Environmental determinants of the movement patterns of elephants in the Kruger National Park

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Environmental determinants of the movement patterns of elephants in the Kruger National Park

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Disclaimer

I, Andrew Purdon 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.

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Abstract

To improve the efficacy of protected areas in conserving ecological processes, initiatives such as the megaparks for metapopulations strive to increase connectivity between small and often isolated protected areas. Increasing connectivity between protected areas may mediate the apparent impact of elephants on vegetation and promote regional population stability through the spatial structuring of their populations. This relies on asynchronous population dynamics between interconnected subpopulations separated by distance. It is likely that the spatial responses of elephants to environmental variation drive this asynchrony. Therefore, developing a thorough knowledge of the spatial responses of elephants to their environment can inform management decisions to conserve suitable habitat, and promote population persistence through the maintenance of ecological processes.

Most of what we know about the spatial responses of elephants is from studies that focused on explaining their spatial distribution or re-distribution in space, and studies that aimed to identify factors that determine resources use and selection. Recently, technological and analytical advances have marked a shift to studies that aim to assess the behavioural responses of animals to their environment by considering how individuals change their movement. Therefore, my approach in this thesis was to evaluate the environmental determinants of the movement patterns of elephants in the Kruger National Park. To do this, I used hourly location time series datasets acquired from 26-collared elephant cows distributed across Kruger.

In chapter 3, I modelled the movement behaviour of the elephants using dynamic Brownian bridge movement modelling. I then evaluated how well different environmental factors explain changes in their movement behaviour using a mixed modelling approach at multiple temporal scales. Distance from water, primary productivity, vegetation structure, and temperature could explain changes in the movement behaviour of the elephants. The factors that could best explain changes in their movement behaviour varied between seasons and among temporal scales. Therefore, elephants adjusted their movement scale-dependently in response to their environment.

Management interventions could induce artificial patterns of elephant movement, potentially uncoupling them from the processes that result in asynchrony in the dynamics of local populations. Therefore, the influence and consequences of management interventions such as the provisioning of water remain controversial. In chapter 4, I examined how the provisioning of water influences the movement patterns and the resulting spatial distribution of elephants. When elephants used artificial waterholes, they used areas more than double the distance away from natural water sources in comparison to when they used natural water sources. This increased the total area used by elephants by more than one third. The resulting change in the distribution of elephants may accentuate their impact on vegetation and have demographic consequences.

Elephants respond to the distribution and availability of resources, and rather than returning to the artificial manipulation of numbers to relieve symptoms, I argue that management should continue to base their decisions on ecological principals. Many questions remain, and my hopes are that this research contributes to what we know about elephants and how best to manage them, or rather, how best to manage their responses to our interferences.

Dedication

I dedicate this thesis to my parents, Kevin and Colleen Purdon.

Acknowledgements

First, I would like to thank Rudi van Aarde. Thank you for your patience, guidance, and support. Your passion for science and conservation has motivated me throughout the duration of this thesis. The shaping of my thoughts, through many discussions on science, conservation, and management will have a lasting impact on my future career. I am very grateful for the knowledge that you have passed on to me during this time and for the incredible opportunities you have provided.

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Chapter 1. General Introduction

Conservation planning and management requires solutions to conservation problems based on sound theoretical and applied ecological research (Cook et al., 2010; Keith et al., 2011). Managers, however, often need to make decisions on how to improve the efficacy of protected areas in conserving ecological processes with incomplete knowledge of an entire ecosystem (see Franklin, 1993; Margules and Pressey, 2000). Conservation planning can therefore benefit from a focal species approach that allows management to make informed decisions with incomplete knowledge (Caro and O'Doherty, 1998; Andelman and Fagan, 2000; Epps et al., 2011). In southern Africa, the magapark for metapopulations initiative aims to augment small isolated savannah elephant (*Loxodonta africana*) populations to prevent local hyper abundance, reduce local impact, and stabilise the elephant population regionally (van Aarde et al., 2006; van Aarde and Jackson, 2007). Conserving elephant habitats and their functional connectivity may effectively conserve habitat and potential landscape linkages for other species (Beier et al., 2008; Epps et al., 2011; Roever, 2013) by aiding in the development of networks of conservation areas that enhance habitat connectivity and promote long-term viability of ecosystem processes.

Although, the use of elephants for conservation planning makes sense, their management remains contentious (see van Aarde et al., 1999; Gilson and Lindsay, 2003; Whyte et al., 2003; Owen-Smith et al., 2006; van Aarde and Jackson, 2007; Chamaillé-Jammes et al., 2007a, b; Smit et al., 2007b, c). The need to manage elephants in southern Africa is also contentious, largely due to differences of opinion on the effects that elephants can have on vegetation (Eckhardt et al., 2000; Guldemond and van Aarde, 2007). The IUCN Red List of threatened species lists the savanna elephant as vulnerable mostly due to poaching (see Blanc, 2008; Wittemyer et al., 2014). Ironically, in many protected areas management is concerned that there are too many elephants (see Owen-Smith, 1996). It has, therefore, long been debated how their effects should be mitigated (Owen-Smith, 1996; Whyte et al., 1998; van Aarde et al., 1999; Owen-Smith et al., 2006; van Aarde et al., 2006; van Aarde and Jackson, 2007). Methods mitigating their effects have often been aimed at reducing their numbers (contraception, relocation, culling), subsequently addressing the symptoms rather than the causes of the problem (Owen-Smith, 1996; Whyte et al., 1998; van Aarde et al., 1999; Owen-Smith et al., 2006; van Aarde et al., 2006; van Aarde and Jackson, 2007). Recently, managers have started to focus on ecological rather than agricultural paradigms that focus on promoting ecological processes to regulate numbers naturally (Pienaar et al., 1997; Owen-Smith et al., 2006; van Aarde and Jackson, 2007). Subsequently, initiatives such as the megaparks for metapopulations (van Aarde and Jackson, 2007) and Transfrontier Conservation Areas (Hanks, 2003) are becoming fashionable.

For megaparks to be efficient in promoting ecological processes that limit the distribution and numbers of elephants naturally, they need to include ecological gradients, occupied and vacant habitats, dispersal between these, and asynchrony in the dynamics of sub-populations (van Aarde and Jackson, 2007; Olivier et al., 2009). It is likely that the spatial responses of elephants to environmental variation drive this asynchrony (van Aarde et al., 2006; van Aarde and Jackson, 2007). This relies on the individual having the ability to select for habitats that will optimize its fitness (Pienaar et al., 1997; Owen-Smith et al., 2006) by adjusting how it moves with respect to its current needs and the distribution and availability of resources (Senft et al., 1987; Rettie and Messier, 2000; Nathan et al., 2008). The distribution and availability of resources and the way elephants use these resources at different scales will influence their spatial dynamics and demography at the landscape scale. Improving our understanding on the spatial responses of elephants to their environment and the consequences thereof may better inform management decisions on conserving suitable habitat, and promoting ecological processes (see Boyce and McDonald, 1999; Nielsen et al., 2006).

Management intervention could induce artificial patterns of elephant space use, potentially uncoupling them from the processes that result in asynchrony in the dynamics of local populations. Consequently, the influence and consequences of management interventions such as the provisioning of water and fencing remain controversial (Owen-Smith, 1996; van Aarde et al., 2006; Packer et al., 2013; Creel et al., 2013; Massey et al., 2014; Woodroffe et al., 2014; Durant et al., 2015). The provisioning of water and fencing may alter the spatial use patterns of elephant and ultimately modify habitat conditions (Owen-Smith, 1996; van Aarde et al., 2008; Grainger et al., 2005; de Beer et al., 2006; Loarie et al. 2009a). The short-term benefits of increased water supply for elephants may be at the expense of their long-term persistence, because of starvation-induced mortality during extended draughts (Walker et al., 1987; Owen-Smith, 1996; Shrader et al., 2010). Additionally, fencing and the provisioning of water may prevent elephants and other species from shifting their range use (Grainger et al., 2005; Leggett, 2006; Smit et al., 2007a; Loarie et al., 2009a), which could accentuate their impact on vegetation (Brits et al., 2002). Finally, fencing and water provisioning may uncouple elephants and other ungulate populations from natural limitations, which may otherwise have limited their distribution and numbers (Owen-Smith et al., 2006; van Aarde and Jackson, 2007). Understanding how management interventions influence the spatial responses of elephants may allow management to mitigate, or ideally prevent their effects.

Kruger National Park's (KNP) elephants have a well-documented history of exposure to management interventions that reduced numbers and tried to alter space use patterns to reduce their apparent impact on vegetation (Pienaar and van Niekerk, 1963; Hanks et al., 1981; Whyte et al., 1998). The cessation of culling in 1994 followed by the closure of two thirds of 365 boreholes and the dropping of some bordering fences introduced a new era of management that centres on promoting ecological processes that may regulate numbers naturally, rather than manipulating numbers artificially (Pienaar et al., 1997; Owen-Smith et al., 2006; van Aarde and Jackson, 2007). Kruger National Park now forms part of the Great Limpopo Transfrontier Park that links KNP with Limpopo National Park and Gonarezhou National Park, thereby providing continuous roaming space in excess of 40 000 km^2 (Figure 1.1). Currently plans include the inclusion of Zinave and Banhine National Parks (Figure 1.1). In line with the magapark for metapopulation initiative, these measures may promote the spatial structuring of the elephant population to regain functional responses to the availability and distribution of resources across the landscape (van Aarde and Jackson, 2006; van Aarde and Jackson, 2007).

Typically the spatial responses of animals are addressed from an Eulerian approach, which focuses on evaluating the changes that occur at locational points and is primarily concerned with the characteristics and the geographical area used by an animal (Nathan et al., 2008; van Moorter et al., 2015). The Eulerian approach is therefore synonymous with home range analyses that quantify the distribution or re-distribution (e.g. de Beer and van Aarde, 2008), and habitat selection patterns (e.g. Roever et al., 2013) of a population (Nathan et al., 2008; van Moorter et al., 2015). Recently, technological and analytical advances have marked a shift to a Lagrangian approach that aims to assess the behavioural responses of animals by considering how individuals change their movement (Nathan et al., 2008; Loarie et al 2009a; van Moorter et al., 2015; Kays et al., 2015). Currently, we base most of what we know about the spatial responses of elephants on studies using an Eulerian approach (de Beer and van Aarde, 2008; Loarie et al 2009a; Roever, 2013; Roever et al., 2014). Therefore, using a Lagrangian approach, I am to evaluate the environmental determinates of elephant space use in the KNP.

Although elephants are large-bodied mixed feeders (Own-Smith, 1988) labelled as habitat generalists, they do select habitats, plant species and plant parts (de Beer et al., 2008; Osborne, 2004; Roever et al., 2012). Studies have attributed their preferences for habitats to a variety of explanations. At a coarse landscape scale, we know that the availability of water, density of conspecifics, and environmental stochasticity drive elephant demography (Chamaillé-Jammes et al., 2008; Trimble et al., 2009; Young et al., 2009; Young and van Aarde, 2010). We also know that when given the choice elephants like to be close to water (de Beer and van Aarde, 2008; Harris et al., 2008; Loarie et al., 2009a), where it is relatively green (Rasmussen et al., 2006; Wittemyer et al., 2008; Loarie et al., 2009b), and where food is of relatively high nutritional quality (Pretorius et al., 2011). Therefore, throughout this thesis I view the environment as a changing template from which elephants acquire resources and as the metric through which it needs to move to locate new resources (MacDonald and Rushton, 2003).

In this thesis, I evaluated the environmental determinants of the movement patterns of elephants in the Kruger National Park. To do this, I used location time series datasets acquired from 26-collared elephant cows, distributed across KNP. Following this introduction, I present a chapter that describes the study site and study animals, two research chapters (chapter 3 and chapter 4) and a conclusion chapter (chapter 5). In chapter 3, I examine the environmental determinants of the movement behaviour of elephants among multiple temporal scales. I modelled the movement behaviour of elephants using dynamic Brownian bridge movement modelling (Kranstauber et al., 2012; Byne et al., 2014). I then evaluated how well different environmental factors (primary productivity, vegetation structure, water availability, and temperature) explain changes in elephant movement behaviour using a mixed modelling approach. Thereafter (chapter 4), I examined how the provisioning of water as a management intervention influences the movement patterns and the resulting spatial distribution of elephants. Together, these chapters contribute to our understanding of the movement patterns of elephants and their environmental determinants, with potential implications for future management of elephants across their range.

Figures

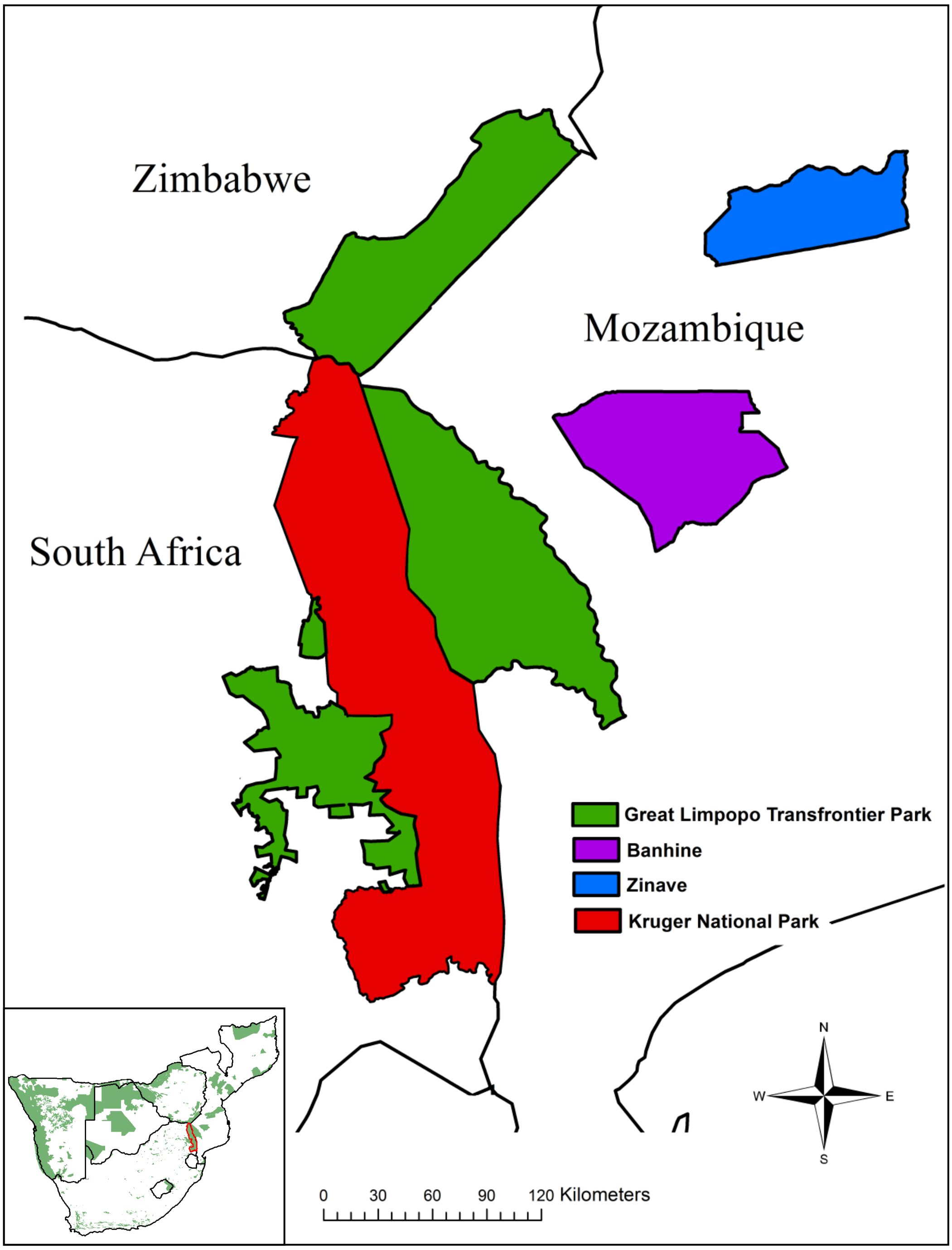


Figure 1.1. Kruger National Park is located within the northeast corner of South Africa adjoining Mozambique in the east and Zimbabwe in the north. Kruger forms part of the Great Limpopo Transfrontier Park that links Kruger with Limpopo National Park in Mozambique and Gonarezhou National Park in Zimbabwe, with plans to include Zinave and Banhine National Parks in the future.

Chapter 2. Brief overview of Kruger National Park and the study animals

Kruger National Park

Kruger National Park is located within the north-eastern corner of South Africa adjoining Mozambique in the east and Zimbabwe in the north (Figure 2.1.). At the time of this study, Kruger National Park extended 360 km north to south and 65 km west to east and covered 19 485 km^2. Kruger National Park has been incorporated into the Great Limpopo Transfrontier Park through the removal of its fences along the Zimbabwean and north-eastern Mozambican border, thereby providing continuous roaming space in excess of 40 000 km^2 (Figure 2.1.). However, fences are still present along the western, southern, and south-eastern border.

Extensive variations in geology and climate underpin KNP. The basic geological template of KNP consists of a western granitic half, and an eastern clayey basaltic and rhyolitic half (Figure 2.2.) (Venter, 1990). Ecca shale soils divide the eastern basalts and western granites. Apart from the Lebombo Mountains running from north to south on the eastern boundary and scattered smaller outcrops dispersed throughout the entire park, the only mountainous areas are those in the south-western and north-eastern sectors.

Kruger National Parks climatic regime is characterised by a single wet and a single dry season (Owen-Smith and Goodall, 2014). A rainfall gradient stretches from an annual mean of 750 mm in the south, to 450 mm in the north of the Park (Figure 2.3.) (SANParks scientific services, Skukuza, South Africa). Rainfall and temperature during the study period (June 2012 to March 2014) are summarised in Figure 2.4. The mean daily temperature in the wet season (December inclusive to March inclusive) was 24.0 °C (range 19.07 °C to 29.9.0

°C) and 17.9 °C (range 11.1 °C to 30.0 °C) in the dry season (June inclusive to September inclusive) (South African Weather Services, Pretoria, South Africa). Water sources in KNP include perennial rivers and ephemeral drainage lines that flow during the wet season, and point water sources such as springs and pans (Figure 2.1.) (Gaylard et al., 2003). Furthermore, artificially pumped water points drilled between the 1930s and 1980s maintained by KNP management provide surface water throughout the park (Figure 2.1.).

Variations in geology and climate across KNP promote changes in vegetation structure and primary productivity. At a coarse scale, the vegetation in KNP consists of a low nutrient high rainfall well-wooded area in the south-west and palatable productive grasslands with some trees in the south-east. Mopane woodlands dominate the northern half of KNP, with fertile open grasslands on the eastern basaltic soils, and more undulating landscapes with woodlands in the north-western area. Woody cover is a useful index as it combines elements of vegetation structure and productivity (see Bucini et al., 2010) (Figure 2.1). Woody cover changes across space in KNP (Figure 2.1). Primary productivity indexed by the Enhanced Vegetation Index (EVI) also varies across KNP and with time (Figure 2.5.) [Moderate Resolution Imaging Spectroradiometer 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].

Study animals

Global Positioning System (GPS) collars (model SM 200E; Africa Wildlife Tracking, Pretoria, South Africa) provided location datasets for 26 elephant cows (held by CERU, www.ceru.up.ac.za). Elephant cows distributed across KNP were selectively fitted with the GPS collars to take advantage of the heterogeneity in KNP (Figure 2.6). Each of the elephant cows was a member of a separate breeding herd and her movements therefore represented those of her breeding herd (Young and van Aarde, 2010). The GPS collars provided fixes every hour and had a mean fix rate (with collars on the elephants) of 90 % ± 2 %. A mean location error of 22.9 m ± 10.8 m (range: 3.7 – 50 m; n= 145) was calculated from the linear distance between recorded locations and the true location for six collars placed at the Skukuza veterinary camp (Longitude: 31.587; Latitude: -24.995) for seven days prior to collaring. Throughout this thesis, I only used locational points that fall within KNP, due to the availability of the woody cover and water layers.

The 26 elephant cows ranged over a larger area during the wet season in comparison to the dry season (Table 2.1.). Furthermore, there was large variation in seasonal home range sizes between elephants distributed across KNP. The seasonal home range sizes were calculated using dynamic Brownian bridge movement modelling (Kranstauber et al., 2012) (please see page 23 for details).

Tables

Table 2.1. Seasonal home range sizes of the 26-collared elephants during the dry and wet season.

	Dry season ranges (km^2)		Wet season ranges (km^2)	
Elephant identity	**2012**	**2013**	**2012**	**2013**
EF0205	124.8	153.0	384.0	263.0
EF0206	108.7	-	169.5	120.0
EF0207	173.1	168.5	332.3	327.3
EF0208	150.8	127.2	317.7	306.7
EF0209	171.7	183.4	242.7	-
EF0210	238.2	204.5	407.6	407.6
EF0211	135.2	121.6	241.3	273.1
EF0212	151.9	90.7	373.2	-
EF0213	227.8	222.8	268.0	229.2
EF0214	196.1	162.9	379.8	316.5
EF0215	164.7	165.7	167.7	215.9
EF0216	129.8	85.1	236.7	318.2
EF0217	114.5	132.7	198.3	210.1
EF0218	95.6	95.9	235.7	248.7
EF0219	106.1	94.4	214.3	192.2
EF0220	62.2	45.4	248.9	310.8
EF0221	125.4	94.9	375.7	267.5
EF0222	96.5	175.3	281.5	314.8
EF0223	130.4	-	219.5	-
EF0224	139.6	157.2	335.9	270.7
EF0225	98.8	79.2	251.8	360.2
EF0226	195.6	183.4	236.4	-
EF0227	117.8	194.4	205.3	249.0
EF0228	211.1	157.3	250.8	273.5
EF0229	172.5	176.4	457.7	245.1
EF0230	70.8	-	121.9	-
Mean ± SD	142.7 ± 46.0	142.3 ± 46.5	275.2 ± 83.6	272.4 ± 62.5

Figures

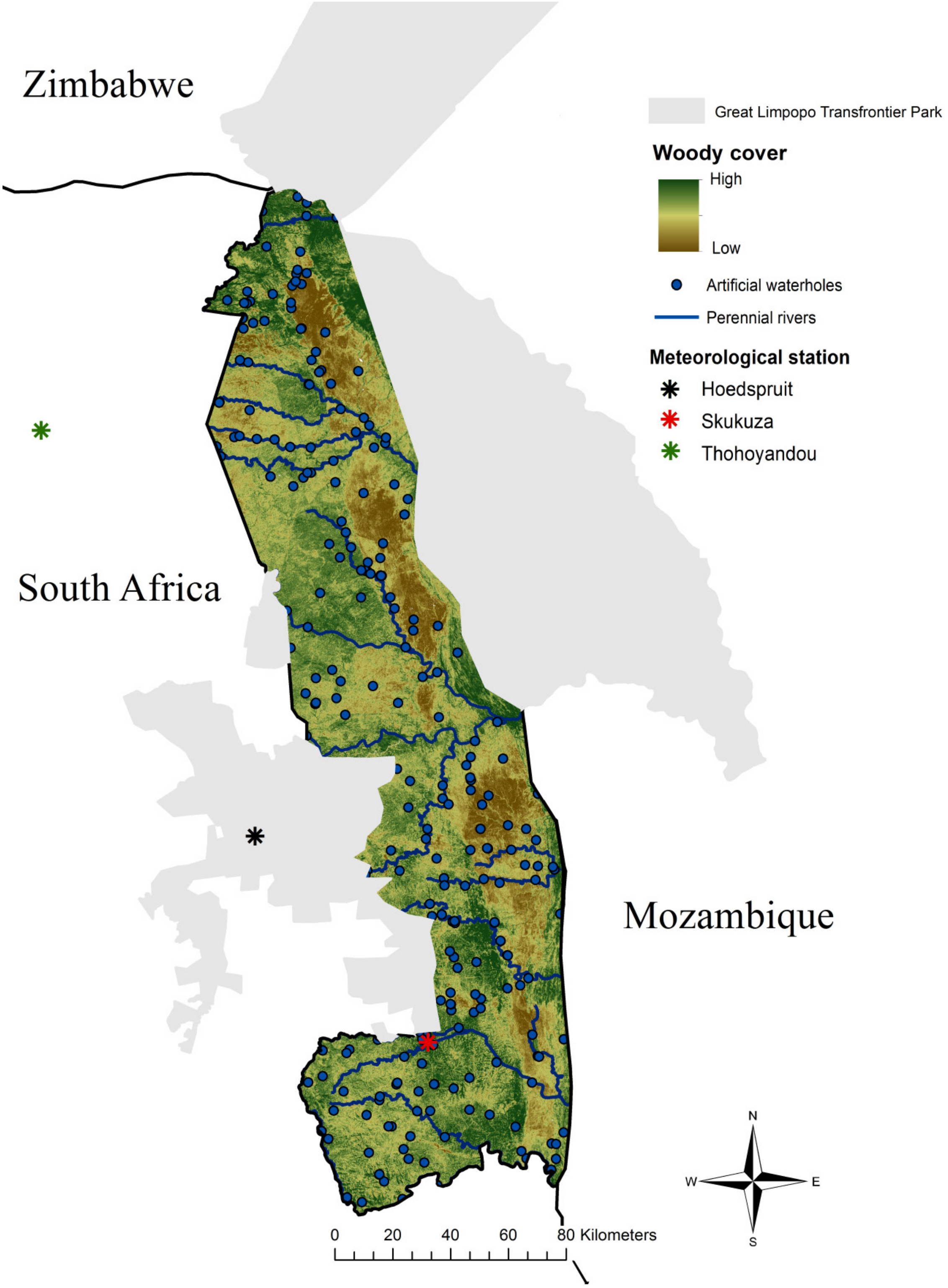


Figure 2.1. Map of Kruger National Park, showing the distribution of perennial rivers, artificial waterholes (Gaylard et al., 2003), meteorological stations (South African Weather services, Pretoria, South Africa), and woody cover (Bucini et al., 2010).

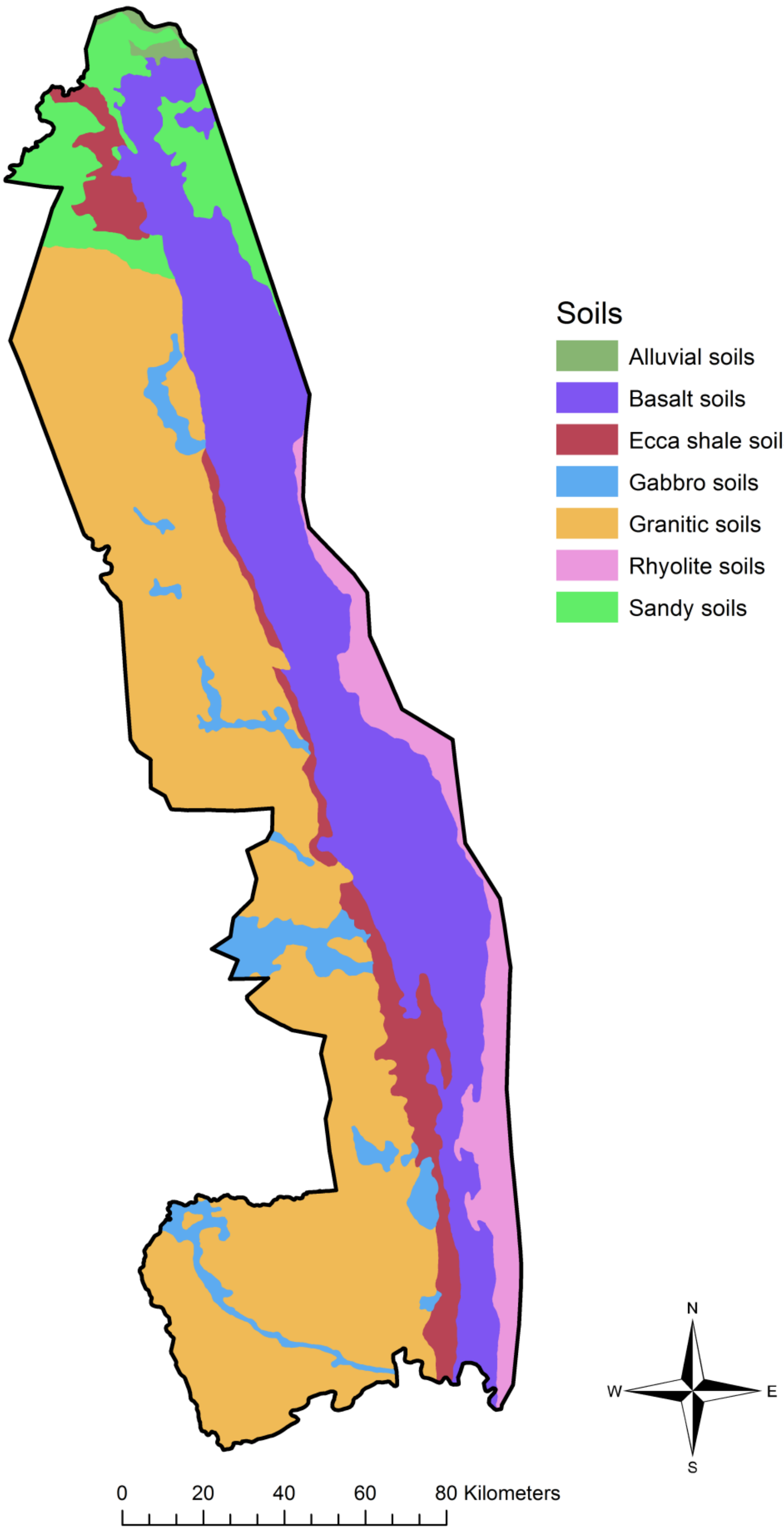


Figure 2.2. Map of Kruger National Park showing the various dominant soil types (Venter, 1990).

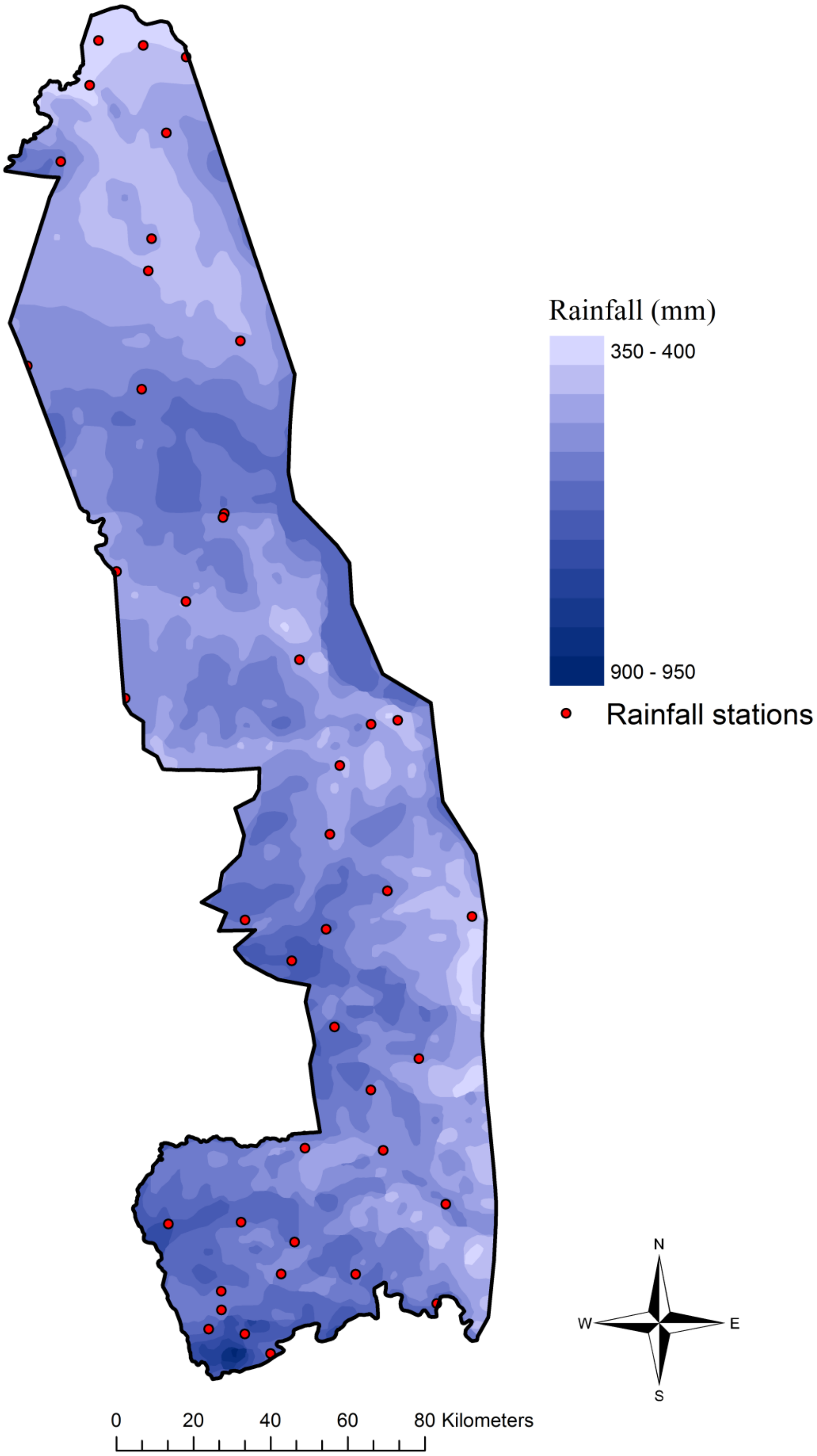


Figure 2.3. Map of Kruger National Park (KNP), showing spatially interpolated long-term mean annual rainfall (SANParks scientific services, Skukuza, South Africa).

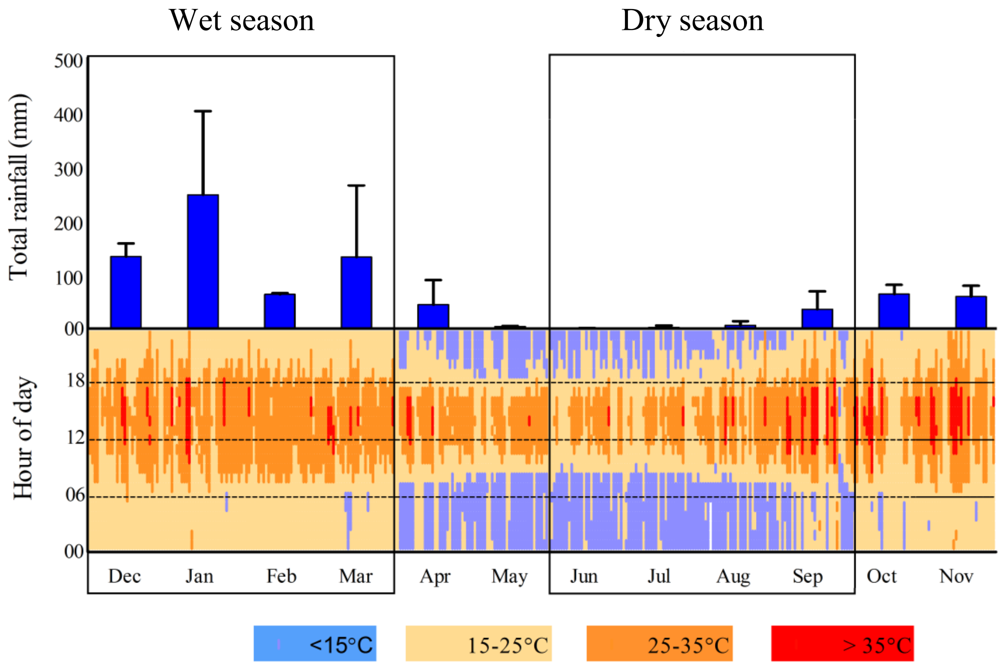


Figure 2.4. Mean total rainfall ± standard deviation (SD) from three meteorological stations located near Kruger National Park (Figure 2.1.) from June 2012 to March 2014 and corresponding mean hourly temperatures (South African Weather Services, Pretoria, South Africa). The blocks indicate the wet season (December inclusive to March inclusive) and the dry season (June inclusive to September inclusive).

Figure 2.5. Maps of Kruger national park showing the spatial and temporal variability in primary productivity as indexed by the Enhanced Vegetation Index (EVI). During the wet season (a to d) and during the dry season (e to h).

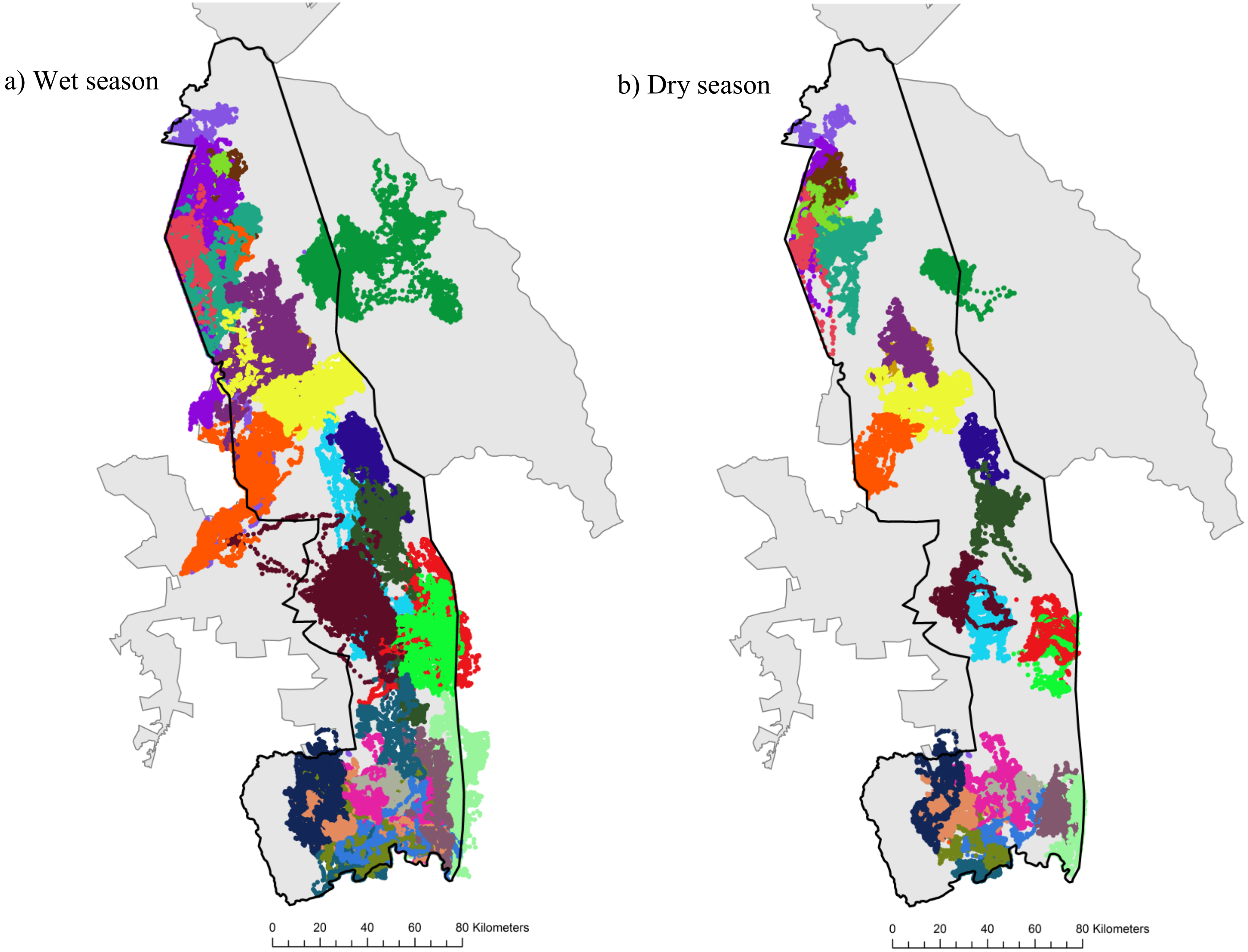


Figure 2.6. Map of Kruger National Park, showing the locations of the 26-collared elephant cows, during the (a) wet and (b) dry season.

Chapter 3. Environmental determinants of the movement patterns of elephants

Introduction

Conservation management actions directed at manipulating the distribution of animals through the availability of key resources have been central to past conservation initiatives. Initially, management supplemented key resources to buffer animals against the potential negative effects of resource scarcity (Pienaar, 1970; Pienaar, 1983; Smith, 2001). This ultimately led to the denaturalisation of animal space use and consequently the attenuation of herbivore impacts on vegetation (Smuts, 1978; Owen-Smith, 1996; Pienaar et al., 1997; Harrington et al., 1999; van Aarde and Jackson, 2007). Currently, the management of savanna elephants (*Loxodonta africana*) in South African National Parks centres on promoting ecological processes that may limit the distribution and number of elephants naturally, rather than manipulating them artificially (Pienaar et al., 1997; Owen-Smith et al., 2006; van Aarde and Jackson, 2007). The most likely driver of the processes that regulate the distribution and number of elephants is their spatial responses to the distribution and availability of resources (van Aarde et al., 2006; van Aarde and Jackson, 2007). Understanding the spatial responses of elephants to variation in environmental conditions and the consequences thereof may better inform management decisions on promoting ecological processes (see Boyce and McDonald, 1999; Nielsen et al., 2006).

Typically, researchers assessed the spatial responses of animals using locational data collected at a coarse temporal resolution, due to the limited battery life of tracking devices. Locational data collected at a coarse resolution limits researchers to an Eulerian approach when analysing their data (Nathan et al., 2008). The Eulerian approach considers changes that occur at locational points in space and is primarily concerned with the characteristics and the geographical area used by an animal (Nathan et al., 2008; van Moorter et al., 2015). The Eulerian approach is therefore synonymous with home range analyses that quantify the distribution or re-distribution (e.g. de Beer and van Aarde, 2008), and habitat selection patterns (e.g. Roever et al., 2013) of a population (Nathan et al., 2008; van Moorter et al., 2015). Recently, technological advances in animal tracking have increased the temporal resolution of locational data. Locational data collected at high temporal resolutions resulted in a number of analytical and computational difficulties, such as spatial and temporal autocorrelation (Nathan et al., 2008). To overcome some of these complications a large number of analytical routines have been developed (Horne et al., 2007; Gurarie et al., 2009; Kranstauber et al., 2012; Gurarie et al., 2015). Advances in animal tracking and analytical routines have marked a shift to a Lagrangian approach that aims to assess the behavioural responses of animals by considering how individuals change their movement (Nathan et al., 2008; Loarie et al 2009a; van Moorter et al., 2015; Kays et al., 2015). Currently, we base most of what we know about the spatial responses of elephants on studies using an Eulerian approach (de Beer and van Aarde, 2008; Loarie et al 2009a; Roever, 2013; Roever et al., 2014). Evaluating the movement behaviour of elephants may provide greater insight into the spatial responses of elephants to their environment (Nathan et al., 2008; Loarie et al 2009a; van Moorter et al., 2015; Kays et al., 2015).

Although tracking devices placed in collars do not directly record movement behaviour per se, analytical approaches that take advantage of high resolution locational data can approximate movement behaviour based on movement path characteristics (see Nathan et al., 2008 and references therein). For example, the dynamic Brownian bridge movement model (dBBMM) can be used to predict an animal's utilisation distribution and movement behaviour along its movement path (Horne et al., 2007; Gurarie et al., 2009; Kranstauber et al., 2012). The dBBMM is an improvement of the Brownian bridge movement model (BBMM) which incorporates the order of locations and the time elapsed between them to predict an animal's utilisation distribution (Horne et al., 2007). Unlike the BBMM, which assumes that an animal's movement remains constant along their entire path, the dBBMM allows for changes in behaviour (Kranstauber et al., 2012). To do this the dBBMM uses maximum likelihood statistics and Bayesian information criterion to determine change points along the animal's movement path (Gurarie et al., 2009; Kranstauber et al., 2012). Therefore, the Brownian motion variance (σ_m^2) which quantifies how irregular the path of an animal is, changes dynamically in response to changes in speed and turning angles along the movement path (Kranstauber et al., 2012). As an index of the individuals movement behaviour, low σ_m^2 values (regular paths and/or low speed) can be interpreted as an inactive behavioural state and high values as active (irregular paths and/or high speed) (Kranstauber et al., 2012; Byne et al., 2014) (see Figure 3.1.). Environmental factors related to the conditions the individual may have experienced along its movement path can be extracted using the utilisation distribution area around the movement path calculated using the dBBMM (Kranstauber et al., 2012; Byne et al., 2014) (Figure 3.1.). Consequently, the σ_m^2 can be a useful one-dimensional measure of movement behaviour (Kranstauber et al., 2012; Byne et al., 2014).

Here, I modelled the movement behaviour of 26 elephant breeding herds distributed across Kruger National Park (KNP) using dBBMM. I then evaluated how well environmental factors explain changes in their movement behaviour using a mixed effects modelling approach at multiple analytical scales (month, week, day, and within-day: night/day). Processes that affect animal behaviour may differ depending on the scale of analysis (Börger et al., 2006; Fryxell et al., 2008; van Beest et al., 2011). Therefore, a multiple-scale approach can potentially improve our understanding on how the movement behaviour of elephants reflects on their environment (Börger et al., 2006; Fryxell et al., 2008; van Beest et al., 2011). The aim of this study is to assess how the environment elephants are moving through affects their movement behaviour.

Animals reduce their activity when travelling through favourable habitats by adopting consistently low movement speeds with large turning angles (low σ_m^2) (Avgar et al., 2011; Kuefler et al., 2012; Avgar et al., 2013). Whereas, in unfavourable habitats animals tend to be in a more active behavioural state by adopting high movement speeds and small turning angles (high σ_m^2) (Avgar et al., 2011; Kuefler et al., 2012; Avgar et al., 2013). Therefore, in preferred habitats, elephants should have low σ_m^2 related to feeding or resting behaviours, whereas, in lower quality habitats elephants should have high σ_m^2. Based on previous studies on elephants, I tested the following predictions:

Season: Studies suggest that the optimal behavioural strategy for elephants comprise a switch from energy maximisation during the wet season to energy conservation during the dry season (e.g. Wittemyer et al., 2007; Loarie et al., 2009b; Birkett et al., 2012; Polansky et al., 2013). Therefore, during the wet season I predict that elephants will be consistently more active (high σ_m^2) in comparison to the dry season, when both food and water may be limited (de Beer et al., 2006; Harris et al., 2008).

Water (distance from water): Elephants need to visit water regularly to maintain body water reserves and for thermoregulation (Wright and Luck, 1984; Dunkin et al., 2013). Therefore, I expect distance from water to be an important explanatory variable in explaining changes in the movement behaviour of elephants during both seasons, among all scales (de Beer et al., 2006; Harris et al., 2008). Elephants prefer to be close to water (de Beer and van Aarde, 2008; Harris et al., 2008; Loarie et al., 2009a), therefore, I expect elephants to be in a less active behavioural state (low σ_m^2) when close to water, and in a more active behavioural state when far from water.

Vegetation structure (woody cover): Elephants predominately feed on grasses during the wet season, but as the dry season progresses they tend to shift their diet towards woody plants (Osborn 2004; Cerling et al., 2007; Cordon et al., 2011). Additionally, when it is hot elephants seek shade to reduce heat gain and maintain thermal comfort (Kinahan et al., 2007; Mole, 2014). Therefore, I expect woody cover to explain changes in the movement behaviour of elephants during both seasons. Furthermore, I expect elephants to be less active (low σ_m^2) in areas with high woody cover, indicative of them either foraging or resting.

Primary productivity (EVI): Elephants prefer areas with high primary productivity (Rasmussen et al., 2006; Wittemyer et al., 2008; Loarie et al., 2009b). Therefore, I expect elephants to be less active (low σ_m^2) in areas with high primary productivity. During the dry season, areas with high primary productivity are more patchily distributed. Therefore, I expect primary productivity to explain changes in the movement behaviour of elephants during the dry season, whereas, during the wet season areas with high primary productivity are more evenly distributed, and should not affect the movement behaviour of elephants.

Temperature: Although temperature is not a resource, elephants may need to make behavioural adjustments due to high temperatures (Kinahan et al., 2007; Mole, 2014) and these adjustments may be evident in their movement behaviour. For instance, elephants may shift their activity and be less active when it is hot to reduce metabolic heat gain (Rowe et al., 2013). Furthermore, high temperatures may restrict which resources elephants can use (Mole, 2014). Therefore, I expect temperature to explain changes in the movement behaviour of elephants during the wet season when it is typically hotter. Coherently, I expect elephants to be less active (low σ_m^2) when it is hot, indicative of them resting.

Methods

Study area

Please see chapter two (page 8) for details on the study area, Kruger National Park.

Study animals

Please see chapter two (page 9) for details on the study animals used in this study.

Movement behaviour of elephants

To assess how the movement behaviour of elephants changed with time and across space the complete movement path of each individual was subset into wet and dry seasons. Therefore, the use of the word season in this chapter denotes a different time of the year and not an analytical scale. I fitted dynamic Brownian bridge movement models to the seasonal paths to obtain Brownian motion variances (σ_m^2), assuming isotopic diffusive motion between consecutive locations (Horne et al., 2007; Kranstauber et al., 2012). Based on the hourly temporal resolution of the locational data I specified a moving window size of 11 hours and a margin of seven, making it possible to detect potential behavioural shifts between daytime and night-time (Kranstauber et al., 2012). Furthermore, the location error was set to 23 m for all locations. The σ_m^2 derived from the dBBMM where then subset into analytical scales (month, week, day, and within day: night/day). To reduce the influence of missed fixes on σ_m^2 (Kranstauber et al., 2012) paths with less than 80 % of their fixes were excluded from subsequent analysis. Finally, I calculated the mean σ_m^2 and 95 % utilisation distribution area (UD) for each individual for all time steps at each analytical scale during both seasons. All analyses were implemented in the R statistical computing environment (R Core Team, 2013) along with the package ‘move’ (Kranstauber et al., 2014). Please see Figure 3.2.a. for a visual representation of the above approach.

Environmental factors

Environmental factors (Table 3.1) known to influence the distribution and habitat selection patterns of elephants as implied in earlier studies (Rasmussen et al., 2006; de Beer and van Aarde, 2008; Harris et al., 2008; Loarie et al., 2009a,b; Roever et al., 2012) that I selected included distance from water sources, vegetation structure, an index of primary productivity, and temperature. The Enhanced Vegetation Index (EVI) from the Moderate Imaging Spectrometer served as an index of vegetation productivity (Rasmussen et al., 2006; Huete et al., 2002) [Moderate Resolution Imaging Spectroradiometer 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]. Hourly temperature data was obtained from the meteorological station nearest to the individual movement path; Skukuza, Hoedspruit or Thohoyandou (Figure 2.1.) (South African Weather Services, Pretoria, South Africa). Separate water layers were created as the Euclidean distance of the centroid of each grid cell to the nearest water source for each season with the exclusion of ephemeral rivers during the dry season (Roever et al., 2012). Temporally dynamic variables were averaged over the relevant analytical scale and the mean value for the environmental factor was then extracted for each 95 % utilisation distribution area. Please see Figure 3.2.b. for a visual representation of the above approach.

Modelling procedure

To evaluate how well environmental factors (Table 3.1.) explain changes in the movement behaviour (σ_m^2) of elephants, I used generalized additive mixed effects models (GAMMs). GAMMs were fitted to the data using the *'nlme'* package in R (Pinheiro et al. 2013). To meet distributional assumptions, log-transformed σ_m^2 was fitted as the response variable in all models (Wood, 2006). I only included individuals at each analytical scale in the analysis with at least two σ_m^2 estimates. Spearman correlation coefficients calculated between pairs of environmental factors were low (spearman rank correlation (r_s) < 0.6) and subsequently none of them were excluded. GAMMs were fitted by restricted maximum likelihood estimation method (REML) with penalized cubic regression splines. REML was used to produce an unbiased estimation of the variance parameters when there are an increased number of fixed parameters in the model (Wood, 2006).

To account for dependencies between observations from the same individual within and between years, I included individual identity (EID) together with year as first- and second-level random effects (Pinheiro and Bates, 2000). I fitted either spatial or temporal autocorrelation structures (Pinheiro and Bates, 2000). The inclusion of either spatial or temporal autocorrelation was evaluated using Akaike information criterion (AIC) (Pinheiro and Bates, 2000). Spatial correlation between estimated σ_m^2 was modelled using the harmonic mean of the coordinates, and temporal correlation was modelled by numbering consecutive σ_m^2 estimates for each individual (van Beest et al., 2011). Depending on which function provided the best fit based on AIC I used the 'corExp' or 'corGaus' function (Pinheiro and Bates, 2000).

Once the distributional assumptions of the mixed model structure were fulfilled, (Table 3.2) best models were selected using a multimodal selection procedure (Burnham and Anderson, 2002). For each analytical scale, I calculated a candidate GAMM for all combinations of environmental factors (see Chapter 7, Appendix I to Appendix X). The resulting models were ranked using their AIC and the Akaike weight of each model (ω_i) (Burnham and Anderson, 2002). These served as competing hypotheses to explain changes in elephant movement behaviour. The strength of support for the best model and alternate best models was assessed using AIC differences (ΔAIC) between the approximate best model (ΔAIC = 0) and alternate candidate models. Candidate models with ΔAIC < 2 were considered as good as the best model and have substantial support as an alternative best model (Burnham and Anderson, 2002). Model selection was undertaken using the '*MuMIn*' package in R (Barton, 2014; R Core team, 2013). To find the relative importance of each environmental factor I calculated parameter weights based on ω_i for all models. These range from zero to one, where parameter values closer to one indicated higher importance as explanatory variables for changes in elephant movement behaviour (Burnham and Anderson, 2002). Please see Figure 3.2.c. for a visual representation of the above approach.

Results

My assessment of elephant movement behaviour as indexed by σ_m^2 suggests that elephants were less active during the dry season than during the wet season (Figure 3.3.). Furthermore, variability in the movement behaviour of elephants was greater during the wet season than during the dry season at all scales (Figure 3.3.). At the within-day scale, during both seasons, elephants were less active during the night and more active during the day (Figure 3.3.).

Environmental factors that could best explain changes in elephant movement behaviour were different between the wet and dry seasons and among temporal scales (Table 3.3.). The apparent best and alternate models explained between 21 % and 50 % of the variation in elephant movement behaviour (Table 3.3.). I considered environmental factors retained in the apparent best and alternate models important in explaining changes in elephant movement behaviour (Table 3.3.). Furthermore, I considered variables important in explaining changes in elephant movement behaviour when their relative importance was close to one (see Chapter 7, Appendix XI for full table). The partial response curves (Figure 3.4. to Figure 3.7.) show the relationship of the partial residuals of the response variable (log σ_m^2) and the smoothed explanatory terms (environmental factors) in the best approximate models (Table 3.3.).

Water (distance from water)

Distance from water was important in explaining changes in elephant movement behaviour at all scales during the dry season (Table 3.3.). Furthermore, distance from water had a high relative variable importance (1) at the weekly, daily, and within-day scale during the day. Distance from water was also important in explaining changes in elephant movement behaviour during the wet season with high relative variable importance (1) at the daily and within-day scale during the day. Although distance from water did contribute as an explanatory variable with high relative variable importance during the wet season at the daily and within-day scale during the day (Table 3.3.), the partial response curves suggest it had a negligible effect ($p > 0.05$) (Figure 3.4.). Whereas, during the dry season, at the daily and within-day scale during the day, elephants increased their activity significantly ($p < 0.002$) as they got further away from water sources, most likely indicative of them moving quickly through unfavourable habitat ($p < 0.002$) (Figure 3.4.).

Vegetation structure (woody cover)

Vegetation structure as indexed by woody cover (Bucini et al., 2010) was important in explaining changes in elephant movement behaviour during both season and at all scales (Table 3.3.). Coherently, woody cover had high relative variable importance (0.75 – 1). During both seasons, and among all scales, elephants decreased their activity significantly ($p < 0.002$) with increasing woody cover, indicative of them either foraging or resting. (Figure 3.5.).

Primary productivity (EVI)

Primary productivity as indexed by EVI was important in explaining changes in elephant movement behaviour during both seasons and among all scales, except during the wet season at the monthly scale (Table 3.3.). EVI had high relative variable importance (0.73 – 1), except during the wet season at the monthly scale (0.06). During the wet season at the monthly and weekly scale, elephants decreased their activity in areas with increasing EVI ($p < 0.006$) (Figure 3.5.). Although EVI did contribute as an explanatory variable with high relative variable importance during the dry season at the weekly and daily scale (Table 3.3.), the partial response curves suggest it had a negligible effect ($p > 0.05$) (Figure 3.6.). However, during the dry season at the weekly and daily scale elephants decreased their activity significantly with increasing EVI ($p < 0.006$) (Figure 3.6.). At the finer within-day scale, the relationship between elephant movement behaviour and EVI was more complex. The elephants were least active in areas with low EVI values and increased their activity with increasing EVI until it peaked and then decreased again with higher EVI values ($p < 0.043$) (Figure 3.6.).

Temperature

Temperature was important in explaining changes in elephant movement behaviour during the wet season, among all scales (Table 3.3.). Coherently, temperature had a high relative variable importance (0.67 - 1) during the wet season, among all scales. Furthermore, temperature was important at scales finer than a week during dry season (0.81 – 1) (Table 3.3.). Even though temperature did contribute as an explanatory variable with high relative variable importance during the wet season at the monthly and weekly scale (Table 3.3.), the partial response curves suggest it had a negligible effect ($p > 0.05$) (Figure 3.7.). Furthermore, temperature had a negligible affect during the dry season at the within-day scale, during the day ($p = 0.173$) (Figure 3.7.). Elephants increased their activity significantly with increasing temperatures ($p < 0.006$) in the wet season among scales shorter than a week (Figure 3.7.). During the dry season, elephants increased their activity with increasing temperature ($p < 0.019$) at the daily and within-day scale at night (Figure 3.7.).

Discussion

The most likely driver of the ecological processes that regulate the distribution and number of elephants is their spatial response to variation in their environment (van Aarde et al., 2006; van Aarde and Jackson, 2007; Owen-Smith, 2014). Here, I measured the spatial responses of elephants as changes in their movement behaviour, indexed by the Brownian motion variance (σ_m^2) (Kranstauber et al., 2012). Elephants should be less active (low σ_m^2) in preferred habitats related to feeding or resting behaviours, whereas, in lower quality habitats elephants should be more active (high σ_m^2). In summary, the movement behaviour of the elephant breeding herds varied greatly and environmental factors that could best explain the variation differed between seasons and among temporal scales.

As predicted, elephants were more active during the wet season than during the dry season. Expectedly, distance from water could explain changes in the movement behaviour of elephants during the dry season among all temporal scales. Unexpectedly, during the wet season distance from water could only explain changes in movement behaviour at the daily and within-day scale at not at the monthly and weekly scales. As expected, vegetation structure could explain changes in elephant movement behaviour during both seasons and elephants were less active in areas with high woody cover. Unpredictably, primary productivity could explain changes in elephant movement behaviour during both seasons and not just during the dry season. I expected elephants to be less active in areas with high primary productivity, indicative of them feeding. At longer temporal scales, elephants were more active in areas with low EVI. Conversely, at the within-day scale elephants were less active in areas with low EVI. When it is hot the energetic cost of being active may increase

(Langman et al., 2012; Rowe et al., 2013) and unexpectedly elephants increased their activity with increasing temperature.

In this study, elephants were consistently less active during the dry season in comparison to the wet season. This supports previous studies that suggest that the optimal behavioural strategy for elephants comprise a switch from energy maximisation during the wet season when food and water are plentiful to energy conservation during the dry season (e.g. Wittemyer et al., 2007; Loarie et al., 2009b; Birkett et al., 2012; Polansky et al., 2013). During the wet season, the increased availability of water sources and forage may allow elephants to be more selective of what and where they eat and subsequently elephants may travel further distances in search of high quality forage. Whereas, during the dry season, elephants probably become less selective in what they eat and spend more time close to water to reduce travelling costs between forage and water sources.

Elephants need water for several physiological reasons (Wright and Luck, 1984; Dunkin et al., 2013) and their distribution and demography are limited by its availability (Chamaillé-Jammes et al., 2007a; Harris et al., 2008; de Beer and van Aarde, 2008; Loarie et al., 2009a,b; Shannon et al., 2009, Young et al., 2009). Therefore, it is not surprising that distance from water was an important determinant of the movement behaviour of elephants during the dry season when its availability and distribution my impose limitations (Loarie et al., 2009a; Roever et al., 2012). When it is hot, elephants can lose up to 100 l of water through cutaneous evaporative water loss and elephants wet their skin directly to cool themselves down (Dunkin et al., 2013; Mole, 2014). Therefore, the importance of water during the hot wet season at the daily and within-day scale can most likely be explained by their need to replenish water reserves and to thermoregulate (Dunkin et al., 2013; Mole, 2014). In the wet season, the importance of water is most likely less important at longer temporal scales because of its increased availability, which results in less variation in distance from water at longer temporal scales (Chapter 7, Appendix XIII).

In the dry season, elephants in Hwange National Park (HNP), Zimbabwe increased their speed when close to water, suggestive of elephants minimising travelling time between forage and water (Chamaillé-Jammes et al., 2013). However, in this study, elephants in both seasons were least active when close to water. This discrepancy may be due to the depletion of forage around artificial waterholes in HNP resulting in elephants increasing their activity by adopting high movement speeds and small turning angles. Compromising their necessity to stay close to water and conserve energy by their need to search for forage (Redfern et al., 2003; Loarie et al., 2009b; Polansky et al., 2013). At fine spatiotemporal scales, we have a limited understanding on when elephants use water and what the consequences thereof are for their spatial use patterns. For instance, we know that water availability has demographic consequences (Chamaillé-Jammes et al., 2007a), but we do not understand the underlying processes. This warrants further research, particularly due to the importance of water manipulation as a management option (Owen-Smith, 1996; Brits et al., 2002; de Beer et al., 2006; Chamaillé-Jammes et al., 2007a, b; van Aarde and Jackson, 2007; Loarie et al., 2009a; Shannon et al., 2009; Shrader et al., 2010).

Trees provide both shade (Kinahan et al., 2007) and forage for elephants (Harris et al., 2008; Loarie et al., 2009a; Roever et al., 2012). Unsurprisingly, woody cover was an important factor in explaining changes in elephant movement behaviour during both seasons and among all scales. Typically, animals adjust their behaviour and reduce their activity when travelling through resource-rich areas, by adopting consistently low movement speeds with large turning angles (Avgar et al., 2011; Kuefler et al., 2012; Avgar et al., 2013). Coherently, resource-poor areas may result in increased activity (Avgar et al., 2013). Elephants adjusted their movement behaviour in response to apparent resource quality and quantity and decreased their activity in areas with high woody cover, indicative of them either foraging or seeking shade. Additionally, elephants decreased their activity with increasing EVI at the weekly and daily analytical scales. However, at the within-day scale elephant activity was lowest in areas with low primary productivity. Interestingly, these low values correspond to recently burnt areas. Post-fire stimulation of plant nutrients may explain their decreased activity in burned areas (Eby et al., 2014), which are hidden at the broader temporal scales.

The behavioural decisions resulting in the modelled movement behaviour are dependent on the physiological requirements and internal state of an individual (Senft et al., 1987; Rettie and Messier 2000; Börger et al., 2006; van Beest et al., 2011). Although most behavioural decisions made by elephants are probably aimed at acquiring food to meet their energetic requirements (Guy, 1976) behavioural adjustments in response to the thermal environment may influence their movement (Kinahan et al., 2009; Mole, 2014). In this study, temperature was important in explaining changes in elephant behaviour at daily and within-day analytical scales during both seasons. Counterintuitively, elephants increased their activity with increasing temperature, where the energetic cost of being active may increase (Langman et al., 2012; Rowe et al., 2013). However, temperatures were mostly below core body temperature (36.4 °C) (Kinahan et al., 2007), and therefore may not have imposed limitations on elephant behaviour. Furthermore, in KNP, the hottest time of the year is wet (Figure 2.4.) and elephants are most likely able to thermoregulate and maintain water requirements relatively easily.

This study provides limited insight into how elephants adjust their movement behaviour in response to the distribution and availability of key resources and it contributes little to what we already know about the spatial use patterns of elephants. This is most likely due to a combination of factors. One of the most pertinent contributing factors is that I did not include the influence of their absolute spatial position in my evaluation of their movement behaviour i.e. that elephants do not make their movement choices based purely on their immediate surroundings, but also on where they are travelling to or from. Indeed, I did include distance from water as a spatial variable, but the distribution of other resources (such as woody cover) in relation to the absolute spatial position of elephants will most likely also influence the way they move. Another limiting factor of this study is the use of a one-dimensional measure (σ_m^2) as an index of movement behaviour, because it can only separate a limited amount of behaviours (Kranstauber et al., 2012). Therefore, two relatively different movement paths (e.g. a movement path with high variation in turning angles and a movement path with high variation in speed) could result in similar Brownian motion variance values (Kranstauber et al., 2012).

Conservation management needs to be able to predict how species may respond to natural and anthropogenic changes in their environment, particularly, when management actions are directed at manipulating the distribution of animals through the availability of key resources. If we fail to understand the processes driving animal spatial use patterns, any predictions and subsequent inferences could be incorrect. Although this study has limitations, it does represent another step in disentangling the spatial responses of elephants to their environment. Furthermore, it confirms that elephants adjust their movement in response to their environment, as required for the non-equilibrium management of elephant populations (Young and van Aarde, 2010; van Aarde and Jackson, 2007).

Tables

Table 3.1. Description of the environmental factors fitted as smoothed effects in the generalized additive mixed effects modelling approach used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephants.

Environmental factor	Description	Temporal resolution	Spatial resolution (m)
Distance from water	Distance from water calculated for each season with the exclusion of ephemeral water sources in the dry season (Roever et al., 2012).	Seasonally	23.5
Vegetation structure	Percentage woody cover (Bucini et al., 2010) as an index of vegetation structure.	Static composite (see Bucini et al., 2010)	23.5
Primary productivity	Enhanced vegetation index (EVI) from the Moderate Imaging Spectrometer as an index of vegetation productivity (Wittemyer et al., 2008; Huete et al., 2002).	16 day composite	250
Temperature	Temperature data from three meteorological stations namely Skukuza, Hoedspruit, and Thohoyandou (South African Weather services, Pretoria, South Africa).	Hourly	Three point sources

Table 3.2. Overview of the generalized additive mixed effects modelling structure used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephants.

Temporal scale and model structure		Dry season	Wet season
Month	Random effects	0.171	0.109
	Temporal correlation	NR	NR
	Spatial correlation	863.989 m	NR
	n	118	73
Week	Random effects	0.166	0.071
	Temporal correlation	0.816	0.89
	Spatial correlation	NR	NR
	n	665	568
Day	Random effects	0.192	0.223
	Temporal correlation	0.529	1.06
	Spatial correlation	NR	NR
	n	5028	4638
Daytime*	Random effects	0.227	0.294
	Temporal correlation	0.410	0.734
	Spatial correlation	NR	NR
	n	4792	3511
Night-time*	Random effects	0.131	0.279
	Temporal correlation	0.469	0.698
	Spatial correlation	NR	NR
	n	4666	3407

Notes: elephant identity shows the standard deviation (SD) in the full mixed-effects model. Spatial correlation indicates the range of the spatial autocorrelation in the models (by using the harmonic mean centre of the coordinates). Temporal correlation shows the range of the temporal autocorrelation in the models (integer valued continuous-time measures starting from the first σ_m^2 estimates taken). Both spatial and temporal correlations were fitted using the 'corExp' -function. NR = not retained in final model. *Within-day temporal scale.

Table 3.3. Summary of selected best and alternative generalized additive mixed effects models (ΔAIC ≤ 2) using environmental factors (Table 3.1.) to explain changes in the movement behaviour (indexed by Brownian motion variance,log σ_m^2) of 26-collared elephants.

Season	Scale	Model	df	R^2	AIC	ΔAIC	ω_i
Dry	Month	EVI* + woody cover*	9	0.43	108.95	0.00	0.47
		EVI*+ woody cover*+ distance from water	11	0.45	110.54	1.59	0.14
	Week	EVI + woody cover* + distance from water	11	0.50	770.45	0.00	0.96
	Day	EVI + woody cover*+ distance from water*+ temperature*	13	0.31	11062.02	0.00	0.99
	Daytime$^{\#}$	EVI*+ woody cover*+ distance from water*+ temperature	13	0.21	12373.19	0.00	1.00
	Night-time$^{\#}$	EVI*+ woody cover*+ temperature*	11	0.29	13951.72	0.00	0.70
Wet	Month	Woody cover*+ temperature	8	0.35	78.89	0.00	0.58
	Week	Woody cover*+ EVI*+ temperature	11	0.39	846.40	0.00	0.73
	Day	Woody cover*+ distance from water + temperature*+ EVI*	13	0.38	9178.05	0.00	0.99
	Daytime$^{\#}$	Woody cover*+ distance from water + temperature*+ EVI*	13	0.28	7822.63	0.00	0.73
	Night-time$^{\#}$	Woody cover*+ EVI*+ temperature*	11	0.34	9841.28	0.00	0.78

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models are ranked using Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df = degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights. Environmental factors retained in the best set of models are ordered by their relative importance in the full set of models (see S5 for full table). *model parameter coefficient significant ($p<0.05$). $^{\#}$Within-day temporal scale.

Figures

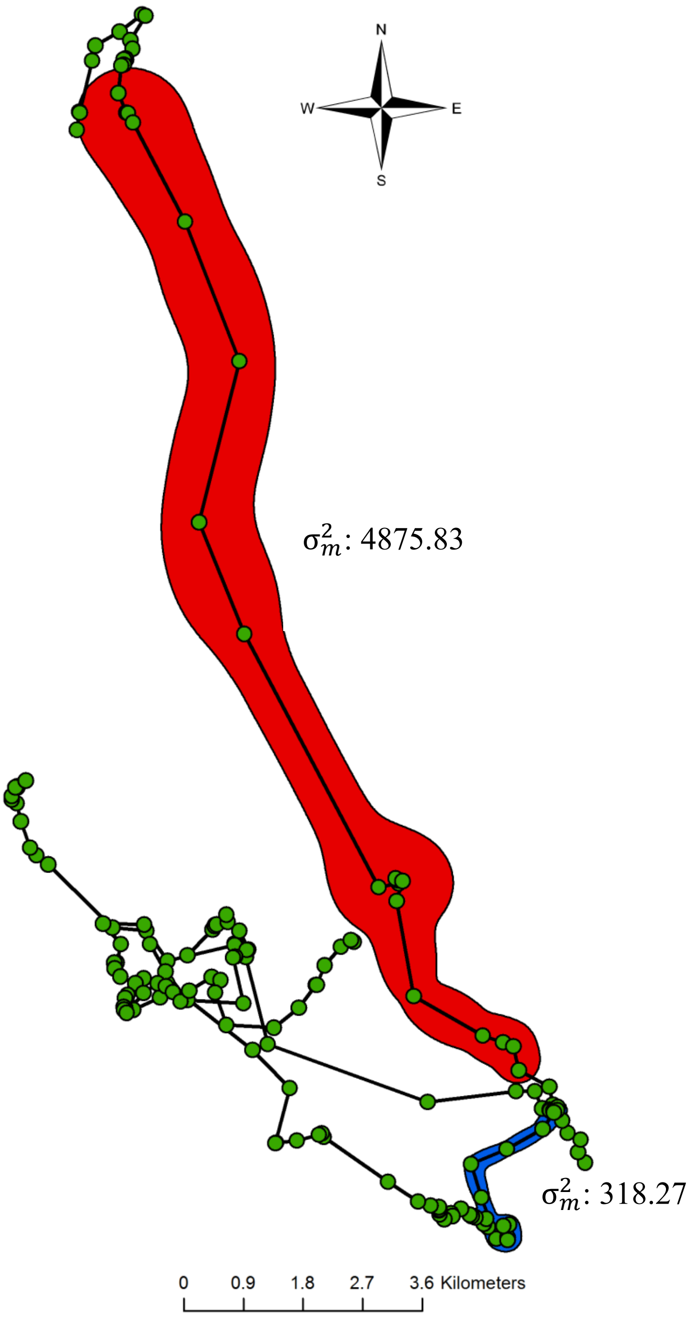
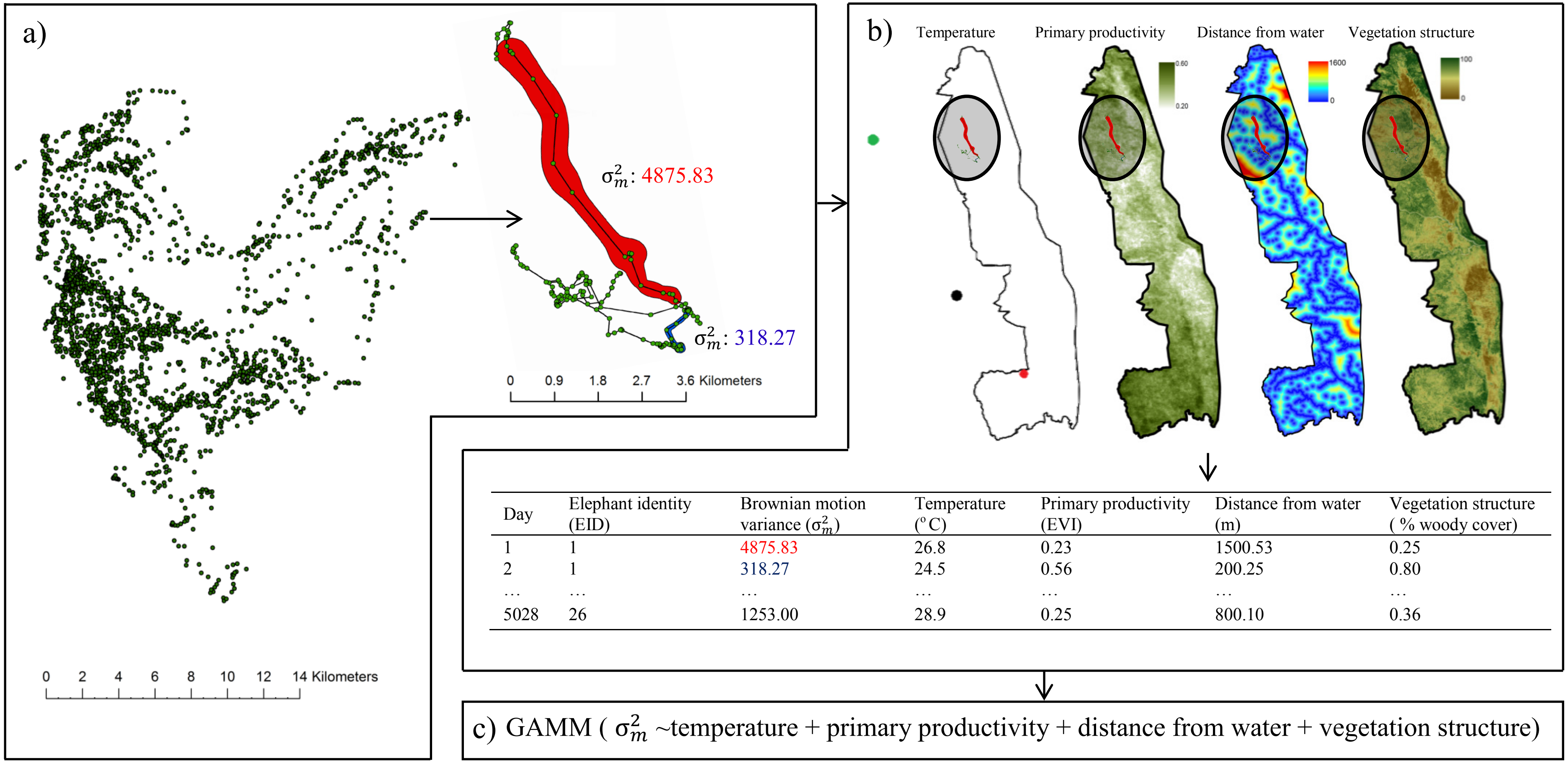


Figure 3.1. Contrasting mean daily Brownian motion variances (σ_m^2) and 95 % utilisation distribution area derived from the dynamic Brownian bridge movement model for a single elephant-breeding herd. Green dots represent hourly locations. The Brownian motion variance is relatively larger in the area shaded in red in comparison to the area shaded in blue, due to the elephant adopting high movement speeds and smaller turning angles.



Day	Elephant identity (EID)	Brownian motion variance (σ_m^2)	Temperature (° C)	Primary productivity (EVI)	Distance from water (m)	Vegetation structure (% woody cover)
1	1	4875.83	26.8	0.23	1500.53	0.25
2	1	318.27	24.5	0.56	200.25	0.80
…	…	…	…	…	…	…
5028	26	1253.00	28.9	0.25	800.10	0.36

c) GAMM (σ_m^2 ~temperature + primary productivity + distance from water + vegetation structure)

Figure 3.2. Visual representation of the approach used in this chapter. The temporal scale of interest in this example is the daily scale. a) Elephant movement behaviour: the locational points for each elephant were divided into wet and dry seasons and a dynamic Brownian Bridge movement model was fitted to the locational points to obtain Brownian motion variances (σ_m^2) and a mean σ_m^2 for each day. Furthermore, a 95 % utilization distribution area was calculated for each day (indicated by red and blue surrounding the points). b) Environmental factors: mean temperature, primary productivity (EVI), distance from water, and vegetation structure (woody cover were) were then extracted for each 95 % utilization distribution area. c) Modelling procedure: a generalised additive mixed effects model was fitted to the data to determine which of the environmental factors (means) best explain changes in daily σ_m^2.

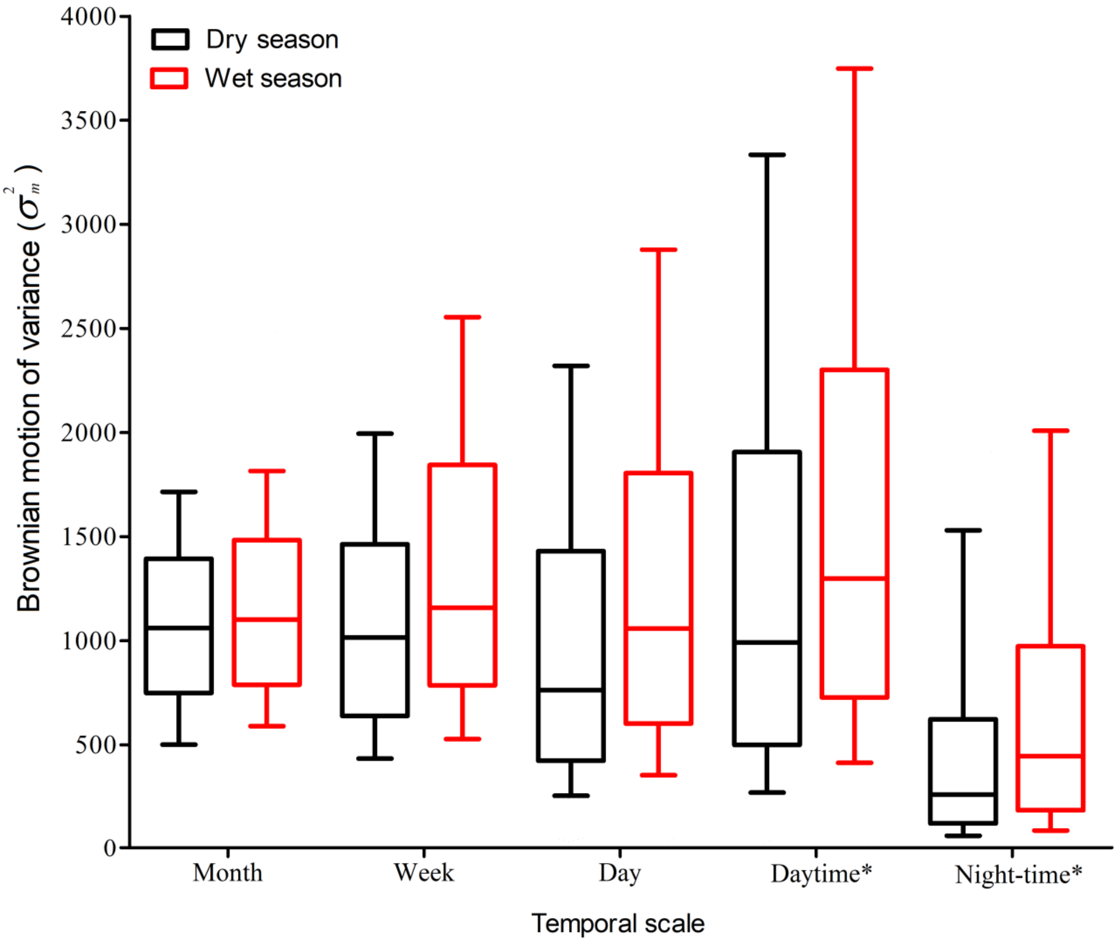


Figure 3.3. Variation in the movement behaviour of 26 female elephants as indexed by Brownian motion variance (σ_m^2), among temporal scales during the dry (black) and wet (red) season. *Within-day temporal scale

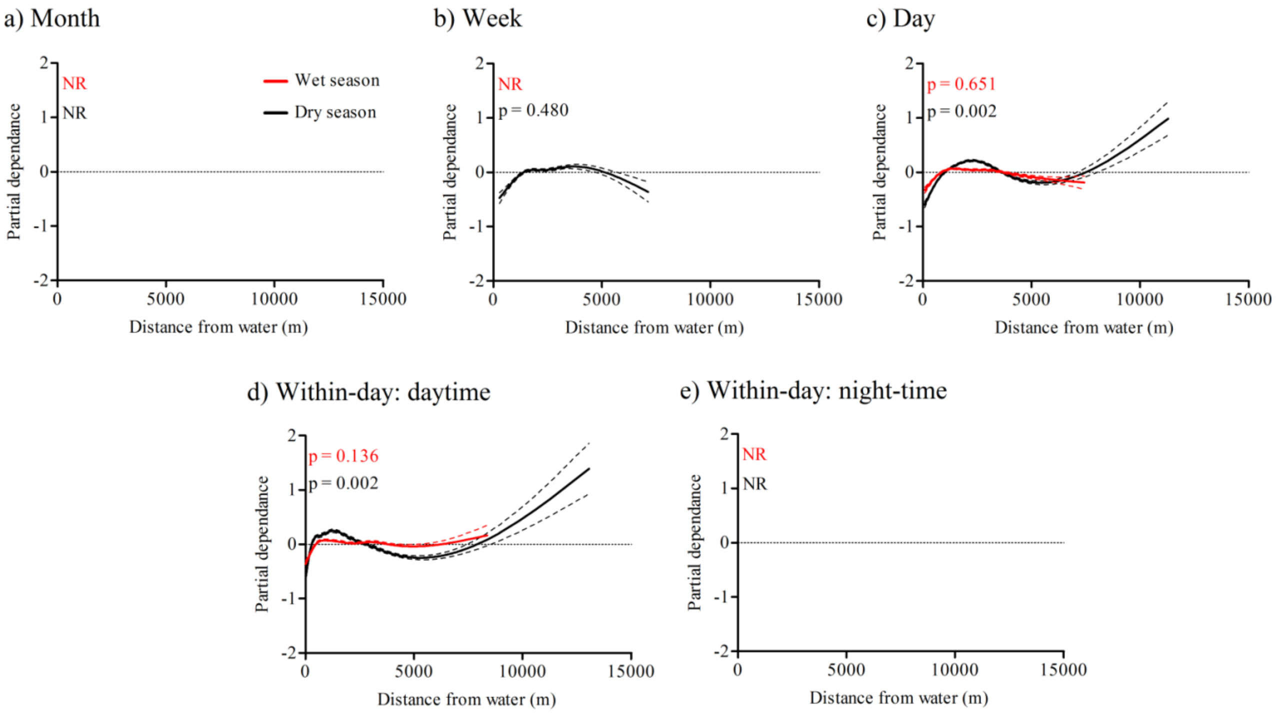


Figure 3.4. Partial dependence of Brownian motion variance (σ_m^2) on distance from water in selected best generalised additive mixed effects models (a to e). Plots are centred to have zero means, and it is the trend, rather than the actual values, that describes the patterns of dependence. Lines show predicted values in corresponding colours for the dry and wet season. Dashed lines represent standard errors. p values represent smooth term significance in the selected best model. NR = not retained in the selected best model. *Within day temporal scale

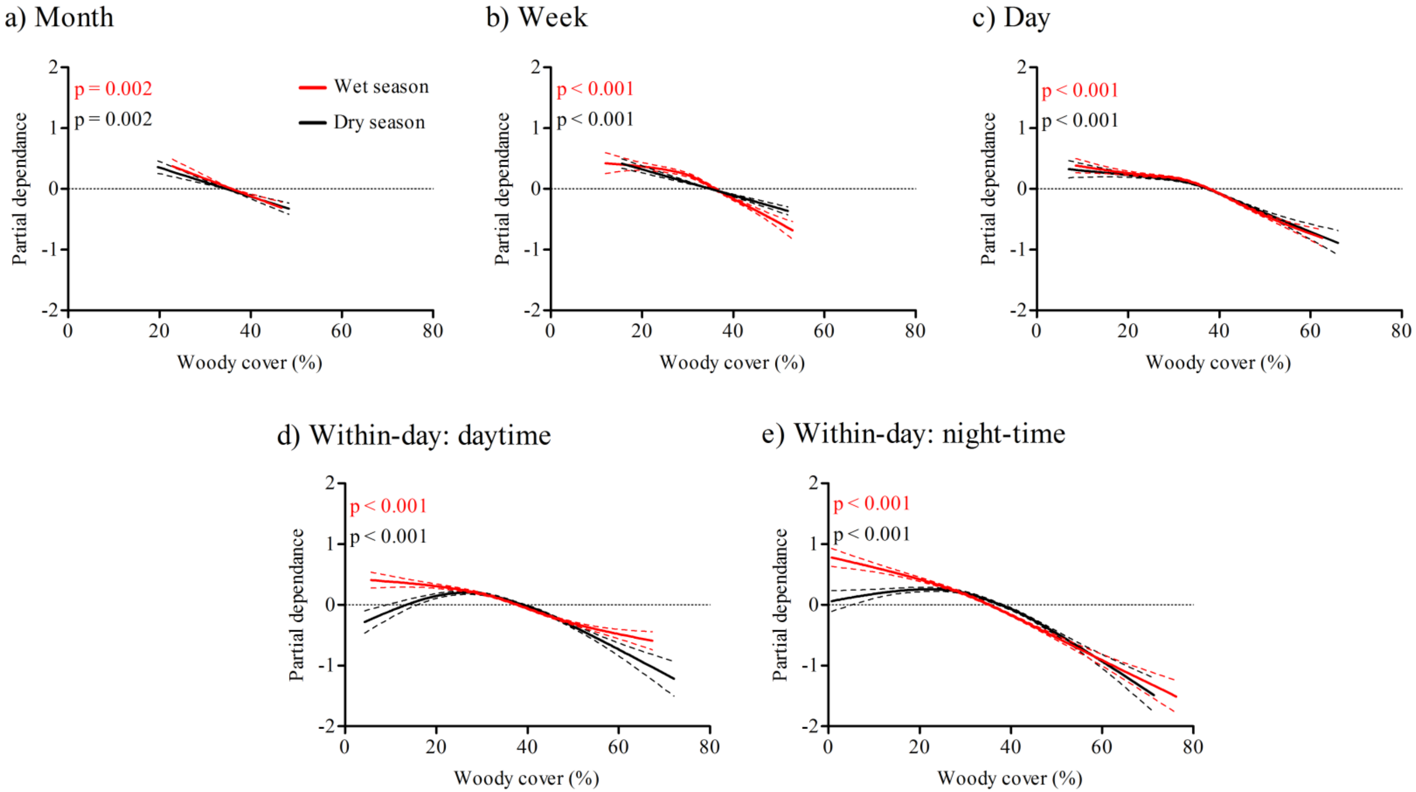


Figure 3.5. Partial dependence of Brownian motion variance (σ_m^2) on woody cover in selected best generalised additive mixed effects models (a to e). Plots are centred to have zero means, and it is the trend, rather than the actual values, that describes the patterns of dependence. Lines show predicted values in corresponding colours for the dry and wet season. Dashed lines represent standard errors. p values represent smooth term significance in the selected best model. NR = not retained in the selected best model. *Within day temporal scale

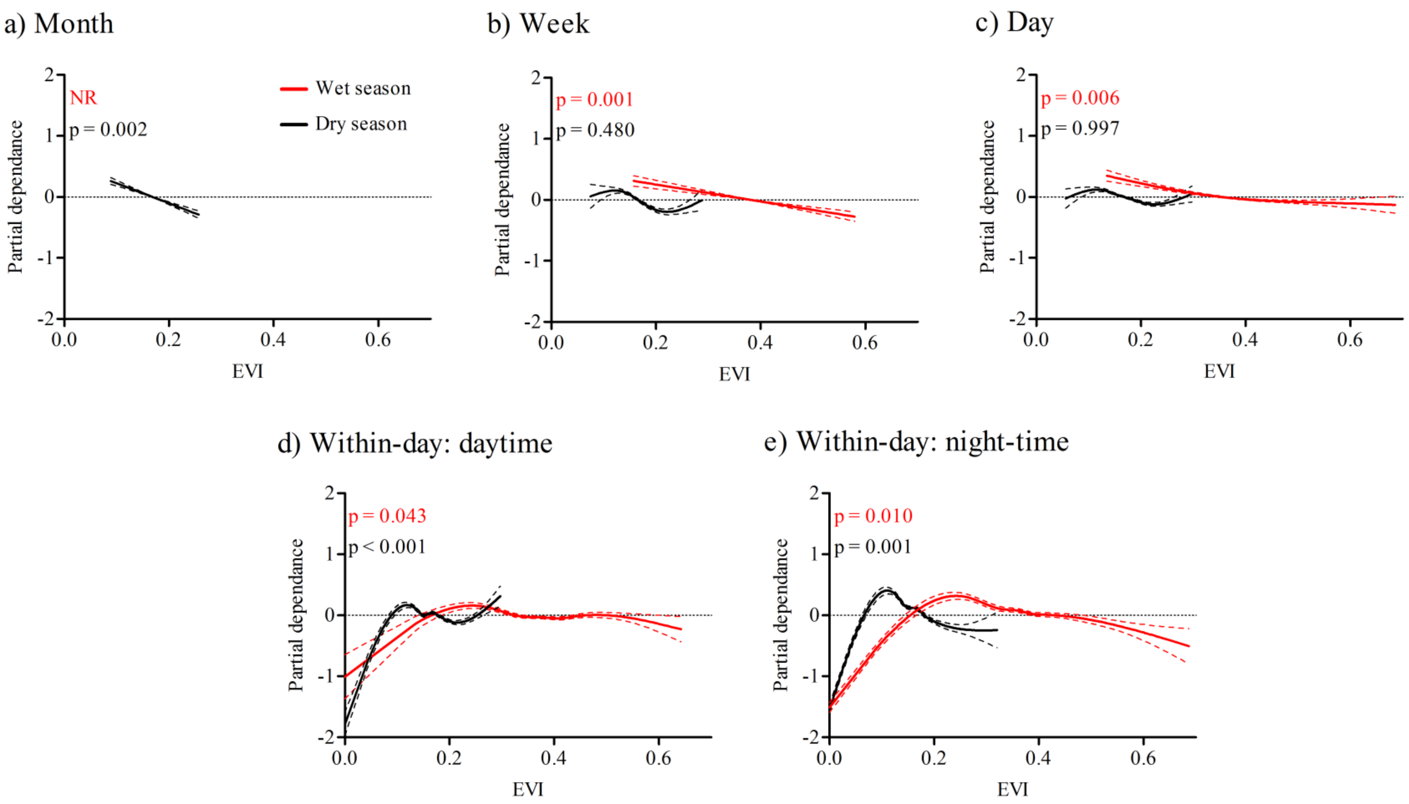


Figure 3.6. Partial dependence of Brownian motion variance (σ_m^2) on EVI in selected best generalised additive mixed effects models (a to e). Plots are centred to have zero means, and it is the trend, rather than the actual values, that describes the patterns of dependence. Lines show predicted values in corresponding colours for the dry and wet season. Dashed lines represent standard errors. p values represent smooth term significance in the selected best model. NR = not retained in the selected best model. *Within day temporal scale

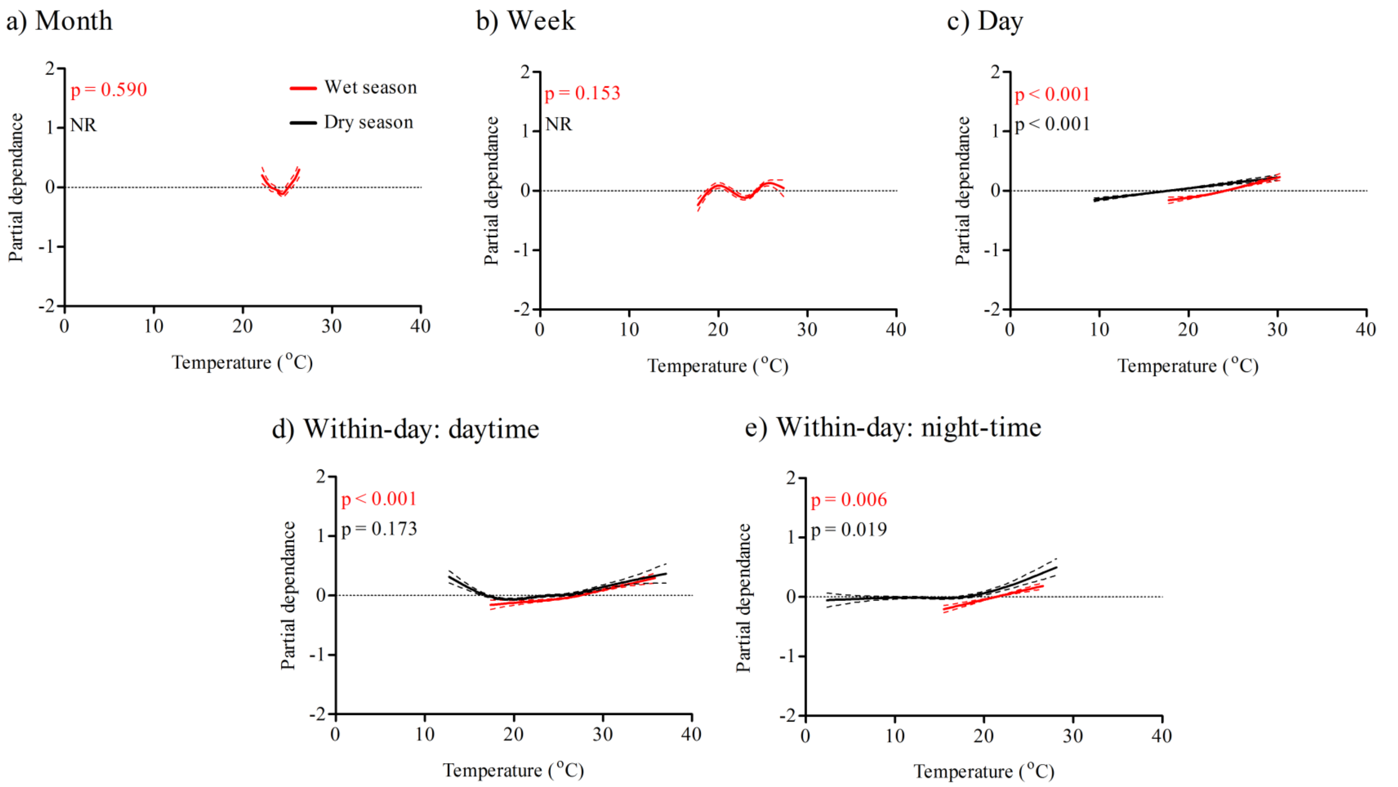


Figure 3.7. Partial dependence of Brownian motion variance (σ_m^2) on temperature in selected best generalised additive mixed effects models (a to e). Plots are centred to have zero means, and it is the trend, rather than the actual values, that describes the patterns of dependence. Lines show predicted values in corresponding colours for the dry and wet season. Dashed lines represent standard errors. p values represent smooth term significance in the selected best model. NR = not retained in the selected best model. *Within day temporal scale

Chapter 4. The provisioning of water as a determinant of the movement patterns of elephants

Introduction

There are stark contrasts in scientific opinion on the topic of the water provisioning and fencing (Owen-Smith, 1983; Owen-Smith, 1996; van Aarde et al., 2006; Loarie et al., 2009a; Shrader et al., 2010; Packer et al., 2013; Creel et al., 2013; Massey et al., 2014; Woodroffe et al., 2014; Durant et al., 2015). One school of thought maintains that the provisioning of water uncouples savanna elephants (*Loxodonta africana*) from natural limitations, causing changes in their distribution and increases in their populations, which may accentuate their impact on vegetation (Owen-Smith, 1996; Brits et al., 2002; de Beer et al., 2006; Chamaillé-Jammes et al., 2007a, b; van Aarde and Jackson, 2007; Loarie et al., 2009a; Shannon et al., 2009; Shrader et al., 2010). The opposing group discounts the influence that the provisioning of water may have on the distribution and abundance of elephants, and their resulting impact on vegetation (Redfern et al., 2005; Owen-Smith, et al., 2006; Smit et al., 2007b, c; Hilbers et al., 2015). To reconcile such widely divergent opinions, this chapter examines how water provisioning influences the movement patterns and the resulting spatial distribution of elephants in Kruger National Park (KNP).

Elephant numbers in KNP have doubled within the 20-year period that followed on the cessation of culling and elephants are now more evenly distributed across the landscape than ever before (Robson, 2015). The remaining waterholes supplement the five perennial and ephemeral rivers (Figure 4.1.) (Gaylard et al., 2003). The roles of these in governing the distribution of elephants has not yet been documented, but for the earlier work of Smit et al., (2007a) who discounted the importance of provisioned water on the spatial use patterns of elephant breeding herds. This solicited some debate on the contribution that surface-water management may have for ameliorating the impact elephants have on vegetation by controlling their distribution and abundance (Chamaillé-Jammes et al., 2007b; Smit et al., 2007a, b; Loarie et al., 2009a; Shannon et al., 2009; Young and van Aarde, 2010; Hilbers et al., 2015). The continued debate could benefit from the present assessment on how water provisioning influences the movement patterns and the resulting spatial distribution of elephants.

The downplayed importance of provisioned water on the distribution and demography of elephants is based on the assumption that provisioned water does not affect the distribution of elephants due to relatively abundant natural water sources (Redfern et al., 2005; Owen-Smith et al., 2006; Smit et al., 2007b, c; Hilbers et al., 2015). Additionally, in previous studies in KNP that used aerial census data collected towards the end of the dry season, found that elephant breeding herds primarily associated with rivers and not artificial waterholes (Smit et al., 2007a, b). Apparently, rivers most likely act as a habitat for forage and water resources (Smit et al., 2007a, b). We know that at the landscape scale elephants distribute themselves in relation to surface-water availability (Western 1975; Stokke and du Toit 2002; Grainger et al., 2005; de Beer and van Aarde, 2008; Loarie et al., 2009a; Shannon et al., 2009). Furthermore, at the population scale we know that reduced surface-water availability negatively affects the demography of elephants (Chamaillé-Jammes et al., 2008). However, we do not know how water utilisation, water source type, and distribution affect the movement patterns and the resulting spatial distribution of elephants (Chamaillé-Jammes et al., 2013).

The time and effort spent on attaining water, limits the amount of time an animal can spend away from water and ultimately the distance it can travel from water sources. Elephant cows and juveniles have high rates of water turnover due to cutaneous and respiratory evaporative water loss, loosing up to a 100 *l* of water per day when it is hot (Dunkin et al., 2013). Furthermore, when it is hot elephants rely on water-related activities such as mud bathing, swimming, and splashing to thermoregulate (Dunkin et al., 2013; Mole, 2014). Therefore, I expect elephants to visit water sources often regardless of whether it is a natural or artificial water source. To reduce travelling costs between forage and water sources, elephants will most likely coincide their drinking times with their need to employ water-related thermoregulation. Consequently, I expect elephants to visit water sources more often during the hot afternoon hours than at other times of the day (Dunkin et al., 2013; Mole, 2014). Ultimately, the water requirements of elephants and the distribution of surface water determines where elephants will forage (Chamaillé-Jammes et al., 2007a; Chamaillé-Jammes et al., 2008). Consequently, water provisioning could induce artificial patterns of elephant space use, which may accentuate their impact on vegetation and have demographic consequences.

Water provisioning may enable elephants to extend their range use (Owen-Smith, 1996; Brits et al., 2002; de Beer et al., 2006; Chamaillé-Jammes et al., 2007a, b; van Aarde and Jackson, 2007; Loarie et al., 2009a; Shannon et al., 2009; Shrader et al., 2010). Currently, the provisioning of water reduces the distance to permanent water sources across almost half (48 %) of the KNP (Figure 4.1.). Consequently, I expect elephants to extend their ranges by making use of artificial waterholes. Furthermore, I expect the use of artificial waterholes to increase the intensity of use close to waterholes. Establishing how elephants respond to the provisioning of water as reflected in their movement patterns and resulting spatial distribution may better inform management decisions.

In this chapter, I evaluated how water utilisation, water source type, and distribution affect the movement patterns and the resulting spatial distribution of 26-collared elephant cows distributed across KNP (Figure 4.1.). To do this, I segmented their seasonal movement paths into trips defined as segments of the trajectory that occur between two consecutive visits to water sources (Chamaillé-Jammes et al., 2013). I determined if elephants visited water using a dynamic Brownian bridge movement-modelling approach (dBBMM) (Kranstauber et al., 2012). The dBBMM accounts for missing locations, collar error, and the speed and direction the individual was travelling (Kranstauber et al., 2012). I then classified the trips as natural or artificial depending on the start and end water source. If the elephants remained at a water sources for longer than an hour, they were classified as staying at artificial/natural water sources. The area used by elephants when using artificial and natural water sources was calculated by calculating the area used for all locations that were classified as part of a natural trip and for locations that were classified as part of an artificial trip. Finally, to calculate how the use of artificial waterholes altered the intensity of use, I calculated the relative contribution of locations classified as part of an artificial trip to the total number of locations in a cell. The higher the increase in intensity of use, the more time elephants spent in an area.

Methods

Study area

Please see chapter two (page 8) for details on the study area, Kruger National Park.

Study animals

Please see chapter two (page 9) for details on the study animals used in this study.

Trip classification

Each of the movement paths of the 26 elephant cows were subset into wet and dry seasons. I then segmented the movement paths into trips, defined as segments of the trajectory that occur between two consecutive visits to water sources (Chamaillé-Jammes et al., 2013). To determine if an elephant visited a water source I used a dynamic Brownian bridge movement model (Kranstauber et al., 2012) fitted to the most recent locations along the movement path. I specified a window size of seven hours and a margin size of three. A small window size increases the chance of picking up short-term changes in movement at the cost of reducing reliability in dBBMM estimates (Kranstauber et al., 2012). The location error was set to 23 m for all locations. I then calculated a 95 % utilisation distribution area (UD) for the latest location based on the Brownian motion variance from the dBBMM. If the UD overlapped with a water source, I considered it as a visit to a water source, whereas, if the UD did not overlap with a water source, then a UD was calculated for the next location. Elephants do not always leave the water source once they reach it and I defined these locations as either staying at natural or staying at artificial water sources. The next trip started when the elephant left the water source. Once I had segmented a trip from the movement path, I classified it as either natural or artificial depending on what water source elephants visited at the start and end of the trip. All analyses were implemented using the R statistical computing environment (R Core Team, 2013) along with the package ‘*move*’ (Kranstauber and Smolla, 2014).

Elephant distribution

To determine how perennial rivers and artificial waterholes affects the spatial distribution of elephants I calculated the area used by elephants for locations classified as part of a natural trip (start and end locations at perennial rivers) and for locations classified as part of an artificial trip (start or end location at artificial waterholes). The area used only during artificial trips is the expanded range (i.e. the expanded range is the area occupied when elephants used artificial waterholes and not when they used perennial rivers). To calculate the areas, I used 95 % Kernel home ranges with a smoothed cross validation (SCV) bandwidth estimator (for validation of Kernel home ranges with SCV bandwidth estimators for elephants please see Roever, 2013).

Elephants may have used the same areas when using artificial and natural water sources. In these areas, the use of artificial waterholes may alter the intensity of use. To calculate how artificial waterholes altered the intensity of use, I calculated the relative contribution of locations classified as part of an artificial trip to the total number of locations in a cell. Considering the hourly relocation schedule of the collars, I chose a cell size of 340 m based on the mean distance elephants travelled per hour. The higher the increase in intensity of use, the more time elephants spent in an area.

Modelling procedure

To model the likelihood of visiting a water source at different times of the day, temperature and season, I fitted generalized additive models with simple random effects (GAM) using the '*mgcv*' package in R (Wood, 2006; R Core team, 2013). The occurrence of visiting water sources was set as a binary response variable and the associated environmental temperature (South African Weather Services, Pretoria, South Africa), time of day and season were set as the explanatory variables. GAMs with simple random effects were selected over generalized additive mixed effects models (GAMMs) because GAMMs are known to perform poorly with binary data. All models were fitted by restricted maximum likelihood estimation method (REML) with penalised cubic regression splines. REML was used to produce an unbiased estimation of the variance parameters when there were an increased number of fixed parameters in the model (Wood, 2006). To account for dependencies between observations from the same individual, I included individual elephant identity as a simple random effect by treating the random effect as a smooth term (Wood, 2008). I fitted either spatial or temporal autocorrelation structures (Pinheiro and Bates, 2000) and evaluated its inclusion using Akaike information criterion (AIC) (Pinheiro and Bates, 2000). Spatial correlation between trips was modelled using the harmonic mean of the coordinates, and temporal correlation was modelled by numbering consecutive trips for each individual (van Beest et al., 2011).

Each set of candidate models was formulated using an all subset approach that comprised of various combinations of the explanatory variables. The best models were selected using a multi-model selection procedure (Burnham and Anderson, 2002). The resulting models were ranked using their AIC and the Akaike weight of each model (ω_i) (Burnham and Anderson, 2002). These served as competing hypotheses to explain the likelihood of visiting a water sources. The strength of support for the best model and alternative best models was assessed using AIC differences (ΔAIC) between the approximate best model (ΔAIC = 0) and alternative candidate models. Candidate models with ΔAIC < 2 were considered as good as the best model and have substantial support as an alternative best model (Burnham and Anderson, 2002). The area under the receiver operating characteristic curve (ROC) was calculated to assess the accuracy and performance of each GAM (Fielding and Bell, 1997). I obtained 95 % confidence intervals of the ROC parameter estimate using a parametric bootstrap based on 10 000 random samples. ROC values vary between 0.5 (the discriminating power of the model is no better than chance) and 1.0 (the model has perfect discriminating power). Models with ROC values ≥ 0.7 were considered to have acceptable discriminating power (Hosmer and Lemeshow, 2000).

Results

In total, I classified 1024 trips where elephants used artificial waterholes and 3314 trips where elephants used perennial rivers. Additionally, I classified 107 and 3333 occasions, where elephants stayed for more than an hour at artificial waterholes and perennial rivers respectively. Model accuracy and predictability was acceptable for the likelihood of visiting artificial watering holes (ROC=0.75, 95 % CI = 0.73, 0.77). Whereas, model accuracy and predictability was relatively poor for the likelihood of visiting perennial rivers (ROC=0.66, 95 % CI = 0.66, 0.67), so its results must be interpreted with caution. The likelihood of visiting a perennial river and artificial waterhole was best explained by the time of day, temperature, and season (Table 4.1.) (see Chapter 7, Appendix XIV. and Appendix XV. for the full table).

Elephants were more likely to visit perennial rivers from 11:00 until 22:00 than any other time of the day, whereas, they were most likely to visit artificial waterholes from 13:00 until 24:00 (Figure 4.2.). The likelihood of visiting water increased with increasing environmental temperatures above 20°C (Figure 4.2.). Elephants were more likely to visit perennial rivers (Estimate = -0.25 ± 0.04; z = -5.77; $p < 0.0001$) and artificial waterholes (Estimate = -0.90 ± 0.16; z = -5.55; $p < 0.0001$) during the dry season than during the wet season.

The frequency distribution of the duration of time elapsed between visits to perennial rivers and artificial waterholes was unimodal (Figure 4.3.). Elephants typically returned to water sources at 12 to 36 hour intervals (Figure 4.3.). When, elephants stayed at a water sources for longer than an hour they stayed at perennial rivers significantly longer (Mdn: 6 hours, IQR: 4 hours, 9 hours) than artificial waterholes regardless of season (Mdn: 3 hours, IQR: 2 hours, 4 hours) (Kruskal-Wallis test, H = 41.45, df = 3, $p < 0.0001$). When using artificial waterholes elephants used areas further away from perennial rivers (Mdn: 5668.84 m, IQR: 3575.26 m – 10153.93 m), in comparison to when they used perennial rivers regardless of the season (Mdn: 2086.21 m, IQR: 1210.73 m – 3478.24 m) (Kruskal-Wallis test, H = 1044.00, 3, df = 3, $p < 0.0001$).

At the individual scale, the use of artificial waterholes by elephants increased their total area used by 34 % ± 22 % (mean ± SD) and 28 % ± 22 % in the in the dry and wet season respectively (Figure 4.4.). At the Park wide scale, the use of artificial waterholes resulted in elephants expanding their range and increasing their total area used by 32 %. Additionally, in the areas already used by elephants when they used perennial rivers, 11 % ± 7 % and 55 % ± 4 % of the area was used more intensively in the in the dry and wet season respectively because of the use of artificial waterholes (Figure 4.5.). At the Park wide scale, 10 % of the area was used more intensely because of the distribution of artificial waterholes.

Discussion

The debate on the effect of provisioned water on the distribution of elephants and the consequences thereof is mainly due to the lack of empirical support (see Smit et al., 2007b, c; Chamaillé-Jammes et al., 2007a, b and references therein). Here, I evaluated how water utilisation, water source type, and distribution affect the movement patterns and the resulting spatial distribution of elephants in KNP. The likelihood of visiting a water source was highest during the hot afternoon hours and most of the time elephants returned to water sources every 12 to 36 hours. As anticipated, artificial waterholes altered the distribution of elephants despite the apparent relative abundance of natural water sources (Redfern et al., 2005; Owen-Smith et al., 2006; Smit et al., 2007b, c; Hilbers et al., 2015). When elephants used artificial waterholes, they used areas more than double the distance away from perennial rivers in comparison to when they used perennial rivers, increasing the total area used by elephants by more than one third. Additionally, the use of artificial waterholes increased the intensity of use in areas already used by elephants when using perennial rivers. I therefore conclude that the provisioning of water alters the movement patterns and the resulting spatial distribution of elephants in KNP.

In KNP, elephant breeding herds returned to water sources every 12 to 36 hours irrespective of the water source type and season. Elephants can however go for longer periods without visiting water sources (Chamaillé-Jammes et al., 2013). In Hwange National Park, Zimbabwe, when elephants visited water sources less often they travelled further distances and reached distances further away from water sources, presumably to reach better quality food (Chamaillé-Jammes et al., 2013). This trade-off between forage and visiting water sources may have demographic consequences, particularly for weaned calves in the dry season (Young and van Aarde, 2010). The provisioning of water sources across KNP may remove the limitations that water availability and distribution exerts on elephants (Owen-Smith, 1983; Owen-Smith, 1996; van Aarde et al., 2006; Chamaillé-Jammes et al., 2008; Young and van Aarde, 2010).

Literature suggests that the removal of artificial waterholes in KNP will not influence elephant spatial use patterns because of the abundance of natural water sources and their preference for rivers (Owen-Smith, 1996; Redfern et al., 2005; Smit et al., 2007b, c; Hilbers et al., 2015). Elephants may prefer rivers because they provide water, forage (Smit et al., 2007b), and shade. Concurrently, elephants in this study spent significantly more time at perennial rivers than artificial water holes, presumably foraging or shading themselves. However, in disagreement with previous studies that use dry season census data (Smit et al., 2007a, b; Hilbers et al., 2015), I find that water provisioning alters the spatial distribution of elephant breeding herds. When elephants used artificial waterholes, they used areas more than double the distance away from perennial rivers then when they only used perennial rivers. Although, elephants may still use these areas if the waterholes are removed, the cost of using them would be greater due to the longer distance between forage and water sources. We do not know the influence of ephemeral water sources on elephant distribution, but there is no significant difference in the duration between visits to water sources in the wet season and dry season. Furthermore, when given the choice elephants may prefer permanent water sources, because of the temporal variability in water availability at ephemeral water sources. Despite the apparent abundance of natural water sources, the provisioning of water in KNP effects the spatial distribution of elephants.

The provisioning of water by management in KNP may uncouple elephants from the limitations that water availability and distribution exert on the distribution and numbers of elephants. The change in elephant movement patterns may accentuate their impact on vegetation and have demographic consequences (Owen-Smith, 1996; Brits et al., 2002; de Beer et al., 2006; Chamaillé-Jammes et al., 2007a, b; Guldemond and van Aarde, 2007; van Aarde and Jackson, 2007; Loarie et al., 2009a; Shannon et al., 2009; Shrader et al., 2010). When possible, management should focus on maintaining and restoring the natural forces that limit elephant distribution, numbers, and impact on vegetation (van Aarde and Jackson, 2007). This study supports the removal of provisioned water or its manipulation so that is resembles that of natural water distribution to recouple elephant populations with natural limitations, generating heterogeneity in their spatial use patterns and numbers (Owen-Smith, 1996; van Aarde and Jackson, 2007; Chamaillé-Jammes et al., 2007a, b; Loarie et al., 2009a). Closing down the remaining artificial waterholes in KNP will most likely limit the distribution of elephants, a desirable outcome for a management approach that centres on promoting ecological processes to regulate numbers naturally.

Although, this study focused on elephants, the provisioning of water will most likely have consequences for other water-limited species (Thrash et al., 1995; Harrington et al., 1999; Smit et al., 2007a; Smit and Grant, 2009; Smit and Ferreira, 2010). The short-term benefits of increased water supply may be at the expense of their long-term persistence. For instance, starvation-induced mortality during extended draughts may occur due to the depletion of reserve resources (Walker et al., 1987; Owen-Smith, 1996). Therefore, it is important to understand the effects that water availability and distribution has on animal populations. This study contributes to the continued debate on the potential effects of water provisioning.

Tables

Table 4.1. Summary of selected best and alternative best ($\Delta \mathrm{AIC}_i < 2$) generalized additive models with simple random effects used to explain the likelihood of visiting a perennial rivers or artificial waterholes using time of day, temperature, and season.

								95 % CI for ROC	
Water source	Model	df	LogLik	AIC	ΔAIC	w_i	ROC	Lower	Upper
Perennial rivers	temperature* + time* + season*	59.39	-16272.31	32663.41	0.00	1.00	0.66	0.66	0.67
Artificial waterholes	temperature* + time* + season*	36.64	-2231.48	4536.25	0.00	1.00	0.75	0.73	0.78

Notes: For each model the degrees of freedom (df), loglikelihood value (LogLik), difference in AIC between the best fit model and model$_i$ ($\Delta \mathrm{AIC}_i$), Akaike weight (w_i), area under receivers operating characteristic curve (ROC) *model parameter coefficient significant ($p < 0.05$). I obtained the 95 % confidence intervals (CI) of the ROC parameter estimate using a parametric bootstrap based on 10 000 random samples.

Figures

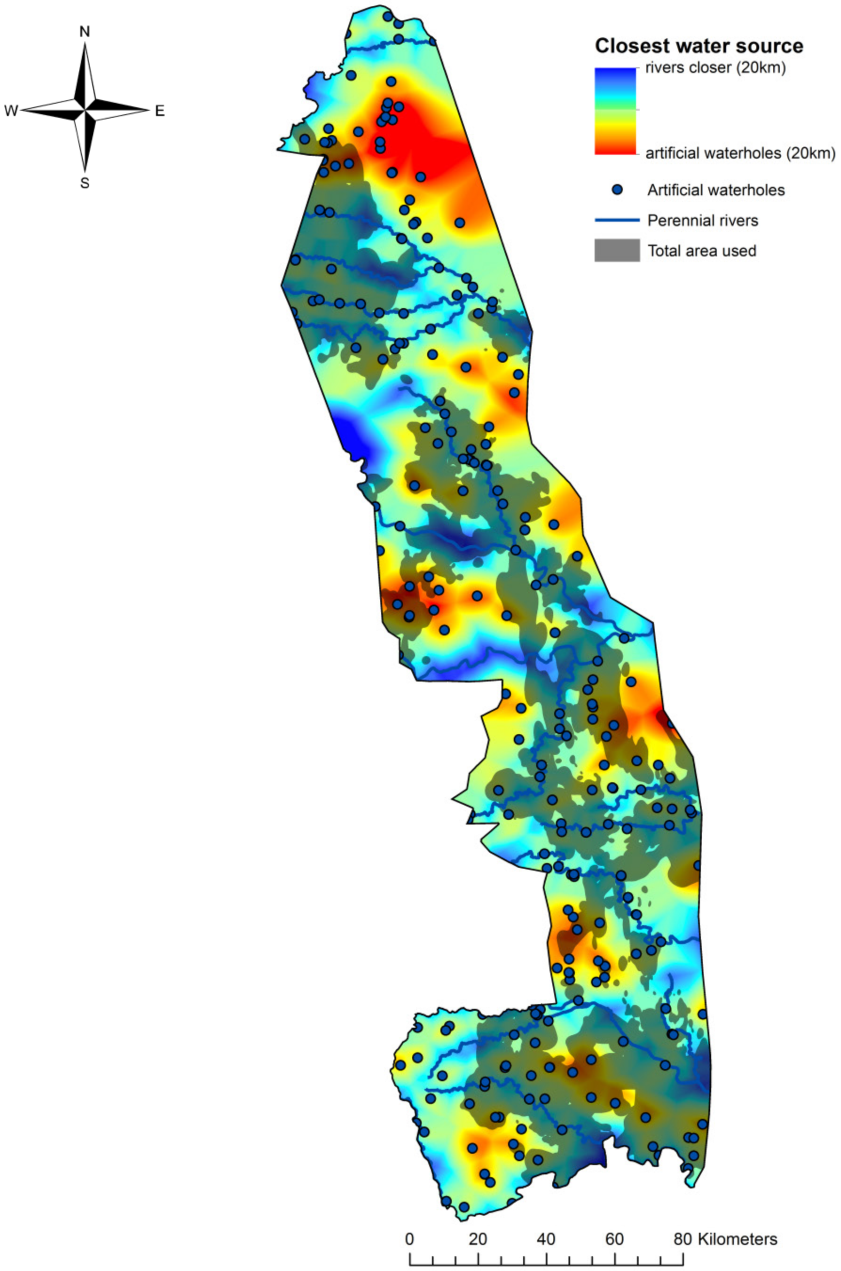


Figure 4.1. The distribution of water sources across the Kruger National Park (KNP). Permanent water across the park consists mainly of the five perennial rivers supplemented by the artificial waterholes. Water provisioning reduced the distance to water across almost half of the Park as indicated by the reds and oranges. The 26-collared elephant cows distributed themselves over 43 % (area shaded in grey) of KNP during the study period.

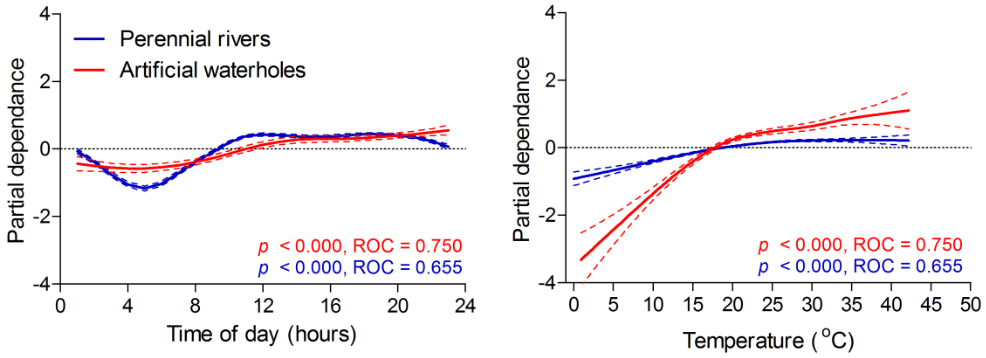


Figure 4.2. Partial dependence of elephants visiting a water source on a) time of day and b) temperature in selected best generalized additive models. Plots are centred to have zero means, and it is the trend, rather than the actual values, that describes the patterns of dependence of elephant movement behaviour on time of day and temperature. p values represent smooth term significance in best approximate model. Lines show predicted values in corresponding colours for perennial rivers and artificial waterholes. Dashed lines represent 95 % confidence intervals. The area under the receivers operating characteristic curve (ROC) for each best approximate model are also presented.

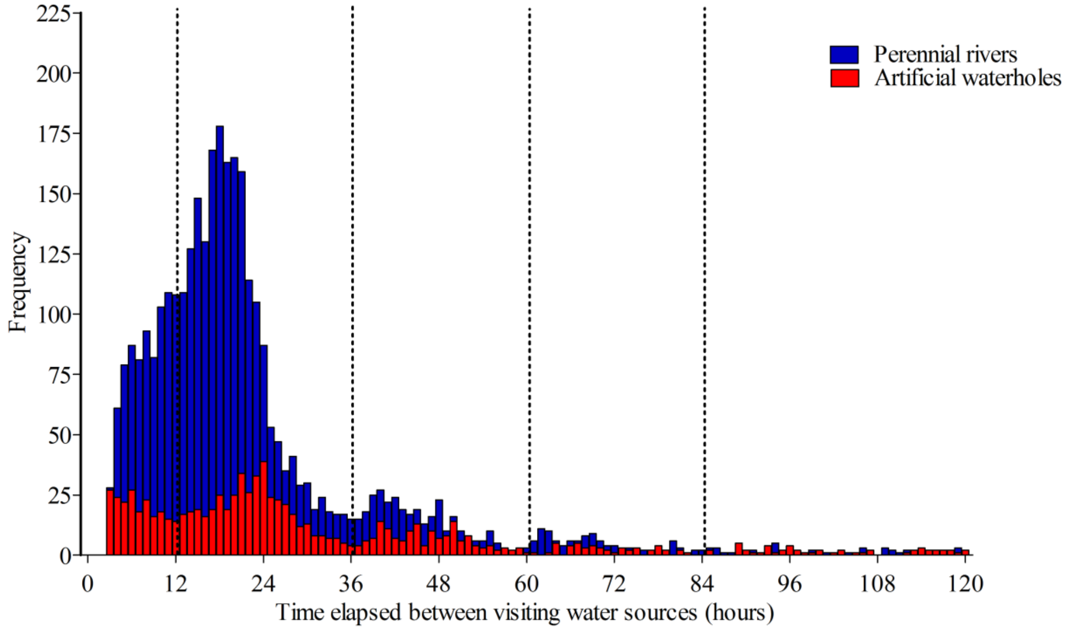


Figure 4.3. Frequency histogram for the time elapsed between visiting perennial rivers and artificial waterholes for 26-collared elephant cows. The frequency distribution of the duration of time elapsed between visits to perennial rivers and artificial waterholes was unimodal.

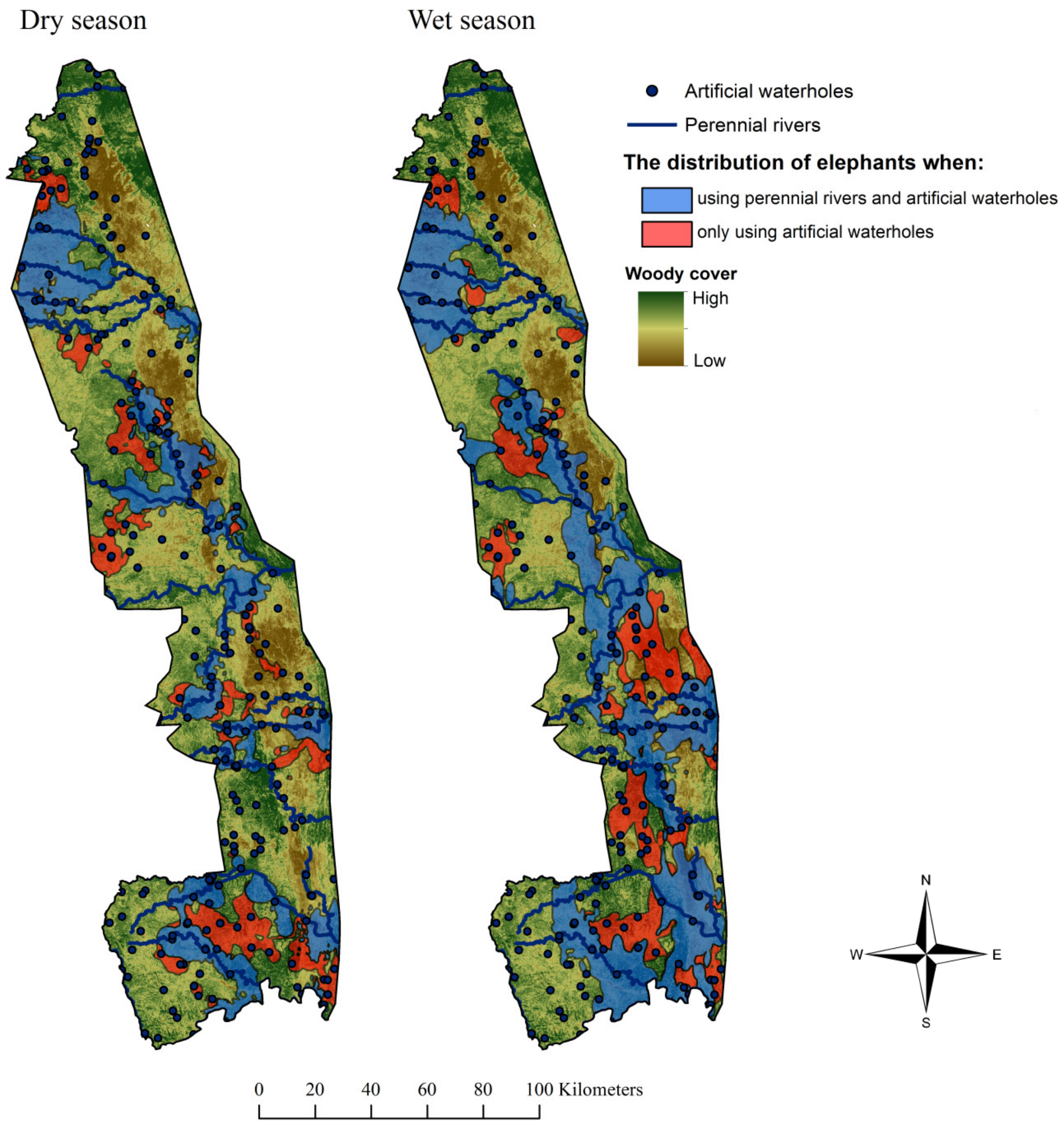


Figure 4.4. Map of Kruger National Park, with the distribution of 26-collared elephant cows when using perennial rivers and artificial watering holes in blue and only artificial waterholes in red. The use of artificial waterholes by elephants increased their total area used by 34 % ± 22 % (mean ± SD) and 28 % ± 22 % in the in the dry and wet season respectively.

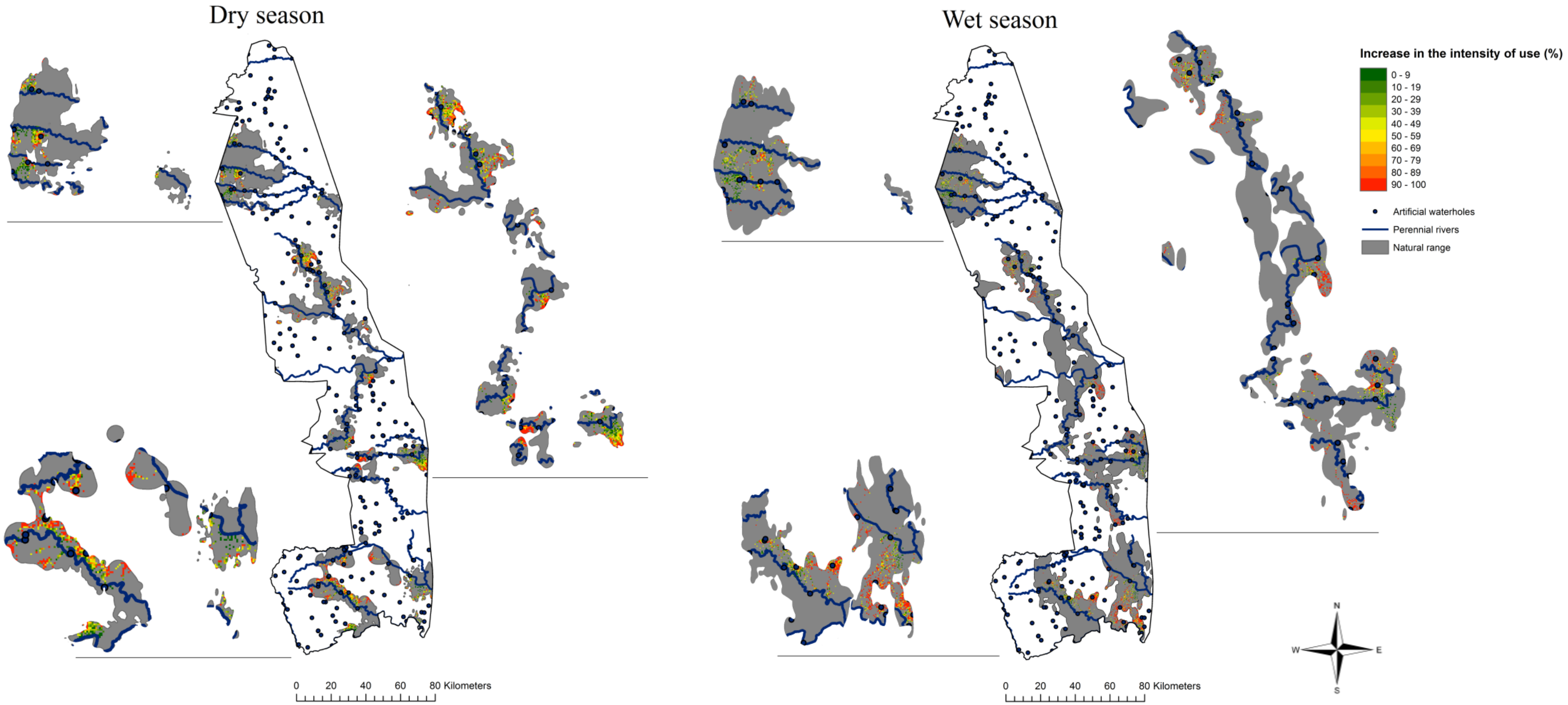


Figure 4.5. Map of Kruger National Park, with the area used by 26-collared elephant cows when using perennial rivers in grey. In the areas already used by elephants when using perennial rivers, 11 % ± 7 % and 55 % ± 4 % of the area was used more intensively in the in the dry and wet season respectively because of the use of artificial waterholes**.**

Chapter 5. General Conclusions

To improve the efficacy of protected areas in conserving ecological processes, initiatives such as the megaparks for metapopulations (van Aarde and Jackson, 2007) and Transfrontier Conservation Areas (Hanks, 2003) strive to increase connectivity between small and often isolated protected areas (van Aarde and Jackson, 2007). For savanna elephants (*Loxodonta africana*), increasing connectivity between protected areas may mediate their apparent impact on vegetation and promote regional population stability through the spatial structuring of their populations (van Aarde and Jackson, 2007). Regional population stability relies on asynchronous population dynamics between interconnected subpopulations separated by distance (Olivier et al., 2009). It is likely that the spatial responses of elephants to environmental variation drive this asynchrony (van Aarde et al., 2006; van Aarde and Jackson, 2007). Developing a thorough knowledge of the spatial responses of elephants to their environment can better inform management decisions to conserve suitable habitat, and promote population persistence through the conservation of ecological processes (see Boyce and McDonald, 1999; Nielsen et al., 2006).

In this thesis, I assessed the environmental determinants of the movement patterns of elephants over four consecutive seasons within Kruger National Park (KNP). In chapter 3, I evaluated the movement behaviour of the elephant breeding herds using dynamic Brownian bridge movement modelling (dBBMM) (Kranstauber et al., 2012; Byne et al., 2014). I then evaluated how well different environmental factors explain changes in their movement behaviour using a mixed effects modelling approach at multiple analytical scales (month, week, day, and within-day: night/day). Changes in the movement behaviour of elephants could be explained by distance from water sources, primary productivity, vegetation structure, and temperature at multiple temporal scales. Ideally, my approach in chapter 3 should have provided better insight into how elephants responded to their environment. One of the limitations of using a one-dimensional measure such as the Brownian motion variance (derived from the dBBMM) as an index of movement behaviour is that it can only separate a limited amount of behaviours (Kranstauber et al., 2012). Therefore, two relatively different movement paths (e.g. a movement path with high variation in turning angles and a movement path with high variation in speed) could result in similar Brownian motion variance values (Kranstauber et al., 2012). In future studies, we may be able to better delineate behavioural states by using higher resolution locational data and alternative modelling approaches, such as the behavioural change point analysis (Gurarie et al., 2009; Gurarie et al., 2015; Polansky et al., 2015). On-going research at the Conservation Ecology Research Unit (CERU) is using fine scale elephant locational data (30 second relocation schedule) accompanied by direct behavioural observations to try unravel the optimal relocation schedule for collecting elephant locational data and an accompanying method to delineate behavioural states of interest.

Elephants can induce considerable changes to their environment (Guldemond and van Aarde, 2007) and it is difficult to isolate the effects of the environment on the spatial responses of elephants from the consequences thereof for the environment. The interdependence of the spatial responses of elephants and their influence on the environment is most likely accentuated by management actions such as the provisioning of water and fencing (de Beer et al., 2006; Loarie et al., 2009a). Contrasting scientific opinion exist on the effect of provisioned water on the distribution and abundance of elephants and the consequences thereof for other species, mainly due to the lack of empirical support (see Smit et al., 2007a, b; Chamaillé-Jammes et al., 2007a, b and references therein). To try to reconcile widely divergent opinions my forth chapter focused on evaluating the movement patterns of elephants in relation to surface-water in KNP. To do this, I examined how the provisioning of water as a management intervention influences the movement patterns and the resulting spatial distribution of elephants. In summary, chapter 4 demonstrates that provisioned water alters the distribution of elephants, despite relatively abundant natural surface-water (Redfern et al., 2005; Owen-Smith et al., 2006; Smit et al., 2007a, b; Hilbers et al., 2015). When elephants used artificial waterholes, they used areas more than double the distance away from natural water sources in comparison to when they only used natural water sources, increasing the total area used by elephants by more than one third. The provisioning of water and the resultant change in elephant distribution may accentuate their impact on vegetation and have demographic consequences. (Owen-Smith, 1996; Brits et al., 2002; de Beer et al., 2006; Chamaillé-Jammes et al., 2007a, b; Guldemond and van Aarde, 2007; van Aarde and Jackson, 2007; Loarie et al., 2009a; Shannon et al., 2009; Shrader et al., 2010).

Interestingly, there was large variation in how the provisioning of water influenced the distribution of individual elephants (see Chapter 7, Appendix XVI.). The variation might be attributed to a variety of explanations including the distribution and density of water sources within their home range (Grainger et al., 2005), forage availability, social rank (Wittemyer et al., 2008), or herd structure such as the presence of a young calf. An apparent limitation of chapter 4 was the exclusion of all ephemeral water sources in my evaluation of the influence of surface-water on the spatial use patterns of elephants. Unfortunately, data on the distribution and availability of all the ephemeral water sources is not available. Improved data on surface-water availability and an evaluation of the variation between the spatial use patterns of individual elephants in relation to surface-water could benefit future studies.

Improvements in tracking technology is increasing the temporal resolution of tracking data (Nathan et al., 2008) and allowing researchers to remotely collect data other than locations e.g. ambient temperature, internal body temperature, and accelerometer data (Kays et al., 2015). Effectively using these data to answer pertinent questions relies on not only the development of analytical routines that can take advantage of these high-resolution data, but also the collection of high-resolution environmental data. Without these high-resolution environmental data to accompany locational data, researchers may find it increasingly difficult to evaluate the determinants and consequences of animal space use. An apparent limitation of this study was the availability of high-resolution environmental data. In addition to data on the availability of ephemeral water sources, the Enhanced Vegetation Index that was used as an index of primary productivity is only available as a validated product at 250 m x 250 m resolution every 16 days. This mismatch between high-resolution tracking data and often lower-resolution environmental data may impose limitations on studies, and could confound the influence of scale. Advances in air-borne remote sensing and initiatives to make these data freely available will most likely overcome some of these limitations in the near future.

Understanding the spatial responses of animals to their environment can improve our understanding of the dynamics of spatially structured populations (Morales and Ellner, 2002; Bowler and Benton, 2005). Here and in numerous other studies, the spatial responses of elephants have been quantified and could be attributed to a variety of environmental factors. However, we know very little about the fitness consequences of these responses (see Young and van Aarde, 2010). CERU has performed repeated Rapid Elephant Population Assessments on a number of the breeding herds used in this study (see Ferreira and van Aarde, 2008; Trimble et al., 2011). Using these demographic data and the locational data it may be possible to relate herd-specific variation in their movement patterns to variation in demographic data. This may allow us to identify possible mechanistic links between elephant movement patterns and demography.

The management of elephants continues to be a contentious management concern (see Whyte et al., 2003; Delsink et al., 2013). In some areas, poaching is placing populations at risk of local extinction (see Wittemyer et al., 2014). Whereas, in many protected areas management is concerned that there are too many elephants (see van Aarde and Jackson, 2007). The magapark for metapopulations initiative potentially addresses both these issues. Albeit that poaching is a socio-economic problem confounded by a lack of political will, rather than an ecological one, creating space for elephants within the megaparks for metapopulations framework (see van Aarde and Jackson, 2007) may improve regional population persistence and buffer local populations against the negative effects of poaching. For example, increased connectivity may allow elephants to move away from high risk ‘poaching sinks’, additionally, source populations may supplement or allow re-colonization of locally extinct populations. On the other hand, where management is concerned that there are too many elephants, increasing connectivity between protected areas and the removal of provisioned water sources may reinstate ecological limitations that regulate the distribution, and numbers of elephants naturally (see Owen-Smith, 1996; van Aarde and Jackson, 2007).

Currently, the management of elephants in South African National Parks aims to maintain natural regulatory processes and reinstate them where necessary by manipulating the spatial utilisation patterns of elephants. In KNP, following the 1994 change in management, elephant numbers have more than doubled. Consequently, there are recommendations to return to the artificial manipulation of elephant numbers (Slotow et al., 2008). Elephants do respond to the distribution and availability of key resources, and rather than returning to manipulative management, I argue that management should continue to base their management decisions on ecological principals and remove the remaining artificial waterholes in KNP. The removal of the artificial waterholes should include a continued evaluation of the response of animals and vegetation to their removal, allowing for the assessment of the effectiveness of their removal in achieving management objectives to improve future management decisions.

Many questions remain, and my hopes are that this research contributes to what we know about elephants and how best to manage them, or rather, how best to manage their responses to our interferences. Furthermore, this study identifies future research avenues that may be meaningful to conservation planning. In an era where contradictory scientific opinion may affect conservation, management needs to continue basing their decisions on sound theoretical and applied ecological research (Cook et al., 2010; Keith et al., 2011).

Chapter 6. References

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Chapter 7: Appendices

Appendix I. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the dry season at the monthly temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI	9	0.43	108.95	0.00	0.47
2	Woody cover + EVI + distance from water	11	0.45	110.54	1.59	0.14
3	EVI	7	0.39	111.21	2.26	0.21
4	Woody cover	7	0.38	113.40	4.44	0.07
5	Woody cover + distance from water	9	0.40	113.79	4.84	0.04
6	EVI + distance from water	9	0.40	114.41	5.46	0.03
7	Woody cover+ EVI + Temperature	11	0.43	115.44	6.49	0.01
8	Woody cover + EVI + distance from water + temperature	13	0.45	116.97	8.02	0.00
9	Woody cover + EVI + distance from water + temperature	9	0.39	117.26	8.31	0.01
10	EVI + temperature	9	0.39	117.59	8.64	0.01
11	Woody cover + distance from water + temperature	11	0.41	118.92	9.97	0.00
12	EVI + distance from water + temperature	11	0.41	120.32	11.37	0.00
13	Distance from water	7	0.33	121.30	12.34	0.00
14	Temperature	7	0.32	123.75	14.79	0.00
15	Distance from water + temperature	9	0.34	126.26	17.30	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix II. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the dry season at the weekly temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + distance from water	11	0.50	770.45	0.00	0.96
2	Woody cover + EVI + distance from water + temperature	13	0.50	776.78	6.33	0.04
3	Woody cover + distance from water	9	0.49	782.92	12.47	0.00
4	Woody cover + distance from water + temperature	11	0.49	788.37	17.92	0.00
5	EVI + distance from water	9	0.48	792.32	21.87	0.00
6	Woody cover + EVI	9	0.48	792.98	22.53	0.00
7	EVI + distance from water + temperature	11	0.48	798.58	28.13	0.00
8	Woody cover + EVI + temperature	11	0.48	800.09	29.64	0.00
9	EVI	7	0.46	808.51	38.06	0.00
10	Woody cover	7	0.46	809.94	39.49	0.00
11	Distance from water	7	0.46	812.06	41.61	0.00
12	EVI + temperature	9	0.46	815.53	45.08	0.00
13	Woody cover + temperature	9	0.46	816.41	45.96	0.00
14	Distance from water + temperature	9	0.46	817.13	46.68	0.00
16	Temperature	7	0.44	839.92	69.47	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models were ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix III. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the dry season at the daily temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + distance from water + temperature	13	0.31	11062.02	0.00	0.99
2	Woody cover + distance from water + temperature	11	0.31	11072.53	10.51	0.01
3	Woody cover + EVI + distance from water	11	0.31	11079.67	17.65	0.00
4	Woody cover + distance from water	9	0.30	11106.37	44.35	0.00
5	EVI + distance from water + temperature	11	0.29	11194.22	132.20	0.00
6	EVI + distance from water	9	0.29	11209.85	147.83	0.00
7	Distance from water + temperature	9	0.29	11219.40	157.38	0.00
8	Distance from water	7	0.28	11254.39	192.37	0.00
9	Woody cover + EVI + temperature	11	0.27	11334.69	272.67	0.00
10	Woody cover + EVI	9	0.27	11339.66	277.64	0.00
11	Woody cover + temperature	9	0.27	11355.28	293.26	0.00
12	Woody cover	7	0.26	11373.70	311.68	0.00
13	EVI + temperature	9	0.26	11412.62	350.60	0.00
14	EVI	7	0.26	11417.67	355.65	0.00
15	Temperature	7	0.25	11445.84	383.82	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix IV. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the dry season at the within-day scale during the day.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + distance from water + temperature	13	0.21	12373.19	0.00	1.00
2	Woody cover + EVI + distance from water	11	0.20	12390.92	17.73	0.00
3	Woody cover + distance from water + temperature	11	0.19	12458.46	85.27	0.00
4	Woody cover + distance from water	9	0.19	12482.98	109.79	0.00
5	EVI + distance from water + temperature	11	0.19	12491.81	118.62	0.00
6	EVI + distance from water	9	0.18	12509.00	135.81	0.00
7	Woody cover + EVI + temperature	11	0.18	12555.74	182.55	0.00
8	Woody cover + EVI	9	0.17	12562.40	189.22	0.00
9	Distance from water + temperature	9	0.17	12592.92	219.73	0.00
10	Distance from water	7	0.16	12619.76	246.58	0.00
11	EVI + temperature	9	0.16	12639.74	266.56	0.00
12	Woody cover + temperature	9	0.16	12644.22	271.04	0.00
13	EVI	7	0.16	12647.93	274.75	0.00
14	Woody cover	7	0.16	12656.06	282.88	0.00
15	Temperature	7	0.14	12739.16	365.98	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix V. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the dry season at the within-day scale during the night**.**

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + temperature	11	0.29	13951.72	0.00	0.70
2	Woody cover + EVI	9	0.29	13954.67	2.95	0.16
3	Woody cover + EVI + distance from water + temperature	13	0.29	13955.35	3.63	0.11
4	Woody cover + EVI + distance from water	11	0.29	13957.92	6.20	0.03
5	EVI + temperature	9	0.26	14109.57	157.85	0.00
6	EVI	7	0.26	14111.35	159.63	0.00
7	EVI + distance from water + temperature	11	0.26	14114.80	163.08	0.00
8	EVI + distance from water	9	0.26	14116.34	164.62	0.00
9	Woody cover + temperature	9	0.20	14499.77	548.05	0.00
10	Woody cover + distance from water + temperature	11	0.20	14501.99	550.28	0.00
11	Woody cover	7	0.20	14510.87	559.15	0.00
12	Woody cover + distance from water	9	0.20	14513.33	561.61	0.00
13	Temperature	7	0.15	14758.61	806.89	0.00
14	Distance from water + temperature	9	0.15	14764.84	813.12	0.00
15	Distance from water	7	0.15	14774.90	823.18	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix VI. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the wet season at the monthly temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + temperature	8	0.35	78.89	0.00	0.58
2	Woody cover	6	0.27	81.79	2.89	0.22
3	Woody cover + EVI	8	0.30	84.27	5.37	0.04
4	Woody cover + distance from water + temperature	10	0.36	84.45	5.56	0.02
5	Temperature	6	0.24	84.73	5.84	0.05
6	Woody cover + EVI + temperature	10	0.34	85.67	6.77	0.01
7	Woody cover + distance from water	8	0.27	87.16	8.26	0.01
8	EVI	6	0.19	89.14	10.25	0.01
9	EVI + temperature	8	0.25	89.17	10.28	0.00
10	Woody cover + EVI + distance from water	10	0.30	89.69	10.79	0.00
11	Distance from water + temperature	8	0.24	90.16	11.27	0.00
12	Distance from water	6	0.17	90.22	11.33	0.00
13	Woody cover + EVI + distance from water + temperature	12	0.34	90.92	12.03	0.00
14	EVI + distance from water	8	0.19	93.83	14.94	0.00
15	EVI + distance from water + temperature	10	0.24	95.63	16.74	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix VII. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the wet season at the weekly temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + temperature	11	0.39	846.40	0.00	0.73
2	Woody cover + EVI	9	0.38	849.90	3.51	0.14
3	Woody cover + temperature	9	0.38	851.11	4.72	0.07
4	Woody cover + EVI + distance from water + temperature	13	0.39	851.79	5.39	0.04
5	Woody cover + EVI + distance from water	11	0.38	854.53	8.14	0.01
6	Woody cover + distance from water + temperature	11	0.38	856.00	9.60	0.01
7	Woody cover	7	0.36	859.69	13.29	0.00
8	Woody cover + distance from water	9	0.37	863.42	17.02	0.00
9	EVI + temperature	9	0.32	899.82	53.42	0.00
10	EVI	7	0.31	904.40	58.00	0.00
11	EVI + distance from water + temperature	11	0.33	905.68	59.29	0.00
12	Temperature	7	0.31	905.87	59.47	0.00
13	EVI + distance from water	9	0.31	909.59	63.19	0.00
14	Distance from water + temperature	9	0.31	911.01	64.61	0.00
15	Distance from water	7	0.29	920.64	74.25	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix VIII. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the wet season at the daily temporal scale.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + distance from water + temperature	13	0.38	9178.05	0.00	0.99
2	Woody cover + distance from water + temperature	11	0.37	9188.18	10.13	0.01
3	Woody cover + EVI + distance from water	11	0.37	9207.89	29.84	0.00
4	Woody cover + distance from water	9	0.37	9215.26	37.21	0.00
5	Woody cover + EVI + temperature	11	0.37	9220.18	42.12	0.00
6	Woody cover + temperature	9	0.37	9229.64	51.59	0.00
7	Woody cover + EVI	9	0.36	9248.07	70.02	0.00
8	Woody cover	7	0.36	9255.07	77.02	0.00
9	EVI + distance from water + temperature	11	0.35	9391.92	213.86	0.00
10	EVI + temperature	9	0.34	9410.79	232.74	0.00
11	Distance from water + temperature	9	0.34	9411.22	233.16	0.00
12	Temperature	7	0.34	9429.06	251.01	0.00
13	EVI + distance from water	9	0.34	9435.63	257.57	0.00
14	Distance from water	7	0.33	9451.74	273.69	0.00
15	EVI	7	0.33	9452.16	274.11	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix IX. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the wet season at the within-day scale during the day.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + distance from water + temperature	13	0.28	7822.63	0.00	0.73
2	Woody cover + distance from water + temperature	11	0.28	7824.65	2.02	0.27
3	Woody cover + EVI+ temperature	11	0.28	7843.49	20.86	0.00
4	Woody cover + temperature	9	0.28	7844.06	21.43	0.00
5	Woody cover + EVI + distance from water	11	0.28	7849.89	27.26	0.00
6	Woody cover + distance from water	9	0.27	7853.27	30.64	0.00
7	Woody cover + EVI	9	0.27	7866.41	43.79	0.00
8	Woody cover	7	0.27	7868.44	45.82	0.00
9	EVI + distance from water + temperature	11	0.25	7954.71	132.08	0.00
10	EVI + temperature	9	0.25	7956.51	133.89	0.00
11	Temperature	7	0.25	7963.65	141.03	0.00
12	Distance from water + temperature	9	0.25	7963.79	141.16	0.00
13	EVI	7	0.24	7991.27	168.64	0.00
14	EVI + distance from water	9	0.24	7992.81	170.18	0.00
15	Distance from water	7	0.24	8004.28	181.65	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix X. Full set of candidate generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows in the wet season at the within-day scale during the night.

	Model	df	R^2	AIC	ΔAIC	ω_i
1	Woody cover + EVI + temperature	11	0.34	9841.27	0.00	0.78
2	Woody cover + EVI + distance from water + temperature	13	0.34	9844.53	3.27	0.15
3	Woody cover + EVI	9	0.34	9846.80	5.53	0.05
4	Woody cover + EVI + distance from water	11	0.34	9849.20	7.93	0.01
5	EVI + temperature	9	0.29	10055.99	214.72	0.00
6	EVI + distance from water + temperature	11	0.29	10062.77	221.51	0.00
7	EVI	7	0.29	10063.88	222.61	0.00
8	Woody cover + EVI + distance from water + temperature	9	0.29	10070.70	229.43	0.00
9	Woody cover + temperature	9	0.27	10178.33	337.06	0.00
10	Woody cover + distance from water + temperature	11	0.27	10181.77	340.50	0.00
11	Woody cover	7	0.26	10189.31	348.05	0.00
12	Woody cover + distance from water	9	0.26	10191.68	350.42	0.00
13	Temperature	7	0.22	10401.19	559.92	0.00
14	Distance from water + temperature	9	0.22	10407.96	566.70	0.00
15	Distance from water	7	0.21	10422.18	580.91	0.00

Notes: the models include a random factor for elephant identity and the number of elephants included in the models varied across scales and seasons. Models ranked using the Akaike's information criteria (AIC). The Akaike weight (ω_i) is the probability that the associated model is the most parsimonious. df= degrees of freedom, R^2 = coefficient of determination, ΔAIC = differences in AIC, ω_i = Akaike weights.

Appendix XI. Summary of the relative importance of each explanatory variable in each set of candidate models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows.

Season	Analytical scale	Woody cover	Water	EVI	Temperature
Dry	Month	**0.75**	0.22	**0.87**	0.03
	Week	**1**	1	1	0.04
	Day	**1**	**1**	0.99	**1**
	Daytime*	**1**	**1**	**1**	1
	Night-time*	**1**	0.14	**1**	**0.81**
Wet	Month	**0.89**	0.04	0.06	0.67
	Week	**1**	0.06	**0.92**	0.85
	Day	**1**	1	**0.99**	**1**
	Daytime*	**1**	1	**0.73**	**1**
	Night-time*	**1**	0.17	**1**	**0.94**

The relative importance of each explanatory variable was calculated by summing the Akaike weights (ωi) across the full set of candidate models in which the particular variable appeared. These values range between 0 and 1; the larger the value the more important the variable is relative to other variables within the set of candidate models (Burnham and Anderson, 2002). Significant ($p<0.05$) model parameter coefficients are in bold. *Within-day temporal scale.

Appendix XII. Summary statistics for Brownian motion variance (σ_m^2) derived from the dynamic Brownian bridge movement model as an index of movement behaviour for 26-collared elephant cows.

Temporal Scale		Dry	Wet
Month			
	median σ_m^2 (IQR)	1055.0 (743.7, 1388.0)	1096.0 (783.6, 1479.0)
	n	118	73
	n_{ele}	26	21
Week			
	median σ_m^2 (IQR)	1010.0 (633.3, 1458.0)	1153.0 (780.1, 1839.0)
	n	665	568
	n_{ele}	26	26
Day			
	median σ_m^2 (IQR)	758.1 (419.0, 1425.0)	1052 (597.0, 1799.0)
	n	5028	4638
	n_{ele}	26	26
Day-Time*			
	median σ_m^2 (IQR)	985.8 (495.0, 1901)	1293 (723.0, 2297.0)
	n	4792	3511
	n_{ele}	26	26
Night-time*			
	median σ_m^2 (IQR)	255.6 (116.9, 617.8)	440.2 (180.3, 968.0)
	n	4666	3407
	n_{ele}	26	26

n = number of Brownian motion variance (σ_m^2) derived from the dynamic Brownian bridge movement model. n_{ele} = number of individual elephants retained for subsequent analysis. IQR= inter quartile range *Within-day temporal scale.

Appendix XIII. Summary statistics (mean and range) for each of the environmental factors fitted as smoothed effects in the generalized additive mixed effects models used to explain changes in the movement behaviour (indexed by Brownian motion variance, log σ_m^2) of 26-collared elephant cows.

Analytical scale	Variables	Dry	Wet
Month	Woody cover (%)	34.69 (19.63 – 48.38)	35.90 (22.86 – 46.80)
	Distance from water (m)	2271.00 (923.90 – 4411.00)	2228.00 (859.70 – 4260.00)
	EVI	0.17 (0.09 – 0.26)	0.39 (0.27 – 0.55)
	Temperature (°C)	17.79 (13.80 – 21.98)	24.09 (22.17 – 26.35)
Week	Woody cover (%)	35.06 (15.64 – 52.02)	35.26 (11.98 – 52.98)
	Distance from water (m)	2182.00 (289.40 – 7132.00)	2266.00 (353.30 – 5753.00)
	EVI	0.17 (0.08 – 0.29)	0.38 (0.16 – 0.58)
	Temperature (°C)	18.61 (12.10 – 25.54)	22.77 (17.70 – 27.34)
Day	Woody cover (%)	35.62 (7.00 – 66.06)	35.72 (8.57 – 62.60)
	Distance from water (m)	2117.00 (84.95 – 11280.00)	2264.00 (84.94 – 7428.00)
	EVI	0.17 (0.06 – 0.30)	0.38 (0.13 – 0.69)
	Temperature (°C)	22.77 (17.70 – 27.34)	22.77 (17.70 – 27.34)
Day-Time*	Woody cover (%)	36.65 (4.29 – 72.15)	36.85 (5.73 – 67.41)
	Distance from water (m)	1990.00 (10.02 – 13060.00)	2135.00 (15.80 – 8374.00)
	EVI	0.17 (0.00 – 0.30)	0.37 (0.00 – 0.64)
	Temperature (°C)	22.77 (17.70 – 27.35)	22.77 (17.70 – 27.3)
Night-time*	Woody cover (%)	34.77 (17.70 – 27.34)	34.22 (0.74 – 76.26)
	Distance from water (m)	2338.00 (0.71 – 71.35)	2316.00 (15.26 – 8518.00)
	EVI	0.16 (0.00 – 0.32)	0.35 (0.00 – 0.69)
	Temperature (°C)	22.77 (17.70 – 27.34)	22.77 (17.70 – 27.34)

*Within-day analytical scale

Appendix XIV. Full set of candidate generalized additive models with simple random effects used to explain the likelihood of elephants visiting perennial rivers using time of day, temperature, and season.

							95 % CI for AUC	
Model	df	LogLik	AIC	ΔAIC	w_i	AUC	Lower	Upper
temperature + time + season	59.39	-16272.31	32663.41	0.00	1.00	0.66	0.66	0.67
temperature + time	59.09	-16286.39	32690.97	27.56	0.00	0.65	0.66	0.67
time + seasons	56.17	-16306.78	32725.92	62.51	0.00	0.65	0.66	0.67
time	55.47	-16309.50	32729.94	66.53	0.00	0.65	0.66	0.67
temperature + season	51.18	-16562.45	33227.27	563.86	0.00	0.63	0.64	0.65
temperature	53.54	-16621.42	33349.92	686.51	0.00	0.62	0.63	0.64
season	45.64	-16994.37	34080.03	1416.62	0.00	0.56	0.57	0.57

Notes: For each model the degrees of freedom (df), loglikelihood value (LogLik), difference in AIC between the best fit model and model$_i$ (ΔAIC$_i$), Akaike weight (w_i), area under receivers operating characteristic curve (ROC) *model parameter coefficient significant ($p < 0.05$). I obtained the 95 % confidence intervals (CI) of the ROC parameter estimate using a parametric bootstrap based on 10 000 random samples.

Appendix XV. Full set of candidate generalized additive models with simple random effects used to explain the likelihood of elephant's artificial waterholes using time of day, temperature, and season.

							95 % CI for AUC	
Model	df	LogLik	AIC	ΔAIC	w_i	AUC	Lower	Upper
temperature + time + season	36.637	-2231.489	4536.251	0.000	1.000	0.750	0.733	0.768
temperature + time	36.243	-2249.257	4570.999	34.748	0.000	0.743	0.725	0.760
temperature + season	30.927	-2262.426	4586.706	50.455	0.000	0.736	0.718	0.755
time + seasons	33.861	-2260.627	4588.975	52.724	0.000	0.739	0.720	0.757
time	32.675	-2266.738	4598.826	62.574	0.000	0.736	0.718	0.754
temperature	30.097	-2296.258	4652.711	116.459	0.000	0.718	0.700	0.737
season	27.536	-2367.746	4790.563	254.312	0.000	0.677	0.656	0.698

Notes: For each model the degrees of freedom (df), loglikelihood value (LogLik), difference in AIC between the best fit model and model$_i$ (ΔAIC$_i$), Akaike weight (w_i), area under receivers operating characteristic curve (ROC) *model parameter coefficient significant ($p <$ 0.05). I obtained the 95 % confidence intervals (CI) of the ROC parameter estimate using a parametric bootstrap based on 10 000 random samples.

Appendix XVI. Area in km^2 used by the 26-collared elephant cows during the dry and wet. Only artificial, is the area used only during artificial trips and the increase percentage is the increase in area used by elephants because of artificial waterhole use.

	Dry season (km^2)					**Wet season (km^2)**				
Elephant	**Total area**	**Perennial rivers**	**Artificial waterholes**	**Only Artificial waterholes**	**Increase (%)**	**Total**	**Perennial rivers**	**Artificial waterholes**	**Only Artificial waterholes**	**Increase (%)**
EF0205	307.92	226.87	120.13	81.05	26.3	941.46	520.41	649.32	421.05	44.7
EF0206	179.79	154.86	76.34	24.93	13.9	181.48	181.48	-	-	-
EF0207	328.22	158.68	246.67	169.54	51.7	884.30	331.75	874.11	552.55	62.5
EF0208	193.65	126.84	126.90	66.81	34.5	362.00	349.94	162.09	12.06	3.3
EF0209	367.61	130.42	260.43	237.19	64.5	219.22	84.15	139.19	135.07	61.6
EF0210	544.61	395.20	302.99	149.41	27.4	552.58	342.83	386.77	209.75	38.0
EF0211	304.01	215.40	166.24	88.61	29.1	529.41	438.14	205.60	91.26	17.2
EF0212	308.88	232.59	134.83	76.29	24.7	614.18	548.37	123.89	65.81	10.7
EF0213	646.11	331.53	389.28	314.59	48.7	508.72	374.66	233.59	134.06	26.4
EF0214	351.48	129.93	306.63	221.55	63.0	761.79	455.38	535.88	306.41	40.2
EF0215	504.35	371.33	336.40	133.02	26.4	289.54	287.71	55.02	1.83	0.6
EF0216	258.17	151.66	148.31	106.51	41.3	332.06	232.88	237.39	99.18	29.9
EF0217	73.28	11.95	61.33	61.33	83.7	107.42	14.06	173.73	93.36	86.9

EF0218	169.85	114.73	97.44	55.12	32.5	341.18	234.92	224.11	106.26	31.1
EF0219	303.05	208.60	178.96	94.44	31.2	270.19	219.30	140.32	50.89	18.8
EF0220	101.14	89.21	27.83	11.92	11.8	1176.57	895.57	547.48	281.00	23.9
EF0221	252.01	127.35	210.59	124.66	49.5	548.16	478.96	298.66	69.19	12.6
EF0222	266.91	259.06	131.73	7.85	2.9	771.56	716.33	329.18	55.24	7.2
EF0223	219.92	79.23	219.56	140.69	64.0	199.39	166.24	68.16	33.15	16.6
EF0224	301.08	162.48	241.44	138.61	46.0	271.12	163.97	294.64	107.16	39.5
EF0225	120.20	110.78	15.94	9.41	7.8	88.14	42.90	48.69	45.24	51.3
EF0226	681.37	569.60	180.00	111.78	16.4	808.85	683.63	348.28	125.22	15.5
EF0227	356.25	350.51	105.96	5.74	1.6	480.49	462.35	258.92	18.14	3.9
EF0228	388.44	383.19	84.82	5.24	1.4	448.78	434.54	109.99	14.24	3.1
EF0229	474.40	369.66	148.41	104.74	22.1	360.25	304.99	75.34	55.27	15.3
EF0230	52.23	23.76	32.11	28.47	54.5	-	-	-	-	-
Mean ± SD	309.81 ± 161.60	210.98 ± 133.45	167.36 ± 98.70	98.83 ± 77.64	33.7 ± 21.8	463.42 ± 290.60	358.62 ± 213.16	263.49 ± 204.72	128.47 ± 136.17	27.5 ± 22.0