006).

The African elephant (*Loxodonta africana*) is arguably the most controversial CITES species. The down-listing of some elephant populations to Appendix II have been complicated by trade limitations and conditions. For instance, at the 2002 Conference of the Parties, CITES allowed Namibia, South Africa and Botswana to sell their ivory stockpile on condition that a system for monitoring the illegal killing of elephants (CITES, 2007a) was in place (Gillson & Lindsay, 2003). This resolution was only approved at the 2007 CITES meeting in Den Haag (Morell, 2007).

Even so, the illegal ivory trade apparently continues to threaten the survival of African elephants. Several ivory seizures in recent years (Wasser et al., 2007) indicate that ivory poaching might be widespread in Africa in the face of numerous resolutions relating to African elephants and the ivory trade ban in 1989 (Stiles, 2004). The case of Zambia is compelling where the ivory demand degraded populations before the ivory ban came into effect (Abel and Blaikie, 1986). The seizure of large amounts of ivory from Zambia in 2002 (Wasser et al., 2007) suggests that elephant populations there may continue to be subjected to poaching after the Ban. In Zambia poachers may have killed 800 (CITES, 2007b) to 6 000 (Wasser et al., 2007) elephants during 2001 alone, but authorities here only noted 135 such killings between 1992 and 2001 (Wasser et al., 2007). This disparity may be due to inefficient monitoring programmes that rely on inaccurate elephant numbers rather than on the consequences that poaching may have for the demographic profiles of populations.

The ongoing poaching of elephants can reduce their numbers by reducing survival (Surovell et al., 2005). Poaching may also disrupt age distributions when poachers target older elephants with relatively large tusks (Milner-Gulland and Mace, 1991). Comparatively few large and old elephants should be present in such populations. We therefore hypothesised that declines in elehant populations within the poaching hotspot defined earlier in Zambia (Wasser et al., 2007) should be associated with a reduction in the number of large (old) elephants there, while this will not be the case in increasing or stable populations beyond the hotspot. Herd sizes and the incidences of tusklessness should also change if poachers target large and old elephants with big tusks (Milner-Gulland and Mace, 1991).

Materials and methods

Defining elephant population trends

We collated all estimates of the number of elephants in four Zambian National Parks (Kafue National Park – *n* = 8, Lower Zambezi National Park – *n* = 4, South Luangwa National Park – *n* = 14, and the North Luangwa National Park – *n* = 9) (see Supplementary Reference List) to assess apparent trends in elephant numbers for populations within the poaching hotspot identified by Wasser et al. (2007). We focused on data from 1970-2006 to compare population estimates prior to the Ivory Ban with those after the Ban. Scarcity of data for most of the Zambian populations forced us to also include informed (*n* = 8) and other guesses (*n* = 1) in our analyses, apart from total aerial counts (*n* = 1) and aerial sample counts (*n* = 25) (Blanc et al., 2007). Irregular sampling intervals, variable survey efforts and a lack of measures of precision for estimates in time series restricted our analytical options.

We also collated estimates since 1970 for four populations (Etosha National Park – *n* = 17, northern Botswana – *n* = 17, Zambezi Valley – *n* = 12, and the Kruger National Park – *n* = 34) (Seber, 1992), all areas with a history of little poaching and that are well beyond the poaching hotspot identified by the 2002 seizure (Wasser et al., 2007). We termed these non-poached populations and included 6 informed guesses, 1 ground sample survey, 39 aerial total counts and 32 aerial sample counts in our analysis.

We converted population estimates to number of elephants km^{-2} to correct for differences in survey areas. Linear regression of the natural logarithm of densities against time allowed us to determine growth rates for all populations during the era after the Ivory Ban in 1989. We excluded estimates made during years of culling for Kruger i.e. 1966 - 1996 (van Aarde et al., 1999) and the Zambezi Valley i.e. 1960 - 1991 (Cumming et al., 1997).

Determining the size structure of elephant populations

We surveyed breeding herds during 2003 - 2006 in Zambian National Parks (North Luangwa – n = 63 herds, South Luangwa – n = 96, Lower Zambezi – n = 13, northern Kafue – n = 23, southern Kafue – n = 35) and populations elsewhere (Etosha – n = 17, Ngamiland – n = 28, Moremi Game Reserve – n = 13, Chobe National Park – n = 29 and Kruger – n = 29) to evaluate whether the size distributions of populations in the poaching hotspot (Zambia) differ from those of populations elsewhere. We converted back lengths measured through digital photogrammetry (Shrader et al., 2006a) to shoulder heights to test whether poached populations had a shortage of large elephants.

Deriving and smoothing age distributions

We assigned age to individual elephants from shoulder heights (Shrader et al., 2006a). We previously (Ferreira and van Aarde, 2007) considered the smoothing and expanding of an age distribution given that we could only assign ages reliably up to the age of 15 years (Shrader et al., 2006). We grouped female elephants into one-year age classes up to age 15 with all older elephants comprising a single age class. We then assumed that most elephants do not live beyond 60 years of age (Wiese and Willis, 2004) and defined $\sum_{x}^{w} n_x = n_0 a^x \left[\frac{(1-a^{(w-x+1)})}{(1-a)} \right]$ as the sum of frequencies of females that were x to w years old. Here n_x = the number of females x years old. The frequencies decay at a rate a, our smoothing parameter, with increase in age. By defining a series of $\sum_{i=x}^{w} n_i$ when increasing x

at increments of 1 up to 15 and setting $w = 60$, we estimated the decay rate (a) through maximum likelihood assuming a normal distribution.

We also calculated the age at first calving (x_{1st}) and calving interval (i) from cow-calf associations (Ferreira and van Aarde, unpublished data). Recruitment or apparent fecundity $m_x = 0.5/i$ was set equal for all females of age $x \geq x_{1st}$.

Predicting the number of elephants killed each year

We determined whether the observed age distributions differed from that predicted by the apparent fecundity and the population growth we estimated from time series, and if these were the same for poached and non-poached populations. Estimated fecundity (m_x) and population growth rates (r) allowed us to define the expected stable age distribution $S_x = l_x e^{-rx}$ for each population from $\sum l_x e^{-rx} m_x = 1$, within which the fraction of individuals of age x decays with age at a rate a. When adults are poached, a should decrease and the change in a is negative (i.e. $\Delta a < 0$). However, for non-poached populations we expected Δa to be both positive and negative. This predicts that the distribution of Δa should center below zero for poached populations, but on zero for non-poached populations. As expected, the distribution of Δa fell below zero for the poached populations, and around zero for the non-poached populations.

The decays of observed (a_o) and expected (a_e) age distributions for a given fecundity m_x, allowed us to estimate the likely number of elephants killed each year. Given that $s = \lambda a$ (Ferreira and van Aarde, unpublished data), we assumed λ was the finite population growth rate (1+r) that we noted for each of the Zambian populations and defined yearly survival from the observed age distribution s_o, while s_e was annual survival defined from the expected age distribution. Note that we assumed equal survival for all ages, as our data did not allow us to estimate age-specific survival rates. If we assume that l_0, i.e., survivorship at birth, is 1, then the effect of annual survival accumulates with age so that the sum of survivorships for all ages x ($\sum_{x=0} l_x = \sum_{x=0} s^x$) should be less for the observed than that for the expected age distribution. The difference between observed sums of survivorships and expected sums of survivorships will reflect on the impact of poaching. We thus calculated the proportion of elephants that poachers removed each year as $1 - \sum_{x=0} l_{x,o} \Big/ \sum_{x=0} l_{x,e}$. Through this approach, the deviances of observed from expected age distributions suggest that 6.4%, 4.6%, 0.7% and 4.0% of the elephants in Kafue, Lower Zambezi, South Luangwa and North Luangwa were poached each year.

We then used the most recent population estimates and the population growth rates we estimated for Kafue, Lower Zambezi, South Luangwa and North Luangwa to predict what the population size was in 2001 from which we calculated how many elephants were killed between 2001 and 2002. In that year, approximately 220, 10, 29 and 153 elephants were killed illegally in Kafue, Lower Zambezi, South Luangwa and North Luangwa respectively.

We also calculated how many years poachers needed to accumulate the 6.5 tons of ivory seized in 2002 (Wasser et al., 2007) that is equivalent to 3 000 - 6 500 elephants. If we assume that the proportional illegal killing of elephants stayed the same in each population, and we backtracked the population sizes, then such an illegal ivory stockpile needed five to 10 years of poaching.

Results

Our collation of estimates of elephant densities suggests that elephant densities in Kafue in Zambia continued to decline after the Ivory Ban (calculated rates of change for North Luangwa were 0.029 ± 0.046, (mean ± SE), $F_{1,3} = 0.39$, $p = 0.57$; for South Luangwa 0.011 ± 0.018, $F_{1,6} = 0.35$, $p = 0.56$; for Kafue -0.081 ± 0.024, $F_{1,4} = 11.59$, $p = 0.03$; and for Lower Zambezi -0.018 ± 0.201, $F_{1,1} = 0.01$, 191 $p = 0.94$; Fig. 1a). In contrast, populations elsewhere in southern Africa that were beyond the poaching hotspot were either stable or increased following the Ban (Zambezi Valley – 0.002 ± 0.020, $F_{1,1} = 0.01$, $p = 0.92$; Botswana – 0.030 ± 0.016, $F_{1,10} = 3.24$, $p = 0.10$; Kruger – 0.041 ± 0.006 $F_{1,7} = 54.88$, $p = 0.01$; and Etosha – 0.034 ± 0.017, $F_{1,5} = 4.32$, $p = 0.09$; Fig. 1b).

Breeding herds of populations in the poaching hotspot consistently had fewer females larger than 230 cm in shoulder height (> 43 years old) – the asymptote of female growth across Africa (Shrader et al., 2006b) - compared to populations elsewhere ($t_{12} = 3.29$, $p = 0.01$) (Fig. 2). Selective poaching also reduced the fraction of large elephants in a population and thus shifted age distributions ($t_8 = 2.58$, $p = 0.02$). Hence, trends in elephant numbers observed for Zambian populations may result from relatively low adult survival when compared to other populations that have had little or no poaching incidences.

Moreover, Zambian populations had few large herds (Fig. 3a) and elephants without tusks were common in two of the populations compared to populations outside the poaching hotspot (Fig. 3b).

The size structures converted to age structures were different from that predicted for the given fecundty schedule and observed population growth rates. As expected, the distribution of $\Delta\alpha$ fell below zero for the poached populations, and around zero for the non-poached populations. These deviances of observed from expected age distributions suggest that 6.4%, 4.6%, 0.7% and 4.0% of the elephants in Kafue, Lower Zambezi, South Luangwa and North Luangwa were poached each year. This predicts that 220, 10, 29 and 153 elephants were killed illegally between 2001 and 2002 in Kafue, Lower Zambezi, South Luangwa and North Luangwa respectively. If we assume that the proportional illegal killing of elephants stayed the same in each population, and we backtracked the population sizes, then the 2002 seizure representing 3000 to 6000 elehants needed five to 10 years of poaching.

Discussion

The transient changes in elephant numbers and the disruptions in age distributions of breeding herds support recent notions that relatively large scale poaching is taking place in Zambia (Wasser et al., 2007) despite the implementation of the Ivory Ban (Martin, 1990; Stiles, 2004). This differs from populations elsewhere in southern Africa. For instance, after years of growth, elephant densities in northern Botswana recently started to stabilize (Junker et al., 2007), whereas densities in some areas in Zimbabwe (Cumming et al., 1997), Namibia (Lindeque, 1991) and South Africa (van Aarde et al., 1999; Slotow et al., 2005) are either increasing or stable. The declines in elephant numbers in Zambia apparently reflect on ivory poaching that affects adult survival. Zambian authorities should therefore have recorded many more incidences of poaching than the 135 illegal killings of elephants reported over 10 years prior to the 2002 seizure (Wasser et al., 2007). This suggests that CITES programmes that monitor the illegal killing of elephants (CITES, 2007a) have limitations.

The 12 major seizures totalling 23.46 tons of ivory in 2005 / 2006, as well as the 6.5 tons of ivory seized by the Zambian authorities in June 2002 may represent the product of the slaughter of elephants during the previous years (Wasser et al., 2007). It accounts for ~23 000 elephants in 2005 / 2006 (Wasser et al., 2007) (presumably from several regions) and 3 000 - 6 500 elephants in 2002 (Wasser et al., 2007) from Zambia alone. If we assume that the deviance in size structure we noted in Zambia is exclusively due to poaching, then ~412 elephants were killed in 2002. This is well short of that predicted by the 2002 ivory seizure (Wasser et al., 2007), but closer to that assumed by the CITES Panel of Experts that evaluated Zambia's application to sell ivory (CITES, 2007b). These apparent anomalies need explanation.

The seized ivory may not all have come from Zambia, but rather from the large populations of elephants in the neighbouring Zimbabwe and Botswana. Assumptions that were made previously when estimating the number of poached elephants (CITES, 2007b; Wasser et al., 2007) also may be flawed. However, a more likely explanation is that the 2002 seizure does not represent a single year of poaching as our assessment suggests that this ivory may have accumulated over five to 10 years of poaching in Zambia. Poaching also may have continued after the Ban and have induced a decline in elephant numbers in Zambia. Poaching effects may be widespread for several other regions, given the large seizures during 2005 / 2006 (Wasser et al., 2007).

Apart from the call for international support to increase law enforcement and the monitoring of the illegal killing of elephants (Wasser et al., 2007), conservationists should continue to monitor elephant numbers and hence evaluate conservation efforts to curb this decline. Furthermore, given the apparent disruption of size distributions induced by ivory poaching, we suggest that authorities should instigate surveys of size and age structures to reflect on the intensity of poaching in a given population. This may be more efficient than efforts to detect population trends based on population estimates with relatively wide confidence limits (Seber, 1992).

Our analysis supports the renewed concern about the effect of illegal ivory trade on elephant populations (Wasser et al., 2007). It also suggests that the Ivory Ban was relatively ineffective in curbing populations declines in Zambia, as may also be the case elsewhere in Africa. The criteria that CITES uses to evaluate ivory trade applications may have shortcomings when defining trends in elephant numbers and incidences in the illegal killing of elephants. We therefore suggest that conservation targets should be based on demographic profiles and signals of shifts in age distributions as robust, cost-efficient complementary criteria on which to base CITES regulations on the international trade of ivory.

The CITES case history of elephants and ivory illustrates the importance of credible and robust information on which international agreements can provide decisions. Robust ecological measures may provide such information.

Literature cited

Abel, N., Blaikie, P., 1986. Elephants, people, parks and development: the case of the Luangwa Valley, Zambia. Environmental Management 10, 735-751.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I., Hart, J.A., 2007. African Elephant Status Report 2007: An Update from the African Elephant Database. IUCN, Gland.

Caplan, A.J., Silva, E.C.D., 2007. An equitable, efficient and implementable scheme to control global carbon dioxide emissions. International Tax and Public Finance14, 263-279.

CITES, 2007a. Monitoring the illegal killing of elephants (MIKE). http://www.cites.org/eng/prog/MIKE (accessed 19 February 2007).

CITES, 2007b. Report of the Panel of Experts on the African Elephant on the review of the proposal submitted by Zambia to transfer its national population of Loxodonta africana from Appendix I to Appendix II. http://www.cites.org/eng/cop/12/doc/E12-66A4.pdf (accessed 15 March 2007).

Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Hovorka, M.D., Johston, D.S., Kalcounis, M., Mahlangu, Z., Portfors, C.V.R., 1997. Elephants, woodlands and biodiversity in southern Africa. South African Journal of Science 93, 231-236.

Ferreira, S.M., van Aarde, R.J., 2007. A rapid method to estimate population variables for African elephants. Journal of Wildlife Management, in review.

Gillson, L., Lindsay, K., 2003. Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. Environmental Science and Policy 6, 411-419.

IUCN, 1976. Convention on the International Trade in Endangered Species of Wild Fauna and Flora, Washington DC, 3 March 1973, in force 1 July 1975. Unity Nations Treaty Series 993, 1-243.

Junker, J., van Aarde, R.J., Ferreira, S.M., 2007. An appraisal of temporal trends in elephant numbers and densities in northern Botswana. Oryx, 42, 58-65.

Kampragou, E., Eleftheriadou, E., Mylopoulos, Y. 2007. Implementing equitable water allocation in transboundary catchments: The case of River Nestos/Mesta. Water Resource Management 21, 909-918.

Kolstad, C.D., 2007. Systematic uncertainty in self-enforcing international environmental agreements. Journal of Environmental Economics and Management 53, 68-79.

Lange, A., Vogt, C., Ziegler, A., 2007. On the importance of equity in international climate policy: An empirical analysis. Energy Economics 29, 454-562.

Lindeque, M., 1991. Age structure of the elephant population in the Etosha National Park, Namibia. Madoqua 18, 27-32.

Martin, E.B., 1990. After the ivory bans. Wildlife Conservation 93, 28-31.

McGinty, M., 2007. International agreements among asymetric nations. Oxford Economic Papers 9, 45-62.

Milner-Gulland, E.J., Mace, R., 1991. The impact of the Ivory Trade on the African Elephant Loxodonta africana population as assessed by data from the Trade. Biological Conservation 55, 215-229.

Morell, V., 2007. Elephants take centre ring at CITES. Science 316, 1678-1679.

Reeve, R., 2006. Wildlife trade, sanctions and compliance: lessons from the CITES regime. Internal Affairs 82, 881-897.

Rubio, S.J., Ulph, A., 2006. Self-enforcing international environmental agreements revisited. Oxford Economics Papers 58, 233-263.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters. MacMillan, New York.

Shrader, A.M., Ferreira, S.M., van Aarde, R.J., 2006a. Digital photogrammetry and laser rangefinder techniques to measure African elephants. South African Journal of Wildlife Research 36, 1-7.

Shrader, A.M., Ferreira, S.M., McElveen, M.E., Lee, P.C., Moss, C.J., van Aarde, R.J., 2006b. Growth and age determination of African savanna elephants. Journal of Zoology (London) 270, 40-48.

Slotow, R., Garaï, M., Reilly, B., Page, B., Carr, R.D., 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. South African Journal of Wildlife Research 35, 23-32.

Steenkamp, G., Ferreira, S.M., Bester, M.N., 2007. Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*). Journal of the South African Veterinary Association, in press.

Stiles, D., 2004. The ivory trade and elephant conservation. Environmental Conservation 31, 309-321.

Surovell, T., Waguespeck, N., Brantingham, P.J., 2005. Global archaeological evidence for proboscidean overkill. Proceedings of the National Academy of Sciences 102, 6231-6236.

van Aarde, R.J., Whyte, I.J., Pimm, S.L., 1999. Culling and the dynamics of the Kruger National Park African elephant population. Animal Conservation 2, 287-294.

Walther, G., Hughes, L., Vitousek, P., Stenseth, N.C., 2005. Consensus on climate change. Trends in Ecology and Evolution 20, 648-649.

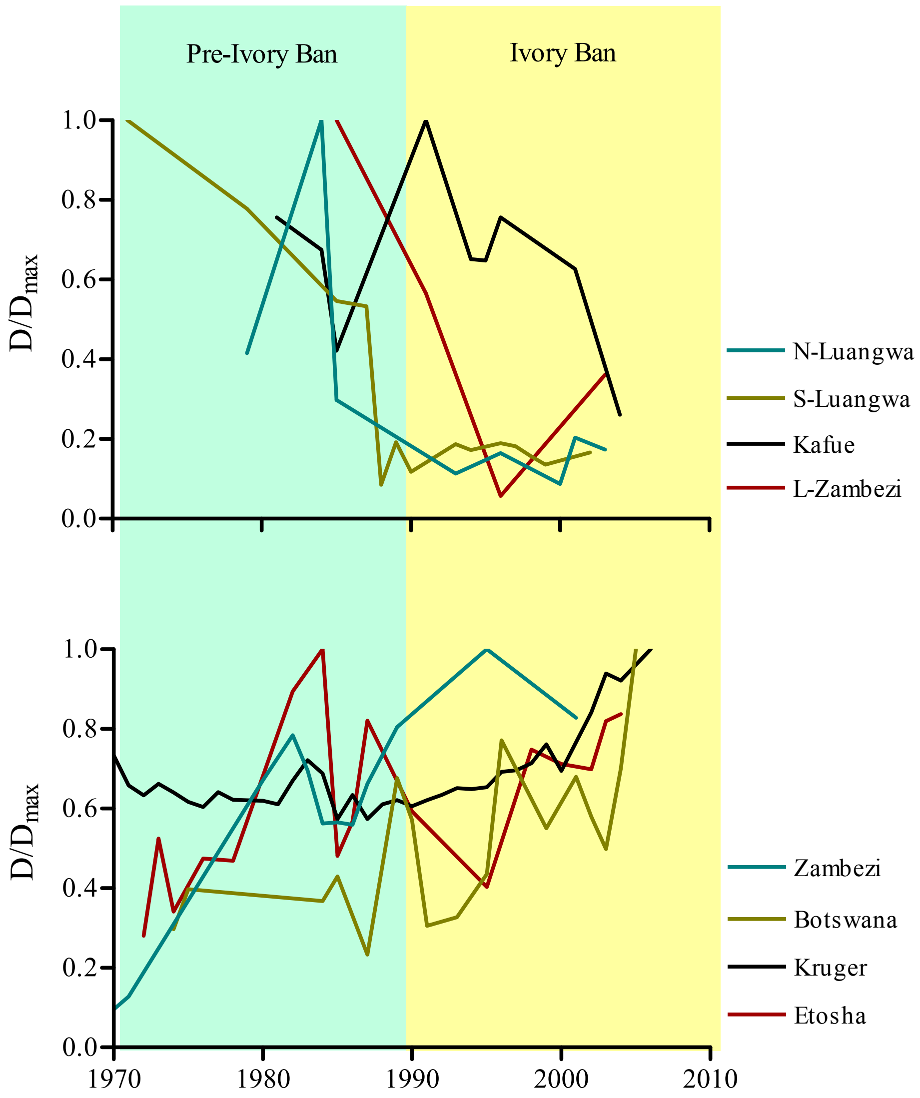
Wasser, S.K., Mailand, C., Booth, R., Mutayoba, B., Kisamo, E., Clark, B., Stephens, M., 2007. Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. Proceedings of the National Academy of Sciences 104, 4228-4233.

Weikard, H.P., Finus, M., Altamirano-Cabrera, J.C., 2006. The impact of surplus sharing on the stability of international climate agreements. Oxford Economic Papers 58, 209-232.

Weston, J., 2007. Implementing international environmental agreements: the case of the Wadden Sea. European Planning Studies 15, 133-152.

Wiese, R.J., Willis, K., 2004. Calculation of longevity and life expectancy in captive elephants. Zoo Biology 23, 365-373.

a) Zambian poached populations



b) Other non-poached populations

Fig. 1. Trends in African elephant population densities since 1970. We illustrate those for Zambia (assumed poached populations) a) and other selected southern African regions (non-poached populations) b). We show each density estimate (*D*) as a fraction of the maximum density estimate (D_{max}) in a time series.

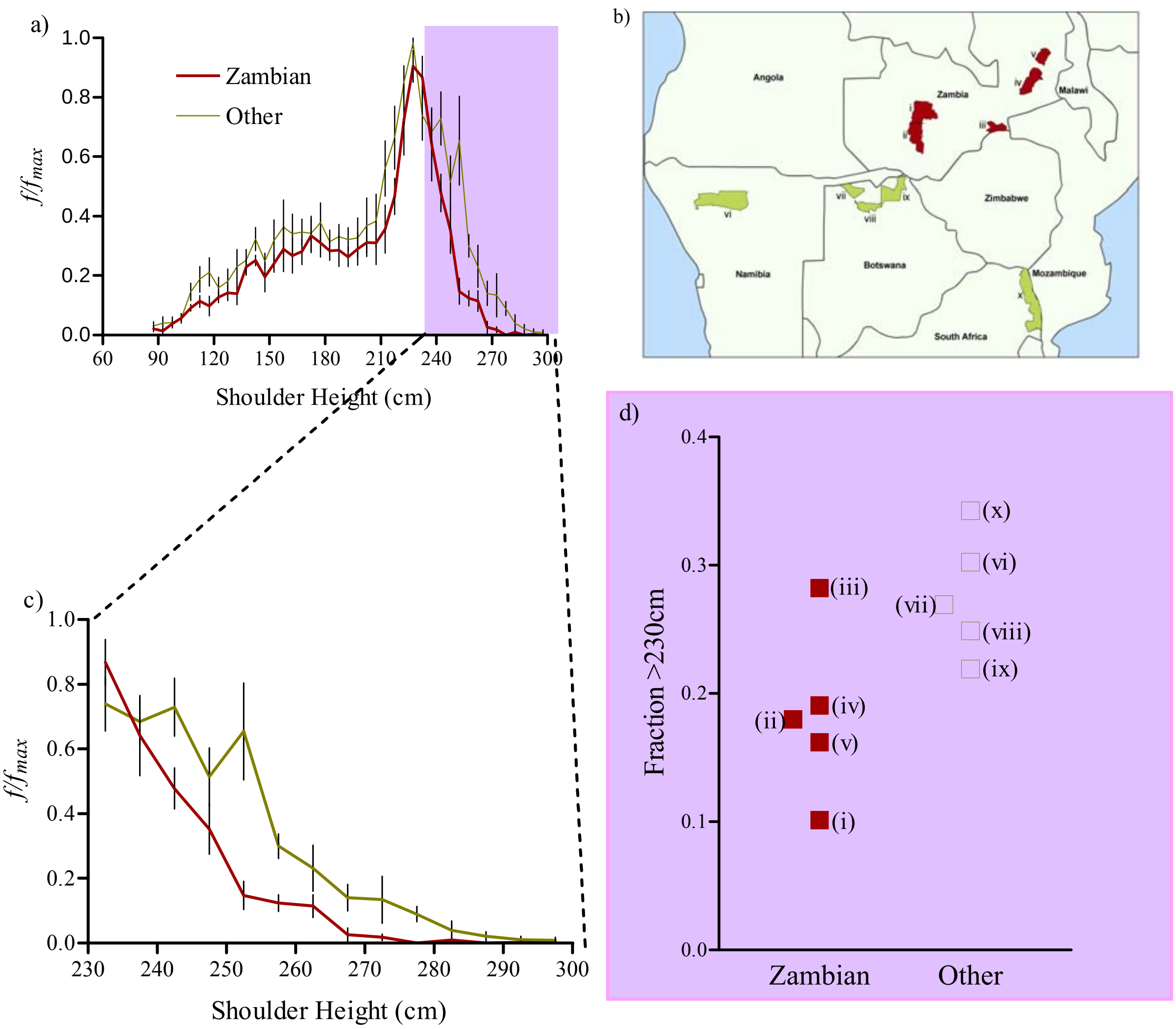


Fig. 2. Poaching effects on the size structure of elephant populations in southern Africa (a). We measured shoulder heights for five populations within the poaching hotspot (i – northern Kafue, ii – southern Kafue, iii – Lower Zambezi, iv – South Luangwa, v – North Luangwa) and five populations elsewhere in southern Africa (vi – Etosha, vii – Ngamiland, viii – Moremi, ix – Chobe, x – Kruger) (b). We expressed size frequencies (*f*) as fractions of the highest frequency (*fmax*) for each population. We calculated mean values for populations within and beyond the poaching hotspot, separately

(vertical bars represent SE) (c). Zambian populations tend to have a smaller fraction of individuals larger than 230 cm at the shoulder (d).

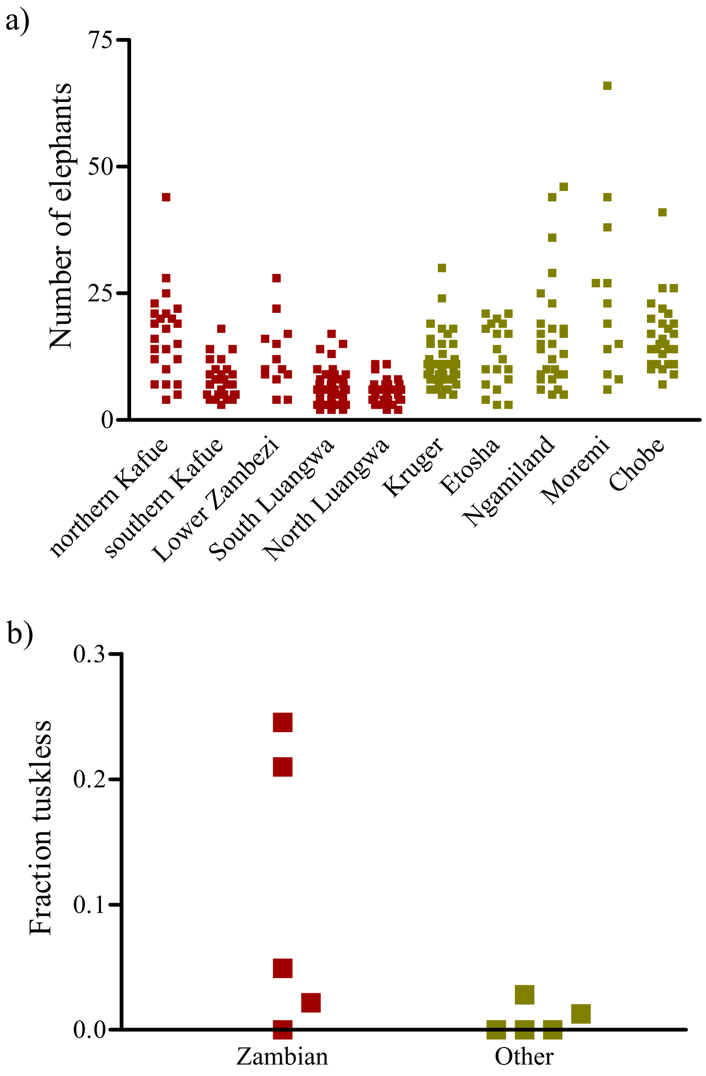


Fig. 3. Poaching effects on African elephant populations. We show herd sizes (a) and incidences of elephants without tusks (b). Brown symbols denote populations in the poaching hotspot while populations beyond this hotspot are indicated in green. We extracted incidences of elephants without tusks for each of the populations from the literature (Wiese and Willis, 2004).

Supplementary reference list

Reference list for population estimates

Anon., 1999. Kafue National Park general management plan. Japan International Cooperation Agency, Chilanga.

Anon., 1996. Aerial census of wildlife and some domestic animals in Botswana. Dry season 1996. Department of Wildlife and National Parks, Gaborone.

Anon., 1999. Aerial census of wildlife and some domestic animals in Botswana. Dry season 1999. Department of Wildlife and National Parks, Gaborone.

Anon., 2001. Aerial census of wildlife and some domestic animals in Botswana. Dry season 2001. Department of Wildlife and National Parks, Gaborone.

Anon., 2002. Aerial census of wildlife and some domestic animals in Botswana. Dry season 2002. Department of Wildlife and National Parks, Gaborone.

Anon., 2003. Aerial census of wildlife and some domestic animals in Botswana. Dry season 2003. Department of Wildlife and National Parks, Gaborone.

Anon., 2004. Aerial census of wildlife and some domestic animals in Botswana. Dry season 2004. Department of Wildlife and National Parks, Gaborone.

Anon., 2005. Aerial census of wildlife and some domestic animals in Botswana. Dry season 2005. Department of Wildlife and National Parks, Gaborone.

Ansell, W.F.H., 1960. Mammals of Northern Rhodesia. Department of Game and Fisheries, Lusaka.

Astle, W.L., 1999. A history of wildlife conservation and management in the Mid-Luangwa Valley, Zambia, Research Paper No. 3. British Empire & Commonwealth Museum, Bristol.

Barnes, R.F.W., Craig, G.C., Dublin H.T., Overton, G., Simons, W., Thouless, C.R., 1999. African elephant database 1998. IUCN, Gland.

Bigalke, R.C., 1958. On the present status of ungulate mammals in South West Africa. Mammalia 22, 478-497.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, C.G., Barnes, R.F.W., 2003. African elephant status report 2002: an update from the African elephant database. IUCN, Gland.

Blanc, J.J., Barnes, R.F.W., Craig, C.G., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I., Hart, J.A., 2007. African elephant status report 2007: an update from the African elephant database. IUCN, Gland.

Caughley, C., Goddard, J., 1975. Abundance and distribution of elephants in Luangwa Valley, Zambia. East African Wildlife Journal 13, 39-48.

Chanda, G., Tembo A., 1993. The status of elephant on the Zambian bank of the Middle Zambezi Valley. Pachyderm 16, 48-50.

Chase, M.J., Griffin, C.R., 2006. Elephant distribution and abundance in the Lower Kwando river basin and West Caprivi (Unpublished Report, 2006).

Cumming, D.H.M., Jackson, P., 1981. The status and conservation of Africa's elephants and rhinos. Proceedings of the joint meeting of IUCN/SSC, Hwange Safari Lodge, 30 July - 7 August.

Cumming, D.H.M., du Toit, R.F., Stuart, S.N., 1990. African elephant and rhinos, status survey and conservation. IUCN, Gland.

Cumming, D.H.M., Jones, B., 2005. Elephants in southern Africa: management issues and options, occasional paper no. 11. WWF, Harare.

de Villiers, P.A., 1981. Eto-ekologiese aspekte van olifante in die Nasionale Etoshawildtuin, S.W.A. MSc thesis, University of the Orange Free State, Bloemfontein.

Douglas-Hamilton, I., 1972. On the ecology and behaviour of the African elephant. PhD thesis, University of Oxford, Oxford.

Douglas-Hamilton, I., 1987. African elephant population study. Pachyderm 8, 1-10.

Dunham, K.M., Simwanza, H.I., 2002. Aerial census of elephants and other large herbivores in South Luangwa NP and Lupande GMA, Zambia: 2002. Zambia Wildlife Authority / WWF, Chipata.

Dunham, K.M., 2004. Aerial survey of elephants and other large herbivores in the Zambezi Heartland (Zimbabwe, Mozambique and Zambia): 2003. African Wildlife Foundation, Lusaka.

Fairall, N., Kampamba, G., 2001. Aerial Census of Kafue National Park. University of Pretoria, Pretoria.

Gibson, D.S.C., Craig, G.C., Masogo, R.M., 1998. Trends of the elephant population in northern Botswana from aerial survey data. Pachyderm 25, 14-27.

Grimwood, I.R., Benson, C.W., Ansell, W.F.H., 1958. The present-day status of ungulates in northern Rhodesia. Mammalia 3, 451-467.

Guldemond, R., Lehman, E., Ferreira, S., van Aarde, R., 2005. Elephant numbers in Kafue National Park, Zambia. Pachyderm 39, 50-56.

Jachmann, H., 1995. Survey experiments and aerial survey of elephants in the South Luangwa National Park and the Lupande Game Management Area, Zambia, 1993. Pachyderm 19, 81-86.

Jachmann, H., 2001. Estimating abundance of African wildlife: an aid to adaptive management. Kluwer, Dordrecht.

Jachmann, H., 2002. Comparison of aerial counts with ground counts for large African herbivores. Journal of Applied Ecology 39, 841-852.

Jachmann, H., Billiouw, M., 1997. Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. Journal of Applied Ecology 34, 233-244.

Kerr, M.A., Frazer, J.A., 1975. Distribution of elephant in a part of the Zambezi Valley, Rhodesia. Arnoldia 7, 1-14.

Laws, R.M., Parker, I.S.C., Johnstone, R.C.B., 1975. Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda. Clarendon, Broadbridge.

Lewis, D.M., 1984. Demographic changes in the Luangwa Valley elephants. Biological Conservation 29, 7-14.

Lindeque, M., 1989. Population dynamics of elephants in Etosha National Park, S.W.A. / Namibia. PhD thesis, University of Stellenbosch, Stellenbosch.

Mackie, C.L., 2002. Aerial census of elephants and other large herbivores in the Zambezi Valley, Zimbabwe: 2001, occasional paper no. 2. Department of National Parks and Wild Life Management / WWF, Harare.

Martin, R.B., 2005. Elephants - Transboundary Species Project. Transboundary Mammal Project. Ministry of Environment and Tourism and Namibia Nature Foundation, Windhoek.

Martin, R.B., Conybeare, A.M.G., 1995. Elephant management in Zimbabwe, 2nd edn. Department of National Parks and Wild Life Management, Harare.

Ndhlovu, D.E., Balakrishnan, M., 1991. Large herbivores in Upper Lupande Game Management Area, Luangwa Valley, Zambia. African Journal of Ecology 29, 93-104.

Parker, I.S.C., Graham, A.D., 1989. Elephant decline (part1). Downward trends in African elephant distribution and numbers. International Journal of Environmental Studies 34, 287-305.

Pienaar, J.S., 1963. Large mammals of the Kruger National Park: their distribution and present day status. Koedoe 6, 16-37.

Pienaar, U. De V., van Wyk, P., Fairall, N., 1966. An aerial census of elephant and buffalo in Kruger National Park, and the implications thereof on intended management schemes. Koedoe 9, 40-107.

Said, M.Y., Chunge, R.N., Craig, G.C., Thouless, C.R., Barnes, R.F.W., Dublin, H.T., 1995. African elephant database 1995. IUCN, Gland.

Sommerlatte, M.W.A., 1976. Survey of elephant populations in north-eastern Botswana, Project 72/020. Department of Wildlife and National Parks and UNDP / FAO, Gaborone.

Spinage, C.A., 1990. Botswna's problem elephants. Pachyderm 13, 14-20.

van Aarde, R., Kilian, W., Pimm, S., 2003. The dynamics of savanna elephants in Etosha National Park in northern Namibia, annual progress report to the US Fish and Wildlife Service. Conservation Ecology Research Unit, Pretoria.

van Wyk, P., Fairall, N., 1969. The influence of the African elephant on the vegetation of the Kruger National Park with special reference to the tree and shrub strata. Koedoe 12, 57-89.

Whyte, I.J., 2001. Conservation management of the Kruger National Park elephant population. PhD thesis, University of Pretoria, Pretoria.

Whyte, I.J., Biggs, H.C., Gaylard, A., Braack, L.E.O., 1999. A new policy for the management of the Kruger National Park's elephant population. Koedoe 42, 111-133.

Estimates for 2003 and 2004 for Kruger National Park provided by the South African National Parks Board.

Appendix 2 Reference list including documents from which I extracted information on elephant population estimates and management.

Abel, N. & Blaikie, P. (1986) Elephants, people, parks and development: the case of the Luangwa Valley, Zambia. *Environmental Management*, **10**, 735-751.

Afolayan, T.A. & Amubode, F.O. (1985) Stock assessment of large mammals in Nigerian wooded savanna and its management implications. *Forest Ecology and Management,* **13**, 256-263.

Aleper, D. & Moe, S.R. (2006) The African savannah elephant population in Kidepo Valley National Park, Uganda: changes in size and structure from 1967 to 2000. *African Journal of Ecology,* **44**, 157-164.

Alers, M.P.T., Blom, A., Kiyengo, C.S., Masunda, T. & Barnes, R.F.W. (1992) Preliminary assessment of the status of the forest elephant in Zaire. *African Journal of Ecology*, **30**, 279-291.

Amwata, D.A., Omondi, P. & Bitok, E. (2006) Human-wildlife conflict in Mochongoi Forest, Baringo, Kenya: a case study of elephants. *Pachyderm*, **41**, 30-36.

Andersen, J.L. (1993) The introduction of elephant into medium-sized conservation areas. *Pachyderm*, **17**, 35-38.

Andersen, K.F. & Eltringham, S.K. (1997) Some preliminary observations on possible stress in the elephants of Mikumi National Park, Tanzania. *African Journal of Ecology*, **35**, 278-282.

Anon. (1996) *Aerial Census of Wildlife and Some Domestic Animals in Botswana. Dry Season 1996.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (1999) *Aerial Census of Animals in Botswana. Dry season 1999.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (1999) *Kafue National Park General Management Plan. April 1999.* Unpublished report. Kafue National Park Management Plan Project. National Parks and Wildlife Service, Japan International Cooperation Agency, Tokyo, Japan.

Anon. (2000) *Strategy for the Conservation of Elephants in Ghana. To Ensure the Conservation of Viable Elephant Populations and their Habitats in Ghana. November 2000.* Wildlife Division/ WWF/ African Elephant Specialist Group, Accra, Ghana.

Anon. (2001) *Aerial Census of Animals in Botswana. Dry Season 2001.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (2002) *Aerial Census of Animals in Botswana. Dry Season 2002.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (2003) *Aerial Census of Animals in Botswana. Dry Season 2003.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (2004) *Aerial Census of Animals in Botswana. Dry Season 2004.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (2004) *Kakum National Park Elephant Survey 2004*. Final report. Convention on International Trade in Endangered Species (CITES), Monitoring the Illegal Killing of Elephants (MIKE).

Anon. (2004) *Managing African Elephant Populations: Act or Let Die?* Expert Consultation on the Control of Wild Elephant Populations. Office for International Co-operation, Faculty of Veterinary Medicine, Utrecht University, Utrecht, The Netherlands.

Anon. (2004) *North East Survey Report.* Second draft, 22. November 2004. Unpublished report. Ministry of Environment and Tourism, Windhoek, Namibia.

Anon. (2004) *Strategie de Gestion Durable des Elephants en Cote D'Ivoire, Août 2004. Programme 2005-2014*. Unpublished report. Ministere des Eaux et Forests, Abidjan, Ivory Coast.

Anon. (2005) *Aerial Census of Animals in Botswana. Dry Season 2005.* Unpublished report. Department of Wildlife and National Parks, Monitoring Unit Research Division, Gaborone, Botswana.

Anon. (2005) *Strategie de Conservation de l'Elephant du Benin*. Septembre 2005. Unpublished report. Fish and Wildlife Service/ African Elephant Specialist Group, Republique du Benin. Ministere de l'Agriculture de l'Elevage et de la Peche, Bohicon, Benin.

Anon. Undated. *IRAS (Information System for Rare Species Management)*. Unpublished Report. The Transboundary Mammal Project, Ministry of Environment and Tourism, The Namibia Nature Foundation, Windhoek, Namibia.

Ansell, W.F.H. (1960) *Mammals of Northern Rhodesia*. The Department of Game and Fisheries, Government Printer, Lusaka, Zambia.

Ayeni, J.S.O. (1977) Waterholes in Tsavo National Park, Kenya. *Journal of Applied Ecology*, **14**, 369-378.

Astle, W.L. (1999) *A History of Wildlife Conservation and Management in the Mid-Luangwa Valley, Zambia.* Research Paper Number 3. British Empire & Commonwealth Museum, Bristol, U.K.

Barnes, J.I. (1996) Changes in the economic use value of elephant in Botswana: the effect of international trade prohibition. *Ecological Economics*, **18**, 215-230.

Barnes, R.F.W. (1999) Is there a future for elephants in West Africa? *Mammal Review*, **29**, 175-199.

Barnes, R.F.W. & Douglas-Hamilton, I. (1982) The numbers and distribution patterns of large mammals in the Ruaha-Rungwa area of southern Tanzania. *Journal of Applied Ecology*, **19**, 411-425.

Barnes, R.F. & Kapela, E.B. (1991) Changes in the Ruaha elephant population caused by poaching. *African Journal of Ecology*, **29**, 289-294.

Barnes R.F.W., Blom, A., Alers, M.P.T. & Barnes, K.L. (1995) An estimate of the numbers of forest elephants in Gabon. *Journal of Tropical Ecology*, **11,** 27-37.

Barnes, R.F.W., Beardsley, K., Michelmore, F., Barnes, K.L., Alers M.P.T. & Blom, A. (1997) Estimating forest elephant numbers with dung counts and a geographic information system. *Journal of Wildlife Management*, **61**, 1384-1393.

Barnes, R.F.W., Craig, G.C., Dublin H.T., Overton, G., Simons, W. & Thouless, C.R. (1998) *African Elephant Database 1998.* IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Barnes, R.F.W. & Dunn, A. (2002) Estimating forest elephant density in Sapo National Park (Liberia) with a rainfall model. *African Journal of Ecology*, **40**, 159-163.

Barnes, R.F.W. & Awo, N. (2004) *Report on the Survey of the Elephants of the Ziama Forest Reserve (July – December 2004).* Unpublished report. Convention on International Trade in Endangered Species (CITES), Monitoring Illegal Killing of Elephants (MIKE), Government of Guinea, and Conservation International, Abidjan, Ivory Coast.

Bekhuis, P.D.B. & Prins, H.T. (2003) Forest elephant density and distribution in the southern part of Campo Ma'an National Park, Cameroon. *Pachyderm*, **35**, 37-42.

Belemsobgo, U., Coulibaly, S., Poda, W.C. & Bassargette, D. (2003) *Strategie et Programme de Gestion Durable des Elephants au Burkina Faso. Juin 2003.* Unpublished report. Ministere de l'Environnement et du Cadre de Vie, Sekretariat General, Direction generale des Eaux et Forets, Ouagadougou, Burkina Faso.

Bell, R.H.V. (1981) An outline of a management plan for Kasungu National Park, Malawi. In *Problems in Management of Locally Abundant Wild Mammals* (eds. P.A. Jewell & S. Holt). Academic Press, New York, U.S.A.

Bhima, R. (1995) Assessing elephant numbers in Liwonde National Park, Malawi using the line transect dung count method. *Nyala*, **18**, 11-16.

Bhima, R. (1999) *Habitat utilization and population dynamics of the African elephant Loxodonta africana in the Liwonde National Park, Malawi.* PhD Thesis. University of Pretoria, Pretoria South Africa.

Bhima, R. & Bothma, J.D.P. (1997) Age structure of elephants in Liwonde National Park, Malawi. *Koedoe*, **40**, 1-8.

Bhima, R., Howard, J. & Nyanyale, S. (2003) The status of elephants in the Kasungu National Park, Malawi, in 2003. *Pachyderm*, **35**, 31-36.

Bigalke, R.C. (1958) On the present status of ungulate mammals in South West Africa *Mammalia*, **22**, 478-497.

Blake, S. (2005) *Central African forests: Final Report on Population Surveys (2003 – 2004).* Unpublished report. Wildlife Conservation Society, Washington, U.S.A.

Blake, S., Bouché, P., Rasmussen, H., Orlando, A. & Douglas-Hamilton, I. (2003) *The Last Sahelian Elephants: Ranging Behavior, Population Status and Recent History of the Desert Elephants of Mali*. Save the Elephants, Nairobi, Kenya.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, C.G. *et al*. (2003) *African Elephant Status Report 2002. An Update from the African Elephant Database.* IUCN/ SSC African Elephant Specialist Group, Gland, Switzerland.

Blanc, J.J., Barnes, R.F.W., Craig, C.G., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. *et al*. (2007) *African Elephant Status Report 2007. An Update from the African Elephant Database.* IUCN/ SSC African Elephant Specialist Group, Gland, Switzerland.

Borner, M. (1983) Selous Aerial survey 1981. *Pachyderm*, **1**, 7.

Bosman, P. & Hall-Martin, A. (1989) *Elephants of Africa*. Struikhof, Cape Town, South Africa.

Bouché, P. H. (2002) Elephant status and conservation in the upper Bandama Game Reserve, Ivory Coast. *Pachyderm*, **32**, 72-73.

Bouché, P. (2003) *Recensement Aerien Totale de la Faune dans l'Ecosysteme Po-Nazinga-Sissili (Ponasi).* May 2003. Unpublished report. Monitoring Illegal Killing of Elephants (MIKE).

Bouché, P.H., Lungren, C.G. & Ouedraogo, L.K. (2002) Statut et tendances des effectifs d'elephants dans les aires protegees de l'est du Burkina Faso. (Status and elephant number trends in the protected areas of the east of Burkina Faso.) *Pachyderm*, **32**, 49-54.

Bouché, P., Lungren, C.G., Hien B. & Omondi, P. (2004) *Aerial Total Count of the "W"-Arli-Pendjari-Oti-Mandouri-Keran (WAPOK) Ecosystem in West Africa. April-May 2003*. Unpublished Report, February 2004. Monitoring Illegal Killing of Elephants (MIKE), Parc Regional W Ecopas, European Union, PAUCOF.

Brockington, D. & Homewood, K. (1999) Pastoralism around Mkomazi Game Reserve: the interaction of conservation and development. In *Mkomazi: the Ecology, Biodiversity, and Conservation of a Tanzanian Savanna* (eds. M. Coe, N. McWilliam, G. Stone & M. Packer). Royal Geographical Society (with the Institute of British Geographers), London, U.K.

Broten, M.D. & Said, M. (1995) Population trends of ungulates in and around Kenya's Masai Mara Reserve. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds. A. R. E. Sinclair & P. Arcese). University of Chicago Press, Chicago, U.S.A.

Burrill, A. & Douglas-Hamilton, I. (1987) *African Elephant Database Project: Final Report.* Unpublished report. United Nations Environment Programme (UNEP), Nairobi, Kenya.

Buss I.O. (1990) *Elephant Life. Fifteen Years of High Population Density*. Iowa State University Press, Ames, U.S.A.

Buss, I.O. & Savidge, J.M. (1966) Change in population number and reproduction rate of elephants in Uganda. *Journal of Wildlife Management*, **30**, 791-809.

Butler, J.R.A. (2000) The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology,* **38**, 23-30.

Butynski, T.M. (1986) Status of elephants in the Impenetrable (Bwindi) Forest, Uganda. *African Journal of Ecology*, **24**, 189-193.

Caro, T.M. (1999) Conservation monitoring: estimating mammal densities in woodland habitats. *Animal Conservation*, **2**, 305-315.

Carroll, R.W. (1988) Elephants of the Dzanga-Sangha dense forest of south-western Central African Republic. *Pachyderm*, **10**, 12-15.

Caughley, C. & Goddard, J. (1975) Abundance and distribution of elephants in Luangwa Valley, Zambia. *East African Wildlife Journal*, **13**, 39-48.

Chambal, M. (1993) Current elephant range and status in Mozambique. *Pachyderm*, **16**, 44-47.

Chanda, G. & Tembo, A. (1993) The status of elephant on the Zambian bank of the Middle Zambezi Valley. *Pachyderm*, **16**, 48-50.

Chardonnet, B. (1988) Les éléphants au Togo. *Revue d Elevage et de Medecine Veterinaire des Pays Tropicaux*, **41**, 303-305.

Chardonnet, B. (2000) Etude des effectifs et de la répartition saisonnière des eléphants des Aires Classées de l'Est du Burkina Faso. *Pachyderm*, **28**, 16-30.

Charif, R.A., Ramey, R.R., Langbauer, W.R. & Payne, K.B. (2005) Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta africana*) clans. *Behavioral Ecology and Sociobiology*, **57**, 327–338.

Chase, M.J. & Griffin, C.R. (2005) *Elephant Distribution and Abundance in the Lower Kwando River Basin and West Caprivi.* Unpublished report. Ministry of Environment and Tourism, Windhoek, Namibia.

Chase M.J. & Griffin C.R. (2007) *Elephants Caught in the Middle: Impacts of War, Fences and People on Elephant Distribution and Abundance in the Caprivi Strip, Namibia*. Unpublished report. Conservation International and Elephants without Borders, Namibia.

Child, G., Smith, P. & von Richter, W. (1970) Tsetse control hunting as a measure of large animal population trends in the Okavango Delta, Botswana. *Mammalia*, **34**, 34-75.

Chiyo, P.I. & Cochrane, E.P. (2005) Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda. *African Journal of Ecology*, **43**, 233-241.

Cobb, S.M. (1976) *The Distribution and Abundance of the Large Herbivore Community of Tsavo National Park, Kenya*. PhD Thesis. University of Oxford, Oxford, U.K.

Cobb, S. (1989) *The Ivory Trade and the Future of the African Elephant.* Unpublished report. Ivory Trade Review Group. Prepared for the Seventh CITES Conference of the Parties, Lausanne, France.

Communal Areas Management Programme For Indigenous Resources in Natural Connections (CAMPFIRE). (1994) *Perspectives in Community-Based Conservation* (eds. D. Western & Michael Wright, S. Strum, associate editor). Island Press, Washington D.C, U.S.A.

Corfield, T.F. (1973) Elephant mortality in Tsavo National Park, Kenya. *African Journal of Ecology*, **11**, 339-368.

Craig, G.C. & Gibson, D.C. (2004) *Aerial Survey of Wildlife in the Niassa Reserve and Surrounds Mozambique, October 2004.* Unpublished report. Prepared for Sociedade para a Gestão e Desenvolvimento da Reserva do Niassa Moçambique, Niassa, Mozambique.

Cumming, D.H.M. (1981) The management of elephant and other mammals in Zimbabwe. In *Problems in Management of Locally Abundant Wild Mammals* (eds. P. A. Jewell & S. Holt). Academic Press, New York, U.S.A.

Cumming, D.H.M. & Jackson, P. (1984) *The Status and Conservation of Africa's Elephants and Rhinos*. Proceedings of the joint meeting of IUCN/SSC African Elephant and African Rhino Specialist Groups. 30. July - 7. August 1981, Hwange Safari Lodge, Zimbabwe.

Cumming, D.H.M., du Toit, R.F. & Stuart, S.N. (1990) *African Elephant and Rhinos, Status Survey and Conservation.* IUCN, Gland, Switzerland.

Cumming, D. & Jones, B. (2005) *Elephants in Southern Africa: Management Issues and Options.* Occasional Paper Number 11, May 2005. WWF-SARPO.

Dahlberg, A.C. (2000) An environmental history of a village in North-East Botswana. *Journal of Southern African Studies*, **26**, 759-782.

Damiba, T.E. & Ables, E.D. (1994) Population characteristics and impacts on woody vegetation of elephants on Nazinga Game Ranch, Burkina Faso. *Pachyderm*, **18**, 46-53.

Danquah, E., Boafo, Y., Dubiure, U.F., Awo, N., Hema, E.M. & Appiah, M.A. (2001) Elephant census in the Ancasa Conservation Area in south-western Ghana. *Pachyderm*, **31**, 63-69.

Davies, C. (1996) *Aerial Census of Elephant and Other Large Mammals in the North West Matabeleland and Gonarezhou Regions of Zimbabwe*. Department of National Parks and Wild Life Management, Harare, Zimbabwe.

de Beer, Y. (2007) *Determinants and Consequences of Elephant Spatial Use in Southern Africa's Arid Savannas.* MSc Thesis, University of Pretoria, Pretoria, South Africa.

de Bie, S. (1991) *Wildlife Resources of the West African Savanna*. PhD Thesis. Wageningen Agricultural University, Wageningen, The Netherlands.

de Bruin, D.J. (1995) *The Ecology and Behaviour of Reintroduced African Elephants on Mabula Game Reserve, Northern Province, South Africa.* MSc Thesis. University of Pretoria, Pretoria, South Africa.

de Longh, H.H., Tchamba, M., Aarhaug, P. & Verhage, B. (2004) Impact of dam construction on two elephant populations in northern Cameroon. *Pachyderm*, **36**, 30-43.

Delsink, A.K., van Altena, J.J., Grobler, D., Bertschinger, H., Kirkpatrick, J. & Slotow, R. (2006) Regulation of a small, discrete African elephant population through immunocontraception in the Makalali Conservancy, Limpopo, South Africa. *South African Journal of Science* **102**, 403 - 405.

Demeke, Y. (1997) The status of the African elephant (*Loxodonta africana*) in Ethiopia. *Walia*, **18**, 15-27.

Demeke, Y. (2003) Law enforcement, illegal activity and elephant status in Mago and Omo National Parks and adjacent areas, Ethiopia. *Pachyderm*, **35**, 16-30.

Demeke, Y. & Bekele, A. (2000) Population estimates and threats to elephants *Loxodonta africana* (Blumenbach 1797) in the Mago National Park, Ethiopia. *Tropical Zoology*, **13**, 227-237.

de Villiers, P.A. (1981) *Eto-Ekologiese Aspekte van Olifante in die Nasionale Etoshawildtuin, S.W.A.* MSc Thesis. University of the Orange Free State, Bloemfontein, South Africa.

de Villiers, P.A. & Kok, O.B. (1983) Verspreidingspatrone van olifante (*Loxodonta africana*) in Suid-Wes Afrika met spesiale verwysing na die Nasionale Etoshawildtuin. *Madoqua*, **13**, 281-296.

de Vos, V., Bengis, R.G. & Coetzee, H.J. (1982) Population control of large mammals in the Kruger National Park. In *Management of Large Mammals in African Conservation Areas* (ed. N. Owen-Smith). HAUM Educational Publishers, Pretoria, South Africa.

Dolmia, N.M., Calenge, C., Maillard, D. & Planton, H. (2007) Preliminary observations of elephant (*Loxodonta africana*, Blumenbach) movements and home range in Zakouma National Park, Chad. *African Journal of Ecology*, **46**, 113-116.

Douglas-Hamilton, I. (1972) *On the Ecology and Behaviour of the African Elephant*. PhD Thesis. University of Oxford, Oxford, U.K.

Douglas-Hamilton, I. (1987) African elephant population study. *Pachyderm*, **8**, 1-10.

Douglas-Hamilton, I. (1987) African elephants: population trends and their causes. *Oryx*, **21**, 11-24.

Douglas-Hamilton, I., Krink, T. & Vollrath, F. (2005) Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, **92**, 158-163.

Druce, H., Pretorius, K., Druce, D. & Slotow, R. (2006) The effect of mature elephant bull introductions on resident bull's group size and musth periods: Phinda Private Game Reserve, South Africa. *South African Journal of Wildlife Research*, **36**, 133-137.

Dublin, H.T. & Douglas-Hamilton I. (1987) Status and trends of elephants in the Serengeti-Mara ecosystem. *African Journal of Ecology*, **25**, 19-33.

Dudley, J.P., Mensah-Ntiamoah, A.Y. & Kpelle, D.C. (1992) Forest elephants in a rainforest fragment: preliminary findings from a wildlife conservation project in southern Ghana. *African Journal of Ecology*, **30**, 116-126.

Dudley, J.P., Craig, G.C., Gibson, D.S., Haynes, G. & Klimowicz, J. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, **39**, 187-194.

Dunham, K.M. (2002) *Aerial Census of Elephants and Other Large Herbivores in Gonarezhou National Park and Some Bordering Lands, Zimbabwe: 2001.* Occasional Paper No. 4. Department of National Parks and Wild Life Management / WWF, Harare, Zimbabwe.

Dunham, K.M. (2002) *Aerial Census of Elephants and Other Large Herbivores in North West Matabeleland, Zimbabwe: 2001.* Occasional Paper No. 6. Department of National Parks and Wild Life Management / WWF, Harare, Zimbabwe.

Dunham, K.M. (2002) *Aerial Census of Elephants and Other Large Herbivores in Save Valley Conservancy, Zimbabwe: 2001.* Occasional Paper No. 5. Department of National Parks and Wild Life Management / WWF, Harare, Zimbabwe.

Dunham, K.M. (2004) *Aerial Census of Elephants and Other Large Herbivores in the Zambezi Heartland (Zimbabwe, Mozambique and Zambia): 2003.* Unpublished report. African Wildlife Foundation, Lusaka, Zambia.

Dunham, K.M. & Simwanza, H.I. (2002) *Aerial Census of Elephants and Other Large Herbivores in South Luangwa NP and Lupande GMA, Zambia: 2002.* Zambia Wildlife Authority/ WWF, Chipata, Zambia.

Ebedes, H., Vernon, C. & Grundling, I. (1991) *Past, Present and Future Distribution of Elephants in Southern Africa.* Wildlife Group of the South African Veterinary Association, Onderstepoort. Proceedings of a symposium on the African elephant as a game ranch animal. 29. April – 30. April, Berg-en-Dal, South Africa.

Edroma, E.L. (1975) A count of the large mammals in a Uganda National Park. *Oryx*, **13**, 176-178.

Edroma, E.L. (1981) The number and distribution of elephants in Kidepo Valley National Park, Uganda. *African Journal of Ecology*, **19**, 299-302.

Eggert, L.S., Eggert, J.A. & Woodruff, D.S. (2003) Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Molecular Ecology*, **12**, 1389-1402.

Ekobo, A. (1993) The status of forest elephants in the south east of the Republic of Cameroon. *Pachyderm*, **16**, 84.

Ekobo, A. (1995) Elephants in the Lobeke Forest, Cameroon. *Pachyderm*, **19**, 73-80.

Ekobo, A. (1997) Elephant problem in the Mungo Division, Littoral Province Cameroon. *Pachyderm*, **24**, 53-63.

Eltringham, S.K. (1977) The numbers and distribution of elephant *Loxodonta africana* in the Rwenzori National Park and Chambura Game Reserve, Uganda. *African Journal of Ecology*, **15**, 19-39.

Eltringham, S.K. & Malpas, R.C. (1980) The decline in elephant numbers in Rwenzori and Kabalega Falls National Parks, Uganda. *African Journal of Ecology*, **18**, 73-86.

Esser, J.D. & van Lavieren, L.P. (1979) Importance, répartition et tendance évolutive des populations de grands herbivores et de l'autruche dans le Parc National de Waza, Cameroun. *Revue d'Ecologie: La Terre et la Vie*, **33**, 3-26.

Fairall, N. & Kampamba, G. (2001) *Aerial Census of Kafue National Park*. Unpublished report. Conservation Ecology Research Unit (CERU), University of Pretoria, Pretoria, South Africa.

Fay, J.M. & Agnagna, M. (1991) A population survey of forest elephants (*Loxodonta africana cyclotis*) in northern Congo. *African Journal of Ecology*, **29**, 177-187.

Fay, J.M. & Agnagna, M. (1991) Forest elephant populations in the Central African Republic and Congo. *Pachyderm*, **14**, 3-19.

Field, C.R. (1971) Elephant ecology in the Queen Elisabeth National Park, Uganda. *East African Wildlife Journal*, **9**, 99-123.

Fischer, F. (2005) Elephants in Cote D'Ivoire - a warning for West African conservation. *Pachyderm*, **38**, 64-75.

Foley, L.S. (2002) *The Influence of Environmental Factors and Human Activity on Elephant Distribution in Tarangire National Park, Tanzania.* Unpublished report. International Institute for Geo-Information Science and Earth Observation, Enschede, The Netherlands.

Garai, M.E., Slotow, R., Carr, R D. & Reilly, B. (2004) Elephant reintroductions into small fenced reserves in South Africa. *Pachyderm*, **37**, 28-36.

Gibson, D.S.C., Craig, G.C. & Masogo, R.M. (1998) Trends of the elephant population in northern Botswana from aerial survey data. *Pachyderm*, **25**, 14-27.

Gillson, L., Sheridan, M. & Brockington, D. (2003) Representing environments in flux: case studies from East Africa. *Area*, **35**, 371–389.

Goredema, L., Taylor, R. Bond, I. & Vermeulen, S. (2005) *Empowering Rural Communities to Manage Wildlife: Lessons Learned from WWF's Support to CAMPFIRE Project 1993-2002.* Unpublished report. WWF/ IIED.

Government of Botswana. (1998) *National Report on Measures Taken to Implement the Convention on Biological Diversity.* Presented to the Fourth Conference of Parties to the CBD May, Bratislava, Slovakia.

Green, A.A. (1988) Elephants of the Pendjari-Singou-Mekrou region, West-Africa. *Mammalia*, **52**, 557-565.

Greyling, M.D., McCay, M. & Douglas-Hamilton, I. Undated. *Green Hunting as an Alternative to Lethal Hunting.* Unpublished report. Save the Elephants, Nairobi, Kenya.

Grimwood, I.R., Benson, C.W. & Ansell, W.F.H. (1958) The present-day status of ungulates in Northern Rhodesia. *Mammalia*, **3**, 451-467.

Guldemond, R., Lehman, E., Ferreira, S. & van Aarde, R. (2005) Elephant numbers in Kafue National Park, Zambia. *Pachyderm*, **39**, 50-56.

Guy, P.R. (1981) Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology*, **18**, 507-519.

Guy, P.R. (1989) The influence of elephants and fire on a Brachystegia-Julbernadia woodland in Zimbabwe. *Journal of Tropical Ecology*, **5**, 215-226.

Hagos, Y., Ghebrehiwet, M. & Shoshani, J. (2003) The elephants (*Loxodonta africana*) of Zoba Gash-Barka, Eritrea: part 1. Historical perspective and related findings. *Pachyderm*, **34**, 13-23.

Hall-Martin, A.J. (1980) Elephant survivors. *Oryx*, **15**, 355-362.

Hall-Martin, A.J. (1992) Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe*, **35**, 65-87.

Hanks, J. & McIntosh, J. E. A. (1973) Population dynamics of the African elephant (*Loxodonta africana*). *Journal of Zoology, London*, **169**, 29-38.

Happold, D.C.D. (1987) *The Mammals of Nigeria*. Clarendon Press, Oxford, U.K.

Hien, B.M. (2003) Les éléphants du Ranch de Gibier de Nazinga (Burkina Faso): données passées, situation actuelle, perspectives de conservation. *Pachyderm*, **35**, 43-52.

Hien, B.M. (2005) *Factors Affecting Variability in the Distribution of Elephants at Nazinga Game Ranch (Burkina Faso, West Africa).* MSc Thesis. South Dakota State University, Brookings, U.S.A.

Hillman-Smith, A.K.K., de Merode, E., Nicholas, A., Buls, B. & Ndey, A. (1995) Factors affecting elephant distribution at Garamba National Park and surrounding reserves, Zaire, with a focus on human-elephant conflict. *Pachyderm*, **19**, 39-48.

Hillman-Smith, K. & Ndey, A. (2005) Post-war effects on the rhinos and elephants of Garamba National Park. *Pachyderm*, **39**, 106-110.

Hiscocks, K. (1999) The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe*, **42**, 47-55.

Inogwabini, B.I., Hall, J.S., Vedder, A., Curran, B., Yamagiwa, J. & Basabose, K. (2000) Status of large mammals in the mountain sector of Kahuzi-Biega National Park, Democratic Republic of Congo, in 1996. *African Journal of Ecology*, **38**, 269-276.

Iyenguet, F.C., Malanda, G.A. Rainey, H.J., Schloeder, C.A. & Jacobs, M.J. (2006) Recensement d'elephants dans la Reserve Communautaire du Lac Tele, Republique du Congo. *Pachyderm*, **41**, 20-29.

Jachmann, H. (1980) Population dynamics of the elephants in the Kasungu National Park, Malawi. *Netherlands Journal of Zoology*, **30**, 622-634.

Jachmann, H. (1984) *The Ecology of the Elephants in Kasungu National Park, Malawi; with Specific Reference to Management of Elephant Populations in the Brachystegia Biome of South Central Africa.* PhD Thesis. University of Groningen, Groningen, The Netherlands.

Jachmann, H. (1986) Notes on the population dynamics of the Kasungu elephants. *African Journal of Ecology*, **24**, 215-226.

Jachmann H. (1988) Numbers, distribution and movements of the Nazinga elephants. *Pachyderm*, **10**, 16-21.

Jachmann, H. (1991) Evaluation of four survey methods for estimating elephant densities. *African Journal of Ecology*, **29**, 188-195.

Jachmann, H. (1995) Survey experiments and aerial survey of elephants in the South Luangwa National Park and the Lupande Game Management Area, Zambia, 1993. *Pachyderm*, **19**, 81-86.

Jachmann, H. (2001) *Estimating Abundance of African Wildlife: an Aid to Adaptive Management*. Kluwer Academic Publishers, Boston, U.S.A.

Jachmann, H. (2002) Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, **39**, 841-852.

Jachmann, H. & Bell, R.H.V. (1979) The assessment of elephant numbers and occupancy by means of droppings counts in the Kasungu National Park Malawi. *African Journal of Ecology*, **17**, 231-240.

Jachmann, H. & Bell, R.H.V. (1984) The use of elephant droppings in assessing numbers, occupance and age structure a refinement of the method. *African Journal of Ecology*, **22**, 127-141.

Jachmann, H. & Billiouw, M. (1997) Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology*, **34**, 233-244.

Jost, C.C. & Suedmeyer, B. (2005) *West African Elephant Conservation in Burkina Faso-Ecosystem Dynamics in a Conservation Environment*. Unpublished report. The International Program/ TuftsCCM, Tufts Cummings School of Veterinary Medicine, North Grafton, U.S.A.

Kaweche, G.B., Lewis, D.M. & Carr, G.S. (1985) *Luangwa Valley Elephants: Toward Developing a Management Policy.* Lupande Research Project publication no. 2, Nyamaluma. Wildlife Conservation International, Bronx, U.S.A.

Kerr, M.A. & Frazer, J.A. (1975) Distribution of elephant in a part of the Zambezi Valley, Rhodesia. *Arnoldia*, **7**, 1-14.

Khaemba, W.M., Stein, A., Rasch, D., de Leeuw, J. & Georgiadis N. (2001) Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. *African Journal of Ecology*, **39**, 374-382.

Klingelhoeffer, E.W. (1987) *Aspects of the Ecology of the Elephant Loxodonta africana (Blumenbach, 1797), and a Management Plan for the Tembe Elephant Reserve in Tongaland, Kwazulu*. MSc Thesis. University of Pretoria, Pretoria, South Africa.

Knight, M.H., Hitchins, P. & Erb, K.P. (1993) An aerial survey of rhinoceros and elephant in a portion of the Chobe National Park and surrounding areas, northern Botswana, September 1992. *Pachyderm*, **17**, 64-75.

Kotchikpa, K., Sophie, D., Kokouvi, A. & Hoinsounde, S. (2004) Impacts humaines sur les aires de distribution et couloirs de migration des elephants de Togo. *Pachyderm*, **36**, 69-79.

Lamprey, H.F. (1964) Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *East African Wildlife Journal*, **2**, 1-46.

Lamprey, H.F., Glover, P.E., Turner, H.I.M. & Bell, R.H.V. (1967) Invasion of the Serengeti National Park by elephants. *African Journal of Ecology*, **5**, 151–166.

Largen, M.J. & Yalden, D.W. (1986) The decline of elephant and black rhinoceros in Ethiopia. *Oryx*, **21**, 103-106.

Laws, R.M. (1969) The Tsavo research project. *Journal of Reproduction and Fertility-Supplement*, **6**, 495-531.

Laws, R.M. (1970) Elephants as agents of habitat and landscape change in East Africa. *Oikos*, **21**, 1-15.

Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1970) Elephants and their habitats in North Bunyoro, Uganda. *East African Wildlife Journal*, **8**, 163-180.

Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1975) *Elephants and Their Habitats: the Ecology of Elephants in North Bunyoro, Uganda.* Clarendon Press, Broadbridge, U.K.

Lewis, D.M. (1984) Demographic changes in the Luangwa Valley elephants. *Biological Conservation*, **29**, 7-14.

Lewis, D.M. & Alpert, P. (1997) Trophy hunting and wildlife conservation in Zambia. *Conservation Biology*, **11**, 59-68.

Lindeque, M. (1989) *Population Dynamics of Elephants in Etosha National Park, S.W.A./ Namibia*. PhD Thesis. University of Stellenbosch, Stellenbosch, South Africa.

Lindeque, M. (1991) Age structure of the elephant population in the Etosha National Park, Namibia. *Madoqua*, **18**, 27-32.

Litoroh, M. (1997) Aerial census of the Gash Setit elephant population of Eritrea and Ethiopia. *Pachyderm*, **23**, 12-18.

Litoroh, M. (2002) Aerial elephant count in the Shimba Hills ecosystem, Kenya. *Pachyderm*, **32**, 55-63.

Litoroh, M. (2003) An elephant dung survey of the Shimba Hills ecosystem, Kenya and implications for management. *Pachyderm*, **35**, 71-76.

Liyama, M., Maitima, J. & Kariuki, P. (2007) Crop-livestock diversification patterns in relation to income and manure use: a case study from a Rift Valley community, Kenya. *African Journal of Agricultural Research*, **2**, 58-66.

Loutit, R. (1995) *Report on an Elephant Census (ELESMAP survey) in Kunene Region, September/ October, 1995*. Unpublished report. Ministry of Environment and Tourism, Windhoek, Namibia.

Loutit, R. & Douglas-Hamilton, I. (1992) *Report on an Elephant Count in the Cunene Province, Namibia, 10th to 21st October 1992.* Unpublished report. Ministry of Environment and Tourism, Windhoek, Namibia.

MacGregor, S.D. (2000) *Influence of Drought or Elephant on the Dynamics of Key Woodland Species in a Semi-Arid African Savanna.* Honours Thesis. University of Natal, Durban, South Africa.

Mackey, R.L., Page, B.R., Duffy, K.J. & Slotow, R. (2006) Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research,* **36**, 33-43.

Mackie, C.S. (2002) *Aerial Census of Elephants and Other Large Herbivores in the Sebungwe Region, Zimbabwe: 2001.* Occasional Paper No. 3. Department of National Parks and Wild Life Management / WWF, Harare, Zimbabwe.

Mackie, C.S. (2002) *Aerial Aerial Census of Elephants and Other Large Herbivores in the Zambezi Valley, Zimbabwe: 2001.* Occasional Paper No. 2. Department of National Parks and Wild Life Management / WWF, Harare, Zimbabwe.

Mapaure, I.N. & Campbell, B.M. (2002) Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of Ecology*, **40**, 212-219.

Martin, R.B. (2005). *Transboundary Species Project. Background study. Elephants.* The Transboundary Mammal Project, Ministry of Environment and Tourism, The Namibia Nature Foundation, Windhoek, Namibia.

Martin, R.B., Craig, G.C. & Booth, V.R. (re-edited R.B. Martin & A.M.G. Conybeare,) (1995) *Elephant Management in Zimbabwe*. Department of National Parks and Wild Life Management, Harare, Zimbabwe.

Mathews, W.S. & Nemane, M. (2006) *Aerial Survey Report for Maputo Special Reserve.* Unpublished report. Ministerio du Turismo, Maputo, Mozambique.

Mauvais, G. (2001) Quelques éléments sur les effectifs d'éléphants au Parc National du Niokolo Koba (année 2000). *Pachyderm*, **31**, 70-72.

Maveneke, T.N. (1996) *Local Participation and Benefit Sharing in Wildlife Management: the CAMPFIRE Experience.* A paper presented at the World Bank/UNEP Africa Forestry Policy Forum, Nairobi, Kenya, 29th - 30th August, 1996.

McKnight, B. (2000) Changes in elephant demography, reproduction and group structure in Tsavo East National Park (1966-1994). *Pachyderm*, **29**, 15-24.

McKnight, B. (2004) Elephant numbers, group structure and movements on privately owned land adjacent to Tsavo East National Park, Kenya. *Pachyderm*, **36**, 44-51.

Melton, D.A. (1985) The status of elephants in northern Botswana. *Biological Conservation*, **31**, 317-333.

Mertens, H. (1983) Recensement aeriens des principaux ongules du Parc National des Virunga, Zaire. *Revue d'Ecologie: La Terre et la Vie*, **38**, 52-64.

Merz, G. (1986) Counting elephants (*Loxodonta africana cyclotis*) in tropical rain forests with particular reference to the Tai-National-Park, Ivory-Coast. *African Journal of Ecology*, **24**, 61-68.

Merz, G. (1986) The status of the forest elephant, *Loxodonta africana cyclotis*, Matchie, 1900, in the Gola Forest Reserve, Sierra Leone. *Biological Conservation*, **36**, 83-94.

Merz, G. & Hoppe-Dominik, B. (1991) Distribution and status of the forest elephant in the Ivory Coast, West Africa. *Pachyderm*, **14**, 22-24.

Mitchelmore, F., Beardsley, K., Barnes, R.F.W. & Douglas-Hamilton, I. (1994) A model illustrating the changes in forest elephant numbers caused by poaching. *African Journal of Ecology*, **32**, 89-99.

Mkanda, F.X. (1993) Status of elephants and poaching for ivory in Malawi: a case study in Liwonde and Kasungu National Parks. *Pachyderm*, **16**, 59-62.

Montford, A. & Montford, N. (1977) Operation elephant in Rwanda part 1 population structure of the Bugesera herds and translocation of young animals to the Akagera National Park. *Revue d'Ecologie: La Terre et la Vie*, **31**, 354-384.

Morgan, B.J. & Lee, P.C. (2003) Forest elephant (*Loxodonta africana cyclotis*) stature in the Réserve de Faune du Petit Loango, Gabon. *Journal of Zoology (London)*, **259**, 337-344.

Morley, R.C. (2005) *The Demography of a Fragmented Population of the Savanna Elephant (Loxodonta africana Blumenbach) in Maputaland*. PhD Thesis. University of Pretoria, Pretoria, South Africa.

Moss, C.J. (1990) Elephants in Tarangire. *Pachyderm*, **13**, 26-30.

Moss, C.J. (2001) The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology (London)*, **255**, 145-156.

Moss, C.J. (2003) *Amboseli Elephant Research Project*. Annual Report 2003. Amboseli Trust for Elephants, Nairobi, Kenya.

Moss, C.J. (2005) *Amboseli Elephant Research Project*. Annual Report 2005. Amboseli Trust for Elephants, Nairobi, Kenya.

Mubalama, L. (2000) Population and distribution of elephants (*Loxodonta africana africana*) in the central sector of the Virunga National Park, Eastern DRC. *Pachyderm*, **28**, 44-55.

Mubalama, L. & Bashigg, E. (2006) Caught in the crossfire: the forest elephant and law enforcement in a region of political instability, eastern Democratic Republic of Congo. *Pachyderm*, **40**, 69-79.

Munthali, S.M. & Mkanda, F.X. (2002) The plight of Malawi's wildlife: is trans-location of animals the solution? *Biodiversity and Conservation*, **11**, 751–768.

Muoria, P.K. (2000) Population estimate of elephants in Arabuko-Sokoke Forest. *Pachyderm*, **29**, 48-51.

Mwalyosi, R.B.B. (1977) A count of large mammals in the Lake Manyara National Park. *African Journal of Ecology*, **15**, 333-335.

Mwathe, K., Muriuki, J., Nyamu, J. & Waruingi L. (2006) *Elephants in Kenya's South Rift: Bridging the Information Gap*. Report to the African Elephant Database of the African Elephant Specialist Group. African Conservation Centre/LCAOF Elephant Program, Nairobi, Kenya.

Nchanji, C.A. (2005) Elephant-poaching weapons and new experiences from the Banyang-Mbo Wildlife Sanctuary, Cameroon. *Pachyderm*, **39**, 3-42.

Ndhlovu, D.E. & Balakrishnan, M. (1991) Large herbivores in Upper Lupande Game Management Area, Luangwa Valley, Zambia. *African Journal of Ecology*, **29**, 93-104.

Norton G.W., Hawkins D.M. & Mofulu, F. (2005) *Elephants of Mikumi National Park, Tanzania: Conservation, Education and Research*. Final Report Project Reference 162/11/008. Darwin Initiative For The Survival Of Species, Sciences Research Centre, Department Of Life Sciences, Anglia Polytechnic University, Cambridge, U.K.

Norton-Griffiths, M. (1975) The numbers and distribution of large mammals in Ruaha National Park, Tanzania. *African Journal of Ecology*, **13**, 121-140.

Ntumi, C.P. (2002) *Space and Habitat Use by Elephants (Loxodonta africana) in the Maputo Elephant Reserve, Mozambique*. MSc Thesis. University of Pretoria, Pretoria, South Africa.

Nyakaana, S. & Arctander, P. (1999) Population genetic structure of the African elephant in Uganda based on variation at mitochondrial and nuclear loci: evidence for male-biased gene flow. *Molecular Ecology*, **8**, 1105-1115.

Obot, E., Edet, C., Ogar, G. & Ayuk, J. (2005) Population survey of elephants on Okwangwo Division, Cross River National Park, Nigeria. *Pachyderm*, **38**, 59-63.

Ogola, O.P. (2003) *Demographic Status of the Meru Elephant Population*. Final Report to the Elephant Research Fund/ KWS and Save the Elephants, Nairobi, Kenya.

Ogola, P. & Omondi, P.O. (2005) Demography of a confined elephant population and the potential consequence of translocation: the case of Sweetwaters Game Reserve, Kenya. *Pachyderm*, **39**, 57-62.

Okello M.M. & Kiringe, J.W. (2004) Threats to biodiversity and their implications in protected and adjacent dispersal areas of Kenya. *Journal of Sustainable Tourism,* **12**, 55-69.

Olindo, P.M., Douglas-Hamilton, I. & Hamilton, P. (1988) The 1988 Tsavo elephant count. *Swara*, **11**, 23-24.

Olivier P.I., Ferreira, S.M. & van Aarde, R.J. (2008) Dung counts and measurements to estimate population sizes and extract age structures: a case study on elephants in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*, *in press*.

Omondi, P., Bitok, E. & Mayienda, R. (2002) Decline of elephants and other wildlife in the Nasolot- South Turkana and Kerio Valley- Kamnarok conservation areas, Kenya. *Pachyderm*, **33**, 69-73.

Osborn, L. (1998) *Elephant/Human Conflict Around Maputo Elephant Reserve, Mozambique*. Unpublished report. IUCN/Mozambique and USAID, U.S.A.

Ott, T. (2007) *Landscape Heterogeneity as a Determinant of Range Utilization by African elephants (Loxodonta africana) in Mesic Savannas.* MSc Thesis, University of Pretoria, Pretoria, South Africa.

Ottichilo, W.K. (1986) Population estimates and distribution patterns of elephants in the Tsavo ecosystem, Kenya, in 1980. *African Journal of Ecology*, **24**, 53-57.

Ottichilo, W. (2000) *Wildlife Dynamics: an Analysis of Change in the Masai Mara Ecosystem of Kenya.* PhD Thesis. Wageningen University and Research Centre, Wageningen, The Netherlands.

Ottichilo, W.K., Kufwafwa, J.W. & Stelfox, J.G. (1987) Elephant population trends in Kenya: 1977-1981. *African Journal of Ecology*, **25**, 9-18.

Parker, I.S.C. and Graham, A.D. (1989) Elephant decline (part1). Downward trends in African elephant distribution and numbers. *International Journal of Environmental Studies*, **34**, 287-305.

Parren, M.P.E., de Leede, B.M. & Bongers F. (2002) A proposal for a transnational forest network area for elephants in Côte d'Ivoire and Ghana. *Oryx*, **36**, 249-256.

Peace Parks Foundation. 2000. *Annual Review 2000*. Unpublished report, Stellenbosch, South Africa.

Pellew, R.A. (1983) Modelling and the systems approach to management problems: the *Acacia*/Elephant problem in Serengeti. In *Management of large mammals in African conservation areas* (ed. R.N. Owen-Smith). HAUM Educational Publishers, Pretoria, South Africa.

Pentzhorn, B.L., Robbertse, P.J. & Olivier, M.C. (1974) The influence of the African elephant on the vegetation of the Addo National Park. *Koedoe*, **17**, 137-158.

Pienaar, J.S. (1963) Large mammals of the Kruger National Park: their distribution and present day status. *Koedoe*, **6**, 16-37.

Pienaar, U., de V., van Wyk, P. & Fairall, N. (1966) An aerial census of elephant and buffalo in Kruger National Park, and the implications thereof on intended management schemes. *Koedoe*, **9**, 40-107.

Poche, R.M. (1974) Ecology of the African elephant *Loxodonta africana africana* in Niger West Africa. *Mammalia*, **38**, 567-580.

Poole, J.H. (1992) Kenya's elephants: a very different story to tell. *Swara*, **15**, 29-31.

Prins, H.H.T. & Douglas-Hamilton, I. (1990) Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia*, **83**, 392-400.

Prins, H.H.T., van der Jeugd, H.P. & Beekman, J.H. (1994) Elephant decline in Lake Manyara National Park, Tanzania. *African Journal of Ecology*, **32**, 185-191.

Puit, M. & Ghiurghi, A. (2006) Premiere estimation de la densite d'elephants dans le Parc National de Monte Alen, Guinee Equatoriale. *Pachyderm*, **41**, 44-52.

Querouil, S., Magliocca, F. & Gautier-Hion, A. (1999) Structure of population, grouping patterns and density of forest elephants in north-west Congo. *African Journal of Ecology*, **37**, 161-167.

Rodgers, W.A. & Lobo, J.D. (1980) Elephant control and legal ivory exploitation: 1920-1976. *Tanganyika Notes and Records*, **84,** 25-54.

Rodwell, T.C., Tagg, J. & Grobler, M. (1995) *Wildlife Resources in the Caprivi, Namibia: the Results of an Aerial Census in 1994 in Comparison with Past Surveys.* Unpublished report. Ministry of Environment and Tourism, Windhoek, Namibia.

Roth, H.H., Merz, G. & Steinhauer, B. (1984) Distribution and status of large mammals in the Ivory Coast. (I Introduction and II Elephants.) *Mammalia*, **48**, 207-226.

Roth H.H. & Douglas-Hamilton I. (1991) Distribution and status of elephants in West Africa. *Mammalia*, **55**, 489-527.

Roux, C. (2006) *Feeding Ecology, Space Use and Habitat Selection of Elephants in Two Enclosed Game Reserves in the Eastern Cape Province, South Africa*. MSc Thesis. Rhodes University, Grahamstown, South Africa.

Runyoro, V.A., Hofer, H., Chausi, E.B. & Moehlman, P.D. (1995) Long-term population trends in the herbivore populations of Ngorongoro Crater, Tanzania. In *Serengeti 2: Dynamics, Management and Conservation of an Ecosystem* (eds. A.R.E. Sinclair & P. Arcese). University of Chicago Press, Chicago, U.S.A.

Said, M.Y., Chunge, R.N., Craig, G.C., Thouless, C.R., Barnes, R.F.W. & Dublin, H.T. 1995. *African Elephant Database 1995*. IUCN/SSC African Elephant Specialist Group, Gland, Switzerland.

Sam, M.K., Danquah, E., Oppong, S.K. & Bozu, E.D. (2006) Elephant survey in the Bia Conservation Area, western Ghana. *Pachyderm*, **40**, 42-50.

Shannon, G., Page, B., Slotow, R. & Duffy, K. (2006) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, **41**, 37-44.

Sheldrick, D. (2000) Vegetation changes in Tsavo National Park, Kenya, 1885-1996: elephant densities and management. *Elephant*, **2**, 26-33.

Sherry, B.Y. (1975) Reproduction of elephant in Gonarezhou, south-eastern Rhodesia. *Arnoldia*, **7**, 1-13.

Sherry, B.Y. (1978) Growth of elephants in the Gonarezhou National Park, south-eastern Rhodesia. *South African Journal of Wildlife Research*, **8**, 49-58.

Short, J. (1983) Density and seasonal movements of forest elephants (*Loxodonta africana cyclotis* Matchie) in Bia National Park, Ghana. *African Journal of Ecology*, **21**, 175-184.

Shortridge, G.C. (1934) Order Proboscidea, Family Elephantidae. In *Mammals of South West Africa*. William Heinemann Limited, London, U.K.

Shoshani, J., Hagos, Y., Yacob, Y., Ghebrehiwet, M. & Kebrom, E. (2004) Elephants (*Loxodonta africana*) of Zoba Gash-Barka, Eritrea: Part 2. Numbers and distribution, ecology and behaviour, and fauna and flora in their ecosystem. *Pachyderm*, **36**, 52-68.

Siege, L. & Baldus, R.D. (2000) *From Decline to Recovery - the Elephants of the Selous*. Tanzania Wildlife Discussion Paper No. 27. Deutsche Gesellschaft für Technische Zusammenarbeit Selous, Saadani and Katavi Rukwa Conservation Programmes, Community based Conservation Wildlife Division, Dar es Salaam, Tanzania.

Sikubwabo, C. & Mubalama, L. (2003) Les éléphants du Parc National des Virunga au travers la guerre en République Démocratique du Congo. *Pachyderm*, **34**, 45-52.

Slotow, R. & van Dyk, G. (2004) Ranging of older male elephants introduced to an existing small population without older males: Pilanesberg National Park. *Koedoe*, **47**, 91-103.

Slotow, R., Garai, M.E., Reilly, B., Page, B. & Carr, R.D. (2005) Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, **35**, 23-32.

Sommerlatte, M.W. (1976) *Survey of Elephant Populations in North-Eastern Botswana*. Department of Wildlife and National Parks, and UNDP/ FAO Project 72/020, Wildlife Management and Utilisation in Botswana, Gaborone, Botswana.

Spinage, C.A. (1963) Elephant numbers. *African Wildlife*, **17**, 325-332.

Spinage, C.A. (1985) The elephants of Burkina-Faso, West Africa. *Pachyderm*, **5**, 2-5.

Spinage, C.A. (1990) Botswana's problem elephants. *Pachyderm*, **13**, 14-20.

Spinage, C.A. & Guinness, F.E. (1971) Tree survival in the absence of elephants in the Akagera National Park, Rwanda. *Journal of Applied Ecology*, **8**, 723-728.

Stelfox, J.G., Kufwafa, J.W. & Ottichilo, W.K. (1984) Monitoring elephant and rhino trends in Kenya. *Pachyderm*, **4**, 15.

Stelfox, J.G., Peden, D.G., Epp, H., Hudson, R.J., Mbugua, S.W., Agatsiva, J.L. *et al.* (1986) Herbivore dynamics in southern Narok, Kenya. *Journal of Wildlife Management*, **50**, 339-347.

Steyn, A. (2003) *The Impact of Re-Introduced Elephant (Loxodonta africana) on Key Woody Plant Species in Songimvelo Nature Reserve*. M-Tech. Tshwane University of Technology, Pretoria, South Africa.

Stretch, A.M. (2005) *A Modelling Approach to Elephant and Tree Population Dynamics for a Small Game Farm.* M-Tech. Durban Institute of Technology, Durban, South Africa.

Stromayer, K.A.K. & Ekobo, A. (1992) The distribution and number of forest dwelling elephants in extreme southeastern Cameroon. *Pachyderm*, **15**, 9-14.

Tafangenyasha, C. (1997) Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. *Journal of Environmental Management*, **49**, 355-366.

Taylor, R.D. (1987) Abundance and distribution of elephants in Matusadona National Park Zimbabwe. *Transactions of the Zimbabwe Scientific Association*, **63**, 58-66.

Taylor, R.D. (1993) Elephant management in Nyaminyami District, Zimbabwe: turning a liability into an asset. *Pachyderm*, **17**, 19-29.

Tchamba M.N. (1993) Number and migration patterns of savanna elephants (*Loxodonta africana africana*) in northern Cameroon. *Pachyderm*, **16**, 66-71.

Tchamba, M.N. & Mahamat H. (1992) Effects of elephant browsing on the vegetation in Kalamaloue National Park, Cameroon. *Mammalia*, **56**, 533-540.

Tchamba, M.N. & Elkan, P. (1995) Status and trends of some large mammals and ostriches in Waza National Park, Cameroon. *African Journal of Ecology*, **33**, 366-376.

Tehou, A.C. (2002) Les éléphants *Loxodonta africana* dans la Réserve de Biosphère de la Pendjari, nord-est République du Bénin: abondance, densité et répartition spatiale. *Pachyderm*, **33**, 64-68.

Tehou, A.C. & Sinsin, B. (2000) The ecology of elephant populations (*Loxodonta africana*) in the Cynegetic Zone of Djona (Benin). *Mammalia*, **64**, 29-40.

Tembo, A. (1995) A survey of large mammals in Sioma-Ngwezi National Park, Zambia. *African Journal of Ecology*, **33**, 173-174.

Theuerkauf, J., Ellenberg, H. & Guiro, Y. (2000) Group structure of forest elephants in the Bossematié Forest Reserve, Ivory Coast. *African Journal of Ecology*, **38**, 262-264.

Theuerkauf, J., Ellenberg, H., Waitkuwait, W.E. & Mühlenberg, M. (2001) Forest elephant distribution and habitat use in the Bossematie Forest Reserve, Ivory Coast. *Pachyderm*, **30**, 37-43.

Thompson, G. (1978) Natal's last elephants. *African Wildlife*, **32**, 42-43.

Thouless, C. (1991) A report of the Laikipia elephant count, 1990. *Pachyderm*, **14**, 32-36.

Thouless, C.R. (1994) Conflict between humans and elephants on private land in northern Kenya. *Oryx*, **28**, 119-127.

Timberlake, J.R. & Childes, S.L. (2004) *Biodiversity of the Four Corners Area*. Technical Reviews Volume Two (Chapters 5-15). Occasional Publications in Biodiversity No. 15. Biodiversity Foundation for Africa/ Zambezi Society, Harare, Zimbabwe.

Turkalo, A. & Fay, M. (1995) Studying forest elephants by direct observation: preliminary results from the Dzanga Clearing, Central African Republic. *Pachyderm*, **20**, 45-54.

TWINBAS. (2007) *Twinning European and Third Countries Rivers Basins for Development of Integrated Water Resources Management Methods.* Work Package 6 Classification of Water Bodies. Volume I: Characterisation (D6.2). An EC FP6 research project co-funded within the topic 'Twinning European/third countries river basins' under the 'Global change and ecosystems' sub-priority.

United Nations Development Programme/Global Environment Facility. (2004) *Effective Management of the National Protected Areas System.* Unpublished report. Zambia.

Usongo, L. (2003) Preliminary results on movements of a radio-collared elephant in Lobeke National Park, south-east Cameroon. *Pachyderm*, **34**, 53-58.

van Aarde, R., Whyte, I. & Pimm, S. (1999) Culling and the dynamics of the Kruger Park African elephant population. *Animal Conservation*, **2**, 287-294.

van Aarde, R., Kilian, W. & Pimm, S. 2002. *The Dynamics of Savanna Elephants in Etosha National Park in Northern Namibia.* Annual Progress Report 2002 (September 2002 – December 2002) to the US Fish and Wildlife Service. Conservation Ecology Research Unit (CERU), University of Pretoria, Pretoria, South Africa.

van Aarde, R., Ferreira, S., Lehman, E. & Fourie, J. (2005) *A Survey of Large Mammal Numbers of the Lundazi Forest Reserve, the Kasungu National Park, the Vwaza*

Game Reserve and the Nyika National Park 2005. Unpublished report. Conservation Ecology Research Unit (CERU), University of Pretoria, Pretoria, South Africa.

van Aarde, R.J. & Jackson, T.P. (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation*, **134**, 289-297.

van Aarde, R., Ferreira, S., Page, B., Jackson, T., Junker, J., Gough, K., *et al*. (2008) Elephant population biology and ecology. In *South African Elephant Assessment* (ed. Bob Scholes). Wits University Press, South Africa.

van Lavieren, L.P. & Esser, J.D. (1979) Numbers, distribution and habitat preference of large mammals in Bouba Ndjida National Park, Cameroon. *African Journal of Ecology*, **18**, 141-153.

van Wyk, P. & Fairall, N. (1969) The influence of the African elephant on the vegetation of the Kruger National Park with special reference to the tree and shrub strata. *Koedoe*, **12**, 57-89.

Viljoen, P.J. (1987) Status and past and present distribution of elephants in the Kaokoveld, South West Africa/ Namibia. *South African Journal of Zoology*, **22**, 247-257.

Viljoen, P.J. (1988) *The Ecology of the Desert-Dwelling Elephants Loxodonta africana (Blumenbach, 1797) of the Western Damaraland and Kaokoland.* DSc Thesis. University of Pretoria, Pretoria, South Africa.

Walker, B.H., Emslie, R.N., Owen-Smith, R.N. & Scholes, R.J. (1987) To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology*, **24**, 381-401.

Walsh, P.D. & White, L.J.T. (1999) What it will take to monitor forest elephant populations. *Conservation Biology*, **13**, 1194-1202.

Wambwa, E., Manyibe, T., Litoroh, M., Gakuya, F. & Kanyingi, J. (2001) Resolving human–elephant conflict in Luwero District, Uganda, through elephant translocation. *Pachyderm*, **31**, 58-62.

Watson R.M. & Bell R.H.V. (1969) The distribution, abundance and status of elephant in the Serengeti region of northern Tanzania. *Journal of Applied Ecology*, **6**, 115-132.

Watson, R.M., Parker, I.S.C. & Allan, T. (1969) A census of elephant and other large mammals in the Mkomazi region of northern Tanzania and southern Kenya. *East African Wildlife Journal*, **7**, 11-26.

Weaver, L.C. & Skyer, P. (2003) *Conservancies: integrating wildlife land-use options into the livelihood, development, and conservation strategies of Namibian communities.* A paper presented at the 5th World Parks Congress to the Animal Health and Development (AHEAD) Forum Durban, Republic of South Africa, 8-17 September, 2003.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, **13**, 265-288.

Western, D. & Lindsay, W.K. (1984) Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, **22**, 229-244.

White, L. (1994) Biomass of rain forest mammals in the Lopé Reserve, Gabon. *Journal of Animal Ecology*, **63**, 499-512.

Whitehouse, A. (2001) *Conservation Biology of a Small Closed Population*. PhD Thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

Whitehouse, A.M. & Hall-Martin, A.J. (2000) Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. *Oryx*, **34**, 46-55.

Whitehouse, A.M., Hall-Martin, A.J. & Knight, M.H. (2001) A comparison of methods used to count the elephant population of the Addo Elephant National Park, South Africa. *African Journal of Ecology*, **39**, 140-145.

Whitehouse, A.M. & Schoeman, D.S. (2003) Ranging behaviour of elephants within a small, fenced area in Addo Elephant National Park, South Africa. *African Zoology*, **38**, 95-108.

Whyte, I.J. (2001) *Conservation Management of the Kruger National Park Elephant Population*. PhD Thesis. University of Pretoria, Pretoria, South Africa.

Whyte, I.J. & Wood, C.A. (1996) *Census Results for Elephant and Buffalo in the Kruger National Park in 1996.* Scientific report 20/96. National Parks Board, Skukuza, South Africa.

Whyte, I.J., Biggs, H.C., Gaylard, A. & Braack, L.E.O. (1999) A new policy for the management of the Kruger National Park's elephant population. *Koedoe*, **42**, 111-133.

Whyte, I.J., van Aarde, R.J., Pimm, S.L., du Toit, J.T., Rogers, K.H. & Biggs, H.C. (2003) Kruger's elephant population: its size and consequences for ecosystem heterogeneity. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds. J. du Toit, K. Rogers & H. Biggs). Island Press, Washington, U.S.A.

Williamson, B.R. (1975) Seasonal distribution of elephants in Wankie National Park. *Arnoldia*, **7**, 1-16.

Williamson, B.R. (1976) Reproduction in female African elephant in the Wankie National Park, Rhodesia. *South African Journal of Wildlife Research*, **6**, 89-93.

Wittemyer, G. (2001) The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology*, **39**, 357-365.

Wood, A.M. (1999) A demographic model to predict future growth of the Addo elephant population. *Koedoe*, **42**, 97-100.

Appendix 3 The following websites and electronic databases were searched to obtain both published and unpublished documents including information on elephant population estimates and management.

Population estimates - websites

1. Wildlife Portal (www.wildlifenetafrica.com/wildlife/wildlife.html)
2. WildNet Africa (www.aroa.org.za)
3. Wildlife Translocation Association (www.wta.org.za)
4. Endangered Wildlife Trust (www.ewt.org.za/home.aspx)
5. United Nations Environment Programme (www.unep-wcmc.org)
6. Convention on the International Trade in Endangered Species (www.cites.org)
7. African Elephant Specialist Group (www.iucn.org/themes/ssc/sgs/afesg/)
8. Elephant Management and Owners Association (www.emoa.org.za)
9. Mpala and Segera WRC (www.mpala.org/researchctr/research/publications.html)
10. Uganda Wildlife Authority (www.uwa.or.ug/new.html)
11. Kenya Wildlife Service (www.kws.org)
12. Tanzania National Parks (www.tanzaniaparks.com)
13. African Wildlife Foundation (www.awf.org)
14. Global Population Dynamics Database (www3.imperial.ac.uk/cpb/research/patternsandprocesses/gpdd)
15. International Fund For Animal Welfare (www.IFAW.org)
16. African Elephant Conservation Coordinating Group (website no longer available)

17. United States Agency for International Development (www.usaid.gov/)
18. Ministère de l'Environnement, des Eaux, Forêts, Chasses et Pêches, Central African Republic (http://bch-cbd.naturalsciences.be/rca/index.htm)
19. World Wildlife Fund (www.worldwildlife.org)
20. Direction de la Faune et de la Chasse, Libreville, Gabon (www.gabon-forests.org)
21. Department of National Parks and Wildlife Management, Causeway, Zimbabwe (www.zimparks.com)
22. US Fish and Wildlife Service (http://www.fws.gov/index.html)
23. Forestry Development Authority, Monrovia, Liberia (http://www.fda.gov.lr/)
24. The Ministry of Tourism, Parks and Wildlife, Malawi (www.malawi.gov.mw/Information/Home)
25. Uganda Wildlife Authority (http://www.uwa.or.ug/parks.html)
26. Ministry of Tourism, Environment and Natural Resources, Zambia (zm.chm-cbd.net/convention/mtenr/)
27. Fauna and Flora International (www.fauna-flora.org/)
28. Conservation International (www.conservation.org/)

Elephant population management - websites

1. United Nations Environment Programme (www.unep-wcmc.org)
2. Wetlands International – Ramsar Sites Information Service (www.wetlands.org/RSIS/_COP9Directory/Directory/ris/1TZ001en.pdf)
3. GTZ Wildlife Programme in Tanzania (www.wildlife-programme.gtz.de/wildlife/download/colonial.pdf)

4. I'm in Africa (iminafrica.com/Provinces/mpumalanga.asp)
5. Department of Environmental Affairs and Tourism (www.environment.gov.za/HotIssues/2005/29062005/MEMO%20TO%20MINISTER.pdf)
6. Getaway Africa (www.getawayafrica.com/)
7. Parks.it (www.parks.it/world/ZM/Eindex.html)
8. NOW Communications Inc. (www.nowtoronto.com/issues/2007-10-18/goods_travel.php)
9. responsibletravel.com (www.responsibletravel.com)
10. Wikipedia – The Free Encyclopedia (en.wikipedia.org/wiki/Main_Page)
11. Best of Kenya (www.bestofkenya.com/TanaRiver.htm)
12. The World Commission on Dams (www.dams.org/docs/kbase/studies/cszzmain.pdf)
13. Zimbabwe Parks and Wildlife Management Authority (www.zimparks.com/html/general.html)
14. The Swazi Observer (www.observer.org.sz/weekend/main.php?id=36945&section=mainweek)
15. Southern African Birding (www.sabirding.co.za/birdspot/130101.asp)
16. IDA – In Defense of Animals (www.idausa.org/campaigns/elephants/sdzoo.html)
17. Warthog Web Designers (warthog.co.za/dedt/tourism/maputaland/print/mkuze.htm)
18. Accurate Reloadingt (www.accuratereloading.com/bchr05.html)
19. BIOZIM – Biodiversity conservation and sustainable development in the Mid-Zambezi Valley (www.biozim.com/en/library/atlas.)
20. BBC (www.bbc.co.uk/nature/animals/features/169index.shtml)

21. Namibia Nature Foundation (www.nnf.org.na/RARESPECIES/InfoSys/elephant/distribution/)

22. University of Pretoria (upetd.up.ac.za/thesis/available/etd-04172007-142520/unrestricted/dissertation.pdf)

23. Environment News Service (www.ens-newswire.com/ens/dec2002/2002-12-12-03.asp)

24. Sun Safaris (www.sunsafaris.com/krugernationalpark.html)

25. Siyabona Africa - Manyeleti Private Game Reserve (manyeleti.krugerpark.co.za)

26. Web forum for biology research at The University of Arizona (research.biology.arizona.edu/mosquito/Willott/Pubs/Commons.html)

27. Kenya Wildlife Service (www.kws.org/marsabit.html)

28. Mashatu Botswana (www.mashatu.com/research_ele.htm)

29. Hidden Trails Safaris (www.hiddentrails.com/africa/botswana/botswana-mashatu.htm)

30. IG Afrika Studien – Universität Basel (pages.unibas.ch/afrika/limpopo/papers/limpopo_html/limpopo_lindenmann.html)

Electronic databases

1. Cambridge Scientific Abstracts
2. Google Scholar
3. Science Direct
4. Blackwell Synergy
5. JSTOR
6. ISI Web of Knowledge
7. Zoological Records

8. InfoTrac
9. Biological Sciences
10. ProQuest
11. African Studies (including South African Studies and Wildlife Ecology Studies Worldwide)
12. CAB Direct
13. Science Citation Index (1980-2000)
14. Navtech (SA Technikon Research)
15. Kovsidex (Research Information at the University of the Free State)
16. UCTD (Theses and Dissertations at South African Universities)
17. SA ePublications
18. SANB (South African Publications)
19. SACat (items available in South African libraries)
20. ISAP by the National Library of South Africa (articles from South African journals)
21. Library of Congress

Appendix 4

List of areas, the region and the country in Africa (in alphabetical order) for which I collated information on elephant population estimates.

Name of the area where elephants were surveyed	Region	Country
Abdoulaye Faunal Reserve	West Africa	Togo
Aberdare NP	East Africa	Kenya
Aberdare NP & Forest	East Africa	Kenya
Aberdare outside	East Africa	Kenya
Abokoamekro Forest Reserve	West Africa	Cote D’Ivoire
Abong-Mbang Forest Reserve	Central Africa	Cameroon
Addo EP	Southern Africa	South Africa
Akagera-Mutara NP	East Africa	Rwanda
Alibori Superieur Forest	West Africa	Benin
Amaya Bonga Area	East Africa	Ethiopia
Amboseli Ecosystem	East Africa	Kenya
Amboseli NP	East Africa	Kenya
Andoni Island	West Africa	Nigeria
Andover Game Reserve	Southern Africa	South Africa
Ankasa Conservation Area (includes Nini-Sihien NP)	West Africa	Ghana
Arabuko Sokoke Forest Reserve	East Africa	Kenya
Arly NP	West Africa	Burkina Faso
Arusha NP	East Africa	Tanzania
Atakora Hunting Zone	West Africa	Benin
Atherstone NR	Southern Africa	South Africa
Azagny NP	West Africa	Cote D’Ivoire
Baba NRafi Forest	West Africa	Niger
Babille Elephant Sanctuary	East Africa	Ethiopia
Bagbe River Forest	West Africa	Sierra Leone
Balule NR	Southern Africa	South Africa
Bama & Gwoza	West Africa	Nigeria
Bamingui-Mangoran Reserve Complex	Central Africa	CAR
Bangassou Forest Reserve	Central Africa	CAR
Bangweulu GMA	Southern Africa	Zambia
Banhine NP	Southern Africa	Mozambique
Banyang-Mbo Forest Reserve	Central Africa	Cameroon
Baringo District	East Africa	Kenya
Barrobo National Forest	West Africa	Liberia
Baths Guera	Central Africa	Chad
Beki-Bossematie Classified Forest	West Africa	Cote D’Ivoire
Benoue NP	Central Africa	Cameroon
Besse-Boka Classified Forest	West Africa	Cote D’Ivoire
Bia NP & Resource Reserve	West Africa	Ghana
Bili Uere	Central Africa	DRC
Binasse Area (Guinea Bissau)	West Africa	Guinea Bissau
Binga Communal Lands	Southern Africa	Zimbabwe

Name of the area where elephants were surveyed	Region	Country
Bisanadi NR	East Africa	Kenya
Bisanadi NR & Dispersal area	East Africa	Kenya
Bolo Forest	West Africa	Cote D'Ivoire
Bongola	Southern Africa	Angola
Boni Forest & Dodori NRs	East Africa	Kenya
Boni Forest NR	East Africa	Kenya
Bontioli Partial and Total Faunal Reserve	West Africa	Burkina Faso
Borakalalo NP	Southern Africa	South Africa
Borana Area	East Africa	Ethiopia
Borgu Forest Reserve	West Africa	Nigeria
Bouba-Ndjida NP	Central Africa	Cameroon
Boucle de Baoule Biosphere Reserve	West Africa	Mali
Boucle de Baoule NP	West Africa	Mali
Boumba-Bek Forest Reserve	Central Africa	Cameroon
Bubi Valley Conservancy	Southern Africa	Zimbabwe
Bubiana Conservancy	Southern Africa	Zimbabwe
Bugungu WR/ Budongo Forest	East Africa	Uganda
Burigi Game Reserve	East Africa	Tanzania
Burigi-Biharamulo Ecosystem	East Africa	Tanzania
Bushimae NP	Central Africa	DRC
Bwindi Impenetrable Forest NP	East Africa	Uganda
Caba Delgado Province	Southern Africa	Mozambique
Caprivi	Southern Africa	Namibia
Cavally Classified Forest	West Africa	Cote D'Ivoire
Central Limpopo Valley	Southern Africa	Botswana
Chad Basin NP Sector	West Africa	Nigeria
Chanjuzi Hunting Block	Southern Africa	Zambia
Charara Safari Area	Southern Africa	Zimbabwe
Chari Baguimi region	Central Africa	Chad
Chete Safari Area	Southern Africa	Zimbabwe
Chew Bahr Wildlife Reserve	East Africa	Ethiopia
Chewore Safari Area	Southern Africa	Zimbabwe
Chiawa GMA	Southern Africa	Zambia
Chibwika-Ntambu GMA	Southern Africa	Zambia
Chichibon Corridor	West Africa	Ghana
Chiredzi River Conservancy	Southern Africa	Zimbabwe
Chirisa Safari Area	Southern Africa	Zimbabwe
Chisomo GMA	Southern Africa	Zambia
Chizarira NP	Southern Africa	Zimbabwe
Chobe NP	Southern Africa	Botswana
Cleveland Game Ranch	Southern Africa	South Africa
Comoe NP	West Africa	Cote D'Ivoire
Concouati NP	Central Africa	Congo
Corubal-Dulombi Area	West Africa	Guinea Bissau
Cross River (Okwango)	West Africa	Nigeria
Dabus Valley Controlled Hunting Area	East Africa	Ethiopia
Dadieso Forest Reserve	West Africa	Ghana
Dande Communal Lands	Southern Africa	Zimbabwe
Davo Forest	West Africa	Cote D'Ivoire

Name of the area where elephants were surveyed	Region	Country
Dembo area	Central Africa	Chad
Deux Bale & Dibon Forest Reserves	West Africa	Burkina Faso
Diefoula (Comoe-Leraba) Classified Forest	West Africa	Burkina Faso
Digya NP	West Africa	Ghana
Dinder NP	East Africa	Sudan
Dja Faunal Reserve	Central Africa	Cameroon
Djambamakrou Forest	West Africa	Cote D'Ivoire
Djona Hunting Zone	West Africa	Benin
Djouah-Belinga	Central Africa	Gabon
Dodori NR	East Africa	Kenya
Doma Safari Area	Southern Africa	Zimbabwe
Dominika Biosphere Reserve	Central Africa	Congo
Doung-Pana	West Africa	Togo
Duekoue Forest	West Africa	Cote D'Ivoire
Dzangha-Ndoki NP	Central Africa	Congo
Dzangha-Sangha & Dzangha-Ndoki NPs	Central Africa	CAR
Dzangha-Sangha NP	Central Africa	CAR
East Caprivi Forestry Area	Southern Africa	Namibia
East Core Area (Susuwe)	Southern Africa	Namibia
Eastern Border	East Africa	Tanzania
Eastern Floodplains (Salambala)	Southern Africa	Namibia
Elephant Sanctuary (north of M.F.N.P.)	East Africa	Uganda
Endulen Game Controlled Area	East Africa	Tanzania
Equateur Province	Central Africa	DRC
Etosha NP	Southern Africa	Namibia
Falgore (Kogin Kano) Game Reserve	West Africa	Nigeria
Far Wamo Wildlife Reserve	East Africa	Somalia
Faro NP	Central Africa	Cameroon
Fazao-Malfakassa NP	West Africa	Togo
Fleme Valley & Mandingue Plateau (probably extinct now)	West Africa	Mali
Forest Elephant Range (E. Guinea)	Central Africa	Equatorial Guinea
Forest Elephant Range (Gabon)	Central Africa	Gabon
Fosse aux Lions NP	West Africa	Togo
Foumbou Classified Forest	West Africa	Cote D'Ivoire
Fresco Forest	West Africa	Cote D'Ivoire
Gagal-Yapala area	Central Africa	Chad
Galana Ranch	East Africa	Kenya
Gamba Reserve Complex	Central Africa	Gabon
Gambella NP	East Africa	Ethiopia
Gangala-na-Bodio	Central Africa	DRC
Garamba NP	Central Africa	DRC
Garamba NP & surrounds	Central Africa	DRC
Garissa District	East Africa	Kenya
Gashaka-Gumti NP	West Africa	Nigeria
Gash-Setit	East Africa	Eritrea
Gile NP	Southern Africa	Mozambique
Goaso Forest	West Africa	Ghana
Go-Bodienou Forest	West Africa	Cote D'Ivoire
Goin-Cavally Classified Forest (& Goin Debe)	West Africa	Cote D'Ivoire

Name of the area where elephants were surveyed	**Region**	**Country**
Gola East Forest Reserve	West Africa	Sierra Leone
Gola North Forest Reserve	West Africa	Sierra Leone
Gola North, West & East Forest Reserves	West Africa	Sierra Leone
Gola, Kpelle & Lorma National Forests	West Africa	Liberia
Gonarhezou NP	Southern Africa	Zimbabwe
Gorongoza NP	Southern Africa	Mozambique
Goungoun Classified Forest	West Africa	Benin
Gourma permanent waterholes	West Africa	Mali
Gourma Range	West Africa	Mali
Great Fish River Reserve Complex	Southern Africa	South Africa
Greater Kuduland Safaris	Southern Africa	South Africa
Greater St. Lucia Wetland Park	Southern Africa	South Africa
Grebo National Forest	West Africa	Liberia
Hanang Forest Reserve	East Africa	Tanzania
Hartley Safari Area	Southern Africa	Zimbabwe
Haut Bandama Fauna & Floral Reserve	West Africa	Cote D’Ivoire
Haut Sassandra Classified Forest	West Africa	Cote D’Ivoire
Hlane Royal NP	Southern Africa	Swaziland
Hluhluwe-Umfolozi GR	Southern Africa	South Africa
Home Farm & Greystone Ranches	Southern Africa	Zimbabwe
Hurungwe Safari Area	Southern Africa	Zimbabwe
Hwange NP	Southern Africa	Zimbabwe
Ihtala GR	Southern Africa	South Africa
Imatong Mtns Nature Conservation Area	East Africa	Sudan
Imenti Forest	East Africa	Kenya
Inhambane Province	Southern Africa	Mozambique
Irobo Classified Forest	West Africa	Cote D’Ivoire
Isangano NP	Southern Africa	Zambia
Isiolo District	East Africa	Kenya
Itigi South	East Africa	Tanzania
Ituri	Central Africa	DRC
Itwara Forest Reserve	East Africa	Uganda
Ivindo NP (& western buffer zone)	Central Africa	Gabon
Jonglei District	East Africa	Sudan
Kafinde NP	Southern Africa	Zambia
Kafue NP	Southern Africa	Zambia
Kahuzi Biega Lowland Sector	Central Africa	DRC
Kahuzi Biega Lowland Sector & Kasese study area	Central Africa	DRC
Kahuzi Biega NP	Central Africa	DRC
Kahuzi Biega Upland Sector	Central Africa	DRC
Kaia Ingwe	Southern Africa	South Africa
Kainji Lake NP	West Africa	Nigeria
Kajiado District	East Africa	Kenya
Kakum Conservation Area	West Africa	Ghana
Kalamaloue NP (near Waza)	Central Africa	Cameroon
Kaloudia-Doumdoum area	Central Africa	Chad
Kambari	West Africa	Nigeria
Kamuka	West Africa	Nigeria
Kangari Hills Hunting Forest Reserve	West Africa	Sierra Leone

Name of the area where elephants were surveyed	Region	Country
Kapama Game Farm	Southern Africa	South Africa
Kariba Communal Lands	Southern Africa	Zimbabwe
Kariega Private Game Reserve	Southern Africa	South Africa
Karkloof Falls Safari Park	Southern Africa	South Africa
Karuma Wildlife Reserve	East Africa	Uganda
Kasanka NP	Southern Africa	Zambia
Kasonso-Busanga GMA	Southern Africa	Zambia
Kasungu NP	Southern Africa	Malawi
Kasyoha-Kitomi Forest Reserve	East Africa	Uganda
Katavi NP	East Africa	Tanzania
Katavi Rukwa outside	East Africa	Tanzania
Katavi-Rukwa Area	East Africa	Tanzania
Katoka Game Reserve	Southern Africa	Zambia
Katonga Game Reserve	East Africa	Uganda
Kavango region	Southern Africa	Namibia
Kavira Forest Land	Southern Africa	Zimbabwe
Kazuma Forest Land	Southern Africa	Zimbabwe
Keran NP	West Africa	Togo
Keregbo Forest	West Africa	Cote D'Ivoire
Kerio Valley Conservation & Dispersal Areas	East Africa	Kenya
Khaudom & Nyae Nyae Conservancy	Southern Africa	Namibia
Khaudom GR	Southern Africa	Namibia
Kibale NP	East Africa	Uganda
Kidepo Valley NP	East Africa	Uganda
Kigezi Wildlife Reserve	East Africa	Uganda
Kilifi & Kwale Districts	East Africa	Kenya
Kilifi District	East Africa	Kenya
Kilimanjaro NP/Forest Reserve	East Africa	Tanzania
Kilombero Game Controlled Area	East Africa	Tanzania
Kipipiri Forest Reserve	East Africa	Kenya
Kitui District	East Africa	Kenya
Kivu Province	Central Africa	DRC
Klaserie Private Game Reserve	Southern Africa	South Africa
Koakrana HZ	West Africa	Burkina Faso
Konkombouri HZ	West Africa	Burkina Faso
Konkombri Hunting Zone	West Africa	Benin
Konoumou Classified Forest	West Africa	Cote D'Ivoire
Kora NP	East Africa	Kenya
Korup NP	Central Africa	Cameroon
Kourtiagou HZ	West Africa	Burkina Faso
Krahn Bassa National Forest	West Africa	Liberia
Kruger NP	Southern Africa	South Africa
Kunene-Damaraland	Southern Africa	Namibia
Kwalata	Southern Africa	South Africa
Kwale District	East Africa	Kenya
Kwandwe Private Game Reserve	Southern Africa	South Africa
Kwiambana	West Africa	Nigeria
Kyambura (Chambura) Wildlife Reserve	East Africa	Uganda
Lac Fitri area	Central Africa	Chad

Name of the area where elephants were surveyed	Region	Country
Lac Tchad	Central Africa	Chad
Lac Tele Community Reserve	Central Africa	Congo
Lag Badana Bushbush	East Africa	Somalia
Lag Dhere Ecosystem	East Africa	Somalia
Laikipia District	East Africa	Kenya
Lake Chad	West Africa	Nigeria
Lake Manyara NP	East Africa	Tanzania
Lalibela Private Game Reserve	Southern Africa	South Africa
Lamu District	East Africa	Kenya
Larmanaye area	Central Africa	Chad
Lavushi Manda	Southern Africa	Zambia
Lefini Reserve	Central Africa	Congo
Lekoli-Pandaka GR	Central Africa	Congo
Letaba Ranch	Southern Africa	South Africa
Limpopo NP	Southern Africa	Mozambique
Linyanti	Southern Africa	Botswana
Liuwa Plain NP	Southern Africa	Zambia
Liwonde NP	Southern Africa	Malawi
Loango NP	Central Africa	Gabon
Lobeke Forest Reserve	Central Africa	Cameroon
Lofa-Mano NP	West Africa	Liberia
Loho Classified Forest	West Africa	Cote D'Ivoire
Loliondo Game Controlled Area	East Africa	Tanzania
Lomani-Lualaba	Central Africa	DRC
Longido Game Conservation Area	East Africa	Tanzania
Lope Faunal Reserve	Central Africa	Gabon
Lope FR & environments	Central Africa	Gabon
Loroki Forest	East Africa	Kenya
Lower Zambezi NP	Southern Africa	Zambia
Lowhills	Southern Africa	South Africa
Luama Hunting Zone	Central Africa	DRC
Luama-Itombwe West Area	Central Africa	DRC
Luambe NP	Southern Africa	Zambia
Luangwa	Southern Africa	Mozambique
Luangwa Valley	Southern Africa	Zambia
Luano GMA	Southern Africa	Zambia
Luawata Hunting Block	Southern Africa	Zambia
Luiana Partial Reserve	Southern Africa	Angola
Lukusuzi NP	Southern Africa	Zambia
Lukwakwa GMA	Southern Africa	Zambia
Lumimba GMA	Southern Africa	Zambia
Lunga-Luswishi & Kasonso-Busanga	Southern Africa	Zambia
Lunga-Luswishi GMA	Southern Africa	Zambia
Lupande GMA	Southern Africa	Zambia
Lusenga Plain NP	Southern Africa	Zambia
Lusulu Communal Lands	Southern Africa	Zimbabwe
Luvero	East Africa	Uganda
Maan Region (formerly known as Campo Reserve)	Central Africa	Cameroon
Mabula Game Lodge	Southern Africa	South Africa

Name of the area where elephants were surveyed	Region	Country
Machakos District	East Africa	Kenya
Machya-Fungulwe GMA	Southern Africa	Zambia
Madagali & Kopre	West Africa	Nigeria
Madikwe Nature Reserve	Southern Africa	South Africa
Madjoari Faunal Reserve (prob. Part of W du Burkina)	West Africa	Burkina Faso
Mago & Omo NPs	East Africa	Ethiopia
Mago NP	East Africa	Ethiopia
Magoe District	Southern Africa	Mozambique
Mahenye	Southern Africa	Zimbabwe
Mahlatini GR	Southern Africa	South Africa
Maiko NP	Central Africa	DRC
Majete Wildlife Reserve	Southern Africa	Malawi
Makalali Private Game Reserve	Southern Africa	South Africa
Makuya NP	Southern Africa	South Africa
Malapati Safari Area	Southern Africa	Zambia
Mali-Guinea Border	West Africa	Mali
Malilangwe Conservancy	Southern Africa	Zimbabwe
Malolotja NR	Southern Africa	Swaziland
Mambali Communal Lands	Southern Africa	Zimbabwe
Mamili NP	Southern Africa	Namibia
Mana Pools	Southern Africa	Zimbabwe
Manda National Park	Central Africa	Chad
Mandera District	East Africa	Kenya
Mangetti Game Reserve	Southern Africa	Namibia
Manica Province	Southern Africa	Mozambique
Manovo-Gounda St. Floris Reserve Complex	Central Africa	CAR
Manyeleti Game Reserve	Southern Africa	South Africa
Manzan Classified Forest	West Africa	Cote D'Ivoire
Maputo Elephant Reserve (& Futi River)	Southern Africa	Mozambique
Marahoue NP	West Africa	Cote D'Ivoire
Marakele NP	Southern Africa	South Africa
Maramani Communal Lands	Southern Africa	Zimbabwe
Marang Forest Reserve	East Africa	Tanzania
Mare Aux Hippotames Biosphere Reserve	West Africa	Burkina Faso
Marguba Forest Reserve	West Africa	Nigeria
Maro, Tui & Pa Forest Reserves	West Africa	Burkina Faso
Marromeu Complex	Southern Africa	Mozambique
Marsabit District	East Africa	Kenya
Marsabit National Reserve	East Africa	Kenya
Marsabit NP	East Africa	Kenya
Masai Mara & Surrounds	East Africa	Kenya
Masai Mara NR	East Africa	Kenya
Masai Mara Outside	East Africa	Kenya
Masai Steppe	East Africa	Tanzania
Massenya-Mandjafa area	Central Africa	Chad
Maswa Game Reserve	East Africa	Tanzania
Maswa-Makau (Makao Hunting Block)	East Africa	Tanzania
Maswa-Ngorongoro	East Africa	Tanzania
Matabeleland Forest Area	Southern Africa	Zimbabwe

Name of the area where elephants were surveyed	Region	Country
Matetsi Complex	Southern Africa	Zimbabwe
Matetsi Safari Area	Southern Africa	Zimbabwe
Matibi II Communal Lands	Southern Africa	Zimbabwe
Matthews Range	East Africa	Kenya
Matusadona NP	Southern Africa	Zimbabwe
Mau Forest Complex	East Africa	Kenya
Mavurandonha Wilderness Area	Southern Africa	Zimbabwe
Mboko Hunting Reserve	Central Africa	Congo
Mecucoe	Southern Africa	Mozambique
Mekrou Hunting Zone	West Africa	Benin
Mengame WS	Central Africa	Cameroon
Meru Conservation Area	East Africa	Kenya
Meru North Dispersal Areas	East Africa	Kenya
Meru NP	East Africa	Kenya
Metamboa	Southern Africa	Mozambique
Mgahinga Gorilla NP	East Africa	Uganda
Midlands Conservancy	Southern Africa	Zimbabwe
MIKE2	Southern Africa	Namibia
Mikumi NP	East Africa	Tanzania
Mikumi NP (outside)	East Africa	Tanzania
Minkebe NP	Central Africa	Gabon
Mizan Teferi Controlled Hunting Area	East Africa	Ethiopia
Mkadikgadi Pans	Southern Africa	Botswana
Mkhaya NR	Southern Africa	Swaziland
Mkomazi Game Reserve	East Africa	Tanzania
Mkomazi region (northern Tanzania & southern Kenya)	East Africa	Tanzania
Mkuzi Falls Safaris	Southern Africa	South Africa
Mkuzi GR	Southern Africa	South Africa
Mochongoi Forest	East Africa	Kenya
Mokolo River Nature Reserve	Southern Africa	South Africa
Mole NP	West Africa	Ghana
Mongokele Forest Reserve	Central Africa	Cameroon
Monogaga Classified Forest	West Africa	Cote D'Ivoire
Monpri Classified Forest	West Africa	Cote D'Ivoire
Mont Peko NP	West Africa	Cote D'Ivoire
Mont Sangbe NP	West Africa	Cote D'Ivoire
Monte Alen NP (north)	Central Africa	Equatorial Guinea
Monte Alen NP (south)	Central Africa	Equatorial Guinea
Montres Mitra Sector (extension of Monte Alen NP)	Central Africa	Equatorial Guinea
Monts de Cristal	Central Africa	Gabon
Monts Kouffe Forest	West Africa	Benin
Moremi GR	Southern Africa	Botswana
Moribane-Chimanimani	Southern Africa	Mozambique
Mosi-oa-Tunya	Southern Africa	Zambia
Mouhoun Protected Area Complex	West Africa	Burkina Faso
Mount Elgon NP	East Africa	Uganda
Moyowosi-Kigosi Game Reserve	East Africa	Tanzania
Mpongo Park	Southern Africa	South Africa
Mt Cameroon	Central Africa	Cameroon

Name of the area where elephants were surveyed	**Region**	**Country**
Mt Elgon NP & Forest Reserve	East Africa	Kenya
Mt Elgon NP only	East Africa	Kenya
Mt Fouari Reserve	Central Africa	Congo
Mt Gbandee & Surrounds	West Africa	Cote D'Ivoire
Mt Kenya NP & Forest Reserve	East Africa	Kenya
Mt Mavoumbou Hunting Reserve	Central Africa	Congo
Mthethomusha Game Reserve	Southern Africa	South Africa
Mtibi Game Farm	Southern Africa	South Africa
Mudumu NP	Southern Africa	Namibia
Muhesi GR	East Africa	Tanzania
Mukungule GMA	Southern Africa	Zambia
Mulobezi GMA	Southern Africa	Zambia
Mumbwa GMA	Southern Africa	Zambia
Mungo Division (Yabassi area)	Central Africa	Cameroon
Munyamadzi GMA	Southern Africa	Zambia
Munyawana	Southern Africa	South Africa
Murchison Falls NP (Kabalega Falls NP)	East Africa	Uganda
Murchison North	East Africa	Uganda
Murchison South	East Africa	Uganda
Musalungu GMA	Southern Africa	Zambia
Musele-Matebo GMA	Southern Africa	Zambia
Mwagne NP	Central Africa	Gabon
Mwanya Hunting Block (southern sector of Lumimba)	Southern Africa	Zambia
Mwea National Reserve	East Africa	Kenya
Mweru-Wantipa Ecosystem	Southern Africa	Zambia
Mweru-Wantipa NP	Southern Africa	Zambia
N#a-Jaqna Conservancy	Southern Africa	Namibia
Namwala GMA	Southern Africa	Zambia
Namwala West GMA	Southern Africa	Zambia
Narok District	East Africa	Kenya
Nasolot, South Turkana, Rimoi & Kamnarok NRs	East Africa	Kenya
Nazinga Game Ranch	West Africa	Burkina Faso
NCB 7	Southern Africa	Mozambique
Nchete Island Wildlife Sanctuary	Southern Africa	Zambia
Ndzalama Game Reserve	Southern Africa	South Africa
Ngamo Forest Land	Southern Africa	Zimbabwe
Ngorongoro Crater	East Africa	Tanzania
Ngorongoro Crater Conservation Area	East Africa	Tanzania
Nguruman Hills	East Africa	Kenya
Niassa & surrounds	Southern Africa	Mozambique
Niegre Classified Forest	West Africa	Cote D'Ivoire
Nienzi & Luganzo Hunting Blocks (Sagara-Nyamagoma)	East Africa	Tanzania
Nimule NP	East Africa	Sudan
Niokolo-Koba NP	West Africa	Senegal
Nkala GMA	Southern Africa	Zambia
Nkhotakota Wildlife Reserve	Southern Africa	Malawi
Nki Forest Reserve	Central Africa	Cameroon
North East National Forest	West Africa	Liberia
North Gokwe Communal Lands	Southern Africa	Zimbabwe

Name of the area where elephants were surveyed	Region	Country
North Kitui National Reserve	East Africa	Kenya
North Luangwa NP	Southern Africa	Zambia
North of Lake Cabora Bassa	Southern Africa	Mozambique
Northeast Botswana (non-conserved)	Southern Africa	Botswana
Northeastern Ghana - Red & White Volta-Morago Ecosystem	West Africa	Ghana
Northern Botswana elephant range	Southern Africa	Botswana
Northern Tuli Game Reserve	Southern Africa	Botswana
Nouabale-Ndoki NP	Central Africa	Congo
Nsumbu NP	Southern Africa	Zambia
NW Matabeleland	Southern Africa	Zimbabwe
Nxai-Pan	Southern Africa	Botswana
Nyae Nyae Conservancy	Southern Africa	Namibia
Nyampala GMA	Southern Africa	Zambia
Nyanga North Hunting Reserve	Central Africa	Congo
Nyanga South Hunting Reserve	Central Africa	Congo
Nyangboue	West Africa	Cote D'Ivoire
Nyatana Wildlife Management Area	Southern Africa	Zimbabwe
Nyika NP	Southern Africa	Malawi
Nyungwe Forest Reserve	East Africa	Rwanda
Odzala NP	Central Africa	Congo
Odzala NP & environs	Central Africa	Congo
Okapi NP	Central Africa	DRC
Okavango Delta	Southern Africa	Botswana
Okomu Game Sanctuary	West Africa	Nigeria
Okromodou Forest	West Africa	Cote D'Ivoire
Ol Ari Nyiro Ranch	East Africa	Kenya
Omo Forest Reserve	West Africa	Nigeria
Omo NP	East Africa	Ethiopia
Orientale Province	Central Africa	DRC
Oti-Mandouri Faunal Reserve	West Africa	Togo
Otze Forest	East Africa	Uganda
Oueme Superieur Forest	West Africa	Benin
Oumou Hunting Reserve	West Africa	Burkina Faso
Oure Kaba	West Africa	Guinea
Outamba-Kilimi NP	West Africa	Sierra Leone
Pagou-Tondougou HZ	West Africa	Burkina Faso
Pai Game Reserve	West Africa	Nigeria
Pama Centre Sud	West Africa	Burkina Faso
Pama Partial Faunal Reserve	West Africa	Burkina Faso
PAMA, SINGOU & ARLY Combined	West Africa	Burkina Faso
Pamula Game Lodge	Southern Africa	South Africa
Pandamasuie Forest Land	Southern Africa	Zimbabwe
Paradise Game Farm	Southern Africa	South Africa
Park W du Benin, Mekrou Classified Forest & Djona Hunting Zone	West Africa	Benin
Pendjari Biosphere Reserve	West Africa	Benin
Pendjari Hunting Zone	West Africa	Benin
Pendjari National Park	West Africa	Benin
Phalaborwa Mining Co.	Southern Africa	South Africa
Phinda Resource Reserve	Southern Africa	South Africa

Name of the area where elephants were surveyed	Region	Country
Phirilongwe Forest Reserve	Southern Africa	Malawi
Pilanesberg NP	Southern Africa	South Africa
Piti East Hunting Block	East Africa	Tanzania
Po National Park (adjacent to Nazinga GR)	West Africa	Burkina Faso
Po-Nazinga-Sissili Ecosystem	West Africa	Burkina Faso
Pongara NP	Central Africa	Gabon
Pongola Game Reserve	Southern Africa	South Africa
Pongolapoort GR	Southern Africa	South Africa
Protea Farm	Southern Africa	Zimbabwe
Pumulanga	Southern Africa	South Africa
Queen Elizabeth Conservation Area (Rwenzori NP)	East Africa	Uganda
Quicama NP	Southern Africa	Angola
Quirimbas NP	Southern Africa	Mozambique
Red & White Volta Valley (Morago Ecosystem)	West Africa	Ghana
Remainder of Pama	West Africa	Burkina Faso
Remainder of Selous	East Africa	Tanzania
Rhinoland Safaris	Southern Africa	South Africa
Rietboklaagte	Southern Africa	South Africa
Riverside	Southern Africa	South Africa
Robondo Island NP	East Africa	Tanzania
Rombo	East Africa	Kenya
Ruaha NP	East Africa	Tanzania
Ruaha-Rungwa (outside)	East Africa	Tanzania
Ruaha-Rungwa Ecosystem	East Africa	Tanzania
Rubi-Tele Area	Central Africa	DRC
Rufunsa GMA	Southern Africa	Zambia
Rukingwa Wildlife Sanctuary & Taita Ranch	East Africa	Kenya
Rukwa GR	East Africa	Tanzania
Rungwa GR	East Africa	Tanzania
Rungwa South Hunting Block	East Africa	Tanzania
Rungwa-Kisigo GR	East Africa	Tanzania
Rwenzori Mountains NP	East Africa	Uganda
Saadani GR	East Africa	Tanzania
Sabi Sand Game Reserve	Southern Africa	South Africa
Salamat region	Central Africa	Chad
Salonga NP & surrounds	Central Africa	DRC
Salonga NP North	Central Africa	DRC
Salonga NP South	Central Africa	DRC
Sambisa Game Reserve	West Africa	Nigeria
Samburu & Buffalo Springs NRs	East Africa	Kenya
Samburu District	East Africa	Kenya
Samburu-Laikipia	East Africa	Kenya
Sandwe GMA	Southern Africa	Zambia
Sango Bay	East Africa	Uganda
Sansale	West Africa	Guinea
Sapi Safari Area	Southern Africa	Zimbabwe
Sapo NP	West Africa	Liberia
Save Valley Conservancy	Southern Africa	Zimbabwe
Scio Classified Forest	West Africa	Cote D’Ivoire

Name of the area where elephants were surveyed	Region	Country
Sebungwe region	Southern Africa	Zimbabwe
Sekula Island Wildlife Sanctuary	Southern Africa	Zambia
Selati GR	Southern Africa	South Africa
Selous Ecosystem	East Africa	Tanzania
Selous Game Reserve	East Africa	Tanzania
Selous-Masasi Corridor	East Africa	Tanzania
Selous-Niassa Corridor	East Africa	Tanzania
Semliki NP	East Africa	Uganda
Sengwa Wildlife Research Area	Southern Africa	Zimbabwe
Sengwe Communal Lands	Southern Africa	Zimbabwe
Sentinel & Nottingham	Southern Africa	Zimbabwe
Serengeti Ecosystem	East Africa	Tanzania
Serengeti NP	East Africa	Tanzania
Seronga	Southern Africa	Botswana
Shambe NP	East Africa	Sudan
Shamwari Game Reserve	Southern Africa	South Africa
Shangani Ranch	Southern Africa	Zimbabwe
Shari West Region	Central Africa	Chad
Sheraro	East Africa	Eritrea
Shimba Hills Nature Reserve & FRs	East Africa	Kenya
Shire	East Africa	Ethiopia
Sichifula GMA	Southern Africa	Zambia
Sijarira Forest Area	Southern Africa	Zimbabwe
Sikumi Forest Land	Southern Africa	Zimbabwe
Silue Classified Forest	West Africa	Cote D’Ivoire
Singou Partial Faunal Reserve	West Africa	Burkina Faso
Siniaka-Minia Faunal Reserve	Central Africa	Chad
Sioma Ngwezi NP	Southern Africa	Zambia
Sirba Game Reserve	West Africa	Niger
Sofala Province	Southern Africa	Mozambique
Songan-Tamin-Mabi-Yaya Classified Forest	West Africa	Cote D’Ivoire
Songimvelo GR	Southern Africa	South Africa
Sousan Forest Reserve	West Africa	Mali
South East Border	East Africa	Tanzania
South Kitui National Reserve	East Africa	Kenya
South Luangwa NP	Southern Africa	Zambia
Southern NP	East Africa	Sudan
Southern NP & Surrounds	East Africa	Sudan
Southern NP (outside)	East Africa	Sudan
Sudd Swamps (west of the Nile river)	East Africa	Sudan
Sutton Game Ranch	Southern Africa	South Africa
Swamp NP	East Africa	Somalia
Sweetwaters Game Reserve	East Africa	Kenya
Tai Ecosystem	West Africa	Cote D’Ivoire
Taita Taveta District (between Tsavo East and Tsavo West NPs)	East Africa	Kenya
Tamou Total Faunal Reserve	West Africa	Niger
Tana River Delta	East Africa	Kenya
Tana River District	East Africa	Kenya
Tana River Primate National Reserve	East Africa	Kenya

Name of the area where elephants were surveyed	Region	Country
Tarangire Ecosystem	East Africa	Tanzania
Tarangire NP	East Africa	Tanzania
Tarangire NP (outside)	East Africa	Tanzania
Taylor Creek	West Africa	Nigeria
Tekezze Valley Wildlife Reserve	East Africa	Ethiopia
Tembe Elephant Park	Southern Africa	South Africa
Tene Forest	West Africa	Cote D’Ivoire
Tete Province	Southern Africa	Mozambique
Thaba Tholo	Southern Africa	South Africa
Thornybush Game Lodge	Southern Africa	South Africa
Thukela Biosphere Reserve	Southern Africa	South Africa
Thuma Forest Reserve	Southern Africa	Malawi
Tiapley Forest	West Africa	Cote D’Ivoire
Timbavati Game Reserve	Southern Africa	South Africa
Tongoe	Southern Africa	Mozambique
Tongo-Sikongo	Southern Africa	Zambia
Tonkoli & Tama Forest Reserves	West Africa	Sierra Leone
Toro (Semliki Valley) Wildlife Reserve	East Africa	Uganda
Touchstone Game Farm	Southern Africa	South Africa
Transmara Forest	East Africa	Kenya
Trois Riviere Forest	West Africa	Benin
Tsavo (outside)	East Africa	Kenya
Tsavo East NP	East Africa	Kenya
Tsavo Ecosystem	East Africa	Kenya
Tsavo NP	East Africa	Kenya
Tsavo West NP	East Africa	Kenya
Tshukudu Game Lodge	Southern Africa	South Africa
Tuli Circle Safari Area	Southern Africa	Botswana
Turkana District	East Africa	Kenya
Ugalla River Game Reserve	East Africa	Tanzania
Ugalla River Outside	East Africa	Tanzania
Umbabat Game Reserve	Southern Africa	South Africa
Upemba NP	Central Africa	DRC
Upper Ogun Game Reserve	West Africa	Nigeria
Upper Tshuapa Area	Central Africa	DRC
Utengule Area	East Africa	Tanzania
Uwanda GR & surrounds	East Africa	Tanzania
Vassako Bolo	Central Africa	CAR
Venetia Limpopo Nature Reserve	Southern Africa	South Africa
Vhembe-Dongola	Southern Africa	South Africa
Victoria Falls	Southern Africa	Zimbabwe
Virunga (Mikeno)	Central Africa	DRC
Virunga Central	Central Africa	DRC
Virunga North	Central Africa	DRC
Virunga NP (formerly Lake Albert NP)	Central Africa	DRC
Virunga Plains	Central Africa	DRC
Virunga South	Central Africa	DRC
Volcans NP	East Africa	Rwanda
Vosdal	Southern Africa	South Africa

Name of the area where elephants were surveyed	Region	Country
Vwaza Marsh Wildlife Reserve	Southern Africa	Malawi
W du Benin NP	West Africa	Benin
W du Burkina NP & Kourtiagou Partial Faunal Reserve	West Africa	Burkina Faso
W du Niger NP	West Africa	Niger
Wajir District	East Africa	Kenya
Wamba/Lopori Area	Central Africa	DRC
Waza NP	Central Africa	Cameroon
Welcome Game Reserve	Southern Africa	South Africa
Welgevonden PGR	Southern Africa	South Africa
West Caprivi GR	Southern Africa	Namibia
West Core Area (Buffalo NP)	Southern Africa	Namibia
West Loliondo Game Controlled Area	East Africa	Tanzania
West Lunga NP	Southern Africa	Zambia
West Petauke	Southern Africa	Zambia
West Pokot District	East Africa	Kenya
West Zambezi	Southern Africa	Zambia
Western Border	East Africa	Tanzania
Western Ghana	West Africa	Ghana
Yaida & surrounds	East Africa	Tanzania
Yankari NP	West Africa	Nigeria
Yoko area	Central Africa	Cameroon
Zabre Department	West Africa	Burkina Faso
Zakouma NP	Central Africa	Chad
Zambezi NP	Southern Africa	Zimbabwe
Zambezi Valley	Southern Africa	Zimbabwe
Zambezi Valley Communal Lands	Southern Africa	Zimbabwe
Zambezi Valley Escarpment	Southern Africa	Zimbabwe
Zambezia Province	Southern Africa	Mozambique
Ziama Strict Nature Reserve	West Africa	Guinea
Zimbabwe-Border	Southern Africa	Botswana
Zinave NP	Southern Africa	Mozambique
Zulu Nyala Safaris	Southern Africa	South Africa
Zumbo	Southern Africa	Mozambique