

**Demographic responses to changes in conservation
management: a case study on elephants in the
Kruger National Park**

by

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Demographic responses to changes in conservation management: a case study on elephants in the Kruger National Park

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Disclaimer

This thesis contains two manuscripts (Chapters 2 and 3). For consistency, styles and formatting for all chapters follow the requirements for the journal *Biological Conservation*.

I, Ashley Stephen Robson declare that the thesis, which I hereby submit for the degree *Magister Scientiae* (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Ashley Stephen Robson

March 2015

Dedication

I dedicate this thesis to my parents, Stephen and Yola, and my sister Claire.

Abstract

Conservation management approaches for elephants in southern Africa, and particularly in the Kruger National Park, have changed. Recently, Kruger's managers adapted their approach from artificially manipulating elephant numbers to reinstating and embracing density-dependent processes that could limit or regulate the elephant population. However, few studies have evaluated whether changes in Kruger's elephant management approach were effective in achieving the desired outcomes. This is a common shortcoming in conservation endeavours and has the potential to undermine future initiatives. In my thesis, I address this shortcoming, and assess whether recent changes in conservation management in Kruger induced demographic responses from the elephant population that ecological theory predicted and managers desired.

My assessment into how calf recruitment and population growth rates responded to ecological limitations (i.e. climate, primary productivity and density) during two contrasting management eras suggests that changes in management induced predicted and desired demographic responses. During the culling era (i.e. density suppression, water supplementation and fencing), population growth rates were primarily driven by the density-independent, climate-mediated, reproductive patterns of the population. In the post-culling era (i.e. natural variation in density, artificial waterhole and fence removals), density-dependence was reinstated and took over as the primary driver of population growth. Although not empirically tested, density-dependent weaned calf survival and dispersal likely contributed to density-dependent population growth during the latter era and should be the focus of future work.

I then determined that the changes in management promoted density-dependent habitat selection, a fundamental driver of population regulation. I found that as densities increased following the cessation of culling, selection for woody cover, an important resource for elephants, generalized (i.e. decreased selection of areas with high woody cover and increased

selection of areas with lower woody cover). Furthermore, selection for areas close to or far from rivers was mediated by rainfall. While not directly related to changes in density, varied selection for rivers may moderate density-dependent feedbacks to demographic parameters by alleviating foraging restrictions and clustering around key resources. The question remains however, whether density-dependent and rainfall-mediated changes to habitat selection have fitness consequences for elephants that could ultimately regulate the population.

Elephants in Kruger responded, at least demographically and partly, to changes in conservation management as theory predicted and managers desired. Although the population has not yet entered the sought after state of long-term stability, my assessment suggests that some of the density-dependent processes necessary to regulate the population are present. I suggest avenues of further study and advocate that ecological principles provide an effective framework for the scientific evaluation and conservation management of elephants within and beyond the Kruger National Park.

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Chapter 1. General Introduction

The success of a conservation initiative often depends on the ability of management to make effective decisions in the face of substantial uncertainty (Cook et al., 2010; Keith et al., 2011). Procedures that reduce the inherent uncertainty and risk associated with any conservation decision may then enhance the effectiveness of management and consequently, contribute to conservation (see Keith et al., 2011). A particularly important procedure in adaptive conservation management is therefore the progressive development of relevant knowledge through the scientific evaluation of past management approaches (Pullin and Knight, 2001; Keith et al., 2011). By assessing the effectiveness of past actions in achieving management objectives, scientists can simultaneously advance ecological theory and develop an evidence base to inform conservation managers (Pullin et al., 2004; Keith et al., 2011). An understanding of what did and did not work in the past can thus improve future management decisions, and ideally, produce effective conservation outcomes (Cook et al., 2010; Keith et al., 2011).

The Kruger National Park, South Africa, has a long history of adaptive conservation management and the evaluation of past management approaches (see van Wilgen and Biggs, 2011). The adaptive approach to African elephant (*Loxodonta africana*) management has been of particular interest to scientists and the public. In the early 1990's, a retrospective evaluation of the initial approaches used to manage elephants in Kruger identified apparent shortcomings (see Owen-Smith et al., 2006; van Aarde and Jackson, 2007). With pressure from the public and mounting scientific evidence, the managers of Kruger adapted their elephant management approach from one based on artificial manipulation of numbers to one aimed at reinstating and embracing ecological processes that govern demography (Owen-Smith et al., 2006; van Aarde and Jackson, 2007). Although elephants are a well-studied species (Trimble and van Aarde, 2011), and elephant management in Kruger has been a topic of scientific and public interest for decades (see Whyte et al., 2003), little has been done to directly evaluate whether the recent

changes to management approaches were effective in achieving the objectives desired by management. In my thesis, I provide such an evaluation and examine how elephants in Kruger have responded demographically to changes in conservation management.

Agricultural paradigms provided an attractive framework for initial conservation efforts for elephants in Kruger and across southern Africa (see Pienaar and van Niekerk, 1963; Hanks et al., 1981; Whyte et al., 1998). Managers used a number of manipulative methods to artificially increase, decrease and stabilise elephant numbers according to agriculturally based targets (see Pienaar, 1983; Owen-Smith, 1996; van Aarde et al., 1999; Owen-Smith et al., 2006). In the years following the establishment of Kruger for instance, managers constructed approximately 300 artificial waterholes and 50 dams in areas devoid of permanent water to increase herbivore numbers and to buffer populations against drought (see Pienaar and van Niekerk, 1963; Pienaar, 1983). Herbivores responded to water supplementation and populations began to grow. In the late 1960s however, the elephant population began to approach the 7 000 mark, the estimated carrying capacity of the Park at the time (Smuts, 1975). From 1967 to 1994, 14 629 elephants were then culled to maintain the population around that level in an attempt to curtail, what managers thought to be, the inevitable destruction of vegetation and biodiversity in the Park (van Aarde et al., 1999; Whyte et al., 2003).

Besides the obvious financial strain and the possible social and political repercussions resulting from culling (see van Aarde and Jackson, 2007), early management approaches ultimately led to a number of ecological anomalies stemming from the incompatibility of managing elephants using agricultural concepts. Previous studies suggest that the culling process, artificially low densities, extensive water supplementation and the complete fencing of the Park by 1976, may have decoupled elephant distribution patterns, and consequently reproduction and survival, from natural variation in key limiting factors for herbivores (i.e. food, water, density) (see Walker et al., 1987; van Aarde et al., 1999; Loarie et al., 2009;

Shrader et al., 2010). Furthermore, water supplementation and fencing may have directly influenced other large herbivore species (see Walker et al., 1987; Owen-Smith, 1996) and, indirectly, a number of woody plant species (see O'Connor et al., 2007). It became apparent that manipulative approaches for elephant management, and indeed approaches affecting other large herbivores, would be ineffective in the long term, as there would be a perpetual need for expensive and controversial human interference.

In 1995, culling was discontinued following public outcry citing a lack of scientific evidence demonstrating that high elephant densities caused damage to vegetation (see van Aarde et al., 1999). During the ensuing period when the management policy was under review, a number of different management options, some including localised culling, were proposed for Kruger's elephants (see Whyte et al., 1998; Whyte, 2001; Whyte et al., 2003). Most of these options were never implemented. Rather, scientists started to voice their opinions and the focus of elephant conservation management began to change from artificial manipulation to natural regulation. Scientists advocated that if managers allowed the elephant population to fluctuate without human interference, and if they naturalised elephant distribution by removing some artificial waterholes and fences, density-dependent processes would potentially lead to the natural regulation of the population (see Turchin, 1995; Owen-Smith et al., 2006; van Aarde et al., 2006). This would subsequently remove the need for intensive human interference and alleviate past ecological, social and financial complications (Owen-Smith et al., 2006; van Aarde and Jackson, 2007).

Management implemented this ecological framework; they removed more than half of artificial waterholes, dropped some fences and continued the moratorium on culling in the Park. The changing focus of elephant conservation management in Kruger laid a precedent for elephant management in southern Africa, however, no studies have directly evaluated whether

these changes were effective in reinstating density-dependent processes that may regulate the population.

In the case of Kruger, ecological theory, and specifically theory on large herbivore population dynamics, provide a scientific framework for assessing whether past changes to management were effective in this regard. Theory suggests that when a large herbivore population is artificially stabilised below its ecological carrying capacity, and food and/or water are supplemented by managers, distribution, fecundity, survival and population growth rates may be decoupled from natural variation in some key limiting factors (i.e. climate, food, water, density) (see Walker et al., 1987; Eberhardt, 2002; Coulson et al., 2004; Owen-Smith et al., 2006; Bonenfant et al., 2009; Milner et al., 2014). When managers cease to intervene, and reinstate dependence on these limiting factors, the population should respond in a predictable demographic manner. For example, as densities begin to recover from artificially maintained low levels, demographic components should respond sequentially (Eberhardt, 2002; Coulson et al., 2004). We expect a decrease in juvenile survival to occur first, preceded by an increase in age at first reproduction, a decrease in reproductive rates and a decrease in adult survival (Eberhardt, 2002). These component density feedbacks will ultimately augment ensemble density feedbacks (i.e. density-dependent population growth) (see Eberhardt, 2002; Coulson et al., 2004; Lande et al., 2006; Bonenfant et al., 2009; Herrando-Pérez et al., 2012), which are necessary to induce and maintain population regulation (see Turchin, 1995; 1999; Coulson et al., 2004; Chamaillé-Jammes et al., 2008).

Intraspecific competition for resources, as suggested by density-dependent habitat selection (see van Beest et al., 2014b), is a fundamental process driving density-dependent demographic variation (see Morris, 1988; 2003; Rosenzweig, 1991; Coulson et al., 2004; Owen-Smith et al., 2006; McLoughlin et al., 2006; 2008; 2010; Bonenfant et al., 2009). As densities increase, intraspecific competition strengthens and some individuals in a population have to

redistribute from higher to lower quality habitats (see Fretwell and Lucas, 1969; van Beest et al., 2014a; b), with potential repercussions for individual fitness (see McLoughlin et al., 2006; 2008; 2010). This may lead to the sequential demographic responses discussed above, and promote population regulation (see Morris, 1988; 2003), the ultimate objective of Kruger's change in elephant conservation management.

In this thesis, I ask whether past changes in conservation management were effective in inducing desirable demographic responses from the elephant population in Kruger, and base my evaluation of “desirable responses” on ecological theory and the expectations of management discussed above. Following this introduction (Chapter 1), I present two research chapters (Chapter 2; 3), that I organise into independent papers, and a conclusion chapter (Chapter 4). In chapter 2, I examine the responses of calf recruitment, incorporating the outcomes of reproduction and first year survival, and population growth rates to variation in limiting factors (e.g. climate, primary productivity, density) during two contrasting periods of human interference. The culling era was characterised by density suppression through culling, water supplementation and fencing, while the post-culling era experienced increased densities and artificial waterhole and fence removals. Thereafter (Chapter 3), I examine whether the increase in elephant densities following the release from culling promoted density-dependent habitat selection, indicative of intraspecific competition for resources and a fundamental driver of demographic variation, and potentially, population regulation. Together, these chapters provide an initial evaluation into the effectiveness of recent changes to elephant conservation management in the Kruger National Park, with potential implications for future scientific assessment and management of elephants across southern Africa.

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Chapter 2. Reinstating demographic responses to ecological limitations: a case study on elephants in the Kruger National Park

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Abstract

Climate, food, water, shelter and density are limiting factors that shape the demographic patterns of large herbivore populations. Human intervention can however decouple population dynamics from spatiotemporal variations in some of these factors. A population should respond demographically when management ceases to intervene, and should do so in a manner predicted by theory. We assessed this prediction using the African elephants (*Loxodonta africana*) of the Kruger National Park as a case study. We used a 28-year time series to examine the responses of calf recruitment and population growth rates to climate, primary productivity and density during different periods of human interference. We divided our time series into two contrasting eras. Relatively low densities, extensive provisioning of water and fencing characterised the culling era. In the post-culling era, management removed some supplemented water and fences and allowed the population to fluctuate without interference. The most notable response was that as densities rose after culling, density-dependent processes took over from density-independent reproduction as the primary driver of population growth. Density-dependent weaned calf survival and dispersal likely contributed to this. We also found that the

drivers of calf recruitment for Kruger were similar to those reported elsewhere in Africa. ENSO likely worked to synchronise reproduction across the Park. We did discover, however, that some ecological limitations were possibly still outstanding, potentially owing to the continuing wide distribution of supplemented water in the Park. Our work offers the most comprehensive evidence to date that the intended move to reinstate ecological processes to Kruger induced desirable demographic responses from the elephant population that were in line with both ecological theory and park management's objectives.

1. Introduction

Large herbivores occurring under natural or near-natural conditions are exposed to a number limiting factors that induce and maintain demographic variation. For instance, spatiotemporal variability in rainfall, water availability, food, shelter and density underpin patterns of dispersal, age specific survival and reproduction observed in many large herbivore populations (Gaillard et al., 2000; Coulson et al., 2001; Brook and Bradshaw, 2006; Trimble et al., 2009; Simard et al., 2010). However, management interventions (e.g. culling, water and/or food provisioning, fencing) may decouple demographic variation from such limitations (see Walker et al., 1987; Eberhardt, 2002; Coulson et al., 2004; Loarie et al., 2009; Smit and Ferreria, 2010; Shrader et al., 2010; Young and van Aarde, 2010; Milner et al., 2014). If management interference is later discontinued and limitations reinstated, herbivore populations should respond demographically (e.g. Eberhardt, 2002; Bonenfant et al., 2009 and references therein). In this paper, we use the African elephant (*Loxodonta africana*) population of Kruger National Park as a case study and examine demographic responses to ecological limitations that prevailed during two contrasting periods of management and across a spatial gradient of varying resource availability.

At the largest scale, climatic phenomena such as the North Atlantic Oscillation (NAO) and the El Niño-Southern Oscillation (ENSO) can drive variations in demographic parameters (Post and Stenseth, 1999; Coulson et al., 2001; Ogutu and Owen-Smith, 2003). In the Northern Hemisphere, these climatic patterns indirectly affect herbivore demography by simultaneously influencing factors linked to resource availability (e.g. rainfall, temperature, snow depth, wind speeds) (Forchhammer and Post, 2004; Hallet et al., 2004; Stenseth and Mysterud, 2005). Similarly, ENSO in southern Africa appears to drive the dynamics of savanna vegetation and herbivores by influencing rainfall during the wet season (Rutherford, 1980; Hulme et al., 2001; Marshal et al., 2011).

The effect of density on demography primarily operates through the negative relationship between density and the amount of resources available. As density varies, so too does per capita resource availability, resulting in age-specific changes to individual fitness and alteration of population level demographic parameters (Lande et al., 2006). Following either human- or environmentally-induced disturbances, rebounding populations can show spatial and demographic patterns that reverberate for years (Coulson et al., 2004) and exhibit a sequential response of demographic rates to rising densities (Eberhardt, 2002; Herrando-Perez et al., 2012). For instance, theory predicts a decrease in juvenile survival first, followed by an increase in age at first reproduction, a decline in reproductive rates and finally a decrease in adult survival (Eberhardt, 2002). Dispersal rates, however, may also respond to changes in density and regulate populations locally (Bonenfant et al., 2009).

Elephants are long-lived, generalist megaherbivores with prolonged gestation periods (22 months), extended maternal investment (three to four years) and the ability to traverse large areas (van Aarde et al., 2008). Elephant populations do respond demographically to ecological limitations, with variation in age structure generally driven by either conditions affecting conception rates, prenatal survival or calf survival, depending on rainfall regime (Trimble et

al., 2009). Conception rates and prenatal survival are linked to variations in primary productivity during the wet season before and the dry season after conception, with ENSO suggested as a synchronising agent in female fecundity (Wittemyer et al., 2007a; Wittemyer et al., 2007b). Furthermore, density may regulate elephant population growth rates by influencing survival and immigration/emigration rates (van Aarde et al., 1999; Chamaillé-Jammes et al., 2008; Young and van Aarde, 2010), while density effects on fecundity are less clear. The survival of suckling calves appears generally unaffected by variations in density and resource availability (Young and van Aarde, 2010), except during extremely harsh periods (Foley et al., 2008), which is expected of a monotocous species (Bonenfant et al., 2009). Instead, the survival of weaned calves decreases with increasing density and decreasing dry season resource availability (Young and van Aarde, 2010). Increasing density may further promote dispersal (van Aarde et al., 1999; Chamaillé-Jammes et al., 2008) and occupation of suboptimal habitats to avoid clustering (Young et al., 2009).

Management of Kruger's elephants has a controversial past, including the combined disturbances of an intensive culling programme, an extensive water provisioning scheme and the complete fencing of the Park (see Whyte et al., 1998; 2003; van Aarde et al., 1999). More recently, management sought to reinstate ecological limitations via the cessation of culling and the removal of most supplementary water and some fences, to allow for the possible regulation of the population with limited management interference (van Aarde and Jackson, 2007). The demographic responses of the elephant population to this change in management are still largely unknown.

Using 28-year time series of climatic, remotely sensed and census data we asked whether elephants in Kruger responded demographically to the intended reinstatement of ecological limitations. Within our analyses we divided the time series into two periods; the culling era (1985-1994) characterised by relatively low densities, water supplementation and

fencing, and the post-culling era (1998-2012) when densities increased, about two thirds of artificial water sources were closed and some fences were allowed to disintegrate and others even removed. We partitioned Kruger into three districts based on a longitudinal gradient in mean annual rainfall and separated by large perennial rivers. We first examined the influence of ENSO on seasonal primary productivity through their shared relationship with rainfall, assuming that this was the pathway through which climate primarily influenced herbivore demography in southern Africa (see Marshal et al., 2011). We then used seasonal primary productivity and density as explanatory variables and evaluated their effects on elephant demographic variation using a two-step approach; firstly by analysing their influences on calf recruitment and thereafter on population growth rates. We lastly examined the effect of calf recruitment on population growth rates. For a visual representation of our conceptual framework, expectations and supporting literature see Fig. 2.1.

2. Material and methods

2.1. Study site

The Kruger National Park extends over 19 485km² in the north-eastern corner of South Africa, bordered by Zimbabwe to the north and Mozambique to the east. The northern, central and southern districts of the Park, separated by the Olifants and Sabie Rivers respectively, lie along a gradient of increasing rainfall from north (receiving an annual average of 450 mm) to south (750 mm). The Park is situated in a region that experiences strong influences from ENSO from November to February (Hulme et al., 2001).

From 1967 to 1994, 14 629 elephants were culled in Kruger in an attempt to stabilise the population around 7 000 individuals (van Aarde et al., 1999), the then estimated carrying capacity of the Park during a dry year (Whyte et al., 2003). This was done to curtail the perceived destruction of vegetation by elephants. During this time, a large number of artificial

waterholes were also installed across the landscape, providing water supplementary to the six perennial and 14 ephemeral rivers that transverse the Park. Increased public pressure informed by science-based advocacy led to culling being discontinued in 1994 (see van Aarde et al., 1999). Managers thereafter attempted to manage the landscape of Kruger rather than the elephants and removed nearly two thirds of supplemented water points and sections of the boundary fence. Elephant numbers doubled from 1995 to 2012, possibly in response to the cessation of culling (Fig. 2.2).

2.2. Measures of climatic and primary productivity variability

We used the Southern Oscillation Index (SOI) as an index of ENSO conditions. Periods with negative SOI values were considered El-Niño (dry) periods while positive values indicated La Nina (wet) periods. Daily rainfall data were collected from 30 rainfall stations across the park. Thereafter, we used the Normalized Difference Vegetation Index (NDVI) as an index of primary productivity. For the period 1983-2006, we used 15 day composites at a resolution of 8km by 8km [National Oceanographic and Atmospheric Association's Advanced Very High Resolution Radiometer (AVHRR) processed by the Global Inventory Monitoring and Modeling Studies Group and available from the Global Land Cover Facility: <http://glcf.unmiacs.umd.edu/data/gimms>]. We calculated mean monthly NDVI values as the mean of the two 15 day composites in a given month for this period. From 2000 to 2012, we used monthly composites at a 1km by 1km resolution [Moderate Resolution Imaging Spectroradiometer (MODIS) processed by the National Aeronautics and Space Administration and available from NASA's Earth Observing System Data and Information System: <http://modis.gsfc.nasa.gov/index.php>]. Global analyses have suggested overall compatibility between MODIS and GIMMS NDVI (see Fensholt and Proud, 2012), so we calibrated and combined them using a 6-year overlap (see Trimble et al., 2009).

We generated time series of seasonal SOI, rainfall and NDVI for the period 1983 to 2012. We identified the core wet and dry seasons as December to March inclusive and June to September inclusive, respectively (see Young and van Aarde, 2010). Seasonal SOI values were calculated as the mean monthly SOI for the corresponding period. We calculated measures of wet and dry season rainfall as the mean of the sums of daily rainfall, and we generated indices of seasonal primary productivity by summing monthly mean NDVI values over the respective periods. We standardized Kruger- and district-specific rainfall and NDVI by dividing by the mean (1983 – 2012) (see Marshal et al., 2011). Spatial synchrony of temporal variations in seasonal rainfall and NDVI between the districts of Kruger was assessed using Pearson correlation coefficients.

2.3. Measures of demographic variability

Aerial surveys of elephants have been carried out annually in Kruger since 1967 (see Whyte et al., 2003). The total counts took place during the dry season when visibility was highest and when elephants were most likely in close proximity to water. The near total coverage of Kruger ensured accurate and precise population estimates (see Ferreria and van Aarde, 2009). Since 1985, all observed individuals were counted and differentiated into first year calves (<1 year) and older animals. We calculated time series of estimated calf recruitment as the percentage of first year calves in the surveyed population. Seasonal distribution of mating and birthing activities in Kruger suggest that the majority of first year calves observed during aerial surveys were born during the wet season preceding the count (Smuts, 1975; Trimble et al., 2009). This estimate of calf recruitment could then include the outcome of conception rates, prenatal survival and survival from birth until the time of the survey. Following the suggestion of Turchin (2003), we calculated time series of annual fluctuations in population size using the equation for per capita population growth rates; $r_t = \ln(N_t/N_{t-1})$, where N_t is the total population count in year t , and N_{t-1} is the population count from the year before ($t-1$) (see Brook and

Bradshaw, 2006; Chamaillé-Jammes et al., 2008; Young et al., 2009; Herrando-Perez et al., 2012; Simard et al., 2012). During the culling era, we accounted for the effect of culling and corrected population growth rates by adding the exact number of individuals culled in April (year t) (Whyte et al., 2003) to the number of individuals counted in August/September (year t). We estimated density as the number of elephants counted for the whole Park and in each district in a given year divided by area of the Park and/or district. Spatial synchrony in temporal variations in calf recruitment and population growth rates between the districts of Kruger for the culling and post-culling eras was assessed using Pearson correlation coefficients.

2.4. Modelling procedure

Prior to analyses, all data were examined for distributional properties. All seasonal rainfall, seasonal NDVI and density variables were natural logged. As temporal trends in time series violate the assumption of stationarity and may produce spurious results, we assessed all variables and detrended those that exhibited significant temporal trends (see Table S.2.1) (see Turchin, 2003; Wu et al., 2007; Coulson et al., 2008; Ahrestani et al., 2013; Husek et al., 2013). Where a trend existed, we only used detrended variables in subsequent analyses (Turchin, 2003). We used least-squares linear regressions to assess the coarse-scale influence of seasonal SOI on seasonal rainfall and seasonal rainfall on seasonal NDVI for the three districts of Kruger. Thereafter, we used simple linear models to examine whether calf recruitment was best explained by seasonal NDVI and/or density at year t , $t-1$ and/or $t-2$. We grouped explanatory variables into periods of interest; the reproductive period (year $t-1$ and/or $t-2$) and first year of life (year t). We also considered the influence of mean seasonal NDVI and mean density over the two-year reproductive period (mean of $t-1$ and $t-2$) on calf recruitment (see Trimble et al. 2009). We analysed combinations of explanatory variables separately for each period of interest to reduce the number of candidate models and avoid over-fitting. We further examined autocorrelation in district-specific calf recruitment by calculating Pearson correlation

coefficients between calf recruitment (t) and calf recruitment (t-1; t-2; t-3; t-4) (see Simard et al., 2012). We ran models separately for the northern, central and southern districts of the Park for the culling and post-culling eras.

We assessed the influence of calf recruitment (year t), density (year t-1) and seasonal NDVI, and combinations thereof, on population growth rates also using simple linear models (see Simard et al., 2012). Direct density-dependence exerts its main effect through mortality whereas delayed density-dependence primarily works through effects on fecundity patterns (Bonenfant et al., 2009). We assumed that if delayed density-dependence existed, it would influence calf recruitment and subsequently be illustrated in those models. We therefore did not include delayed density effects. As population surveys took place partway through the dry season, we assumed that dry season NDVI of the preceding year (t-1) and wet season NDVI of the survey year (t) would influence population growth rates (see Marshal et al., 2011). High negative correlations between district-specific population growth rates for both the culling and post-culling eras (see Results; Fig. 2.2) suggested possible inter-district asymmetric dispersal of elephants. To negate the possible effects of dispersal on district-specific growth rates and to avoid over- or under-estimation of density-dependence, we not only ran models for each district but also for the whole of Kruger. The year 2000 exhibited an unexpected negative growth rate that coincided with the highest wet season rainfall on record (see Fig. 2.2) and the high retention of vegetative cover into the dry season (Whyte, 2001). As this may have compromised detection of elephants during the aerial survey and most likely resulted in a significant undercount (see Whyte, 2001), we additionally ran models excluding the years 2000 and 2001 (growth rate in 2001 would have been affected by the underestimation in 2000).

For each candidate model we calculated AIC corrected for small sample size (AIC_c) and delta AIC_c (ΔAIC_c). Candidate models were ranked according to ΔAIC_c where the estimated best model has $\Delta AIC_c = 0$. Values from 0-2 indicate substantial support; 4-7

considerably less support and >10 , essentially no support (Burnham and Anderson 2002). We also calculated AIC_c weights ($AIC_c(w_i)$), the normalized relative likelihood of the model given the data. We included quadratic terms in candidate models to assess the possibility of nonlinear relationships between response and explanatory variables. We included either a linear or quadratic term in the model selection process, using AIC to determine which produced a more plausible model. To avoid spurious results we excluded models that exhibited effects that did not appear ecologically relevant (i.e. the effect of density was positive or the effects of NDVI and /or calf recruitment were negative) from the model selection process (see Ogutu and Owen-Smith, 2003). We visually inspected all quadratic terms and excluded those that resulted in a u- or n-shaped relationship. All analyses were performed in R3.0 (R Core Development Team, 2013).

3. Results

Several response and explanatory variables showed significant linear or quadratic temporal trends during the culling and post-culling eras (Table S.2.1). The most pronounced of these were the significant increasing trends of Kruger-wide and district-specific densities at all time lags following the cessation of culling in 1994 (Fig. 2.2; Table S.2.1).

3.1. Synchrony and relationships between SOI, rainfall and NDVI

Temporal variation in wet season rainfall was highly correlated among the districts of Kruger during our study period (Fig. S.2.1). District-specific variation in wet and dry season NDVI also showed high correlations (Fig. S.2.1). For all three districts of the Park, variation in wet season rainfall was significantly and positively related to fluctuations in wet season SOI (Fig. 2.3; Table S.2.2). Conversely, dry season rainfall was unrelated to dry season SOI (Table S.2.2). District-specific wet season rainfall had a strong, positive and significant influence on both wet and dry season NDVI (Fig. 2.3), whereas dry season rainfall had a negligible effect

on NDVI during that season (Table S.2.2). The above relationships were relatively consistent across the districts of the Park (Fig. 2.3; Table S.2.2).

3.2. Calf recruitment as a function of NDVI and density

During the culling era, synchrony in calf recruitment was high between adjacent districts though low between the north and south (Fig. 2.2). In all instances, seasonal NDVI during the reproductive period best explained variations in district-specific calf recruitment (Table 2.1). District-specific models explained 51%, 86% and 54% of variation in calf recruitment for the northern, central and southern districts respectively (Table 2.1). The explanatory variables in plausible and high ranked models were similar among districts (Table 2.1; Table S.2.3). Though density was included in a few plausible models (Table 2.1; Table S.2.3), it individually explained very little variation in calf recruitment and the effects were not significant (Table 2.2).

After the cessation of culling, synchrony in calf recruitment was high among all three districts of the Park (Fig. 2.2). For the northern and southern districts it was again seasonal NDVI during the reproductive period that best explained variation (53% and 49% respectively) in calf recruitment, and similar variables were observed in plausible and highly ranked models (Table 2.1; Table S.2.3). However, seasonal NDVI components during the first year of life were detected in low ranking models and in the case of the central district were included in the most plausible model, explaining 15% of variation in calf recruitment (Table 2.1). Model stability was low in the central district with a further four plausible models (Table 2.1; Table S.2.3). A significant positive effect of calf recruitment ($t-3$) on calf recruitment (t) was identified in the northern district, coinciding with estimates of calving intervals, and therefore was incorporated as an explanatory variable in all candidate models for that district. Density was not included in plausible models for any district (Table 2.1; Table S.2.3) and again played an insignificant role in a small number of low ranking models (Table 2.2).

3.3. Population growth rate as a function of calf recruitment, NDVI and density

For the culling era, district-specific population growth rates were negatively correlated among all districts (Fig. 2.2). During this period, calf recruitment (t) was included in half of all plausible Kruger-wide and district-specific models, with density ($t-1$) also unexpectedly selected in most models (Table S.2.4). Kruger-wide population growth rates were best explained by the effects of calf recruitment (t), wet season NDVI (t) and density ($t-1$) (Table 2.3). This model explained 93% of variation. A model including only calf recruitment (t) explained 46% of variation in population growth rates (Table 2.3; Table S.2.4). District-specific models were however less stable. Density ($t-1$) explained 45% of variation in northern growth rates, though model uncertainty was high as an additional four models exhibited $\Delta AIC_c < 2$ (Table S.2.4). The only plausible model for central district growth rates included calf recruitment (t) and density ($t-1$) as explanatory variables and explained 89% of the variation (Table 2.3). In the central district, calf recruitment (t) singularly explained 58% of variation in growth rates (Table 2.3). Wet season NDVI (t) explained 33% of variation in growth rates in the southern district with a second plausible model additionally including calf recruitment (t) (Table 2.3; Table S.2.4). The effect of calf recruitment (t) on growth rates was significant in all models during the culling era, while the effect of density ($t-1$) was only significant for the whole of Kruger and the central district (Table 2.3).

During the post-culling era, correlations between the population growth rates of the northern and central, and northern and southern districts were low (Fig. 2.2). There was however, a high negative correlation between central and southern population growth rates (Fig. 2.2). Density ($t-1$) was included in all plausible Kruger-wide and district-specific models, with calf recruitment (t) selected in less than half and singularly explaining very little variation (Table 2.3; Table S.2.4). A model containing only density ($t-1$) best explained Kruger-wide

population growth rates (Table 2.3; Table S.2.4). This model accounted for 30% of variation and a second plausible model, additionally including dry season NDVI (t-1), explained 31% (Table S.2.4). Similar to the Kruger-wide model, density (t-1) best explained population growth rates in the northern district of the Park (Table 2.3). In the central district, the highest ranking model, including dry season NDVI (t-1) and density (t-1), explained 56% of variation in population growth rates and was closely followed by the second ranked model containing only density (t-1) (Table 2.3; Table S.2.4). Density (t-1) was also included in the highest ranking model in the southern district (Table 2.3), with three further plausible models also detected (Table S.2.4). When the years 2000 and 2001 were excluded from analysis, the amount of variation explained by density only increased for the whole of Kruger (45%) and the northern district (39%) (Table 2.3). The effect of density (t-1) on growth rates was negative and significant in all districts during the post-culling era (Table 2.3). Conversely and contrary to the culling era, the effect of calf recruitment (t) was insignificant in all models (Table 2.3). For a general comparative summary of results for the culling and post-culling eras, as well as an era-specific description of management interventions, see Table 2.4.

4. Discussion

Theory advocates that large herbivore populations should respond demographically to spatiotemporal variations in limiting factors (Coulson et al., 2001; Simard et al., 2010). Management actions such as culling and water provisioning can decouple populations from these limitations (see Walker et al., 1987; van Aarde et al., 1999; Loarie et al., 2009; Shrader et al., 2010). Reversing such interventions should reinstate dependence on ecological factors and generate predictable demographic responses (Eberhardt, 2002; Bonenfant et al., 2009). Elephants in the Kruger National Park did indeed respond demographically to the reinstatement of these limitations.

Our results support the work of others and suggest that primary productivity during the reproductive period is particularly important for elephant reproduction (Wittemyer et al., 2007a; Wittemyer et al., 2007b; Trimble et al., 2009). This relationship seems to drive demographic fluctuations in relatively wet savannas (mean annual rainfall > 522mm) but is altered in drier savannas where conditions influencing first year survival seem to take over from fecundity in explaining age structure variations (Trimble et al. 2009). However, contrary to this and our expectations (Fig. 2.1c), NDVI during the reproductive period generally best explained calf recruitment across all districts of Kruger, for both the culling and post-culling eras, regardless of the observed rainfall gradient. Conditions affecting first year calf survival explained limited variation in calf recruitment, and therefore it seems that our measure of calf recruitment served as an index of birth rates across Kruger throughout our study period. Our one outlier, the central district during the post-culling era, may have resulted from the apparent high asymmetric dispersal rates between this area and the southern district that could have masked the relationship.

Our findings also suggest that ENSO, like NAO in the Northern Hemisphere (Hansen et al., 2013), can spatially synchronise components of large herbivore demography in southern Africa. ENSO forcing is strongest during the wet season in southern Africa and therefore primarily influences wet season rainfall (Hulme et al., 2001). The amount of rainfall received during the wet season appears to be both responsible for primary productivity over this period and the retention thereof into the dry season (Marshal et al., 2011). In line with our expectations (Fig. 2.1a, b), wet season SOI influenced wet season rainfall, which in turn explained variation in both wet and dry season NDVI across Kruger. Additionally, our results show that ENSO synchronised wet season rainfall across the districts of Kruger as well as fluctuations in both wet and dry season NDVI. These spatially synchronous temporal variations in NDVI were then largely responsible for the patterns of highly synchronic calf recruitment observed throughout

our study due to the consistent relationship between calf recruitment and NDVI among the districts of Kruger (i.e. explanatory variables of high ranking district-specific models were similar among districts).

Both the reproductive and first year survival components of calf recruitment were independent of density throughout our study. We anticipated this (Fig. 2.1d) as the survival of first year elephant calves is generally independent of seasonal resource availability or density (Young and van Aarde, 2010), except in regions of low rainfall or during droughts (see Foley et al., 2008; Trimble et al., 2009). Moreover, few studies have illustrated density-dependent fecundity in African elephants (but see Laws et al., 1975). This is to be expected, as elephants are a large monotoxic species. Small polytoxic herbivores have greater reproductive potential and, as they can reach and possibly exceed carrying capacities over a shorter time, may generate stronger density-dependent patterns in fecundity (Bonenfant et al., 2009 and references therein). Additionally, density trade-offs that lead to growth and reproductive delays are only likely observed at very high densities (Eberhardt, 2002) and, in the case of elephants, the effects of being born in a year of resource scarcity and/or high density may only be observed through reproductive outputs years later (see Whyte et al., 1998; Lee et al., 2013).

We expected that our index of calf recruitment would incorporate possible density-dependent changes in age at first calving and inter-calving intervals, two reproductive components that play key roles in varying population growth rates (see Whyte et al. 1998; Bonenfant et al., 2009). However, to corroborate the results of our modelling procedure, we tested for differences in these components between the culling and post-culling eras. We found no differences in either component between eras (Table 2.4, S.2.5, S.2.6), supporting our finding that the reproductive component of calf recruitment was independent of density throughout our study.

Density should typically have a stronger effect on population growth rates during periods of elevated density and/or when conditions are harsh (Bonenfant et al., 2009). We found that post-culling population growth rates, for the whole of Kruger and for each district regardless of rainfall, were negatively related to density (t-1). By removing the outlying year 2000, when apparent demographic responses were likely related to extreme weather and undercounting rather than density or resource availability, the effect of density was more pronounced. However, contrary to theory and our predictions (Fig. 2.1e), we also observed density-dependent population growth during the culling era when densities were about half of what they were at the end of our time series. The culling era likely experienced greater levels of resource availability through water supplementation and therefore it is unlikely that the population was density regulated during this time. District-specific growth rates were likely driven by dispersal linked to culling events (van Aarde et al., 1999). However, when we assessed the Kruger-wide population growth rate data during the culling era, we discovered that the effect of density was possibly an artefact of culling. Our data showed a high correlation ($r = 0.62$) between density (t-1) and the number of individuals culled in year t (see Whyte et al., 2003). Subsequently, the population growth rate in year (t) was negatively correlated ($r = -0.45$) with the number of elephants culled in the same year. Therefore, although we took the number of individuals culled into account prior to our modelling process, the effect of culling likely remained. Culling has been revealed to mimic and act in place of density-dependent mechanisms in other large herbivore populations (e.g. White et al., 2007) and this likely occurred in our study.

Supporting our expectations (Fig. 2.1f), calf recruitment was incorporated into both of our most plausible models and singularly explained a large amount of variation in Kruger-wide population growth rates during the culling era. This, along with our findings that calf recruitment was indicative of birth rates and unaffected by density, suggests that population

growth rates in Kruger during the culling era and at low densities were essentially driven by the density-independent reproductive patterns of the population. Similarly, district-specific growth rates were best explained by models incorporating the effects of calf recruitment, though model instability was high likely owing to inter-district dispersal (see van Aarde et al., 1999). Contrastingly, calf recruitment explained little variation in population growth rates during the post-culling era, both for the whole of Kruger and each district. We therefore propose that an increase in density from the culling to the post-culling era led to unmeasured density-dependent demographic parameters (e.g. weaned calf survival, dispersal) primarily driving variation in growth rates rather than density-independent reproduction (see Eberhardt, 2002; Bonenfant et al., 2009).

We found no evidence of density-dependent first year calf survival and in most cases the survival of adults in large herbivore populations tends to be unrelated to density until densities are extremely high or conditions very harsh (Bonenfant et al., 2009). Consequently, the density-dependent survival of calves older than one, and more particularly weaned calves, could have been partly responsible for annual variations in population abundance after culling ended. Young and van Aarde (2010) found that density and primary productivity explained dry season daily-displacement distances of elephant family groups and that these distances influenced the survival of weaned calves. Although annual census records revealed few elephant carcasses in Kruger, the remains of young individuals are likely more difficult to detect from the air than those of adults and are broken down more rapidly by scavengers (Corfield, 1973). Our models align well with those of Young and van Aarde (2010), and therefore we cannot discount the effect of density-dependent weaned calf survival on post-culling growth rates, though the effects may be slight.

Dispersal has been promoted as a primary response of large herbivore and elephant populations to changes in density and resource availability (Chamaillé-Jammes et al., 2008;

Bonenfant et al., 2009; Young et al., 2009). In our study, a few annual fluctuations in abundance narrowly exceeded the theoretical and/or field-observed maximum population growth rates estimated for elephants (Calef, 1988; Moss, 2001), which suggests immigration effects. Furthermore, the high negative correlation of growth rates between the central and southern districts during the post-culling era suggests that large numbers of elephants had the ability to disperse asymmetrically in the Park. In 1993, the fences between Kruger and game reserves to the west of the Park were completely removed. Additionally, in 2002 sections of the fence separating Kruger and the Limpopo National Park in Mozambique were also removed to create the Great Limpopo Transfrontier Park (Venter et al., 2008). Eliminating these physical barriers could have facilitated elephant movement between Kruger and adjacent areas (unpublished telemetry data from the CERU database). Furthermore, mortality events necessary to slow population growth with no effect of emigration likely did not occur in Kruger during our study period (Walker et al., 1987; Whyte et al., 1998). We therefore suggest that the density-dependent growth observed in Kruger from 1998 to 2012, and the effect that dry season NDVI had on it, was primarily indicative of density-dependent and resource-driven dispersal (Chamaillé-Jammes et al., 2008; Young et al., 2009). The interaction between dispersal and weaned calf survival could have conceivably played a role (see Chamaillé-Jammes et al., 2008; Young and van Aarde, 2010).

We appreciate that detailed time series of population age structure and age-specific survival would have enhanced our understanding of density-dependent and -independent processes in Kruger's elephant population (Lande et al., 2006), however such data has only been made available recently (see Ferreira and van Aarde, 2008; Trimble et al., 2011). Furthermore, formal statistical evaluation of census error was not possible from our total counts (but see Ferreira and van Aarde, 2009). We concede that in some circumstances this could lead to spurious results (Freckleton et al., 2006). However, results from our calf recruitment models

align well with those of other studies using different measures in different localities (see Wittemyer et al., 2007a; Wittemyer et al., 2007b; Trimble et al., 2009). Moreover, the relatively short length of our time series, the large proportion of Kruger annually surveyed and the consistent and precise survey methodology employed satisfy us that our results reflect on ecological processes and not sampling errors (Whyte, 2001; Jachmann, 2002; Freckleton et al., 2006; Ferreira and van Aarde, 2009). Solow (2001) further suggests that regressing $\ln(N_t/N_{t-1})$ against N_{t-1} may generate spurious detection of density-dependence. However, we view our use of this method as appropriate as it has been widely used in describing the dynamics of various mammal populations (e.g. Saitoh et al., 1997, 1999, 2008; Wang et al., 2009; Owen-Smith, 2006; White et al., 2007; Marshal et al., 2011; Herrando-Perez et al., 2012), it has previously been used to describe density-dependence in elephant populations (Chamaillé-Jammes et al., 2008), it is the top-ranked model in meta-analyses of large numbers of species (see Brook and Bradshaw, 2006) and has been incorporated in models used in the theoretical development of density feedback (Dennis et al., 2006).

Our study provides evidence that elephants in Kruger responded demographically at the population level to the intended reinstatement of ecological limitations and did so in a manner supported by the literature (see Eberhardt, 2002; Wittemyer et al., 2007a; Wittemyer et al., 2007b; Chamaillé-Jammes et al., 2008; Bonenfant et al., 2009). The primary response was seen as a shift from density-independent reproduction, influenced by NDVI and ENSO, driving population growth rates in the culling era to unmeasured density-dependent demographic parameters taking over after culling ceased and density began to increase. Though not empirically examined, density-dependent dispersal and weaned calf survival are two parameters that possibly contributed to this. There was however also evidence of a legacy effect of management interventions. For instance, we expected the drivers of calf recruitment to differ across Kruger based on the rainfall gradient (see Trimble et al., 2009). This was not the case

and may provide insights into the demographic effects of supplemented water distribution relative to forage rather than the effects of rainfall per se (see Walker et al., 1987; Loarie et al., 2009; Chamaillé-Jammes et al., 2008; Trimble et al., 2009), as a large number of artificial water sources are still present in Kruger. Nevertheless, our work presents encouraging results, not only for ecologists interested in the population dynamics of large and megaherbivores, but also for those tasked with managing elephant populations across southern Africa.

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Figures

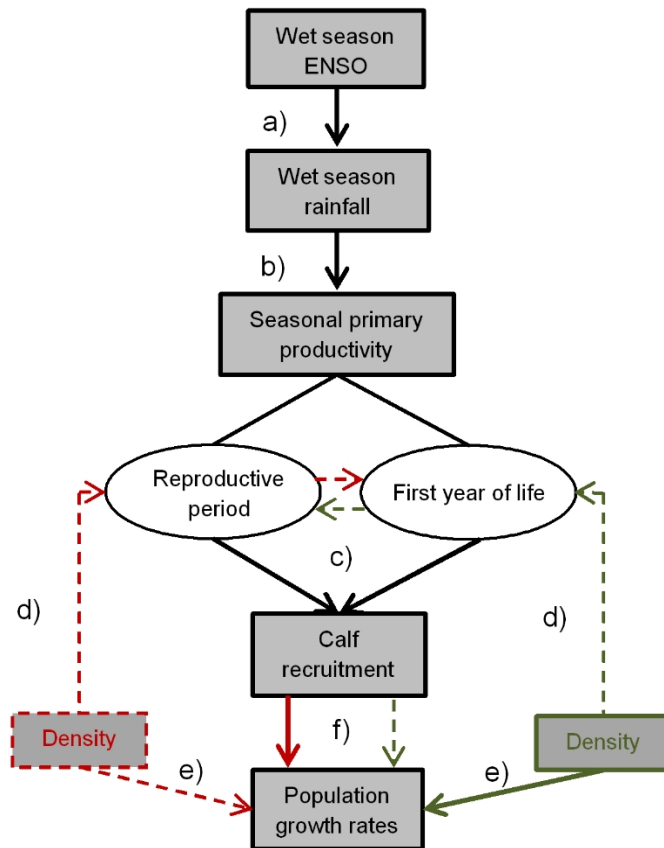


Fig. 2.1. Visual representation of our conceptual framework and expectations. We present era-specific (**culling** and **post-culling**) expectations when we expected differences to occur. Shaded boxes represent explanatory and/or response variables, with solid arrows indicating relationships that we expected to emerge through our model selection process. Circles are periods of influence and dotted lines are relationships that we expected to be weak or non-existent. The direction of arrows indicates the assumed directionality of relationships based on ecological theory. Letters adjacent to arrows refer to literature supporting our framework and expectations.

- a) Hulme et al. (2001).
- b) Rutherford (1980), Hulme et al. (2001).
- c) Depending on rainfall (see Trimble et al. 2009).
- d) Eberhardt (2002), Young and van Aarde (2010).
- e) Bonenfant et al. (2009).
- f) Eberhardt (2002), Chamailé-Jammes et al. (2008), Bonenfant et al. (2009), Young and van Aarde (2010).

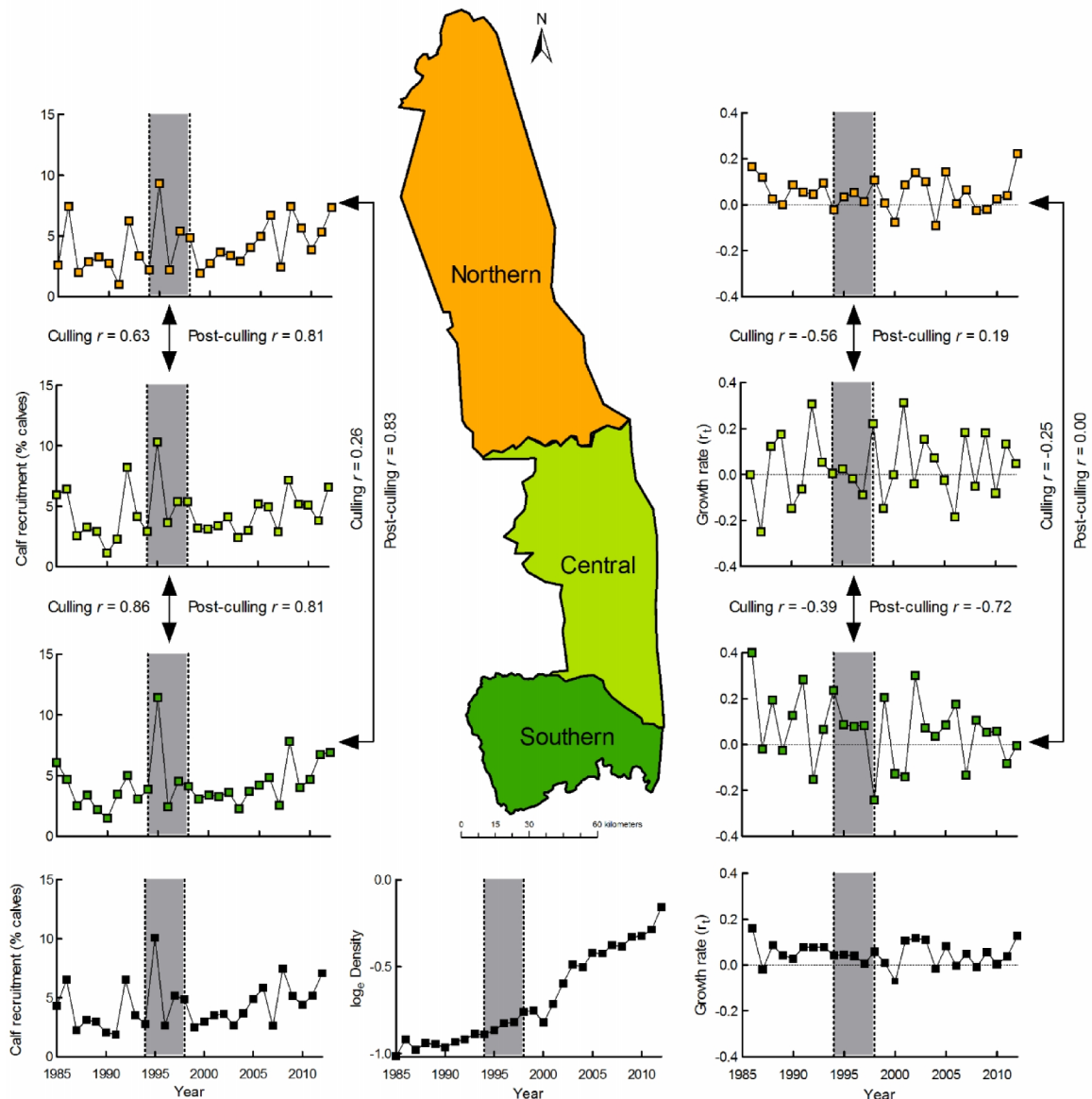


Fig. 2.2. Map of the Kruger National Park with temporal variation in Kruger-wide (below the map) and district-specific calf recruitment (left) and growth rate (r_t) (right) presented. Kruger-wide \log_e density is also presented (below centre). Grey areas separate and provide a three-year buffer between the culling (1985-1994) and post-culling (1998-2012) eras. Values adjacent to the arrows are Pearson correlation coefficients (r) for between district temporal variations in calf recruitment and growth rate for both eras.

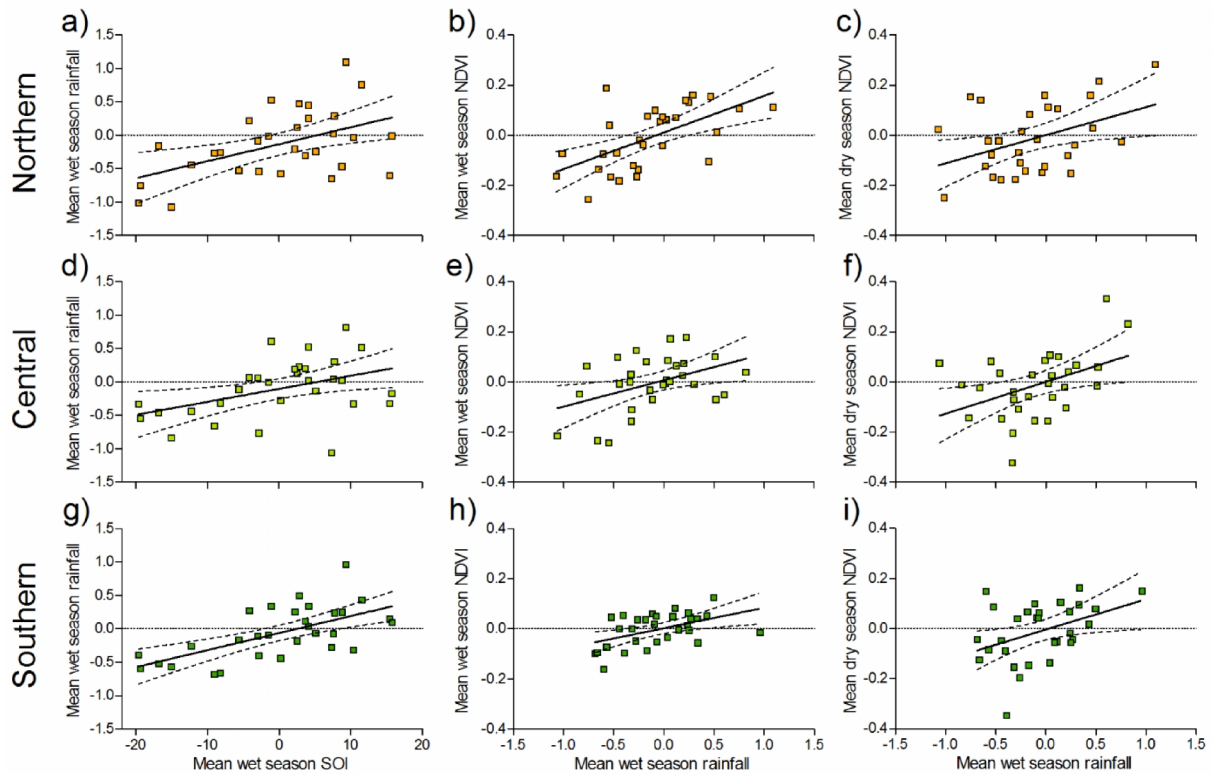


Fig. 2.3. Least-squares linear regressions between mean wet season SOI and mean wet season rainfall (a, d, g), mean wet season rainfall and mean wet season NDVI (b, e, h) and mean wet season rainfall and mean dry season NDVI (c, f, i) for the northern (a, b, c), central (d, e, f) and southern (g, h, i) districts of the Kruger National Park. Rainfall and NDVI were standardized by dividing each value by the mean over the study period (1983 – 2012) and natural logged. Mean wet season SOI was detrended using a linear regression. All regressions were significant ($p < 0.05$). Dashed lines are 95% confidence intervals. For full regression statistics see Supplementary Material (Table S.2.2.).

Tables

Table 2.1. Linear models best explaining variation in calf recruitment during the culling (1985-1994) and post-culling (1998-2012) eras for three districts of the Kruger National Park.

Era	District	Period of interest	Best model	R ²	Number of plausible models
Culling	Northern	Reproductive	Wet NDVI (mean) ²	0.51	3
	Central	Reproductive	Wet NDVI (mean)* + Dry NDVI (mean) + Density (mean)	0.86	1
	Southern	Reproductive	Wet NDVI (mean) ²	0.54	2
Post-culling	Northern ^{1*}	Reproductive	Dry NDVI (t-2)	0.53	2
	Central	First year	Wet NDVI (t)	0.15	5
	Southern ^{**}	Reproductive	Wet NDVI (t-2) ² + Dry NDVI (t-2)	0.49	1

Note: We only show effects where we deemed them ecologically relevant (i.e. density effect was negative, NDVI effect was positive). Quadratic relationships are indicated by a ². The period of interest indicates whether the model represents NDVI and/or density conditions during the first year of life (t) or the reproductive period (t-1; t-2). “mean” represents the mean NDVI and/or density over the reproductive period, including year t-1 and t-2. ¹Included the effect of calf recruitment (t-3). Variables detrended by linear or quadratic regression are indicated by a * or ** respectively. For a complete set of models and selection parameters see Supplementary Material (Table A4).

Table 2.2. Linear model statistics presenting the singular effects of density on calf recruitment during the culling (1985-1994) and post-culling (1998-2012) eras for three districts of the Kruger National Park.

Era	District	Period of interest	Explanatory variable	β	SE	p	R ²
Culling	Northern	Reproductive	Density (t-2)*	-0.05	0.13	0.71	0.02
		Reproductive	Density (mean)*	-0.003	0.06	0.96	0.00
	Central	Reproductive	Density (mean)	-0.08	0.08	0.34	0.15
		Reproductive	Density (t-1)	-0.07	0.06	0.27	0.20
		Reproductive	Density (t-2)	-0.02	0.06	0.71	0.02
	Southern	-	-	-	-	-	-
Post-culling	Northern ^{1*}	Reproductive	Density (t-2)**	-0.04	0.07	0.58	0.19
		Reproductive	Density (mean)**	-0.001	0.09	0.99	0.17
	Central	Reproductive	Density (t-2)*	-0.04	0.04	0.31	0.08
		First year	Density (t)*	-0.03	0.04	0.52	0.03
	Southern**	Reproductive	Density (t-1)*	-0.01	0.03	0.72	0.01

Note: We only show effects where we deemed them ecologically relevant (i.e. negative effects). The period of interest indicates whether the candidate model represents density conditions during the first year of life (t) or the reproductive period (t-1; t-2). “mean” represents the mean density over the reproductive period, including year t-1 and t-2. ¹Included the effect of calf recruitment (t-3). Variables detrended by linear or quadratic regression are indicated by a * or ** respectively. For a complete set of models and selection parameters see Supplementary Material (Table A4).

Table 2.3. Linear model statistics for models best explaining variation in population growth rates during the culling (1985-1994) and post-culling (1998-2012) eras for the Kruger National Park as well as three districts of the Park. Where appropriate, we additionally present the singular effects of density and calf recruitment on variation in population growth rates.

Era	District	Model rank	Explanatory variables	β	SE	p	R ²	Number of plausible models
Culling	Kruger	1	Calf recruitment (t)	1.83	0.55	0.02	0.93	1
			Wet NDVI (t)	0.19	0.11	0.15	-	-
			Density (t-1)*	-0.99	0.29	0.02	-	-
		3	Density (t-1)*	-1.60	0.35	0.002	0.74	-
		6	Calf recruitment (t)	1.87	0.76	0.04	0.46	-
	Northern	1	Density (t-1)	-0.57	0.25	0.07	0.56	5
	Central	1	Calf recruitment (t)	4.11	1.44	0.04	0.89	1
			Density (t-1)	-0.86	0.23	0.02	-	-
		2	Density (t-1)	-1.16	0.31	0.01	0.70	-
	4	Calf recruitment (t)	6.45	2.25	0.03	0.58	-	
Southern	1	Wet NDVI (t)	1.60	0.92	0.14	0.33	2	
	3	Density (t-1)	-0.72	0.91	0.46	0.09	-	
Post-culling	Kruger	1	Density (t-1)**	-0.67 (-0.95)	0.27 (0.31)	0.03 (0.01)	0.30 (0.45)	3
	Northern	1	Density (t-1)**	-0.86 (-1.22)	0.37 (0.42)	0.04 (0.02)	0.29 (0.39)	2
		5	Calf recruitment (t)*	0.65	1.71	0.71	0.01	-
	Central	1	Dry NDVI (t-1)	0.22	0.16	0.20	0.56	2
			Density (t-1)**	-0.98	0.28	0.01	-	-
		2	Density (t-1)**	-1.03	0.29	0.003	0.50	-
	Southern	1	Density (t-1)*	-0.94	0.24	0.002	0.58	4
		7	Calf recruitment**	2.54	3.16	0.44	0.05	-

Note: We only show effects where we deemed them ecologically relevant (i.e. density effect was negative, calf recruitment/NDVI effect was positive). Bracketed values represent results when the years 2000 and 2001 were removed from analysis. Variables detrended by linear or quadratic regressions are indicated by a * or ** respectively. For a complete set of models and selection parameters see Supplementary Material (Table A5).

Table 2.4. General comparative summary of management interventions and drivers of elephant demographic variation during the culling (1985-1994) and post-culling (1998-2012) eras in the Kruger National Park. Additionally, we present era-specific estimates of mean age at first calving and inter-calving interval (see Discussion and Supplementary Material).

		Culling era (1985-1994)	Post-culling era (1998-2012)
Management interventions	Culling	Yes	No
	Water supplementation	Higher	Lower
	Fencing	Complete	Partial
Calf recruitment	¹ Driver of calf recruitment	NDVI during reproduction	NDVI during reproduction
	² Density effect ($p < 0.05$)	No	No
Population growth rates	³ Driver of population growth rates	Calf recruitment	Density
	³ Calf recruitment effect ($p < 0.05$)	Yes	No
	³ Density effect ($p < 0.05$)	Yes (but artefact of culling)	Yes
Supplementary demographic information	⁴ Age at first calving (years)	12.00 (-)	12.28 (10.82 – 14.10)
	⁵ Inter-calving interval (years)	4.13 (2.92 – 5.92)	3.97 (3.79 – 4.23)

Note: For the purpose of simple comparison, we summarise general findings across districts. The values represented are means and ranges (bracketed) over the respective eras for the whole of Kruger. See ¹ Table 2.1, ² Table 2.2, ³ Table 2.3, ⁴ Supplementary Material (Table S.2.5), ⁵ Supplementary Material (Table S.2.6).

Supplementary material

Table S.2.1. Summary of trend identification results performed by regressing variables against year. We only present trends significant at the 95% confidence level in the culling era, post-culling era or both.

District	Variable	Culling era		Post-culling era	
		Trend	p-value	Trend	p-value
Kruger	Calf Recruitment (t)	-	-	Linear	0.02
	Wet season NDVI (t)	Linear	0.05	-	-
	Density (t-1)	Linear	0.03	Quadratic	<0.01
Northern	Calf Recruitment (t)	-	-	Linear	0.02
	Density (t)	-	-	Linear	< 0.01
	Density (t-1)	-	-	Quadratic	< 0.01
	Density (t-2)	Linear	0.05	Quadratic	< 0.01
	Wet season NDVI (Mean)	-	-	Quadratic	< 0.01
	Dry season NDVI (Mean)	-	-	Quadratic	0.01
	Density (Mean)	Linear	0.03	Quadratic	< 0.01
Central	Wet season NDVI (t)	Linear	0.04	-	-
	Dry season NDVI (t)	Quadratic	0.02	-	-
	Density (t)	-	-	Linear	< 0.01
	Wet season NDVI (t-1)	Linear	0.03	-	-
	Density (t-1)	-	-	Quadratic	< 0.01
	Density (t-2)	-	-	Linear	< 0.01
	Wet season NDVI (Mean)	Linear	< 0.01	-	-
Southern	Density (Mean)	-	-	Quadratic	< 0.01
	Calf Recruitment (t)	-	-	Quadratic	0.02
	Density (t)	-	-	Linear	< 0.01
	Density (t-1)	-	-	Linear	< 0.01
	Density (t-2)	-	-	Quadratic	< 0.01
	Density (Mean)	-	-	Quadratic	< 0.01

Note: We fitted both linear and quadratic regressions, assessing which provided a better fit using Akaike's information criterion (AIC). Where a significant ($p < 0.05$) temporal trend was identified, we detrended the time series by replacing the original values with the residuals from the regression against year (Turchin 2003). This method of detrending is appropriate when estimating per capita population growth rates using the equation; $r_t = \ln(N_t/N_{t-1})$ (see Saucy 1994; Simard et al. 2012). Though not shown above, wet season SOI from 1983-2012 exhibited a significant linear trend.

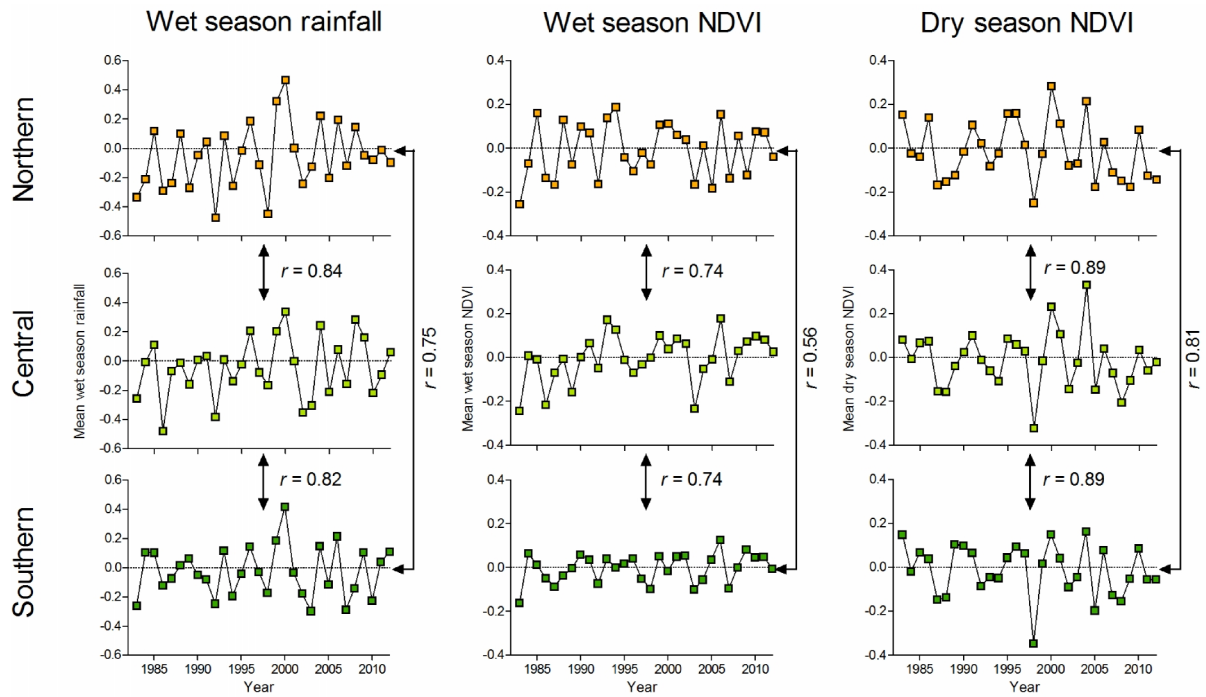


Fig. S.2.1. Temporal variation in district-specific mean wet season rainfall, mean wet season NDVI and mean dry season NDVI. Rainfall and NDVI values were standardized by dividing each value by the mean over the study period (1983 – 2012) and natural logged. Values adjacent to the arrows are Pearson correlation coefficients (r) for between district temporal variations.

Table S.2.2. Summary of least-squares linear regressions between seasonal SOI, rainfall and NDVI for the three districts of Kruger National Park (1983-2012).

District	Regression	Estimate	R ²	F	p
Northern	Wet season rainfall ~ Wet season SOI*	0.03	0.24	9.06	0.01
	Dry season rainfall ~ Dry season SOI	-0.04	0.09	2.94	0.10
	Wet season NDVI ~ Wet season rainfall	0.15	0.36	15.46	<0.01
	Dry season NDVI ~ Dry season rainfall	0.01	0.01	0.19	0.67
	Dry season NDVI ~ Wet season rainfall	0.11	0.17	5.92	0.02
Central	Wet season rainfall ~ Wet season SOI*	0.02	0.19	6.49	0.02
	Dry season rainfall ~ Dry season SOI	-0.03	0.10	3.18	0.09
	Wet season NDVI ~ Wet season rainfall	0.11	0.18	6.23	0.02
	Dry season NDVI ~ Dry season rainfall	0.02	0.01	0.21	0.65
	Dry season NDVI ~ Wet season rainfall	0.13	0.19	6.43	0.02
Southern	Wet season rainfall ~ Wet season SOI*	0.03	0.41	19.11	<0.01
	Dry season rainfall ~ Dry season SOI	-0.03	0.09	2.60	0.12
	Wet season NDVI ~ Wet season rainfall	0.08	0.24	8.70	0.01
	Dry season NDVI ~ Dry season rainfall	0.00	0.00	0.01	0.94
	Dry season NDVI ~ Wet season rainfall	0.12	0.16	5.52	0.03

Note: Regressions significant at the 95% confidence level are indicated in bold. Variables on the left of the ~ are response variables, whereas explanatory variables are on the right. Variables detrended by linear regression are specified by a *.

Table S.2.3. Full linear model selection results relating calf recruitment to seasonal NDVI and density during the a) culling era (1985-1994) and b) post-culling era (1998-2012) for the three districts of the Kruger National Park.

a)

	Rank	Period of interest	Candidate model	AIC _c	ΔAIC _c	AIC _c (wi)	R ²
Northern	1	Reproductive	Wet NDVI (mean)²	-42.94	0.00	0.28	0.51
	2	Reproductive	Wet NDVI (mean)² + Dry NDVI (mean)	-41.09	1.85	0.11	0.53
	3	Reproductive	Wet NDVI (mean)² + Density (mean)*	-41.09	1.85	0.11	0.53
	4	Reproductive	Dry NDVI (mean)	-39.89	3.05	0.06	0.08
	5	Reproductive	Wet NDVI (t-2)	-39.83	3.12	0.06	0.07
	6	Reproductive	Dry NDVI (t-1)	-39.70	3.24	0.06	0.06
	7	Reproductive	Dry NDVI (t-2)	-39.48	3.47	0.05	0.03
	8	Reproductive	Density (t-2)*	-39.41	3.54	0.05	0.02
	9	Reproductive	Wet NDVI (t-1)	-39.23	3.71	0.04	0.00
	10	Reproductive	Density (mean)*	-39.22	3.72	0.04	0.00
	11	Reproductive	Wet NDVI (t-1) + Wet NDVI (t-2)	-38.17	4.78	0.03	0.12
	12	Reproductive	Wet NDVI (t-2) + Dry NDVI (t-2)	-38.12	4.82	0.03	0.11
	13	Reproductive	Dry NDVI (t-1) + Dry NDVI (t-2)	-37.86	5.08	0.02	0.08
	14	Reproductive	Wet NDVI (t-2) + Density (t-2)*	-37.85	5.09	0.02	0.08
	15	Reproductive	Wet NDVI (t-1) + Dry NDVI (t-1)	-37.70	5.24	0.02	0.06
	16	Reproductive	Dry NDVI (t-2) + Density (t-2)*	-37.45	5.49	0.02	0.03
Central	1	Reproductive	Wet NDVI (mean)* + Dry NDVI (mean) + Density (mean)	-45.66	0.00	0.64	0.86
	2	Reproductive	Dry NDVI (mean) + Density (mean)	-43.33	2.34	0.20	0.76
	3	Reproductive	Dry NDVI (t-1) + Density (t-1)	-41.07	4.59	0.06	0.68
	4	Reproductive	Wet NDVI (t-1) + Dry NDVI (t-1) + Density (t-1)	-39.45	6.22	0.03	0.70
	5	Reproductive	Wet NDVI (mean)* + Dry NDVI (mean)	-37.36	8.30	0.01	0.49
	6	Reproductive	Dry NDVI (mean)	-36.51	9.16	0.01	0.27
	7	Reproductive	Wet NDVI (mean)*	-36.13	9.53	0.01	0.23
	8	Reproductive	Wet NDVI (t-1) + Dry NDVI (t-1)	-35.90	9.76	0.00	0.39

9	Reproductive	Dry NDVI (t-2) + Density (t-2)	-35.82	9.84	0.00	0.38	
10	Reproductive	Density (t-1)	-35.79	9.88	0.00	0.20	
11	Reproductive	Dry NDVI (t-1)	-35.64	10.02	0.00	0.18	
12	Reproductive	Wet NDVI (t-1) + Dry NDVI (t-1) + Wet NDVI (t-2) + Dry NDVI (t-2)	-35.60	10.06	0.00	0.62	
13	Reproductive	Dry NDVI (t-2)	-35.54	10.12	0.00	0.17	
14	Reproductive	Density (mean)	-35.32	10.34	0.00	0.15	
15	Reproductive	Wet NDVI (t-1) + Wet NDVI (t-2)	-35.27	10.39	0.00	0.34	
16	Reproductive	Wet NDVI (mean)* + Density (mean)	-35.07	10.60	0.00	0.32	
17	Reproductive	Wet NDVI (t-2)	-34.59	11.08	0.00	0.07	
18	Reproductive	Wet NDVI (t-1)	-34.57	11.09	0.00	0.07	
19	Reproductive	Dry NDVI (t-1) + Dry NDVI (t-2)	-34.46	11.21	0.00	0.27	
20	Reproductive	Density (t-2)	-34.21	11.45	0.00	0.02	
21	Reproductive	Wet NDVI (t-2) + Dry NDVI (t-2)	-34.06	11.60	0.00	0.23	
22	Reproductive	Density (t-1) + Density (t-2)	-33.86	11.81	0.00	0.21	
23	Reproductive	Wet NDVI (t-1) + Density (t-1)	-33.73	11.93	0.00	0.20	
24	Reproductive	Wet NDVI (t-2) + Density (t-2)	-32.54	13.13	0.00	0.07	
<hr/>							
Southern	1	Reproductive	Wet NDVI (mean)²	-48.83	0.00	0.34	0.54
	2	Reproductive	Dry NDVI (t-2)	-48.38	0.44	0.27	0.37
	3	Reproductive	Wet NDVI (t-2)	-46.39	2.43	0.10	0.19
	4	Reproductive	Dry NDVI (mean)	-46.18	2.64	0.09	0.16
	5	Reproductive	Wet NDVI (t-1)	-46.09	2.74	0.09	0.15
	6	Reproductive	Wet NDVI (t-1) + Wet NDVI (t-2)	-45.80	3.02	0.07	0.32
	7	Reproductive	Dry NDVI (t-1)	-44.75	4.08	0.04	0.00

b)

District	Rank	Period of interest	Candidate model	AIC _c	ΔAIC _c	AIC _c (wi)	R ²
Northern*	1	Reproductive	Dry NDVI (t-2)	-89.72	0.00	0.54	0.53
	2	Reproductive	Wet NDVI (t-2) + Dry NDVI (t-2)	-88.81	0.91	0.35	0.56
	3	Reproductive	Wet NDVI (t-2)	-85.29	4.43	0.06	0.37

	4	First year	Wet NDVI (t)	-81.97	7.74	0.01	0.21
	5	Reproductive	Density (t-2)**	-81.72	8.00	0.01	0.19
	6	Reproductive	Wet NDVI (mean)**	-81.57	8.14	0.01	0.19
	7	Reproductive	Dry NDVI (mean)**	-81.45	8.26	0.01	0.18
	8	Reproductive	Density (mean)**	-81.31	8.41	0.01	0.17
	9	Reproductive	Wet NDVI (mean)** + Dry NDVI (mean)**	-79.50	10.21	0.00	0.19
Central	1	First year	Wet NDVI (t)	-82.44	0.00	0.26	0.15
	2	Reproductive	Density (t-2)*	-81.31	1.13	0.15	0.08
	3	Reproductive	Dry NDVI (t-2)	-80.98	1.46	0.13	0.06
	4	Reproductive	Dry NDVI (mean)	-80.59	1.85	0.11	0.04
	5	First year	Density (t)*	-80.55	1.89	0.10	0.03
	6	Reproductive	Dry NDVI (t-2) + Density (t-2)*	-80.17	2.27	0.09	0.13
	7	Reproductive	Dry NDVI (t-1)	-80.05	2.39	0.08	0.00
	8	Reproductive	Dry NDVI (t-1) + Dry NDVI (t-2)	-78.94	3.50	0.05	0.06
	9	Reproductive	Dry NDVI (mean) + Density (mean)**	-78.54	3.89	0.04	0.04
Southern**	1	Reproductive	Wet NDVI (t-2)² + Dry NDVI (t-2)	-89.56	0.00	0.61	0.49
	2	Reproductive	Dry NDVI (t-2)	-86.89	2.67	0.16	0.20
	3	Reproductive	Dry NDVI (mean)	-85.13	4.43	0.07	0.10
	4	Reproductive	Dry NDVI (t-1) + Dry NDVI (t-2)	-84.89	4.68	0.06	0.20
	5	Reproductive	Wet NDVI (t-2) ²	-83.84	5.72	0.04	0.15
	6	First year	Wet NDVI (t)	-83.77	5.79	0.03	0.02
	7	Reproductive	Density (t-1)*	-83.67	5.89	0.03	0.01

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Note: We only included effects into our model selection process where we deemed them ecologically relevant (i.e. density effect was negative, NDVI effect was positive). Quadratic relationships are indicated by a ² whereas variables detrended by linear and quadratic regressions are specified by a * and ** respectively. The period of interest indicates whether the candidate model represents NDVI and/or density conditions during the first year of life (t) or the reproductive period (t-1; t-2). “mean” represents the mean NDVI and/or density over the reproductive period, including year t-1 and t-2. The most plausible models for each district selected according to our selection criteria are shown in bold.

Table S.2.4. Full linear model selection results relating population growth rate to calf recruitment, seasonal NDVI and density during the a) culling era (1985-1994) and b) post-culling era (1998-2012) for the Kruger National Park as well as the three districts of the Park.

a)

District	Rank	Candidate model	AIC _c	ΔAIC _c	AIC _c (wi)	R ²
Kruger	1	Calf recruitment (t) + Wet NDVI (t) + Density (t-1)*	-42.98	0.00	0.72	0.93
	2	Calf recruitment (t) + Density (t-1)*	-40.84	2.14	0.25	0.88
	3	Density (t-1)*	-35.93	7.06	0.02	0.74
	4	Calf recruitment (t) + Wet NDVI (t)*	-34.40	8.58	0.01	0.76
	5	Dry NDVI (t-1) + Density (t-1)*	-33.92	9.06	0.01	0.74
	6	Calf recruitment (t)	-29.27	13.71	0.00	0.46
	7	Wet NDVI (t)*	-23.68	19.30	0.00	0.00
Northern	1	Density (t-1)	-25.54	0.00	0.22	0.45
	2	Dry NDVI (t-1) + Density (t-1)	-25.23	0.31	0.19	0.56
	3	Wet NDVI (t) + Dry NDVI (t-1) + Density (t-1)	-24.17	1.36	0.11	0.61
	4	Dry NDVI (t-1)	-24.13	1.41	0.11	0.35
	5	Calf recruitment (t) + Density (t-1)	-23.93	1.61	0.10	0.48
	6	Wet NDVI (t) + Density (t-1)	-23.51	2.03	0.08	0.46
	7	Calf recruitment (t) + Wet NDVI (t) + Dry NDVI (t-1) + Density (t-1)	-23.17	2.37	0.07	0.66
	8	Calf recruitment (t) + Dry NDVI (t-1) + Density (t-1)	-23.16	2.37	0.07	0.56
	9	Calf recruitment (t) + Wet NDVI (t) + Density (t-1)	-22.82	2.71	0.06	0.54
Central	1	Calf recruitment (t) + Density (t-1)	-15.06	0.00	0.91	0.89
	2	Density (t-1)	-9.37	5.70	0.05	0.70
	3	Dry NDVI (t-1) + Density (t-1)	-8.13	6.94	0.03	0.73
	4	Calf recruitment (t)	-6.70	8.36	0.01	0.58
Southern	1	Wet NDVI (t)	-5.99	0.00	0.42	0.33
	2	Calf recruitment (t) + Wet NDVI (t)	-4.22	1.77	0.17	0.35
	3	Density (t-1)	-3.55	2.44	0.12	0.09

4	Calf recruitment (t) + Density (t-1)	-3.16	2.83	0.10	0.26
5	Calf recruitment (t) + Wet NDVI (t) + Density (t-1)	-2.33	3.66	0.07	0.37
6	Dry NDVI (t-1) + Density (t-1)	-1.51	4.48	0.04	0.09
7	Calf recruitment (t) + Dry NDVI (t-1) + Density (t-1)	-1.45	4.55	0.04	0.30
8	Calf recruitment (t) + Wet NDVI (t) + Dry NDVI (t-1) + Density (t-1)	-0.25	5.75	0.02	0.37

b)

District	Rank	Candidate model	AIC _c	ΔAIC _c	AIC _c (w _i)	R ²
Kruger	1	Density (t-1)**	-43.34	0.00	0.42	0.30
	2	Dry NDVI (t-1) + Density (t-1)**	-41.52	1.82	0.17	0.31
	3	Calf recruitment (t)* + Density (t-1)	-41.40	1.94	0.16	0.31
	4	Dry NDVI (t-1)	-41.06	2.27	0.14	0.19
	5	Calf recruitment (t)* + Dry NDVI (t-1) + Density (t-1)**	-39.55	3.79	0.06	0.32
	6	Calf recruitment (t)* + Dry NDVI (t-1)	-39.01	4.33	0.05	0.19
Northern	1	Density (t-1)**	-30.99	0.00	0.51	0.29
	2	Calf recruitment (t)* + Density (t-1)**	-29.71	1.28	0.27	0.33
	3	Dry NDVI (t-1)	-28.13	2.86	0.12	0.14
	4	Calf recruitment (t)* + Dry NDVI (t-1)	-26.30	4.69	0.05	0.16
	5	Calf recruitment (t)*	-25.99	5.00	0.04	0.01
Central	1	Dry NDVI (t-1) + Density (t-1)**	-21.04	0.00	0.50	0.56
	2	Density (t-1)**	-20.97	0.07	0.49	0.50
	3	Dry NDVI (t-1)	-12.63	8.41	0.01	0.13
Southern	1	Density (t-1)*	-21.25	0.00	0.36	0.53
	2	Wet NDVI (t) + Density (t-1)*	-20.86	0.39	0.30	0.58
	3	Calf recruitment (t)** + Density (t-1)*	-19.88	1.38	0.18	0.55
	4	Calf recruitment (t)** + Wet NDVI (t) + Density (t-1)*	-19.34	1.91	0.14	0.60
	5	Wet NDVI (t)	-14.48	6.77	0.01	0.27
	6	Calf recruitment (t)** + Wet NDVI (t)	-12.90	8.35	0.01	0.29

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7	Calf recruitment (t)**	-10.56	10.69	0.00	0.05
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Note: We only included effects into our model selection process where we deemed them ecologically relevant (i.e. density effect was negative, calf recruitment/NDVI effect was positive). Variables detrended by linear and quadratic regressions are specified by a * and ** respectively. The most plausible models for each district selected according to our selection criteria are shown in bold.

Table S.2.5. Age at first calving estimates for the culling and post-culling eras, collected from culled individuals or through Rapid Elephant Population Assessments (REPAs), in the Kruger National Park.

Year	Era	Age at first calving	
		(years)	Source
1970 - 1974	Culling	12.00	Smuts, 1975
2004	Post-culling	14.10	REPA
2009	Post-culling	10.83	REPA
2010	Post-culling	11.66	REPA
2011	Post-culling	12.53	REPA
Mean (SD)	Culling	12 (-)	
	Post-culling	12.28 (1.21)	

Note: As we only had one value for mean age at first calving during the culling era, we were not able to test for statistical differences between the two eras. However, a difference likely did not exist. Though the Smuts (1975) estimate does not fall directly into our study period, it reflects on age at first calving during the culling era (see Whyte, 2001). For details on REPA protocol and age at first calving calculations see Ferreira and van Aarde (2008) and Trimble et al (2011).

Table S.2.6. Inter-calf interval estimates during the culling and post-culling eras, collected from culled individuals or through Rapid Elephant Population Assessments (REPAs), in the Kruger National Park.

Year	Era	Inter-calf interval	
		(years)	Source
1985	Culling	2.92	Freeman et al., 2009
1987	Culling	4.82	Freeman et al., 2009
1989	Culling	4.02	Freeman et al., 2009
1990	Culling	5.92	Freeman et al., 2009
1991	Culling	3.77	Freeman et al., 2009
1992	Culling	4.78	Freeman et al., 2009
1993	Culling	3.89	Freeman et al., 2009
1994	Culling	2.92	Freeman et al., 2009
2004	Post-culling	3.94	REPA
2009	Post-culling	4.23	REPA
2010	Post-culling	3.92	REPA
2011	Post-culling	3.79	REPA
Mean (SD)	Culling	4.13 (0.95)	
	Post-culling	3.97 (0.16)	

Note: An unpaired t-test indicated that mean calving intervals did not differ significantly between the culling and post-culling eras ($t = 0.31$; $p = 0.77$). For details on REPA protocol and calving interval calculations see Ferreira and van Aarde (2008) and Trimble et al (2011).

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Chapter 3. Changes in elephant conservation management promote density-dependent habitat selection in the Kruger National Park

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Abstract

In conservation, adaptive management relies on the assessment of past management actions to improve conservation efficiencies in the future. Recently, conservation management approaches for African elephants (*Loxodonta africana*) changed. However, little has been done to assess the effectiveness of the changes. Traditionally, the management of elephants focused on numbers. Of late, and specifically in the Kruger National Park, the focus has progressed to promoting ecological processes that may naturally regulate elephant populations. Density-dependent habitat selection, indicative of competition for resources, is fundamental in stimulating the regulatory processes that managers aim to promote. In this paper, we evaluated how effective the changes in Kruger's elephant management approach were in promoting density-dependent habitat selection. We used aerial surveys and resource selection functions (RSFs) to test our primary prediction that an increase in population density following the cessation of culling generalized habitat selection by elephants in Kruger. As densities increased, female occupancy of the Park rose and selection of woody cover, an important

resource for female elephants, generalized during the dry season. Conversely, density had little effect on the selection of rivers. Rather, high dry season rainfall allowed female elephants to select areas farther from permanent water. The effects of density and rainfall on habitat selection varied among the districts of the Park that exhibit different habitat characteristics and rainfall regimes. Our novel identification of fine-grain density-dependent habitat selection for elephants suggests that the conservation management change in Kruger was effective in promoting a potential driver of population regulation.

1. Introduction

We need to know which conservation management approaches were effective in the past if we are to improve future endeavours (Pullin and Knight, 2001). Ideally, we should scientifically evaluate how effective previous approaches were in reaching objectives and base future decisions on the resulting evidence (Pullin et al., 2004). By doing so, we may progress the basis for conservation management decision-making from personal opinions and interdisciplinary interpretations towards a scientific foundation (see Pullin et al., 2004). Historically, personal opinions and agricultural insights dominated conservation management approaches for African elephants (*Loxodonta africana*) (see van Aarde et al., 2006; van Aarde and Jackson, 2007; Young and van Aarde, 2011). More recently, approaches changed and managers started to place ecological theory at the centre of management decisions (van Aarde and Jackson, 2007). Although elephants are a well-studied species (see Trimble and van Aarde, 2010), we lack comprehensive studies that examine the effectiveness of the changes in their management.

Early management of elephants focused primarily on manipulating numbers (Pienaar and van Niekerk, 1963; Hanks et al., 1981; Whyte et al., 1998). Managers supplemented water across landscapes in an attempt to increase numbers (Pienaar and van Niekerk, 1963; Davidson, 1967) and buffer populations against the possible negative effects of droughts (Pienaar, 1983). As anticipated, numbers began to rise as elephants responded demographically to the increased

availability of a limiting resource (van Aarde and Jackson, 2007; Shrader et al., 2010). In some areas, management then viewed relatively high densities as detrimental to the conservation of other species (see Owen-Smith, 1996). Culling, contraception and translocation became attractive options to artificially reduce and stabilise elephant populations at densities lower than those dictated by locally available resources (van Aarde et al., 1999; van Aarde and Jackson, 2007). More recently, some managers have begun to focus on ecological rather than agricultural paradigms. In these cases, managers have increased the area available to elephants by dropping fences, resources are being limited through artificial water source removals and numbers are allowed to fluctuate naturally and are not controlled by culling. The focus of elephant conservation management has therefore changed from manipulating elephant numbers artificially to promoting ecological processes that may regulate numbers naturally (Owen-Smith et al., 2006; van Aarde and Jackson, 2007).

The most prominent and contentious example of this changing focus likely occurred in the Kruger National Park, South Africa. From 1967 to 1994, Kruger managers culled 14 629 elephants to stabilise the population at a whimsically estimated 7000 individuals in an attempt to reduce the presumed negative effects of high densities on vegetation (van Aarde et al., 1999). During this time, approximately 300 artificial waterholes were established across the Park and, by 1976, Kruger was fully fenced and dispersal movement restricted. Thereafter, following public protest informed by science-based advocacy, culling ceased and elephant densities more than doubled from 0.40 in 1995 to 0.83 elephants/km² in 2012. This numerical response occurred despite managers removing more than half of artificial waterholes and dropping some fences between 1993 and 2002. Although science-based objectives ultimately supported the sometimes seemingly haphazard changes in management (see Owen-Smith et al., 2006), little has been done to directly evaluate how effective the changes were in achieving the desired outcomes.

A central ecological objective was to promote density-dependent processes that could regulate the elephant population with limited human interference. A process that is fundamental in promoting such a scenario is density-dependent habitat selection, suggestive of intraspecific competition for resources (see Owen-Smith et al., 2006; Bonenfant et al., 2009). Theory advocates that at low population densities, animals distribute themselves across landscapes relative to high quality habitats that provide optimal fitness returns (Fretwell and Lucas, 1969). As population densities rise, intraspecific competition strengthens and per capita availability of high quality habitats decreases (Fretwell and Lucas, 1969). Consequently, some individuals in a population redistribute into lower quality habitats, proximity of individuals to one another changes (see McLoughlin et al., 2010) and habitat selection becomes more generalized (see van Beest et al., 2014a; b). This may negatively influence individual fitness (McLoughlin et al., 2006; 2008) and ultimately contribute to population regulation through changes in survival and fecundity (see Morris, 1988; 2003).

Here, we evaluate how effective the changes in Kruger's elephant management approach were in promoting density-dependent habitat selection, a key promoter of population regulation. We used annual dry season aerial surveys from 1998 to 2012 and resource selection functions (RSFs) (see Manly et al., 2002; McLoughlin et al., 2010) to test the primary theoretical prediction that a two-fold increase in population density generalized fine-grain habitat selection by elephants (i.e. decreased selection of high quality habitat and increased selection of lower quality habitat) (Fretwell and Lucas, 1969; van Beest et al., 2014a; b). As few studies have quantified fitness returns of specific habitats for elephants, we assumed that habitat selection at low densities would be indicative of high quality habitats for elephants (Fretwell and Lucas, 1969). We included two key factors that influence elephant habitat selection across southern Africa, namely woody vegetation cover and permanent water in the form of rivers (see Roever et al., 2012 and references therein). We assessed how changes in

population density, as well as rainfall, influenced temporal variation in fine-grain habitat selection, recognising that density seldom operates in isolation (see Mobæk et al., 2009; McLoughlin et al., 2010). We expected that as densities increased, elephants would make use of a greater area of Kruger (see Young et al., 2009) and selection would generalize (Fretwell and Lucas, 1969; van Beest et al., 2014a; b). We further expected to find a functional response to temporal changes in rainfall, and specifically that increased rainfall would lead to selection farther from rivers (see Redfern et al., 2003; Chamaillé-Jammes et al., 2008; Smit and Ferreira, 2010). Finally, we anticipated that a density-dependent effect would be less evident in the southern compared to the northern and central districts of the Park due to the prevailing steep rainfall gradient (Gertenbach, 1980). We reasoned that the relatively high mean woody cover and low mean distance to rivers would potentially buffer selection against variation in density in the south (see Mobæk et al., 2009).

2. Material and methods

2.1. Study site

The Kruger National Park covers approximately 19 485km² in the northeastern corner of South Africa. The northern, central and southern districts of the Park lie along a gradient of increasing rainfall from north (receiving an annual average of 450 mm) to south (750 mm) (Gertenbach, 1980), and show differences in dominant vegetation types (Gertenbach, 1983; Kiker et al., 2014). Mean distance to rivers is lowest and spatially least variable in the south (4939m ± 3568m), followed by the central (5633m ± 4548m) and northern (7395m ± 6152m) districts respectively (also see Fig. 3.1). Mean woody cover is highest and varies the least across space in the southern district (40.11% ± 6.34%); while the northern (33.86% ± 12.05%) and central (33.19% ± 11.53%) districts are relatively similar (also see Fig. 3.1).

2.2. Elephant population surveys

We used annual elephant surveys from 1998 to 2012 to estimate elephant locations and population density in Kruger. These aerial surveys occurred during the dry season when visibility was highest and the near-total coverage of Park ensured accurate and precise population estimates (see Whyte, 2001; Ferreira and van Aarde, 2009). Observers in fixed-wing aeroplanes or helicopters recorded elephant locations and whether elephants were in a bull group or female dominated breeding herd. For simplicity, we differentiate between bull groups and female dominated breeding herds as “males” and “females” respectively.

2.3. Spatial scale and habitat covariates

We divided Kruger into 5km² grid-cells (see Fig. 3.1). We chose this scale as it represents estimates of the mean area used daily by elephants in the Park (unpublished data from the CERU telemetry database). Considering that the temporal scale of the survey only allowed us to estimate a habitat selection “snap shot” based on once-off location data, this spatial scale seemed the most appropriate for a highly mobile herbivore (see Young et al., 2009). Grid-cells of 5km² also allowed us to capture heterogeneity in the landscape, which would have likely been overlooked if we used larger grid-cells (e.g. 100-400km², representing variability in dry season home range sizes) (Boyce, 2006; Young et al., 2009).

Elephants are water-dependent. Therefore, we used distance to large perennial, and seasonal rivers as a covariate in estimating habitat selection (see Fig. 3.1) (see Smit and Ferreira, 2010). We additionally used estimations of woody vegetation cover (Bucini et al., 2010). The percentage woody cover layer incorporated elements of vegetation productivity and structure (see Bucini et al., 2010), making it a good index of both forage and shade availability (see Fig. 3.1). Various studies have reported that these variables have strong influences on elephant habitat selection across southern Africa (Harris et al., 2008; Loarie et al., 2009a; Roever et al., 2012; 2013). Furthermore, with prospective links between habitat selection and

density-dependent population regulation in mind, we focused on covariates that appear to drive variation in a number of components of elephant demography (i.e. calf survival, fecundity and dispersal) (see Wittemyer et al., 2007; Chamaillé-Jammes et al., 2008; Young and van Aarde, 2010). We were unable to use distance to waterholes as a habitat covariate (see below).

2.4. Validating the accuracy of aerial survey location data

Aerial surveys may be susceptible to habitat sightability biases that can result in inaccurate estimates of habitat selection (Pollock and Kendall, 1987). To validate the accuracy of our aerial survey data, we compared habitat-use estimated using this data to habitat-use estimated using telemetry data (see van Beest et al., 2014a). During the dry season (June to September inclusive) of 2012, 26 collared female elephants, each representing separate herds spread across Kruger, provided us with hourly location data. A dry season aerial survey was also performed in 2012. We included all daytime telemetry locations during the dry season to assess whether the female habitat-use “snapshot” estimated using aerial survey data was indicative of habitat-use across the season (see van Beest et al., 2014a). As our habitat covariates were continuous, we divided each into equally sized bins (distance to rivers = 2000m bin width; percentage woody cover = 5% bin width) and estimated habitat-use as the percentage of occupied 5km² grid-cells in each bin for aerial survey and telemetry data separately (see Fig. 3.2). We then tested if habitat-use was significantly different between the two data sources using a Wilcoxon matched-pairs signed rank test.

2.5. Estimating habitat selection

We used resource selection functions (RSFs) to separately estimate female and male dry season habitat selection for each year from 1998 to 2012 ($n = 15$). We calculated RSFs for the whole Park, and separately for the northern, central and southern districts (see Study Site). Our analyses matched most closely with a population-level use-availability sampling design (see

Thomas and Taylor, 2006). We specified a grid-cell as used (1) when ≥ 1 elephant was observed in that cell during the survey. For each year, we randomly drew available cells (0) from all cells throughout Kruger or the appropriate district. The ratio of used cells: available cells was 1:1.

Within a logistic regression model, we related used (1) and available (0) cells to mean percentage woody cover and distance to rivers in that cell. The purpose of the RSFs were not necessarily to determine the best-fit model but rather to estimate β coefficients that we could relate to changes in population density. Therefore, we ran full models throughout the procedure. We evaluated the predictive success of each model using k-fold cross-validation ($k = 5$) and the Spearman rank correlation coefficient (see Boyce et al., 2002). All RSFs were calculated using R (R Development Core Team, 2013).

From 1998 to 2012, management in Kruger actively reduced the number of borehole-fed waterholes by approximately 65% (see Fig. S.3.1). The exact timing and locality of closures were however unavailable, therefore distance to waterholes could not be included as a covariate in all of our RSFs. To determine whether our habitat selection estimates independent of waterholes were appropriate, we included distance to waterholes in RSFs when the data were available (1998, 2011 and 2012). We then compared the original models to the models including distance to waterholes by calculating the change in AIC, percentage difference in β coefficients for percentage woody cover and distance to rivers, and the β coefficient and significance of the distance to waterholes effect. We did this separately for female and male elephants, for the whole of Kruger and each district, and found that only female habitat selection estimates were unaffected by distance to waterholes (see Results; Smit et al., 2007). Therefore, we excluded male elephant habitat selection estimates from subsequent analyses and discussion.

2.6. Assessing the influence of density and rainfall on habitat selection

Generalized additive models (GAMs) were used to relate changes in female β coefficients for each habitat covariate (response variable) to variations in population density, mean core dry season rainfall (June to September inclusive) and mean core wet season rainfall (December to March inclusive) (explanatory variables). For this, we used monthly rainfall estimates from 30 rainfall stations across Kruger. We calculated separate GAMs for the whole of Kruger and for each district. We observed that the RSF from 2007 was an outlier (see Table S2) and excluded it from subsequent analyses. Additionally, we removed the year 2000 as the abnormally high wet season rainfall and the high retention of vegetative cover into the proceeding dry season likely resulted in an underestimation of elephant numbers (see Whyte, 2001). For each candidate model we calculated AIC corrected for small sample size (AIC_c) and delta AIC_c (ΔAIC_c). Candidate models were ranked according to ΔAIC_c where the estimated best model has $\Delta AIC_c = 0$. Values from 0-2 indicate substantial support; 4-7 considerably less support and >10 , essentially no support (Burnham and Anderson, 2002). All GAMs were calculated in R (R Core Development Team, 2013) using the `mgecv` package (Wood, 2014).

3. Results

3.1. Aerial survey validation and grid-cell occupancy

We did not find a significant difference between habitat-use estimated using aerial survey and telemetry data (woody cover: Wilcoxon $p = 0.97$, $r_s = 0.98$; distance to rivers: Wilcoxon $p = 0.23$, $r_s = 0.98$) (Fig. 3.2). Therefore, we considered habitat-use estimates using aerial survey data to be indicative of habitat-use throughout the dry season, with no biases introduced due to habitat-specific sightability issues. Female occupancy of grid-cells increased with density at the Kruger-wide scale as well as in each district (Fig. 3.3). Occupancy increased linearly with density for the whole Park and the central and southern districts, whereas a quadratic

relationship indicated a slight levelling-off of occupancy at high densities in the north (Fig. 3.3). At high densities, occupancy was highest in the southern district, followed by the central and northern (Fig. 3.3).

3.2. Habitat selection estimates

Comparisons between the original models and the models including distance to waterholes showed that female habitat selection was mostly uninfluenced by the inclusion (see Table S.3.1). Conversely, distance to waterholes had a strong effect on male selection (see Table S.3.1). It was for that reason that we excluded estimates of male elephant habitat selection from our paper and viewed female habitat selection estimates independent of waterholes as appropriate. The majority of our habitat selection models provided good predictability, though this varied among years and districts (Table S.3.2). Mean β coefficients for woody cover and distance to rivers were highest in the southern district (Table S.3.2). Variability in β coefficients for both covariates also differed, with female elephants in the southern district showing higher variability in selection among years (Table S.3.2).

In general and relative to availability, female elephants selected for areas with a high percentage of woody cover (Table S.3.2; see Fig. 3.4 for an example). However, GAMs revealed that density influenced woody cover selection at the Kruger-wide and district-specific scales (Table 3.1). For the whole of Kruger and the northern district, increasing density led to a significant linear decrease in selection for high woody cover (Fig. 3.5a, b). The models explained 47% and 68% of variation respectively, with no other plausible models (Table 3.1). The model best explaining variation in woody cover selection in the central district showed that an increase in mean wet season rainfall resulted in an increase in selection for high woody cover (Table 3.1). The model containing density closely followed and explained 57% of variation (Table 3.1). It showed that as density increased, selection for high woody cover decreased significantly to a point and then increased slightly (Fig. 3.5c). Model stability was

low in the southern district with four plausible models (Table 3.1). However, the best model again incorporated density and explained 27% of variation in selection for woody cover, and was closely followed by the null model (Table 3.1). As in the Kruger-wide and northern district models, an increase in density resulted in a linear decrease in selection for high woody cover (Fig. 3.5d), though the effect was not significant.

Across all districts, female elephants showed a general tendency to select for areas relatively close to rivers (Table S.3.2; see Fig. 3.4 for an example). Density was largely unimportant in explaining variation in selection for rivers among years (Table 3.2). Instead, for the whole Park, the central district and the southern district, mean dry season rainfall was incorporated in the best GAMs (Table 3.2). In the Kruger-wide and central district models, selection for areas close to rivers stayed constant at low to intermediate levels of dry season rainfall, after which it decreased (or selection of areas relatively far from rivers increased) (Fig. 3.6a, c). These models explained 53% and 64% of variation respectively and the effects were significant (Table 3.2). In the southern district, mean dry season rainfall explained 62% of variation, with selection for areas far from rivers increasing linearly and significantly with mean dry season rainfall (Fig. 3.6d). A second plausible model, additionally including mean wet season rainfall, explained 73% (Table 3.2). The null model was returned as the only plausible model for the northern district (Table 3.2).

4. Discussion

Our “snapshot” estimates of female elephant habitat selection in the Kruger National Park confirmed what we expected to find; female elephants select areas relatively close to water and with high woody cover (see Harris et al., 2008; Loarie et al., 2009a; Roever et al., 2012; 2013). However, in this study, we show that habitat selection, and specifically selection for woody cover, was clearly density-dependent in Kruger. This suggests that changes in conservation

management approaches for elephants in Kruger were effective in achieving at least some of the ecological objectives set by management.

As per our predictions, and following on from the work of Young et al. (2009), female elephant occupancy increased with density in Kruger, although not uniformly across the three districts. This provided an initial indication of density-dependent habitat selection (see Matthyssen, 2005), as some individuals had to redistribute into previously unoccupied areas as density increased. A more compelling finding suggesting density-dependent habitat selection was that an increase in Kruger-wide and district-specific densities also led to a generalization in woody cover selection and land use. At low densities, female elephants across all districts were able to select for areas with a relatively high percentage of woody cover. As densities increased, some female elephants redistributed into areas of lower woody cover and woody cover selection became more diffuse through the landscape. As with occupancy, this did not occur equally across Kruger. The effect of density was insignificant and explained limited variation in the relatively woody southern district. Elephants in the south increased occupancy in response to increasing density as seen in the other districts. However, they may have been able to redistribute into previously unoccupied areas of high woody cover in this relatively woody district. As such, density-dependent woody cover selection was less evident in the southern compared to the northern and central districts of Kruger. This spatial difference may operate in the same way that temporal variation in resource availability can influence the strength of intraspecific competition (suggested in Mobæk et al., 2009). Moreover, we could not account for potential district-specific differences in diet (Codron et al., 2011), species-specific feeding in the heterogeneous southern district (Loarie et al., 2009a) or possible changes in woody cover (Buitenwerf et al., 2012). Nonetheless, the generalization in woody cover selection suggests a novel identification of fine-grain density-dependent habitat selection for elephants that is in line with ecological theory and the objectives of Kruger management.

Woody vegetation constitutes an important resource for female elephants. Elephants switch from a grass-dominated diet in the wet season to a browse-dominated diet in the dry (Cordon et al., 2011; Shannon et al., 2013). During this critical period, woody vegetation may provide nutrients to sustain pregnancy and to recover from parturition events (Wittemyer et al., 2007) and can influence the survival of weaned calves by determining the distance of foraging trips by breeding herds (Young and van Aarde, 2010). Conceptually, a density-dependent generalization in woody cover selection could then have demographic consequences for elephants. Subsequently, this could promote population regulation, the intended outcome of the changes in conservation management in Kruger. It is a logical step that future research should therefore seek to establish empirically the linkages between density-dependent habitat selection, demographic variation (see McLoughlin et al., 2006; 2008), and ultimately, population regulation.

Unlike selection for woody cover, the selection of rivers was surprisingly unrelated to changes in density (see Smit and Ferreira, 2010). Instead, for Kruger and the central and southern districts, the amount of rainfall received during the dry season explained the strength of selection for areas close to rivers. We found that an increase in mean dry season rainfall led to female elephants increasingly selecting for areas farther from rivers (negative β coefficients increased; see Fig. 6). In Kruger, intermittent dry season rainstorms can result in water sources forming independent of large rivers, possibly in smaller rivers and drainage lines (see Redfern et al., 2003; Smit and Ferreira, 2010). Although these temporary water points may only be present for a few days, they can still influence the dry season distribution of large, mobile herbivores such as elephants (see Western, 1975; Trash and Derry, 1999; Redfern et al., 2003; Smit and Ferreira, 2010). High dry season rainfall may extend key-resource areas farther from permanent surface-water, temporarily lifting normal dry season foraging restrictions (see Illius and O'Connor, 2000; Chamaillé-Jammes et al., 2008) and allowing female elephants to imitate

their wet season selection patterns (see Roever et al., 2012). Although unrelated directly to changes in density, variation in dry season river selection may modify the strength of density-dependence by varying local forage availability and aggregation around key-resource areas (see Chamaillé-Jammes et al., 2008). Future studies should therefore consider the effects of density and rainfall, and interactions between them, on elephant habitat selection at a scale finer than the population-level assessment used here (e.g. McLoughlin et al., 2006).

Initial conservation management decisions to fence Kruger, supplement water in relatively dry areas and stabilize the elephant population through culling affected elephant movement patterns and decoupled demographic variation from ecological limitations (see Walker et al., 1987; van Aarde et al., 1999; Loarie et al., 2009b; Shrader et al., 2010). For example, the Kruger elephant population continued to grow despite a severe drought from 1981 to 1983, while the mortality rate of other large herbivore populations increased markedly (Walker et al., 1987). Density-dependent processes were likely absent during that period as managers capped the elephant population well below any realistic ecological carrying capacity (see Walker et al., 1987; Owen-Smith et al., 2006). Furthermore, supplemented water likely alleviated natural foraging restrictions, allowing these highly mobile herbivores to access remote foraging areas (see Loarie et al., 2009b) and avoid local crowding that may occur during dry phases (see Owen-Smith et al., 2006; Chamaillé-Jammes et al., 2008). The agricultural and manipulative focus of past management approaches then resulted in a number of ecological irregularities, and carried additional financial burdens and social controversies (see van Aarde and Jackson, 2007).

Changes in conservation management approaches during the mid-1990s made theoretical sense. In particular, ecological theory suggested that density-dependent processes would ultimately regulate the population if elephant numbers were allowed to fluctuate spatiotemporally without intensive management intervention (see Owen-Smith et al., 2006).

Our identification of density-dependent habitat selection, indicative of competition for resources, suggests that the changes in conservation management approaches for elephants in Kruger were effective in promoting a potential driver of population regulation. We acknowledge that this is an initial foray into unravelling the far-reaching effects of changes in management as we could only directly assess responses to changes in one component of management (i.e. the moratorium on culling). Indeed, given the emphasis that Kruger managers have placed on the revised water supplementation scheme, and the work of, for example, Chamaillé et al. (2007; 2008) and Hilbers et al. (2014), our study would have benefitted from an assessment regarding the influence of reduced water supplementation on habitat selection. We are, however, confident that the absence of such an assessment (see Smit et al., 2007) does not detract from our main finding that elephants in Kruger clearly responded as desired to changes in management approaches. Therefore, we suggest that a no- or limited-intervention approach focusing on ecological processes remains, at this stage, a viable and effective conservation management option in Kruger. We further advise that prospective plans to return some form of artificial manipulation (see examples in Delsink et al., 2013) are likely premature and require scientific evaluation. Our work supports the need to use informative scientific evidence rather than conjecture when developing future conservation management approaches (see Pullin et al., 2004; Owen-Smith et al., 2006).

5. Conclusions

Our study suggests that the changes in conservation management approaches for elephants in Kruger were effective in promoting density-dependent habitat selection, a potential driver of population regulation, in line with ecological objectives set by management. A two-fold increase in density led to an increase in occupancy and generalization in selection for woody cover, an important resource for female elephants. We further demonstrated a functional response of selection for rivers by females, whereby high levels of dry season

rainfall lifted normal dry season foraging restrictions. Finally, our results indicated that the relationship between density and woody cover selection, and rainfall and river selection, varied across districts of the Park that exhibit differences in habitat characteristics and rainfall. In this paper, we contribute to the growing, but still somewhat lacking, body of literature concerning the effects of density on fine-grain habitat selection in large, free-ranging herbivores (see Morris and MacEachern, 2010). Our study not only provides a scientific basis for future decisions regarding elephant conservation management in southern Africa, but also suggests valuable avenues of future enquiry.

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Figures

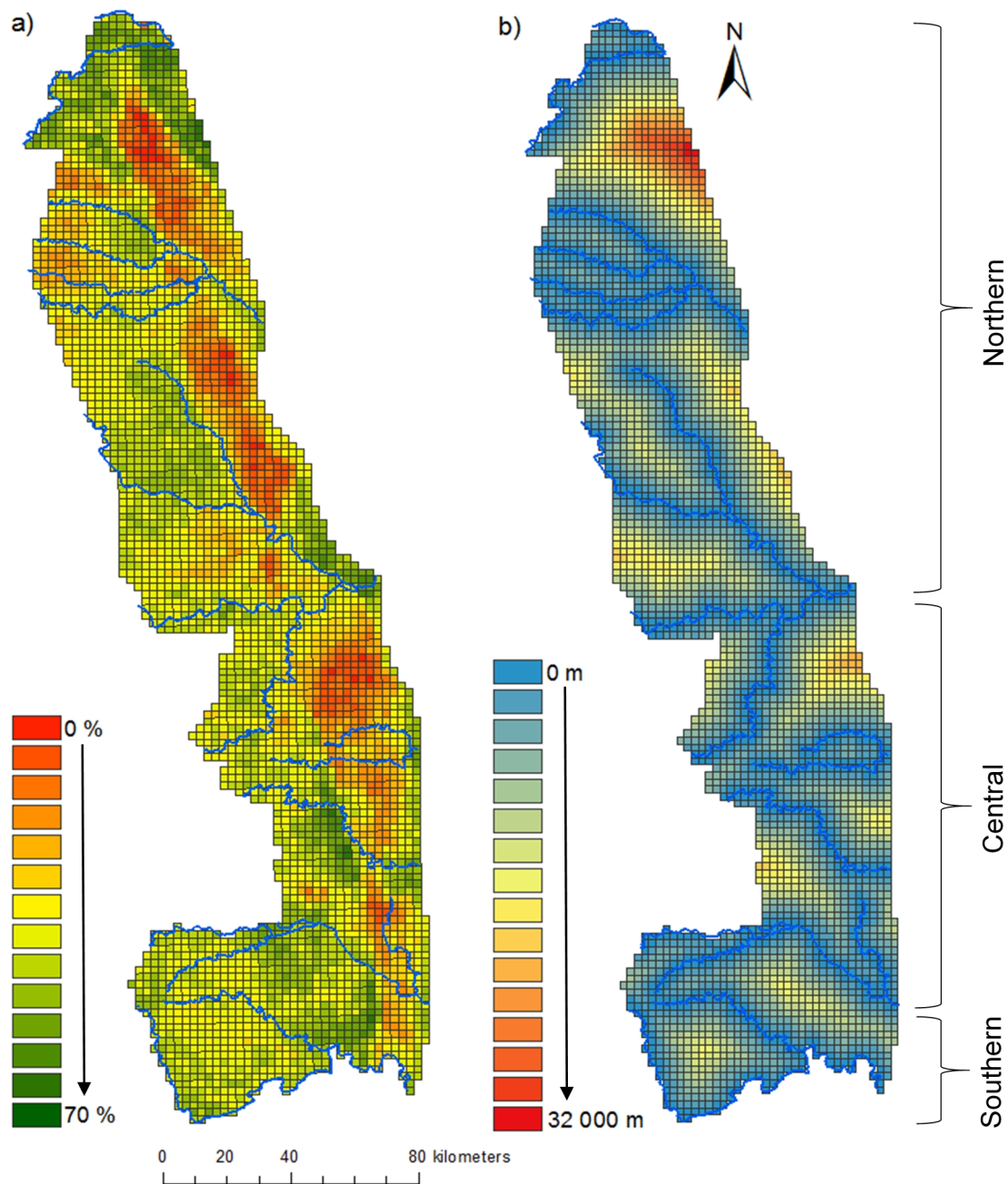


Fig. 3.1. 5km² grid-cells of the Kruger National Park indicating a) mean percentage woody cover (see Bucini et al., 2010) and b) mean distance to rivers for each cell. We further show the districts of Kruger, with the northern district north of the Olifants river, the southern district south of the Sabie river, and the central district in-between.

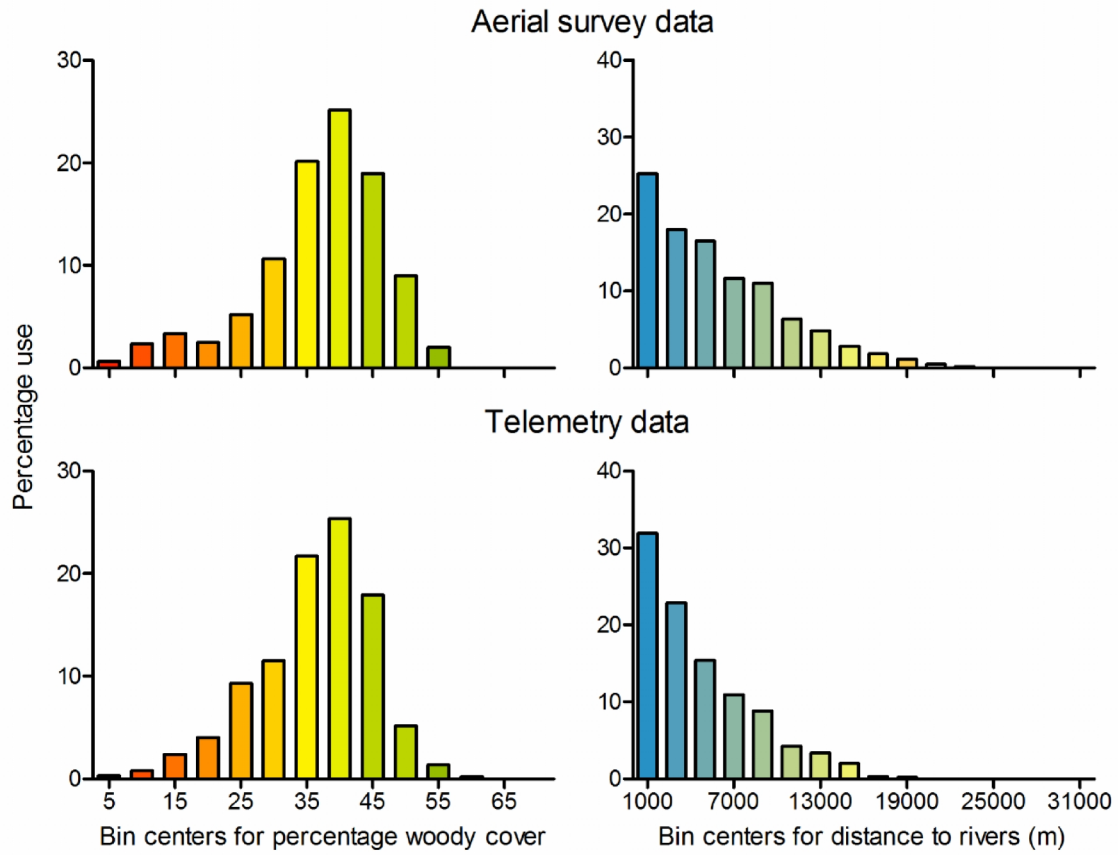


Fig. 3.2. Comparison between female elephant habitat-use estimated using aerial survey and telemetry data during the dry season of 2012.

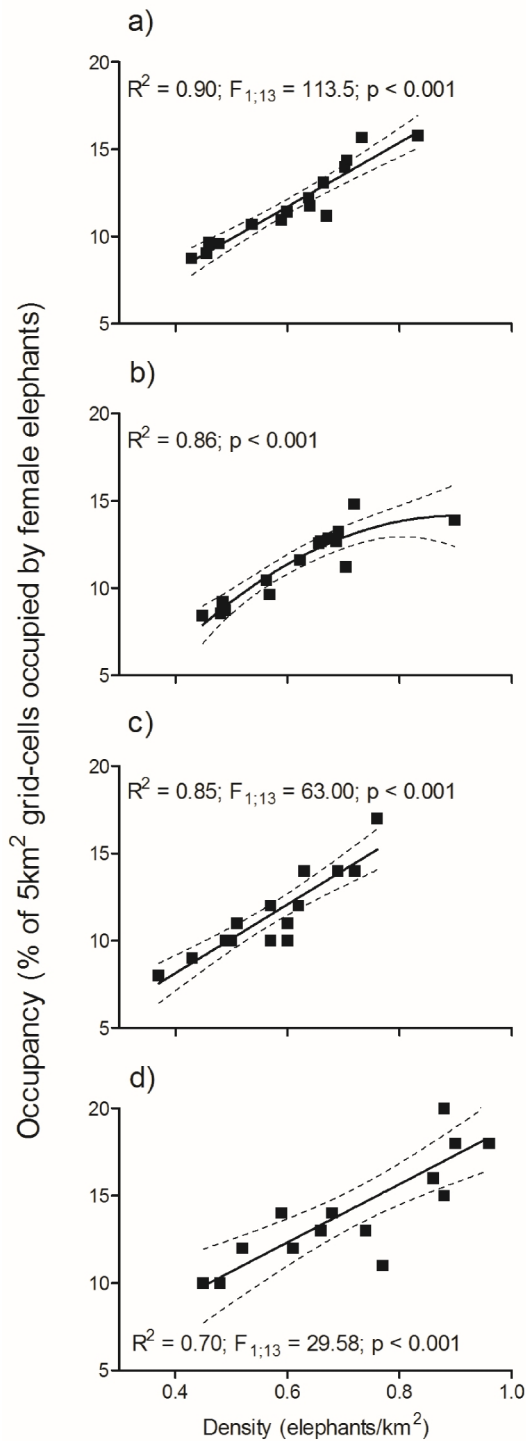


Fig. 3.3. Occupancy as a function of density for a) the whole of Kruger, and the b) northern, c) central and d) southern districts. We used linear regression to relate the percentage of 5km² grid-cells occupied by female elephants to density, and assessed whether the inclusion of a quadratic term improved the fit using the Akaike information criterion (AIC). Dashed lines are 95% confidence intervals.

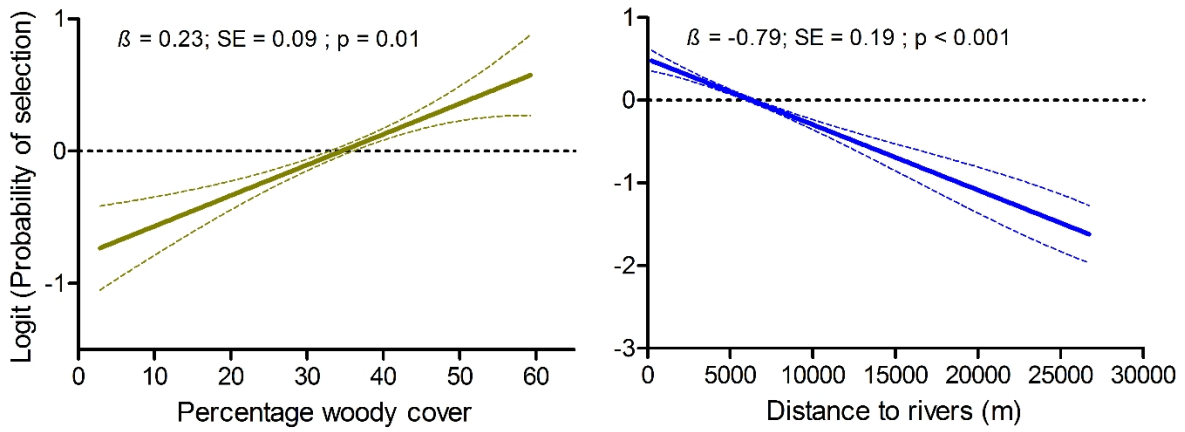


Fig. 3.4. An example of a resource selection function estimating habitat selection by female elephants in the northern district of Kruger during the dry season of 2006. For representation purposes, β coefficients were multiplied by 10 and 10 000 for woody cover and distance to rivers respectively.

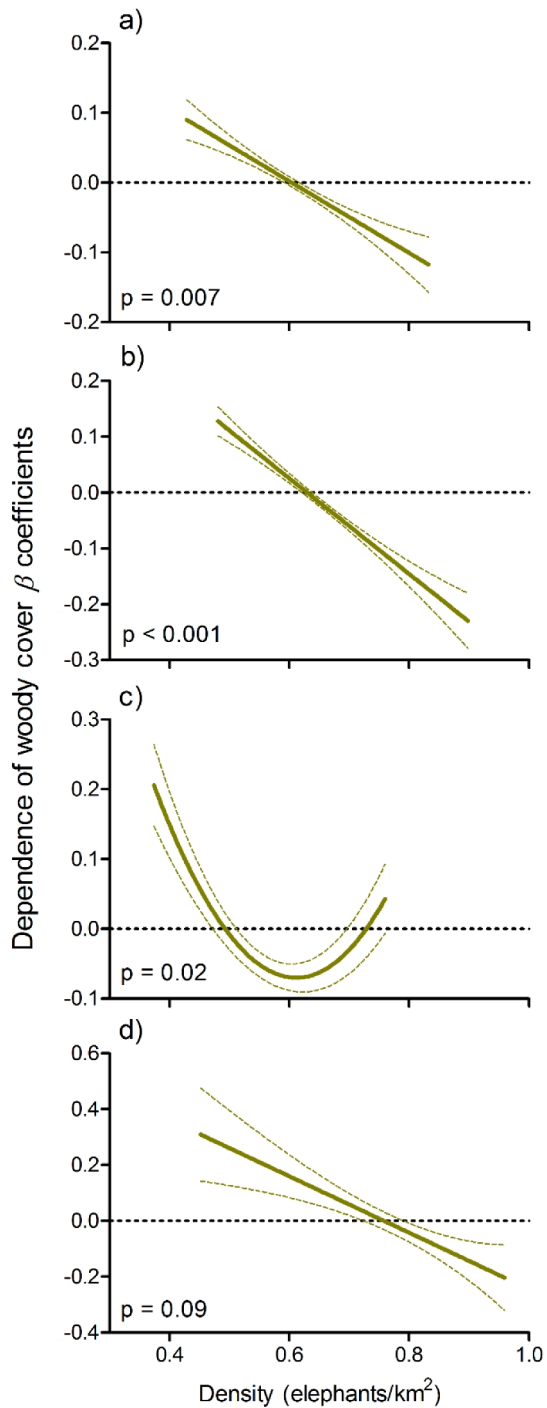


Fig. 3.5. Generalized additive models describing the dependence of woody cover β coefficients on density for a) the whole of Kruger, and the b) northern, c) central and d) southern districts. Smoothers are centred to have zero means, and it is the trend, rather than actual values, that describe the pattern of dependence of woody cover β coefficients on density. Dashed lines represent standard errors and p-values are significance.

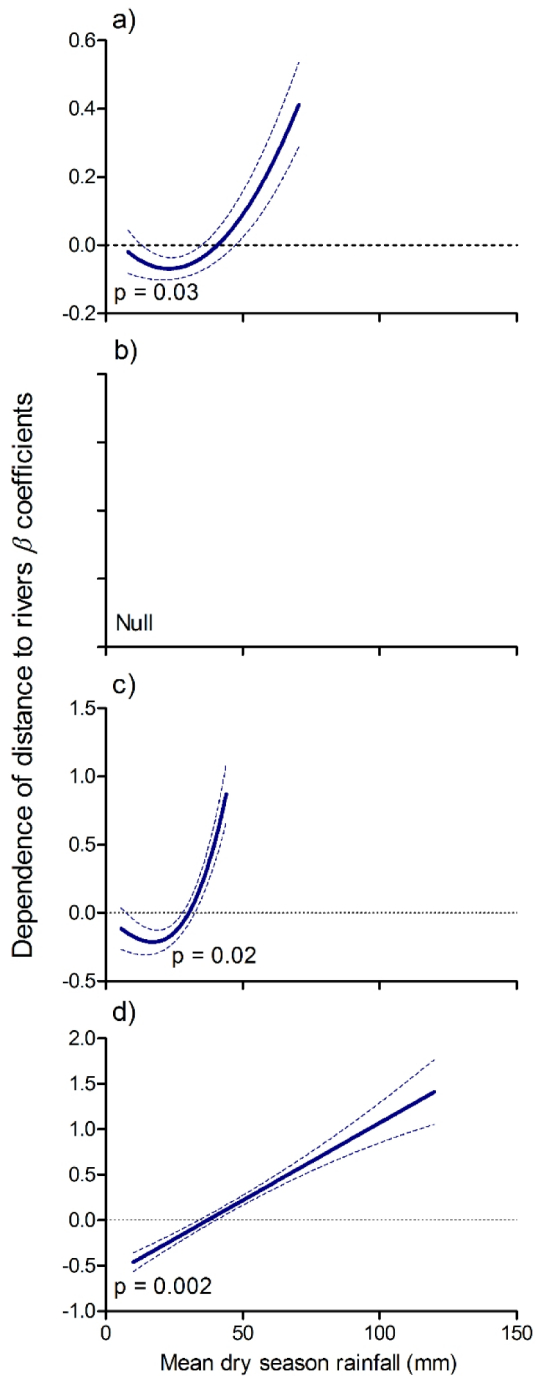


Fig. 3.6. Generalized additive models describing the dependence of distance to rivers β coefficients on mean dry season rainfall for a) the whole of Kruger, and the b) northern, c) central and d) southern districts. Smoothers are centred to have zero means, and it is the trend, rather than actual values, that describe the pattern of dependence of distance to rivers β coefficients on mean dry season rainfall. Dashed lines represent standard errors and p-values are significance.

Tables

Table 3.1. Statistical properties of eight candidate generalized additive models (GAMs) explaining temporal variation in woody cover β coefficients for female elephants in the Kruger National Park, as well as its northern, central and southern districts. The most plausible models selected according to our selection criteria are shown in bold.

District	Candidate model	df	R ²	AIC _c	Δ AIC _c	AIC _c (wi)
Kruger	Density	3	0.47	-29.00	0.00	0.61
	Density + Dry rain	4	0.52	-26.30	2.63	0.16
	Density + Wet rain	5	0.64	-25.40	3.55	0.10
	Density + Dry rain + Wet rain	6	0.77	-24.60	4.34	0.07
	Null	2	0.00	-23.40	5.54	0.04
	Dry rain	4	0.28	-20.50	8.46	0.01
	Wet rain	3	0.01	-20.20	8.78	0.01
	Dry rain + Wet rain	5	0.37	-15.80	13.13	0.00
Northern	Density	3	0.68	-25.00	0.00	0.86
	Density + Dry rain	4	0.68	-20.90	4.15	0.11
	Density + Wet rain	6	0.88	-17.80	7.22	0.02
	Null	2	0.00	-13.90	11.17	0.00
	Wet rain	3	0.19	-13.20	11.84	0.00
	Dry rain	4	0.20	-9.90	15.13	0.00
	Density + Dry rain + Wet rain	7	0.89	-8.70	16.29	0.00
	Dry rain + Wet rain	5	0.37	-7.50	17.52	0.00
Central	Wet rain	4	0.67	-17.00	0.00	0.52
	Density	4	0.57	-16.00	1.01	0.32
	Null	2	0.00	-13.80	3.27	0.10
	Density + Wet rain	3	0.12	-11.60	5.41	0.04
	Dry rain	5	0.68	-11.20	5.87	0.03
	Dry rain + Wet rain	7	0.79	-0.50	16.56	0.00
	Density + Dry rain	7	0.81	2.10	19.12	0.00
	Density + Dry rain + Wet rain	8	0.87	17.10	34.14	0.00
Southern	Density	3	0.27	10.40	0.00	0.30
	Null	2	0.00	10.40	0.03	0.29
	Wet rain	4	0.46	11.20	0.83	0.20
	Density + Wet rain	5	0.72	12.20	1.86	0.12
	Dry rain	3	0.00	14.00	3.68	0.05
	Density + Dry rain	4	0.27	15.10	4.71	0.03
	Dry rain + Wet rain	5	0.49	16.00	5.68	0.02
	Density + Dry rain + Wet rain	11	0.99	121.10	110.76	0.00

Table 3.2. Statistical properties of eight candidate generalized additive models (GAMs) explaining temporal variation in distance to river β coefficients for female elephants in the Kruger National Park, as well as its northern, central and southern districts. The most plausible models selected according to our selection criteria are shown in bold.

District	Candidate model	df	R ²	AIC _c	Δ AIC _c	AIC _c (wi)
Kruger	Dry rain	4	0.53	-5.50	0.00	0.60
	Null	2	0.00	-2.90	2.57	0.17
	Density + Dry rain	5	0.52	-1.60	3.87	0.09
	Density	4	0.40	-0.80	4.64	0.06
	Wet rain	4	0.36	-0.70	4.75	0.06
	Dry rain + Wet rain	6	0.73	0.80	6.30	0.03
	Density + Wet rain	6	0.62	6.50	11.98	0.00
	Density + Dry rain + Wet rain	9	0.89	24.40	29.92	0.00
Northern	Null	2	0.00	2.00	0.00	0.70
	Wet rain	3	0.07	4.90	2.84	0.17
	Density	3	0.08	5.70	3.66	0.11
	Dry rain	6	0.65	9.40	7.35	0.02
	Density + Wet rain	5	0.35	12.00	9.98	0.01
	Dry rain + Wet rain	7	0.85	14.00	11.91	0.00
	Density + Dry rain	7	0.65	20.50	18.46	0.00
	Density + Dry rain + Wet rain	8	0.88	50.10	48.05	0.00
Central	Dry rain	4	0.64	14.10	0.00	0.74
	Null	2	0.00	18.00	3.88	0.11
	Density	5	0.56	19.00	4.94	0.06
	Dry rain + Wet rain	5	0.65	19.60	5.54	0.05
	Wet rain	3	0.12	19.80	5.70	0.04
	Density + Dry rain	7	0.83	27.70	13.66	0.00
	Density + Wet rain	7	0.81	29.10	14.99	0.00
	Density + Dry rain + Wet rain	10	0.93	88.70	74.63	0.00
Southern	Dry rain	3	0.62	21.50	0.00	0.48
	Dry rain + Wet rain	4	0.73	22.20	0.71	0.33
	Density + Dry rain	5	0.79	24.40	2.90	0.11
	Density + Dry rain + Wet rain	6	0.89	25.60	4.09	0.06
	Null	2	0.00	29.40	7.93	0.01
	Wet rain	5	0.68	30.20	8.76	0.01
	Density	3	0.01	32.90	11.47	0.00
	Density + Wet rain	7	0.88	49.50	28.06	0.00

Supplementary Material

Table S.3.1. The effects of including distance to waterholes in resource selection functions for a) female and b) male elephants for the whole of Kruger, and the northern, central and southern districts. Bold values indicate where models improved, according to changes in AIC, by including distance to waterholes. Significant distance to waterhole effects are also in bold. For tabular representation, distance to waterholes β coefficients were multiplied by 10 000.

a)

	Year	District	Δ AIC	% Change in β		Distance to waterholes	
				Percentage woody cover	Distance to rivers	β	p
Females	1998	Kruger	1.51	2%	4%	-0.20	0.48
		Northern	2.14	4%	6%	-0.25	0.53
		Central	1.93	-1%	1%	-0.15	0.79
		Southern	0.29	63%	-35%	0.94	0.20
	2011	Kruger	0.60	6%	-1%	-0.17	0.24
		Northern	1.94	-5%	1%	0.05	0.81
		Central	-1.65	1%	-1%	-0.53	0.06
		Southern	1.68	2%	-11%	0.19	0.57
	2012	Kruger	-0.20	8%	0%	-0.22	0.14
		Northern	1.47	56%	-2%	-0.15	0.47
		Central	1.15	2%	4%	-0.23	0.36
		Southern	-0.37	-2%	-13%	-0.59	0.13

b)

	Year	District	% Change in β			Distance to waterholes	
			Δ AIC	Percentage woody cover	Distance to rivers	β	p
Males	1998	Kruger	-11.10	-8%	189%	-1.01	< 0.01
		Northern	-12.33	-36%	1636%	-1.37	< 0.01
		Central	-0.01	5%	11%	-0.75	0.16
		Southern	-2.53	-43%	-14%	1.79	0.04
	2011	Kruger	-24.30	-17%	22%	-0.70	< 0.01
		Northern	-4.11	-17%	-23%	-0.46	0.01
		Central	-3.19	12%	30%	-0.66	0.02
		Southern	1.98	3%	-2%	0.05	0.90
	2012	Kruger	-12.20	-42%	25%	-0.51	< 0.01
		Northern	-10.08	-36%	-330%	-0.62	< 0.01
		Central	0.89	-34%	15%	-0.27	0.29
		Southern	0.86	-6%	-28%	-0.41	0.29

06

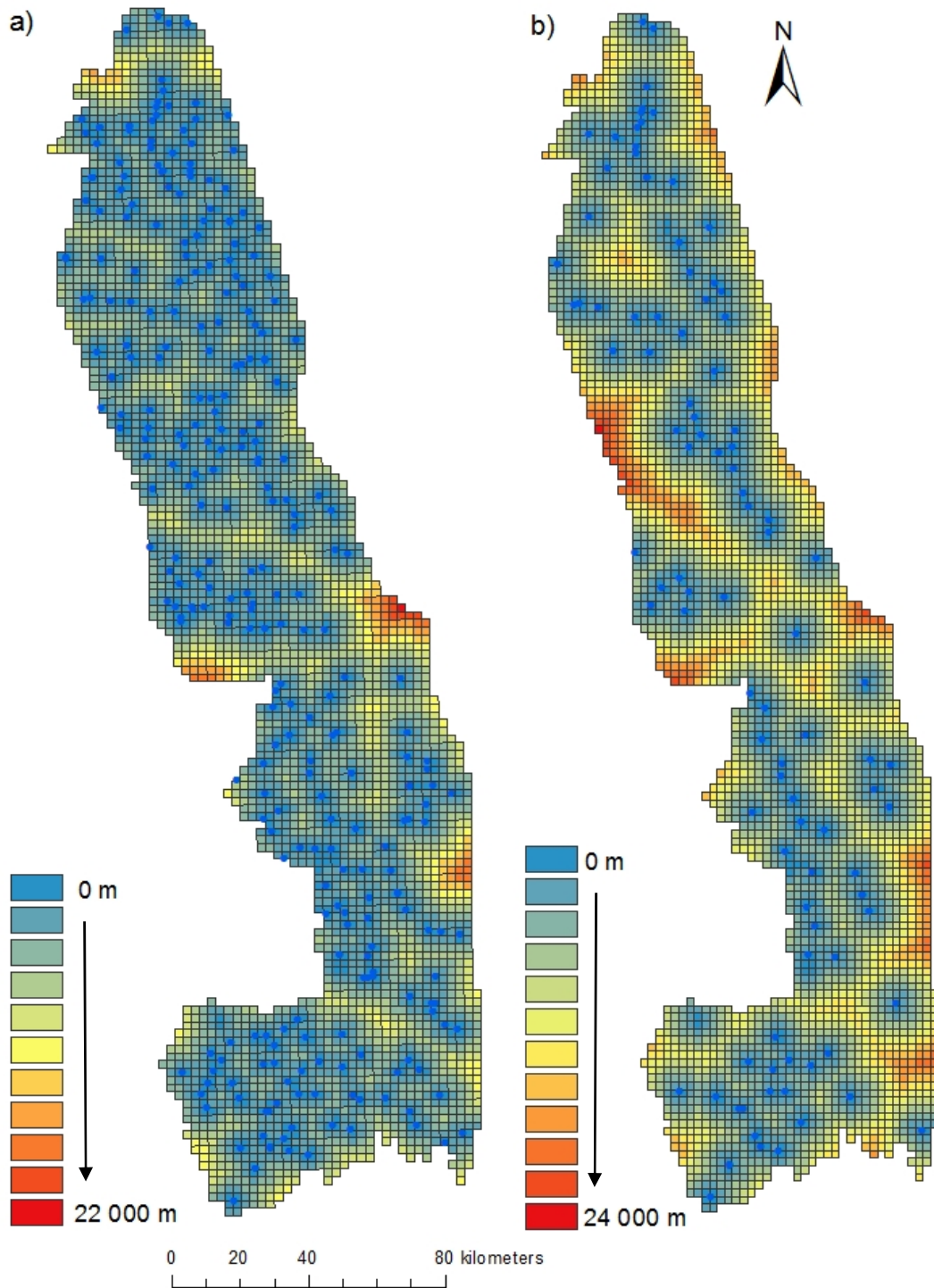


Fig. S.3.1. Estimates of distance to borehole-fed waterholes in a) 1998 and b) 2012 after a 65% reduction of waterholes by Kruger National Park management

Table S.3.2. Results of female elephant resource selection functions calculated for Kruger, and separately for the northern, central and southern districts. For tabular representation purposes, β coefficients and standard errors were multiplied by 10 and 10 000 for woody cover and distance to rivers respectively.

Year	Kruger					Northern district					Central district					Southern district				
	Distance to rivers		Percentage woody cover			Distance to rivers		Percentage woody cover			Distance to rivers		Percentage woody cover			Distance to rivers		Percentage woody cover		
	β	SE	β	SE	r_s	β	SE	β	SE	r_s	β	SE	β	SE	r_s	β	SE	β	SE	r_s
1998	-0.76	0.17	0.35	0.08	0.95	-0.40	0.21	0.32	0.11	0.66	-0.84	0.37	0.16	0.13	0.67	-0.56	0.51	-0.08	0.26	0.42
1999	-0.63	0.15	0.34	0.08	0.98	-0.69	0.18	0.36	0.11	0.87	-0.97	0.37	0.50	0.17	0.82	0.08	0.39	0.30	0.26	0.42
2000	-0.72	0.17	0.17	0.08	0.84	-0.51	0.21	0.13	0.10	0.50	-0.25	0.40	0.44	0.14	0.86	-1.52	0.51	0.58	0.27	0.81
2001	-0.40	0.16	0.29	0.08	0.85	-0.24	0.20	0.47	0.12	0.83	-0.59	0.36	0.30	0.13	0.68	-0.23	0.50	0.44	0.30	0.43
2002	-0.76	0.15	0.18	0.07	0.89	-0.68	0.18	0.12	0.09	0.78	-0.46	0.31	0.19	0.12	0.79	-0.97	0.44	0.88	0.31	0.70
2003	-0.64	0.15	0.27	0.07	0.95	-0.46	0.17	0.22	0.09	0.92	-0.57	0.35	0.21	0.13	0.75	-0.75	0.46	0.91	0.27	0.95
2004	-0.33	0.15	0.32	0.07	0.76	-0.65	0.20	0.34	0.10	0.91	-0.85	0.32	0.37	0.13	0.98	0.05	0.40	0.30	0.23	0.50
2005	-0.64	0.14	0.16	0.07	0.93	-0.58	0.15	0.16	0.09	0.96	-1.41	0.38	0.16	0.12	0.82	-1.64	0.49	0.37	0.25	0.78
2006	-0.71	0.15	0.13	0.07	0.81	-0.79	0.19	0.23	0.09	0.85	-0.63	0.37	0.18	0.13	0.83	-0.42	0.42	0.24	0.21	0.49
2007	-1.27	0.16	0.00	0.07	0.87	-1.17	0.21	0.03	0.10	0.88	-0.87	0.33	-0.13	0.12	0.61	-1.89	0.58	0.11	0.26	0.60
2008	-0.47	0.13	0.09	0.06	0.82	-0.24	0.15	0.17	0.08	0.52	-0.81	0.30	0.03	0.11	0.77	-1.38	0.43	0.04	0.23	0.71
2009	-0.67	0.13	0.14	0.06	0.95	-0.69	0.17	0.13	0.08	0.79	-0.69	0.29	0.17	0.11	0.71	-0.74	0.36	-0.22	0.23	0.55
2010	-0.84	0.14	0.17	0.06	0.98	-0.95	0.19	0.20	0.09	0.81	-1.03	0.28	0.14	0.10	0.90	-0.83	0.39	0.46	0.22	0.69
2011	-0.52	0.12	0.16	0.06	0.85	-0.37	0.15	0.11	0.08	0.77	-0.73	0.29	0.22	0.11	0.83	-0.53	0.33	0.20	0.21	0.55
2012	-0.17	0.12	0.11	0.06	0.73	-0.39	0.16	0.03	0.08	0.70	0.32	0.25	0.25	0.10	0.67	0.91	0.33	0.31	0.21	0.77
Mean	-0.64		0.19		0.88	-0.59		0.20		0.78	-0.69		0.21		0.78	-0.70		0.32		0.63
SD	0.24		0.10		0.08	0.25		0.12		0.13	0.37		0.15		0.09	0.71		0.30		0.16

Chapter 4. General Conclusions

African elephants offer a paradoxical scenario for conservation managers and scientists (van Aarde and Jackson, 2007). In some areas of East Africa for instance, poaching places populations at clear risk of local extinction (see Wittemyer et al., 2014). In other areas, relatively high population densities appear to pose potential threats to the conservation of other species, a situation commonly dubbed the “elephant problem” in southern Africa (see van Aarde and Jackson, 2007). While the poaching of elephants is probably less of a managerial than it is a political or social issue (see Wittemyer et al., 2014), some of the causes of the perceived “elephant problem” are firmly based in historical mismanagement and lingering misconceptions (see van Aarde and Jackson, 2007). Recently, managers have attempted to rectify past shortcomings by placing ecological theory at the centre of management decisions. In the case of the Kruger National Park, managers have changed their management approach by discontinuing culling, removing most artificial waterholes and dropping some fences, in an attempt to reinstate density-dependent processes that may promote natural regulation of the elephant population. Although Kruger is very much at the epicentre of past and current controversy regarding elephant management in southern Africa (see Whyte et al., 2003; Delsink et al., 2013), few have evaluated whether the changes to management have been effective in achieving the expected outcomes.

In this thesis, I examined how Kruger’s elephants responded demographically to changes in conservation management and found that the changes were effective in inducing demographic responses that ecological theory predicted and management desired. In chapter 2, I assessed how calf recruitment, potentially incorporating outcomes of reproduction and first year survival, and population growth rates were affected by limiting factors (i.e. climate, primary productivity and density), during two contrasting eras in Kruger’s management history. My finding that density-independent reproduction, determined by climate-mediated

changes in primary productivity, drove population growth rates during the culling era (i.e. density suppression, water supplementation and fencing) (see Whyte, 2001) is important. It suggests that intensive management did indeed decouple population growth rates from variation in density (Walker et al., 1987; Owen-Smith et al., 2006; van Aarde and Jackson, 2007), a limiting factor that plays a fundamental role in large herbivore population dynamics (Bonenfant et al., 2009). It further suggests that female elephant fecundity is limited by primary productivity (see Wittemyer et al., 2007a, b; Trimble et al., 2009) even at relatively low densities. It is likely that the ability of the elephant population to recover from culling events during the culling era was based on the populations overall reproductive capacity following the event (see Coulson et al., 2004). Furthermore, suggestions of density-dependence and a possible carrying capacity of 0.37 elephants/km² during the culling era were likely incorrect, and rather artefacts of the actual culling process (see van Aarde et al., 1999; White et al., 2007).

Following the 1994 change in management, elephant numbers more than doubled in Kruger. However, my findings show that population growth rates decreased with increasing density. This suggests that by allowing the population to change without human interference, management reinstated density-dependent population growth in the post-culling era. Although the population has not yet entered a period of long-term stability or regulation (see Turchin, 1995) as seen in Hwange National Park (see Chamaillé-Jammes et al., 2008), my results present evidence for some of the density-dependent processes necessary to eventually regulate the population (Turchin, 1995). It is still unclear however, which demographic components were affected by increased density and therefore contributed to density-dependent population growth. My study would have ideally included an assessment into the effects of density on age-specific survival and reproduction, as well as dispersal (see Eberhardt, 2002; Lande et al., 2006; Chamaillé-Jammes et al., 2008; Bonenfant et al., 2009). Though some of these data now exist, they were only made available recently and did not cover my entire study period (see Ferreira

and van Aarde, 2008; Trimble et al., 2011). Nevertheless, my findings do show that both reproduction and first year calf survival appeared to be unaffected by the increase in density in Kruger. This then directs attention to the survival of weaned calves and dispersal, two components of elephant demography that are suggested to respond to changes in density elsewhere (see Chamaillé-Jammes et al., 2008; Young et al., 2009; Young and van Aarde, 2010). An assessment of the effects of variation in density on age-specific survival, reproduction and dispersal into and out of Kruger is therefore a logical next step in future studies.

An apparent limitation of chapter 2 was my time-series of population abundance estimates. It is now commonplace for researchers to use Bayesian state-space models to estimate the process and observation error of a time-series, allowing them to focus on the ecological processes giving rise to variation in process error (e.g. growth rates), free of observation error (see Ahrestani et al., 2013). This is a powerful method when assessing time-series of population counts however, two main reasons kept me from using this approach. First, state-space models provide insufficient estimates of true population size when researchers cannot explicitly estimate detection probability (Kéry and Schaub, 2012), which was the case for the elephant counts in Kruger. Second, state-space models require relatively long time-series, which I did not have because of the division into the culling and post-culling eras. I agree that, where possible, researchers should use Bayesian state-space models over dynamic population models (see Ahrestani et al., 2013). However, in the case of Kruger, I am confident that variations in population abundance estimates reflected on ecological processes and not observation errors (with the exception of the year 2000). Survey methodology did not change during my study period (see Whyte, 2001) and the surveys covered nearly all of Kruger annually, a far greater coverage than the 50% suggested to provide accurate and precise population estimates (see Ferreria and van Aarde, 2009; also see Jachmann, 2002). This led to

accurate and precise counts in Kruger over my study period (see Whyte, 2001), although I acknowledge that sampling error, however small, may still influence the detection of density-dependence (Solow, 2001).

In chapter 3, I examined whether an increase in elephant densities following the cessation of culling promoted density-dependent habitat selection, a fundamental driver of population regulation (Morris, 1988; 2003; Rosenzeig, 1991; Owen-Smith et al., 2006; Bonenfant et al., 2009). I purposefully used habitat covariates that are linked to elephant habitat selection across southern Africa (see Harris et al., 2008; Loarie et al., 2009a; Roever et al., 2012; 2013) and various components of elephant demography (see Wittemyer et al., 2007a, b; Chamaillé-Jammes et al., 2008; Young and van Aarde, 2010). I found that as densities increased following the release from culling, selection for woody vegetation, an important resource for elephants, did indeed generalize (see van Beest et al., 2014b), indicating density-dependent habitat selection. Furthermore, selection for areas close to rivers was altered by dry season rainfall. While not directly linked to changes in density, rainfall-mediated selection for rivers may moderate density-dependent feedbacks to demographic parameters by alleviating foraging restrictions and local clustering (see Chamaillé-Jammes et al., 2008).

These findings reaffirm the main conclusion of chapter 2 that the changes in conservation management promoted some density-dependent processes that may lead to population regulation. However, as in that chapter, these findings immediately present a number of new questions. The main question then is whether density-dependent habitat selection has direct fitness consequences for elephants as it does for other large herbivores (e.g. McLoughlin et al., 2006; 2008; also see Roever et al., 2013). This would again require an assessment of age-specific survival, fecundity and dispersal. It is likely that dispersal rates will increase as per capita availability of optimal habitats decreases and some animals redistribute (see Matthysen, 2005; Young et al., 2009). This relates to my chapter 2 suggestion of density-

dependent dispersal potentially driving population growth during the post-culling era. However, an assessment into the effects of density-dependent habitat selection on age-specific survival and fecundity is more complicated. For such an examination, one would conceptually have to examine the effects of density on habitat selection, possibly at the individual-scale, and relate those effects to measured demographic parameters for that individual and/or associated individuals (i.e. calves) (see McLoughlin et al., 2006; 2008; 2010). For elephants, that would likely be a challenge, as researchers would potentially have to monitor individual animals and measure demographic rates for the better part of a lifetime (up to 60 years) to assess all possible effects (see McLoughlin et al., 2006; 2008; Lee et al., 2011; Lee et al., 2013). Such a dataset is certainly a rarity in elephant research (but see Lee et al., 2011).

Rapid Elephant Population Assessments (REPA's) may however provide a solution to this logistical challenge by offering a detailed demographic snapshot of the elephant population (see Ferreira and van Aarde, 2008; Trimble et al., 2011). Indeed, the Conservation Ecology Research Unit (CERU) has performed repeated REPAs on a number of satellite-tracked breeding herds across Kruger. With both these demographic and spatial-use data, and the results of this study, it may be possible to relate herd-specific variation in age-specific survival and reproduction to differences in the relative use of estimated optimal and suboptimal habitats (see McLoughlin et al., 2006). This may then circumvent the need for an extremely long and detailed time series. Nonetheless, such an assessment remains a daunting task but would go a long way towards identifying possible mechanistic links between density, habitat selection, demographic variation and population regulation for elephants, and indeed large herbivores in general (see Turchin, 1999).

A limitation of chapter 3 was that I could not account for possible changes in woody cover throughout my study period (see Buitenwerf et al., 2012), as my woody cover layer was static (see Bucini et al., 2010). However, I consider my static woody cover layer as appropriate

within the scope of my study for five reasons; (1) the layer was generated using multiple years of data collected during the middle of my study period (Bucini et al., 2010) thereby avoiding an estimation of woody cover biased towards either low or high elephant densities; (2) my study period was relatively short (15 years) therefore decreasing the possibility of significant changes in woody cover over the period; (3) over the last 50 years, increases in woody cover have not been uniform across Kruger (Buitenwerf et al., 2012); (4) even where increases did occur, there has been no apparent change during the period overlapping my study (Buitenwerf et al., 2012) and; (5) my 5km² grid-cell sampling and the Kruger-wide extent of my study likely reduced the effects of fine-scale and spatially isolated changes in woody cover on my results. If a temporal increase in woody cover, correlating with increased density, was the main reason for the strong observed generalization in woody cover selection over time, I would expect the generalization in selection to be most noticeable in the south where woody cover changes have been most obvious (Buitenwerf et al., 2012). This was not the case. While I admit that changes in woody cover likely had slight effects on my findings, I am confident that my conclusions remain valid.

Throughout this study, I emphasise that the changes in conservation management approaches for elephants in Kruger incorporated three major actions: the discontinuation of culling, the removal of many artificial waterholes and the dropping of some fences. However, I am aware that my study only directly assessed the influence of culling, and the subsequent discontinuation thereof, on elephant demography. I refer to the changes in their entirety because it would be ignorant to believe that only the cessation of culling has had demographic consequences for elephants (Owen-Smith et al., 2006). Indeed, artificial waterholes have strong influences on elephant distribution and demography in other areas (see Chamaillé-Jammes et al., 2007b; 2008; Shrader et al., 2010) and fences can influence elephant movements and prohibit dispersal (see Loarie et al., 2009b). This may or may not be the case in Kruger (see

Chamaillé-Jammes et al., 2007a; Smit et al., 2007; Hilbers et al., 2014). However, in this study I could not directly assess the influence of waterhole reductions on demographic variation or habitat selection because Kruger managers did not record yearly removals of artificial waterholes. Nevertheless, ongoing research at CERU will likely unravel the influences of present artificial waterhole distribution, and the theoretical repercussions of an alteration thereof, on elephant movement, distribution and demography in Kruger.

The management of elephants in Kruger has been for decades, and continues to be, a subject of debate in southern Africa (see Whyte et al., 2003; Delsink et al., 2013). After the progress made in the late 1990's and early 2000's, there are still recommendations to return some forms of manipulative management (see examples in Delsink et al., 2013) to ensure the equal conservation of all species in the park. Indeed, a main goal of Kruger's management is to conserve biodiversity in its entirety. The findings of my study suggest that elephants in Kruger have responded, at least demographically and partly, to changes in conservation management as ecological theory predicted and management desired. This is not to say that other species are unaffected by increased elephant densities and occupancy of the park; it would be very surprising if there was no effect (see Valeix et al., 2007; Guldmond and van Aarde, 2008; van Beest et al., 2014a). Rather, I argue that ecological principles continue to provide an effective framework for scientific evaluation and elephant conservation management in Kruger. Managers should seek to maintain the integrity of this ecological framework in the face of uninformed social and political disapproval, and consider adapting it only when sound scientific evidence supports the need for a change.

I stress that my study provides an initial evaluation into the effects of the changes in conservation management on elephant demography in Kruger. There are still many unanswered questions, a few of which I have discussed above. However, from this evaluation, I can conclude that changes in conservation management in Kruger were effective in achieving at

least some of the demographic outcomes that managers envisaged years ago. However, only time, and continued surveying, will reveal whether density-dependent processes ultimately drive the elephant population into a state of long-term regulation (see Turchin, 1995). It is my hope that this study has contributed, at least in a small way, to our understanding of elephant demography and conservation management in the Kruger National Park, and potentially elsewhere in southern Africa. I encourage those tasked with managing elephants to consider this study, and associated ecological literature, when making conservation decisions in the future. Inevitably, elephants will continue to attract public and scientific attention in the coming years. It is therefore important that managers are aware of past failures, past successes and future possibilities when it comes to the conservation management of this controversial species.

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