African Elephant in a Cleft Stick

Choosing between starving or dying from thirst in arid savanna

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This research was conducted under the auspices of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation

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submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University by
the authority of the Rector Magnificus
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Tuesday 20 December 2016
at 8.30 a.m. in the Aula.

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African Elephant in a Cleft Stick
Choosing between starving or dying from thirst in arid savanna,
120 pages.

PhD thesis, Wageningen University, Wageningen, NL (2016)
With references, with summaries in English, Kiswahili and Dutch

ISBN: 978-94-6343-000-5
DOI: 10.18174/394719

To Jib, Swun and all those who put their life at great risk for the sake of wildlife

Contents

Chapter 1

General Introduction

Studies of population dynamics form a central theme in ecology, wildlife conservation and management (Gaillard et al., 1998). Most population ecologists aim at identifying and explaining variabilities of vital demographic rates such as births, deaths, immigration and emigration, that influence change in population size (Tuljapurkar and Caswell, 2012). The variability of the demographic rates are affected by, among others, density-dependent factors (Sæther, 1997, Krebs, 2002). ‘’Density–dependent” refers to a population change where population growth rate declines with population density, other factors kept constant (Lotka, 1925, Fisher, 1930, Nicholson and Bailey, 1935, Andrewartha and Birch, 1954), and the relationship between population density and population growth rate can be non-linear (Sibly and Hone, 2002, Gaillard et al., 1998). This density-dependence hypothesis only accounts for the intrinsic demographic and biotic factors (e.g., food resources, habitat quality, interspecific competition, predation) but does not consider abiotic factors (e.g., rainfall amount, diseases, earth quakes) which also affect population growth (Gaillard et al., 2000, Krebs, 2002). In recent times, population ecologists generally agree that no predictive models of population dynamics can solely rely on the relationships between intrinsic rates and population density without considering the influence of stochastic environmental factors (Krebs, 1995). Because of the variations in environmental factors in time and space, studies of the same animal species in different environments hardly produce similar population growth patterns (Krebs, 2002), as exemplified in salmon fishes (Walters, 1987), birds (Both, 1998) and elephant (Moss, 2001, Gough and Kerley, 2006).

Density-dependent population regulation occurs in a closed equilibrium system (Sinclair and Krebs, 2002, Sinclair, 2003, Gillson and Lindsay, 2003). For instance, in ecosystems with reliable rainfall, stable food and water resources, animal populations persist at a steady state, often referred to as the "ecological carrying capacity" (Krebs, 2002, Sibly and Hone, 2002). It is argued that animal populations can self-regulate at this steady state through negative feedback mechanisms when population is above or below the ecological carrying capacity (Krebs, 2002). In the absence of environmental changes or time-lags, population density will remain close to the ecological carrying capacity (Turchin, 1999, Sinclair, 1996, Sinclair and Krebs, 2002). The major drawback of equilibrium theory is that it does not account for environmental stochasticity such as floods, fires, tornados etc., that are common in natural systems (Reice, 1994). Indeed, most studies conducted in marine and terrestrial ecosystems on different taxa of plants and animals contradict the predictions of equilibrium theory (Connell, 1978, Peet et al., 1983, Sale, 1977, Reice, 1985, Reice, 1994). Also, in rangelands where rainfall is highly variable, the concept of ecological carrying capacity does not apply (Ellis and Swift, 1988, De Leeuw and Tothill, 1993, Gillson, 2004, Vetter, 2005). The frequency of variability of environmental factors in the rangelands are very high, hence impeding equilibrium states from being attained (Reice, 1985). Such systems are best described to be governed by non-equilibrium dynamics (Illius and O'Connor, 1999).

Non-equilibrium population models predict that plant composition and biomass are primarily driven by rainfall rather than by grazing pressure in tropical savannas (Ellis and Swift, 1988, Vetter, 2005). Furthermore, herbivore numbers maintained at low densities by frequent droughts in the tropics have little impact on vegetation change (Ellis and Swift, 1988, Illius and O'Connor, 1999, Sullivan and Rohde, 2002). In such a case, variability in rainfall is thought to be an important driver of tropical savanna ecology that determines spatial and temporal heterogeneity required for ecosystem diversity, stability and resilience (Walker and Noy-Meir, 1982, Walker, 1989, McNaughton et al., 1988).

The debate about the negative impacts of high elephant density through damage to woody vegetation and significant loss of tree cover has gone on for decades (Glover and Sheldrick, 1964, Myers, 1973, Cumming et al., 1997, de Beer et al., 2006), and the resultant habitat change is perceived as an undesirable disruption of equilibrium condition of tropical savannas (Cumming et al., 1997, Gillson and Lindsay, 2003), although a contrary view exists (Kerley and Landman, 2006, Kohi et al., 2011). These habitat modifications by elephant are a potentially irreversible threat to the savanna ecosystem and its biodiversity (Cumming et al., 1997). For wildlife managers, understanding the processes that govern ecosystems have very profound implications on their decision making: if ecosystems are governed by non-equilibrium dynamics then a "*laissez-faire* management style" is appropriate (Van Aarde and Jackson, 2007, Guldemond and Aarde, 2008), but if equilibrium dynamics is prevalent, then a "command and control management style" is appropriate (Gillson and Lindsay, 2003, Owen-Smith et al., 2006, Guldemond and Aarde, 2008). The examples of management options based on an equilibrium view include controlling elephant numbers through culling, translocation, and administering of birth control contraceptives (Walker et al., 1987, Owen-Smith et al., 2006, Scholes and Mennell, 2008).

Elephant population management in arid savannas in Africa

There has been a growing concern about the survival of African elephant because of the threats from poaching, destruction of their habitat, competing land-uses and increased frequencies of droughts (Douglas-Hamilton, 1987, Blanc et al., 2005, Bouché et al., 2011, de Boer et al., 2013, Chase et al., 2016). For this reason, African elephant is listed as "Vulnerable" on the IUCN Red List (Blanc et al., 2007). African elephant populations vary across the continent, with the Southern Africa population increasing (Bouché et al., 2011), and the Central and West Africa population declining to a level of local extinction (Blanc et al., 2005, Bouché et al., 2011, Wittemyer et al., 2014, Chase et al., 2016). As at 2013, the estimated African elephant numbers was about half a million (AESG, 2013). Southern Africa accounted for 55% of this population, followed by Eastern (28%) and Central African states (16%). The remaining population (1%) is spread out in 13 states in West Africa (AESG, 2013). The most recent continental wide census results of African elephant show that the population has reduced further by 8% to about 350,000 (Chase et al., 2016); again, the reduction is largely attributed to poaching and habitat loss.

In regions where elephant density is high, there is a long standing perception and inconclusive debates that elephant have adverse impacts on habitats (de Beer et al., 2006, Guldemond and Aarde, 2008, Staub et al., 2013) and also, sometimes, on other species (Cumming et al., 1997) through their foraging behaviour of pushing over, uprooting and snapping trees (Staub et al., 2013). The question of whether elephant numbers should be controlled or not has been the subject of debates for decades with contradicting proposition on how this should be addressed (Laws, 1970b, Caughley, 1976, Myers, 1973, Owen-Smith et al., 2006, Van Aarde and Jackson, 2007, Guldemond and Aarde, 2008). In some instances, elephant are culled or translocated to reduce the perceived negative impact on woody trees and other species and to keep the population below the "ecological carrying capacity" (Whyte et al., 1998, Gillson and Lindsay, 2003, Owen-Smith et al., 2006). Yet vegetation is also influenced by other factors such as drought, fire, and other herbivores (Prins and van der Jeugd, 1993, Skarpe et al., 2004, Wiseman et al., 2004), leading to transformation of woodlands into grasslands (Illius and O'Connor, 1999, Van Langevelde et al., 2003). Therefore reduction of elephant numbers may not necessarily translate to regeneration of woody trees (Dublin, 1991, Pickett et al., 2003). Another management option is the provision of water to keep elephant population artificially dispersed, thus reducing the negative impacts of high elephant density on woody vegetation (Gillson and Lindsay, 2003). The drawback of water provision is that it results in homogenization of the landscape which is not conducive for mega- and meso-herbivores (Hilbers et al., 2015). Culling of elephant and water provision are examples of management options based on equilibrium theory.

Conversely, in non-equilibrium management approach, less human intervention is applied and habitat heterogeneity persists through the natural functioning of an ecosystem (Vetter, 2005, Van Aarde and Jackson, 2007). For instance, herbivores adopt a seasonal grazing pattern, where some areas, especially near rivers, are foraged intensively in the dry season as other areas of low use get the window to regenerate, hence maintaining habitat heterogeneity (Owen-Smith et al., 2006, Van Aarde and Jackson, 2007). Further, passive management such as corridors that interconnect suitable habitats for the dispersal of elephant and other herbivores are maintained for the same purpose (Hoare and Du Toit, 1999, Van Aarde and Jackson, 2007).

Despite the criticism on the equilibrium approach of elephant population management, it remains the popular management option in most dry savannas, where rainfall is highly variable (Van Aarde et al., 2006, Van Aarde and Jackson, 2007). Reference to justify elephant population control is drawn from the mass elephant mortality that occurred during severe droughts in tropical savannas such as Tsavo National Park in Kenya (Corfield, 1973, Myers, 1973, Phillipson, 1975), Chobe National Park in Botswana (Skarpe et al., 2004) and Hwange National Park in Zimbabwe (Dudley et al., 2001). The mass mortality of elephant was thought to be a negative consequence of elephant overpopulation (Owen-Smith et al., 2006). For instance, in Tsavo, over 5000 elephant died during prolonged droughts of the 1960s and 1970s (Corfield, 1973). This incident attracted immense global research interest to investigate the likely causes of such massive mortalities (Myers, 1973, Phillipson, 1975, Corfield, 1973, Laws and Parker, 1968, Laws, 1970a, Laws, 1970b, Glover and Sheldrick, 1964). The ‘’Tsavo debate” was partly inconclusive because it was based on a one-off drought incident and the studies were conducted amidst that catastrophic drought incident. However, elephant mortality continued to occur even during short droughts, though not in the magnitude of the 1960s and 1970s. The frequency of these droughts have been increasing and it is predicted to increase into the future (Shrader et al., 2010, Yang et al., 2014). For instance, as recent as 2016, South African protected areas faced the worst droughts in its history and similar debate on how to address the consequences of droughts on elephant population took place (Peel and Anderson, 2016). The poignant question that arises is; what have we learnt after 50 years of Tsavo elephant mortality incidents? Proper management of the African elephant in tropical savannas requires a good understanding of their ecology - their distribution, density, movements, behaviour and human-induced impacts on their ecosystems (Kangwana, 1996, Owen-Smith et al., 2006, van Aarde et al., 2008, Scholes and Mennell, 2008, Moss et al., 2011, Skarpe et al., 2014).

The aim of my study was to address the question: Are elephant populations in tropical savannas affected by droughts? I studied elephant population change with respect to droughts in the Tsavo Conservation Area (TCA) and Amboseli National Park in Kenya, to gain a better understanding of drought-related aspects of elephant ecology in a tropical savanna. The understanding of drought-related mortality and its impact on elephant populations require a long term dataset of elephant population change in relation to drought occurrences. I relied on the longest existing time-series data in Africa of a wild elephant population that has been consistently monitored for over 40 years, where life-histories of 3000 individual elephant are known, from Amboseli National Park in Kenya. Besides, I analysed geo-referenced elephant mortality data collected daily for 10 years from the Tsavo ecosystem, Kenya. Moreover, I analysed 2-years data from 8 collared African elephant to investigate their movements patterns in response to seasonal water and forage distribution in the Tsavo ecosystem. I further explored how the findings of this study could be applied to elephant conservation in tropical savannas.

The study area

This study was conducted in two locations: The Tsavo Conservation Area (comprising of Tsavo East National Park, Tsavo West National Park, Chyulu National Park, South Kitui National Reserve and the surrounding community owned ranches) and the Amboseli ecosystem (comprising of Amboseli National Park and the surrounding community owned ranches). The Tsavo Conservation Area spans an area of ~48,300 km^2 and is located at 2°- 4° S and 37.5°- 39.5° E in the southern part of Kenya (Omondi et al., 2008) (Figure 1). It is an arid ecosystem with bi-modal rainfall from mid-March to May and from November to December (Omondi et al., 2008, Tyrrell and Coe, 1974). The long dry season typically ranges from June through October, whereas the short dry season occurs from January to March (Leuthold and Leuthold, 1978, Tyrrell and Coe, 1974). The mean annual rainfall in Tsavo ranges from 250 to 500 mm (Ngene et al., 2014).

Tsavo Conservation Area is dominated by a flat and undulating terrain with an altitude range of 100-500m (Mukeka, 2010). Tsavo landscape is interrupted by granitic hills and inselbergs with the highest peak of Taita hills standing at ~2,220 metres above sea level (Mukeka, 2010). It has only one perennial river, the Galana River and two seasonal river, Tiva and Voi (Ayeni, 1975, Mukeka, 2010). Tsavo Conservation Area is home to over 12,000 elephant, a third of all population of elephant in Kenya (Ngene et al., 2011).

The Amboseli ecosystem extends to over 3500 km^2 (Western, 1975, Moss, 2001), comprising of Amboseli National Park with an approximate area of 390 km^2, located between 37°E and 37° 30' E and 2° 30' and 2° 45' S in southern Kenya, and was established in 1974 (Okello et al., 2015). It abuts the Masai Ecosystem to the South (Prins, 1987). The remaining area comprises community owned conservancies and ranches. The Amboseli ecosystem is an arid area with a bimodal rainfall pattern; long rainy season lasts from March to May, while the short rains occur from November to December (Moss, 2001). The Amboseli ecosystem experiences two dry seasons, the long dry season lasting from June to October and the short dry season from January to March (Moss, 2001, Prins and Loth, 1988). Rainfall amounts range from 100-900mm annually with an average of 300mm annually (Moss et al., 2011). The vegetation is predominantly grassland interspersed with acacia woodland with permanent swamps (Moss et al., 2011). The Amboseli ecosystem is home to about 1500 elephant (Okello et al., 2015).

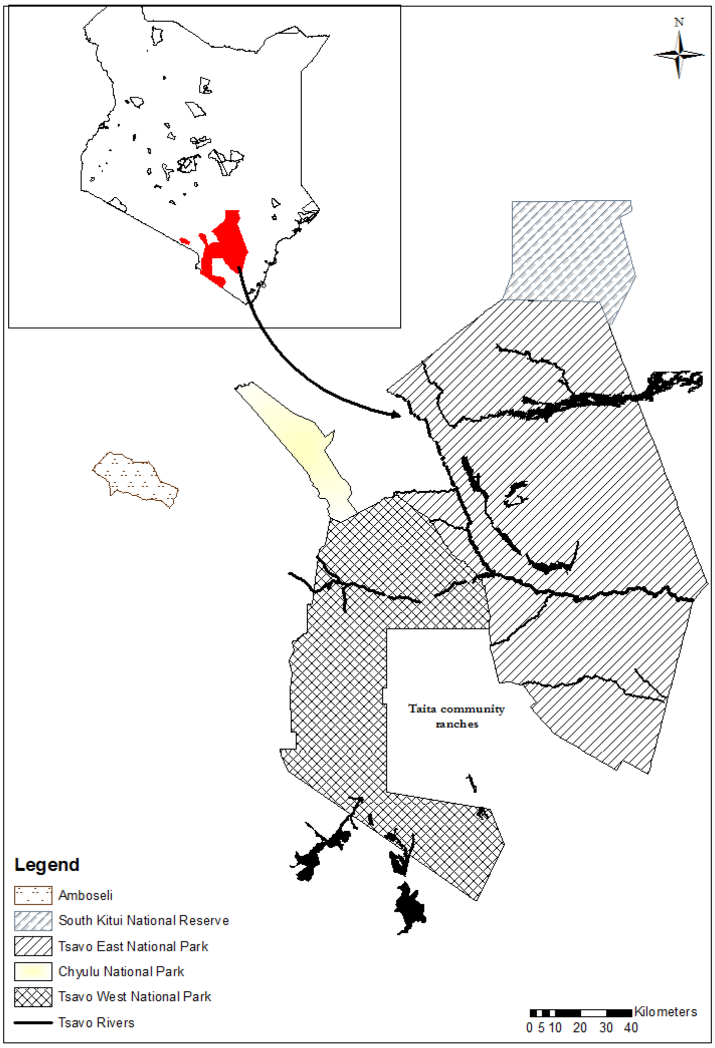

Figure 1: Geographic location of study Area in Kenya (Tsavo Conservation Area and the Amboseli National Park)

Thesis outline

In my study, I aim to contribute to a better understanding of the elephant population dynamics in two important conservation areas in Kenya (The Tsavo Conservation Area and Amboseli National Park) with respect to severe drought conditions and to inform future elephant population management approaches in tropical savannas.

I present four studies: The first two studies focus on the theme of spatial and temporal changes in elephant mortality in relation to variability in rainfall (Chapters 2 & 3). Chapter 2 describes the effects of drought duration and intensity on temporal elephant mortality patterns in Amboseli National Park, Kenya. I looked at drought effects based on the length and intensity of rainfall in contrast to past studies that analysed discrete seasonal and annual drought effects on elephant population (Dudley et al., 2001, Foley et al., 2008, Lee et al., 2011a). In chapter 3, I present the study on the effect of the length (number of consecutive dry months) and intensity (amount of rainfall) of the dry periods, the distance to water, forage and elephant density on spatial elephant mortality. My aim in this chapter is to investigate the factors that explain the spatial distribution of elephant mortality in a dry savanna using Tsavo as a case study. In chapters 4 and 5, I investigate the movement response of African elephant to seasonal water and forage distribution in tropical savanna, using Tsavo Conservation Area as a case study. My purpose in these two chapters is to understand the relative importance of two critical resources in the dry season, water and forage distribution, in determining elephant habitat use. In chapter 4, I begin by investigating the movement response of African elephant to seasonal water distribution in Tsavo. I then follow in chapter 5 to present a study on forage site selection by elephant in a tropical savanna with a specific focus on forage quality and quantity. Finally in chapter 6, I discuss the themes of each chapter separately and synthesize the prominent issue that arises in each. I proceed to generalize the findings to a broader context of elephant population change in tropical savannas and its implication on the future direction of elephant population management. I relate my findings to the on-going debates about density-dependency versus density-independency in elephant population dynamics and about equilibrium versus non-equilibrium dynamics in tropical savannas. Finally, I draw conclusions and identify gaps and recommendations for further research.

Chapter 2

Temporal mortality patterns of African elephant *(Loxodonta africana)* in dry savannas is a reflection of past drought duration and intensity.

Yussuf A. Wato, Ignas M.A. Heitkönig, Herbert H.T. Prins, Phyllis Lee, Cynthia Moss, Sipke E. van Wieren, Geoffrey Wahungu, & Frank van Langevelde.

Abstract

Most ecologists view dry savannas (rainfall less than 400mm year), to be governed by equilibrium dynamics. It is assumed that such systems can support only a certain maximum number of elephant. However, other studies suggest that savannas are non-equilibrium systems prone to drought that may result to crashes of elephant population, and the effects may vary with age or sex of the elephant. While half of the African elephant (*Loxodonta africana*) populations live in these dry savannas, the effects of drought duration and intensity on their population structure is unclear. Drought has been shown to cause juvenile elephant mortality but to have less effect on survival of adult elephant. Most previous studies have focused on inter-annual variability and, rarely, on the duration and intensities of drought at a fine timescale of months that cause variability of forage availability to elephants. We hypothesized that the mortality of elephant is dependent on the duration and intensity of drought. In harsh conditions, elephant mortality is expected to be: (1) high among juvenile elephant and decrease with age, (2) higher in females than males; and, (3) mortality rates will increase with population size. We investigated the effects of drought duration and intensity on African elephant using a demographic data set of over 3000 individually known elephant, monitored for over four decades between 1972 and 2012 at Amboseli National Park, Kenya. The increased occurrence of dry months (<20mm rain) increased the probability of elephant mortality. Similarly, elephant mortality increased slightly with an increase in the elephant population size, whereas the increase in previous year's rainfall amounts reduced the risk of elephant death. Although the odds of dying was higher for male than female elephant, the mortality risk was dependent on the interaction between the age and the sex of elephant. Male elephant above 25 years have significantly lower risks of mortality than females > 25 years. Overall, the risk of death reduced with the age of elephant, with the calves below 1 year of age having the highest mortality risk. We conclude that the effect of drought on elephant survival is more pronounced at a fine resolution of monthly variability of rainfall, and that elephant populations in dry savanna are driven by non-equilibrium dynamics.

Introduction

A central goal in population ecology is to understand the biotic and abiotic factors that explain changes in population sizes of wildlife (Gaillard et al., 2000, Coulson et al., 2004). Wildlife population sizes are assumed to be regulated by equilibrium dynamics if the population is dominantly regulated by biotic factors through negative feedback mechanisms and, in the absence of environmental changes, population size remains at a steady state often referred to as the ecological carrying capacity (Turchin, 1999, Sinclair, 1996, Sinclair and Krebs, 2002). Conversely, if the relative importance of abiotic factors is greater than biotic factors in causing population change, then populations are assumed to be controlled by non-equilibrium dynamics (Ellis and Swift, 1988, Oba, 2001, Gillson and Lindsay, 2003, Vetter, 2005). For example, it has been argued that tropical savannas experience non-equilibrium dynamics as they are characterized by high variation in annual and seasonal rainfall (Rasmussen et al., 2006). Rainfall variability may result in scarcity of forage and water for wildlife, and if prolonged, in death of animals (Wittemyer et al., 2005, Foley et al., 2008, Young and Van Aarde, 2010).

The effects of harsh abiotic conditions on animals can be observed through changes in their body condition (Loison et al., 1999), reduction in the probability of conception and successful reproduction (Rasmussen et al., 2006, Moss et al., 2011, Bouwhuis et al., 2010), and increase in mortality rates (Foley et al., 2008, Lee et al., 2013). For many species, it has been shown that the effect of changes in abiotic factors on their mortality vary with the age and the sex of the animal (Gaillard et al., 2000). For instance, the survival of infant red deer *(Cervus elaphus)* decreased with increase in snow depth (Albon et al., 1983), and the mortality of adult mountain goats *(Oreamnos americanus)* increased with low temperature and snow depth (White et al., 2011). In roe deer (*Capreolus capreolus*) during severe winters, more females survived than males, and the survival of an individual decreased after 7 years of age (Gaillard et al., 1993). Although most studies on effects of climate variability on wildlife have focused on short-lived mammals, the recent availability of long-term data have resulted in studies on the effect of climate variability on long-lived animals such as elephants.

During dry periods, high juvenile elephant mortality is common (Moss, 2001, Leggett, 2006, Foley et al., 2008, Trimble et al., 2009, Lee and Moss, 2011, Moss et al., 2011), whereas adult elephant are thought to be buffered against drought-induced mortality (Gaillard et al., 2000, Young and Van Aarde, 2010, Lee et al., 2011a). Among the juvenile elephant, the male calves born in dry years have reduced life expectancy and reduced body sizes as they grow to maturity, termed the cohort-effect (Lee et al., 2013). Incidences of drought-induced adult elephant mortality have also been recorded in severe droughts in the past few decades (Corfield, 1973, Dudley et al., 2001, Owen-Smith et al., 2006, Foley et al., 2008). Asian elephants *(Elephas maximus)* showed the highest survival rates during the wettest months for all ages and sexes (Mumby et al., 2013). This was also found for African elephant where mortality decreased in the wet season (Moss et al., 2011, Lee et al., 2011a). For instance, the highest population growth rate of elephant at Addo National Park coincided with El Niño (increased) rainfall (Gough and Kerley, 2006) whereas, the highest mortality occurred during severe droughts at Samburu National Reserve (Wittemyer et al., 2005).

Despite these findings, the effect of the duration and intensity of dry periods on adult elephant mortality is still debated (Wato et al., 2016) and remains inconclusive (Dudley et al., 2001, Moss et al., 2011). Some of these studies were based on a single drought event (Dudley et al., 2001, Foley et al., 2008), whereas others spanned multiple drought events of over 30 years (Moss et al., 2011, Lee et al., 2013). In contrast to the increased juvenile mortality during dry periods, the few studies that specifically investigated drought-related adult elephant mortality reported more deaths in wet years than in dry years (Moss et al., 2011, Dudley et al., 2001). For example, in Hwange, comparative mortality between two drought years showed that high adult elephant mortality occurred in the year that registered high annual rainfall (Dudley et al., 2001). From this counterintuitive result, it appears that adult elephant mortality may not be related to whether it rains or not, but rather, the amount, intensity and distribution of the rainfall (Dudley et al., 2001). Supporting this argument, Rasmussen et al. (2006) reported that months with less than 20mm of rainfall had low Normalized Difference Vegetation Index (NDVI), that indicated too little plant production to sustain elephant energetic requirements. If this is the case, we do not expect elephant population in dry savannas to be regulated by density-dependent factors, but rather be controlled by the climatic factors such as rainfall variability.

In contrast to the role of rainfall, other studies suggest that elephant population in dry savannas may be governed by equilibrium dynamics. The case-studies invoked to illustrate density-dependent elephant mortalities include Tsavo National Park in Kenya (Corfield, 1973, Myers, 1973, Phillipson, 1975), Chobe National Park in Botswana (Skarpe et al., 2004), Hwange National Park in Zimbabwe (Dudley et al., 2001) and other tropical savannas (Foley et al., 2008). In the Tsavo case, where over 5000 elephant mortalities were reported in the severe drought of the 70s (Corfield, 1973), the explanations inclined towards density-dependent effects implying that food availability was not sufficient to sustain the elephant (Owen-Smith et al., 2006, Van Aarde and Jackson, 2007). Other studies reported positive correlation between calf mortalities and density in elephant (Moss et al., 2011), and other long-lived mammals (Gaillard et al., 1998, Gaillard et al., 2000, Eberhardt, 2002), suggesting the existence of equilibrium dynamics. Although dry savannas are generally assumed to be governed by non-equilibrium dynamics (Vetter, 2005, von Wehrden et al., 2012), elephant populations in these areas are managed based on assumed equilibrium population dynamics (Gillson and Lindsay, 2003, Van Aarde and Jackson, 2007). The question remains as to whether non-equilibrium dynamics play a role in elephant population dynamics in dry savannas.

To separate the role of non-equilibrium and equilibrium dynamics in elephant populations, we explore effects of the duration and intensity of dry periods and population density on adult elephant mortality. We tested whether elephant mortality depends on a) the duration and intensity of dry periods, b) the age and sex of elephant, and c) the size of the elephant population. We hypothesized that in dry periods, elephant mortality would be high a) in juvenile elephant and decreases with age, b) in females as opposed to males given reproductive costs, and c) would increase with population size. The rainfall in Amboseli ecosystem show high variability in both the duration and intensity (Croze and Lindsay, 2011). To test our hypotheses, we used the long-term rainfall records of Amboseli ecosystem at monthly resolution to capture rainfall variability. We used data from elephant that died of natural causes only and excluded those that died of any other causes such as injury and poaching.

Materials and methods

Study area

Amboseli National Park with an approximate area of 390 km^2, is located between longitude 37°E and 37° 30' E and Latitude 2° 30' and 2° 45' S in southern Kenya, and was established in 1974 (Okello et al., 2015). The entire Amboseli ecosystem where elephant roam extends to over 3500 km^2 (Western, 1975, Moss, 2001) (Figure 1). The rainfall pattern is bimodal and the long rainy season lasts from March to May, while the short rains occur from November to December (Moss, 2001). Amboseli experiences two dry seasons, the long dry season lasting from June to October and the short dry season from January to March (Moss, 2001). Rainfall amounts range from 100-600 mm annually with an average of about 300 mm annually (Altmann et al., 2002). The vegetation is predominantly grassland interspersed with acacia woodland along permanent swamps (Moss et al., 2011).

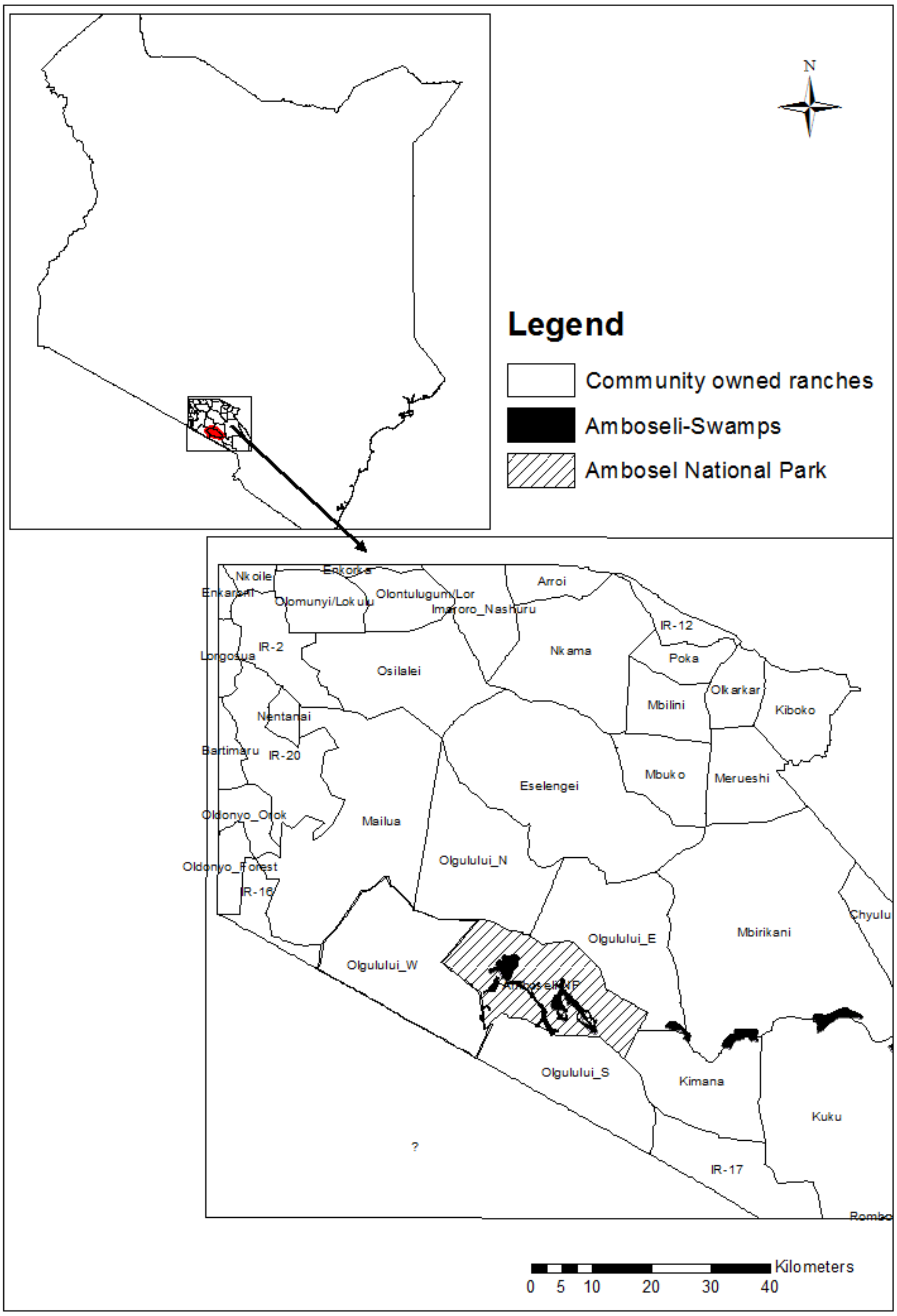

Figure 1: Geographical location of Amboseli National Park and the surrounding Community owned ranches in Kenya

Elephant demographic and rainfall data

The free-ranging elephant in Amboseli have been monitored continuously since 1972, and records of over 3000 individually known elephant are maintained in the Amboseli Elephant Research Project's (AERP) database (Moss, 2001, Moss and Lee, 2011). Births of elephant between 1972 and 1975 are known with a precision of 3-6 months, and from 1976 with a precision of 2 weeks to 3 months (Lee et al., 2013). Since the elephant herds are monitored routinely and every herd must be seen and counted at least once in a month, mortality of each elephant is known with a precision of 1-3 months (Moss, 2001), although the death of male elephants may take longer to discover especially during the dry periods when they roam further from the park. The Amboseli elephant population is ideal for studies of demographic change as they range over an unfenced area of 3500 km^2, are not heavily poached, and they have been relatively unaffected by land-use changes and habitat compression as a result of human population increase (Moss, 2001, Moss and Lee, 2011). Therefore, we excluded the effect of human activities in the analysis and focussed on disentangling the effects of abiotic controlling factors from density-dependent regulatory factors. The detailed monitoring protocol for this elephant population is described in Moss (2001).

Rainfall data were obtained from three different rain gauges from 1972 (Lindsay, 2011). Between 1972-82, rainfall data were obtained from Ol-Tukai meteorological station, whereas the rainfall data from 1982 were collected by the Amboseli Elephant Research Projects (AERP) meteorological station (Lindsay, 2011), both within Amboseli NP. Missing data were supplemented by records from the Amboseli Baboons Research Project (Altmann et al., 2002, Lindsay, 2011). Because rainfall amounts in the entire ecosystem is similar to Amboseli National Park (Moss et al., 2011), we used rainfall data from the three rain gauges to represent rainfall amounts in the entire elephant ranges in the study area. Various measures of rainfall variability have been used in behavioural ecology studies such as measures of rainfall evenness, the annual coefficient of variation across months, and the number of dry months in a given year (Bronikowski and Webb, 1996), although there is no *a priori* criterion to select any of these measures and the choice is guided by the purpose of the study. We based our rainfall variability measure on long-term studies that compared rainfall amounts with forage availability (Altmann et al., 2002, Rasmussen et al., 2006). We classified months into “a dry month” if it had less than 20mm of rainfall and “a dry season” if the cumulative rainfall in four consecutive months was below 150 mm based on the duration of a typical long dry season in Amboseli ecosystem. We used “150 mm” based on the average lowest rainfall amount calculated from 50 dry seasons spanning over 25 years in Amboseli ecosystem (Moss, 2001, Altmann et al., 2002, Moss et al., 2011). Drought in this paper refers to four or more consecutive months with cumulative rainfall of less than 150 mm.

Data analysis

We used the total number of dead elephant by age classes as the dependent variable. The explanatory variables we used in modelling elephant mortality included: elephant age classes and sex, seasonal rainfall amount, monthly rainfall amount, cumulative monthly rainfall amount, and annual elephant population size. We categorized age classes as young calves (0-12 months), older calves (13-24 months), immatures (2-8 years), young adults (9-24 years), prime reproductive adults (25-49) and old adults (50+). The cumulative monthly rainfall amount accounted for effects of past rainfall on elephant mortality in the analysis. We used cumulative monthly rainfall iteratively in the analysis starting with the month preceding each elephants’ death and successively added the previous months to the model. In the final model, we included the sum of precipitation amounts for each of the 17 months preceding each elephant death because its inclusion resulted in the lowest AIC. We initially used a Poisson Generalized Linear Model (GzLM) for the analysis as it is appropriate for modelling count data such as elephant mortality (Zuur et al., 2010). Since the results from Poisson model showed over-dispersion and the data had many zeros (Figure 2), we replaced it with a zero-inflated GzLM to model elephant mortality (Cameron and Trivedi, 1998, Zuur et al., 2010). Furthermore, we assessed multi-collinearity between the rainfall variables and the other variables by calculating their variance inflation factor (VIF) values, and we excluded all variables with VIF greater than five (Zuur et al., 2010).

We assessed all two-way interactions between independent variables and retained only significant interactions in the final GzLM model. We generated all possible candidate models from the global model and performed model selection for all the competing models by comparing their AIC values (Royall, 1997, Anderson and Burnham, 2002). Using the above criteria, we selected the best approximating model with the lowest AIC. For the ease of interpretation of results, we calculated the odds of dying of elephant based on their age, sex and all the other variables selected (Zuur et al., 2010). All the analyses were done in R 3.2.0 software (Team, 2010)

Results

A total of 1347 elephant were reported to have died of natural causes between 1972-2012 at Amboseli National Park. Of these deaths, 198 were adult elephant (>25 years), 217 were sub-adults (9-25 years), and the rest were < 9 years. The annual percentage of mortality differed between years, with the highest reported mortality in 2009 (~30%). Amboseli elephant population is estimated at about 1145 based on the recent census of 2013 (Okello et al., 2015).

The best model included the variables with seasonal rainfall, monthly rainfall, age, sex, population size, cumulative rainfall of the 17 months preceding each elephant death and age and sex interactions (Table 1). Elephant odds of dying were 1.31 times higher in the dry months (rainfall < 20mm) and 1.24 times higher in the dry season (rainfall <150 mm) (Table 2). There was a very small, but highly significant increase in elephant mortality with an increase in yearly elephant population size ($P < 0.001$, see odds ratio, Table 2), whereas the risk of elephant mortality significantly decreased ($P < 0.001$) as the cumulative rainfall prior to each elephant's death increased. The effect of cumulative rainfall was significant from seven months to seventeen months preceding each elephant's death. Although the odds of dying for the male elephant were 1.66 times higher than for the females, this risk was dependent on the interaction between the age and the sex of an elephant. Generally, the risk of dying decreased with the age of an elephant, and male elephant between 25 to 49 years of age had a lower risk of dying of natural causes as compared to females of similar age (Table 2).

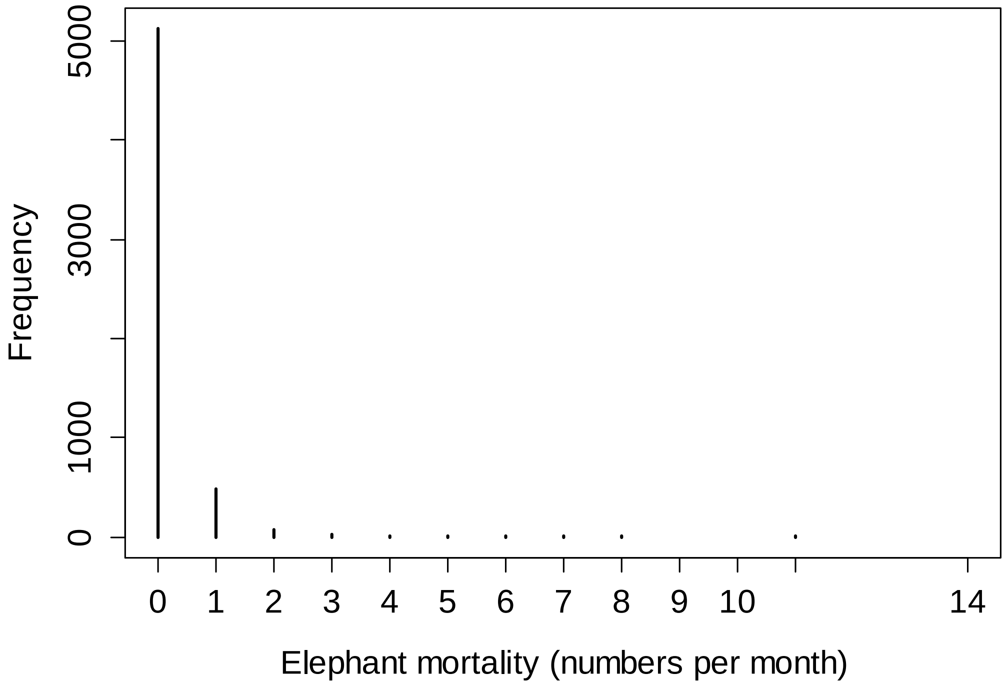

Figure 2: Frequency of recorded dead elephant per month from 1972-2012 at Amboseli ecosystem showing zero-inflation

Table 1: The best four models (with the lowest AIC values) from the competing models explaining natural elephant mortality. **AIC** - the Akaike Information Criteria values; **AIC** $_{(\Delta i)}$ - the difference between the AIC value of each model and the best model; and the **AIC** $_{(Wi)}$ - the ratio of delta AIC $_{(\Delta i)}$ values for each model relative to the whole set of candidate models. **t_{0+17}** -the sum of rainfall amounts for the 17 months preceding each elephant death.

Models	**GLzM model**	**AIC**	**AIC** $_{(\Delta i)}$	**AIC** $_{(W}$
M1	Season, month, age, sex, population, rain t_{0+17}, age x sex	5225	0.00	0.423
M2	Age, sex, population, rain $_{t0+17}$, age x sex	5230	5.11	0.040
M3	Month, age, sex, population, rain t_{0+17}, age x sex	5232	6.52	0.020
M4	Season, age, sex, population	5261	35.42	0.000

M1 with lowest AIC was selected for the final analysis.

Table 2: Summary statistics of zero-inflated GzLM model (count part): β = regression coefficient, odds ratio, CI = confidence interval of the odds ratio, the dependent variable = number of dead elephant

Variables	**β**	**odds ratio**	**(95% CI)**		**P**
Intercept)	0.21	1.23	0.67	2.28	0.5
Monthly rainfall					
Wet month (rain > 20mm)	[*]				
Dry months (rain < 20mm)	0.27	1.31	1.02	1.69	0.04 *
cumulative 17 months rainfall prior to each elephants death	-0.004	0.99	0.99	0.99	< 0.001 ***
Dry season (summed 4 months Rainfall <150mm)	0.21	1.24	0.91	1.67	0.2
Total elephant population in a year	0.005	1.01	1.00	1.01	< 0.001 ***
Sex					
Female	[*]				
Male	0.50	1.66	1.17	2.34	0.004 **
Age					
Elephant < 1 year	[*]				
Elephant < 2 years	-0.18	0.83	0.50	1.40	0.5
Elephant 2 – 8 years	-1.72	0.18	0.09	0.32	<0.001 ***
Elephant 8 – 25 years	-1.99	0.14	0.07	0.26	<0.001 ***
Elephant 25 – 49 years	-1.96	0.14	0.07	0.28	<0.001 ***
Elephant > 50 years	-3.49	0.03	0.01	0.07	< <0.001 ***
Age x Sex					
Female elephant x < 1 year	[*]				
Male elephant x < 2 years	-0.24	0.79	0.41	1.53	0.5
Male elephant x 2 – 8 years	-0.04	0.96	0.57	1.60	0.9
Male elephant x 8 – 25 years	0.20	1.22	0.64	2.31	0.5
Male elephant x 25 – 49 years	-0.81	0.44	0.20	0.98	0.04 *
Male elephant x > 50 years	-1.32	0.27	0.01	33.17	0.6

** P<0.05; **P<0.01; *** P<0.00; Reference variables represented by* [*] *in β column*

To disentangle the sex-age interaction effect further, we combined elephant mortality data for the males and the females below 25 years separately as they were not significantly different (Table 2), and then built a model of age-sex interaction with the two age classes (> 25 years and < 25 years). Male elephant between 25 to 49 years of age had a lower risk of dying of natural causes as compared to females of similar age (Figure 3).

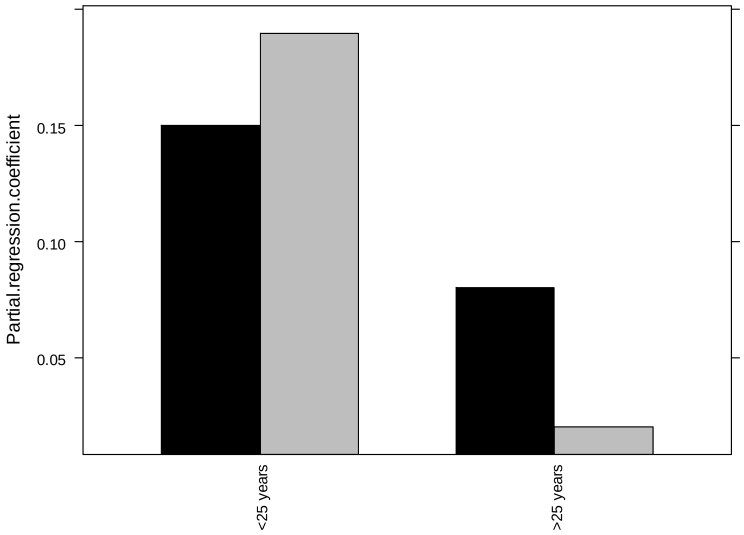

Figure 3: A partial regression showing the interaction between mortality of elephants of different age classes by sex (Black = Female, Grey = Male)

Discussion

In this study, we investigated whether elephant populations in the dry savannas are regulated by equilibrium dynamics through biotic factors or controlled by non-equilibrium dynamics through drought, and if so, how the effects vary with the age and the sex of the elephant. The results of a 40 year analysis covering 5 drought cycles and a doubling of population size showed that both juvenile and adult elephant mortality is high after periods of dry months. Although male elephant have a higher risk of dying than female elephant, this risk is dependent on the interaction between the sex and the age of an elephant. Male elephant over the age of 25 years showed a lower risk of mortality during the dry months. There is a very small (odds ratio of 1.01) but significant increase in elephant mortality associated with an increase in yearly elephant population. Overall, the risk of mortality in elephant decreased with increasing age with calves below one year showing the highest risk of mortality. The results indicate that drought duration and intensities play an important role in elephant mortality, hence pointing to the dominance of non-equilibrium dynamics in understanding the population dynamics of the largest and longest-living vertebrates in dry savannas.

Consistent with our hypothesis, the mortality of both calves and adult elephant was significantly higher in dry (<20mm) than wet months (>20mm) (e.g., Wato et al. (2016). While there is evidence that calves are at greatest risks of dying during drought (Moss, 2001, Foley et al., 2008), some studies have suggested that there is no relationship between adult elephant mortality and drought (Young and Van Aarde, 2010, Moss and Lee, 2011). Indeed, one could expect that elephants with their enormous body mass would be sufficiently buffered against climate variability. The difference between our results and those of other previous studies is due to the temporal resolution at which we measured the dry period; inter-annual vis-a-vis the monthly rainfall amounts. Similarly, Dudley et al. (2001) reported that the effective duration of rainy season appeared to be the best predictor of severity of drought-induced mortality among elephant but not the total annual precipitation. Furthermore, a study of Asian elephants found that elephant survival was related to intra-annual rainfall variability, with the highest survival rates during the wettest months that had the greatest available forage (Mumby et al., 2013). Similar trends have been observed for other mammalian species. For instance, a drought experienced in 2007-2009 in the Amboseli ecosystem caused the decline of many species of mammals such as common waterbuck (*Kobus ellipsiprymnus*), baboon (*Papio anubis*), cape buffalo (*Syncerus caffer*), common warthog (*Phacochoerus africanus*), lesser kudu (*Tragelaphus imberbis*) and elephant although the total annual rainfall in this period was close to those reported in other years. Surprisingly, these mortalities occurred despite the availability of perennial swamps in Amboseli that may cushion herbivores from drought-induced mortality, underscoring the importance of rainfall variability in wildlife survival (Okello et al., 2015). In dry savanna, the duration and the intensities of droughts thus may be more important in determining wildlife survival than annual rainfall variability (Lindsay, 1994).

Our analysis showed that calves below one year had the highest risk of mortality due to drought, consistent with many other studies of large mammals (Gaillard et al., 1998, Gaillard et al., 2000, Moss, 2001, Foley et al., 2008, Moss et al., 2011, Lee et al., 2013, Eberhardt, 2002). High juvenile mortality in large mammalian species has been associated with predation, drought, harsh winters, low birth weight and stunted growth due to nutritional deficiency among many other causes (Gaillard et al., 2000, Forchhammer et al., 2001, Lee and Moss, 2011, Lee et al., 2013). For example, drought in early life resulted in reduced growth rates for males and higher mortality for both sexes in elephant (Lee et al., 2013). In Soay sheep *(Ovies aries)*, warm, wet and windy winters preceding juveniles birth affected the newborn’s future survival, related to mothers' compromised physical condition (Forchhammer et al., 2001). Furthermore, Young and Van Aarde (2010) reported that the weaned young elephant have a higher risk of mortality in dry periods compared to wet seasons. Taken together, all these studies are consistent in showing high mortality in elephant calves during drought. Moreover, elephant risk of mortality decreased with increasing age, as in many other mammals, independent of the main proximate causes of mortality, and regardless of whether mortality is density-dependent or density-independent (Gaillard et al., 1998, Gaillard et al., 2000).

We found that male elephant have a comparatively higher risk of mortality than female elephant. An adult male elephant could weigh up to 7 tonnes while a female elephant weighs up to 4 tonnes (Moss, 2001, Moss et al., 2011). Male elephant have prolonged growth until they attain the age of 50 and females grow for at least three quarters of the post-maturity reproductive lifespan (Moss et al., 2011). Thus, the male elephant need to consume more forage than do female elephant to meet their additional energy cost (Lee, 2011). Furthermore, the male elephant have to incur additional energetic costs in annual reproductive musth phase (Poole and Moss, 1981). During musth, they spend less time feeding and drinking and more time in daily movements searching for the females, and incurring costs of contests and fights (Poole et al., 2011). Together, these factors may reduce male's energetic intake, making them more susceptible to death than female elephants in long dry periods. The energetic requirements for females are however also high, especially during the period of peak lactation (Moss and Lee, 2011). Females with calves under 2 years of age may be especially energy limited and thus both their calves and the females are more susceptible to negative energy balance and death (Moss and Lee, 2011). However, peak lactation is unlikely to coincide with drought for all females in the population, resulting in a lower risk of death across females in the population as a whole.

The risk of dying proves to be not only dependent on the sex of the elephant but also on the age of an individual elephant. Male elephant over the age of 25 years have a significantly lower risk of natural mortality. This finding may be explained by the social organization in elephant (Archie et al., 2006, Archie et al., 2011) and the foraging strategy of male elephant at different ages (Lindsay, 1994, Lindsay, 2011, Lee et al., 2011a). A male elephant remains with its family group usually up to about the age of 10-15 years (Lee et al., 2011b). As the male matures, he undergoes a transition in the way it uses space depending on age and sexual state (Rasmussen et al., 2006). After dispersal, young males remain highly sociable both with female groups and other male groups (Evans and Harris, 2008). As they grow older and mature sexually, usually at about 25-30 years, their foraging range increases and they begin to take more risks and disperse to unfamiliar habitats to seek for forage and mates (Chiyo et al., 2011). Although this risk taking behaviour may sometimes expose male elephant to mortality risks(Poole et al., 2011), this strategy may have advantages such as accessing distant foraging grounds such as crops (Chiyo et al., 2011) and water points in dry season (Lindsay, 2011, Lee et al., 2011b). The higher survival of older male elephant in the dry season may be explained by difference in total energy and protein intake of males and females, the time spent feeding and the nutrient content of forage (Lindsay, 2011). Difference in foraging strategies between the sexes are common in other sexually dimorphic species like red deer (*Cervus elaphus*) (Gordon, 1989) and moose (*Alces alces*) (Miquelle et al., 1992), among many others. Generally, foraging strategies between sexes in many species are more pronounced during periods of food scarcity, and the driving force in the differences appears to be energy need requirements, reproductive status of an individual, body sizes and the social context, all of which differ between sexes (Miquelle et al., 1992, Shannon et al., 2006).

The effects of non-equilibrium dynamics on elephant mortality through drought duration and intensities appeared more important than the effects of elephant population density. We conclude that both juvenile and adult elephant are sensitive to drought but the risk of dying is dependent on the interaction between the age and the sex of an elephant. The effects of drought are more pronounced when measured at a fine resolution of monthly rainfall variability than the annual rainfall variability. In view of predictions that the frequency of dry spells may increase globally, and particularly in Africa (Ogutu and Owen-Smith, 2003, Yang et al., 2014), most elephant populations will be exposed to long periods of drought as a mortality agent. We conclude that non-equilibrium dynamics remains an important factor that controls elephant population dynamics and should therefore form the basis of elephant population management in dry savannas.

Chapter 3

Prolonged drought results in starvation of African elephant *(Loxodonta africana)* in arid savannas.

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Biological Conservation 203 (2016) 89–96

Abstract

Elephant inhabiting arid and semi-arid savannas often experience periods of drought, which, if prolonged, may cause mortality. During dry periods, elephant aggregate around water sources and deplete local forage availability. However, the relationships between adult elephant mortality and both high local elephant density and forage availability close to water during dry periods remain unexplored. We hypothesized that elephant mortality is higher: a) when dry periods are longer, b) closer to water points, and c) in areas with higher local elephant density. Using nine years of elephant carcass data from Tsavo Conservation Area in Kenya, we analysed the probability of adult elephant mortality using maximum entropy modelling (MaxEnt). We found that elephant carcasses were aggregated and elephant mortality was negatively correlated with four months cumulative precipitation prior to death (which contributed 41% to the model), Normalised Difference Vegetation Index (NDVI) (19%) and distance to water (6%), while local elephant density (19%) showed a positive correlation. Three seasons (long dry, short dry and short wet seasons) showed high probability of elephant mortality, whereas low probability was found during long wet seasons. Our results strongly suggest that elephant starve to death in prolonged drought. Artificial water holes may lead to lower mortality, but also to larger populations with subsequent high browsing pressure on the vegetation. Our results suggest that elephant populations in arid and semi-arid savannas appear to be controlled by drought-induced mortalities, which may be the best way of controlling elephant numbers without having to cull.

Introduction

Human-induced climate change is threatening wildlife communities globally (Thuiller et al., 2006). For example, incidents of drought have occurred more frequently globally and particularly, in tropical savannas (Collier et al., 2008). Recent studies predict that failure of long rains in East Africa may become a frequent occurrence in the future (Yang et al., 2014). Although drought is an integral part of arid and semi-arid systems, prolonged periods without rainfall may result in mass die-offs of wildlife (Knight, 1995). To prevent mass wildlife die-offs due to the predicted increase in drought periods, there is a need to better understand the causes of drought-induced mortality. In this paper, we aim to unravel the drought-related causes of mortality of the African elephant (*Loxodonta africana*). Although some studies have investigated elephant mortalities as a result of drought (Caughley et al., 1985, Moss, 2001, Foley et al., 2008), and the effect of environmental factors such as spatial and temporal variability in drinking water, food distribution (extrinsic drivers) and local population density (intrinsic driver) (Young and Van Aarde, 2010), few studies have focussed on long-term drought events, particularly on adult elephant mortality. This is because elephant mortality data were mainly from unpredictable, opportunistic single-drought events, whereas long-term, consistent records of elephant mortality are rare (Dudley et al., 2001, Foley et al., 2008), but see (Aleper and Moe, 2006).

Continent-wide declines in African elephant populations are attributed largely to elephant poaching for ivory (Prins et al., 1994, Kahindi et al., 2010, Bouché et al., 2011, Burn et al., 2011, Maingi et al., 2012, Wittemyer et al., 2014, Chase et al., 2016) and loss of habitat associated with increased human population (Douglas-Hamilton, 1987, de Boer et al., 2013, Chase et al., 2016), but rarely to abiotic factors such as rainfall variability. Given the predicted increase in drought periods, the mortality of wildlife will likely rise, especially for species that are relatively more water dependent than others and those that require large amounts of daily food (Okello et al., 2015). For instance, in Kenya's Amboseli National Park, the droughts of 2007 and 2009 drastically reduced the population of large mammals, and species such as wildebeest (*Connochaetes taurinus*) declined by over 50% (Okello et al., 2015). Elephant mortality as result of drought over the past few decades remains unprecedented (Corfield, 1973, Dudley et al., 2001, Walker et al., 1987, Foley et al., 2008). For example, drought is suspected to have contributed substantially to the elephant population drop in Tsavo from 35,000 elephant in 1974 (Cobb, 1976, Blanc et al., 2007) to below 12,000 elephant in 2011(Ngene et al., 2011).

Given their large body size and long generation time, survival of an adult elephant may be buffered against temporal variation in limiting resources (Gaillard et al., 1998, Gaillard et al., 2000, Prins and Van Langevelde, 2008, Moss and Lee, 2011). In the dry season, for instance, elephant shift their diet from a predominance of grass towards increasing amounts of woody browse (Lindsay, 1994, Moss et al., 2011, Kohi et al., 2011). This diet shift enables elephant to cope with prolonged drought. However, elephant feeding requirements and the dispersed distribution of resources in savannas may cause heterogenous elephant aggregation across the landscape (Wittemyer et al., 2007, Chamaille-Jammes et al., 2008). Consequently, at high densities, elephant may deplete local forage resources, often in the proximity of waterholes and rivers, particularly during the dry season (De Beer et al., 2006, Chamaillé-Jammes et al., 2008). Several previous studies identified distance to water as the primary environmental factor influencing the density of elephant during the dry season (Verlinden and Gavorv, 1998, Maingi et al., 2012), but the relationships between adult elephant mortality and both high local elephant density and forage availability close to water during dry periods remain unexplored.

We investigated whether elephant natural mortality varies seasonally, whether elephant carcasses are clustered around water points, and what are the relationships between observed patterns of elephant mortality and precipitation, distance to water, forage and local elephant density? Water is scarce in arid and semi-arid savannas and most seasonal rivers and water holes dry up during prolonged droughts. Consequently, elephant, especially the breeding herds, are constrained to close proximity of the remaining permanent water sources (O'Connor et al., 2007, Young and Van Aarde, 2010). We hypothesized that elephant mortality will be higher: a) when dry periods are longer, b) closer to water points, and c) in areas with higher local elephant density.

Materials and Methods

Study area

We conducted this study in the Tsavo Conservation Area (~48,300 km^2), located at 2 - 4° S and 37.5 - 39.5° E in the southern part of Kenya (Omondi et al., 2008). It is an arid ecosystem with bi-modal rainfall from mid-March to May and from November to December (Omondi et al., 2008, Tyrrell and Coe, 1974). The long dry season typically ranges from June through October, whereas the short dry season occurs from January to March (Leuthold and Leuthold, 1978, Tyrrell and Coe, 1974). The mean annual rainfall in Tsavo ranges from 250 to 500 mm (Ngene et al., 2014). Tsavo Protected Area is dominated by a flat and undulating terrain with a difference in altitude of 100-500m that is interrupted by granitic hills and inselbergs with the highest peak of Taita hills standing at ~2,220 metres above sea level (Mukeka, 2010). The perennial Galana River flows at the foot of the Yatta plateau situated in the northern part of Tsavo Conservation Area. The vegetation consists of remnants of *Commiphora-Acacia* woodlands that dominated the landscape in the past and is thought to have been thinned by elephant (Bax and Sheldrick, 1963, Leuthold and Sale, 1973, Cobb, 1976). Tsavo Conservation Area hosts a third of Kenya's estimated 38,000 elephant (Omondi et al., 2008, Ngene et al., 2011).

Data

We extracted adult elephant mortality data from the Tsavo Conservation Area database. These data were generated from daily foot-and-vehicle patrols that were carried out by security personnel in Tsavo Protected Area for nine consecutive years (2004-2012). The study area was historically divided into five sections for ease of patrol (Figure 1). A team comprising of between 5-25 rangers patrolled each of these sections daily using a combined vehicle-and-foot patrol. Furthermore, the park authorities received information on elephant mortalities from local people and tourists; these reports were also accepted if the carcass was confirmed by one of the patrol teams. We used elephant carcasses that were approximately less than four months old in our analysis. Most carcasses were fresh and were estimated to be less than a month old. A few were estimated to be more than 4 months old and these carcasses at least had remnants of skins and the bones not fully disintegrated, which enabled us to estimate the approximate death date. The elephant carcasses we used in this paper are from elephant of ages ranging from 3 years to 60 years (estimated ages) and over 80% of the carcasses were from adult elephant.

The following information was recorded for each carcass: date, area name, sex (for fresh carcasses), likely cause of death, estimated age, and GPS coordinates. An elephant was assumed to have died of a natural cause if the carcass had no snare, spear, gun or poison arrow wound and if it was declared by the resident veterinary officer that it had not died of any disease. Although climatic conditions such as temperature change or lack of sufficient food in dry periods play a role in wildlife susceptibility to diseases (Harvell et al., 2002), we excluded all elephant deaths due to diseases, which were <1% of the total recorded mortalities, and used only records of mortality other than poaching and diseases in our analysis. In total, we used 221 elephant carcasses in this study (Figure 1C).

Analysis of wildlife mortality data may violate a number of assumptions that underlie standard statistical tests. This is because there are many sources of biases from, for instance, variable patrol efforts (Burn et al., 2011, Huso, 2011) and imperfect carcass detection. The sources of bias were reduced by dividing the study area into sections and conducting systematic carcass searches with equal search efforts (number of rangers and duration of patrol) (no differences between the sections: ANOVA, F =2.24, P > 0.05). Furthermore, the big size of the elephant carcass, its immobility, the open savanna landscape that dominates the Tsavo ecosystem, the strong smell from the rotting cadaver, vultures overflying and feeding on fresh carcasses, and the intensive and systematic patrols collectively minimized the bias as a result of imperfect detectability. We therefore assumed minimal detectability bias (MacKenzie and Royle, 2005), and used maximum entropy modelling with MaxEnt, which is a rigorously proven inference procedure based on presence-only data that yields least-biased predictions of occurrences (Harte and Newman, 2014).

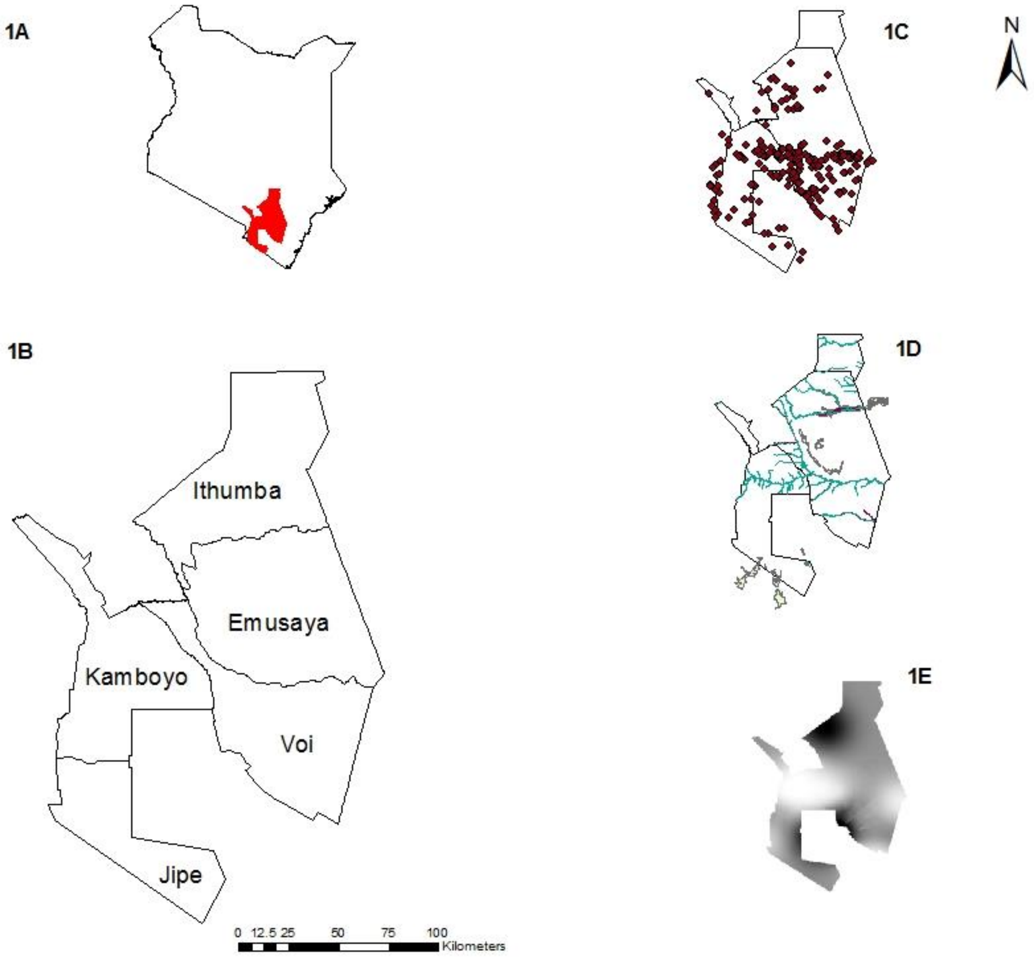

Figure. 1. Maps of 1A) Kenya showing the location of Tsavo Conservation Area (TCA), 1B) the five management sectors of TCA where security patrols were carried out, 1C) elephant carcass locations, 1D) major rivers and, 1E) kriged rainfall amount of January 2009; dark shades representing high rainfall amount (see text for explanation).

We mapped all the water sources in the study area and categorized them as permanent (perennial rivers – Figure 1D – and boreholes) or seasonal (rain-fed ephemeral water pools and seasonal rivers). Permanent water sources have a water supply throughout the year, whereas seasonal water sources hold water for a maximum of four months in the rainy season (Ayeni, 1975). Boreholes are located near tourist facilities and supply water throughout the year. Using ArcGIS Spatial Analyst Tool (ESRI, 2011), we made a map with the distance from grid cells (resolution of 250 m), including the elephant mortality locations, to the permanent rivers, boreholes and seasonal water sources separately. To reduce edge effects (Griffith, 1985), we generated a 10km buffer around the study area and used it to clip the spatial extent of all other subsequent maps used in this study.

We obtained monthly rainfall data from rain gauges distributed in different sites in the study area to capture the variation in rainfall amounts across the study area. We classified seasons in the study area into long wet, short wet, long dry and short dry seasons following Wittemyer et al. (2005) and Moss et al. (2011). We created point maps from rain gauge records for all the months where elephant mortality had occurred. Using kriging (ESRI 2011), we developed a rainfall grid (resolution of 250 m) for each of these months (see Fig. 1E as an example). We extracted rainfall values from these rainfall grids for all 221 elephant carcasses at the time of their estimated death. To account for effects of past rainfall amounts on elephant mortality, we also kriged the rainfall values from rain gauge records for one, two, three, four and five months prior to each elephant's death. We calculated the cumulative rainfall from one month up to five months prior to each death and linked the values to the particular elephant carcass.

Several studies analysing the relationships between elephant and vegetation have successfully applied the satellite-derived Normalised Difference Vegetation Index (NDVI) as a proxy for available forage (Loarie et al., 2009, Maingi et al., 2012). We used the NDVI images from the MODIS product (MOD13Q1), which is a 16-day composite of highest-quality pixels from daily images available at a spatial resolution of 250 m. The MODIS NDVI images were downloaded from the USGS Land Processes Distributed Active Archive Center (LP DAAC). For all 221 elephant mortality records, we extracted NDVI values at the time of each elephant's death.

The variable for local elephant density was derived from 2005, 2008 and 2011 total aerial elephant censuses conducted in Tsavo Conservation Area in the dry season (Omondi et al., 2008, Ngene et al., 2011). We generated kernel-density surfaces using ArcGIS Spatial Analyst Tool (ESRI, 2011) for local population densities of elephant in Tsavo on the basis of these three elephant censuses, and averaged the kernel density grid values. We then extracted a single estimated elephant density value for each of the 221 elephant mortality locations.

Data analysis

We used point pattern analysis to evaluate whether the spatial pattern of elephant carcasses in Tsavo Conservation Area was random, clustered or dispersed (Wong and Lee, 2005) and to evaluate the distances at which the clustering is most pronounced using Moran's I in ArcGIS's incremental spatial autocorrelation tool (ESRI, 2011). Besides, we modelled the occurrence of an elephant carcass as a function of distance to water, NDVI, local elephant density, season and amount of precipitation in preceding months using MaxEnt v. 3.3.3e. MaxEnt has been used widely in analysis of presence-only data (Phillips et al., 2006, Phillips and Dudík, 2008, Elith et al., 2011). MaxEnt relates environmental variables at presence locations with random locations in the whole study area and generates a spatial probability distribution of occurrence (Phillips et al., 2006, Coppes and Braunisch, 2013, Ngene et al., 2014), in our case the probability of carcass occurrence which we call probability of elephant mortality in the paper. We used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips and Dudík, 2008) to assess the accuracy of the model. We used the default convergence threshold of 10^{-6}, maximum number of iterations of 5000 and the default logistic model to ensure that predictions gave estimates between 0 and 1 of the probability of elephant mortality in the study area. We generated 10,000 random points using Geospatial Modelling Environment (GME) (Beyer, 2004) from the entire study area that we used as background data in the MaxEnt modelling. For these 10,000 random points, we extracted data on local elephant density and distance to the nearest source of water. As we had time series of rainfall and NDVI, we randomly selected 20 elephant carcasses that represented different dates from 2004 to

2012. For each of these dates, we randomly drew 500 points from the rainfall and NDVI maps so that we could link rainfall and NDVI data to each of the random locations.

We ran our model using a 10-replicate cross-validation setting. We randomly selected 70% of the elephant mortality locations as training data and used the remaining 30% for testing the resulting model. We tested for the correlations between all variables and found that all rainfall variables were correlated ($r > 0.5$). In the final model, we selected the rainfall variable that had the highest contribution in explaining the occurrence of elephant carcasses. There was also a correlation between NDVI and rainfall ($r > 0.5$) but we accounted for this in our analysis by showing results of each variables separately holding all other variables constant.

Results

Results from the Moran's I analysis (Moran's I = 0.316, Z score 6.74, $P < 0.05$) showed that elephant mortality mainly occurred within a distance of 1 to 8 km from each other in the Tsavo Protected Area, with maximum clustering occurring at a distance of ~8 km (Fig. 2). Our MaxEnt model had an AUC of 0.956 (Fig. 3).

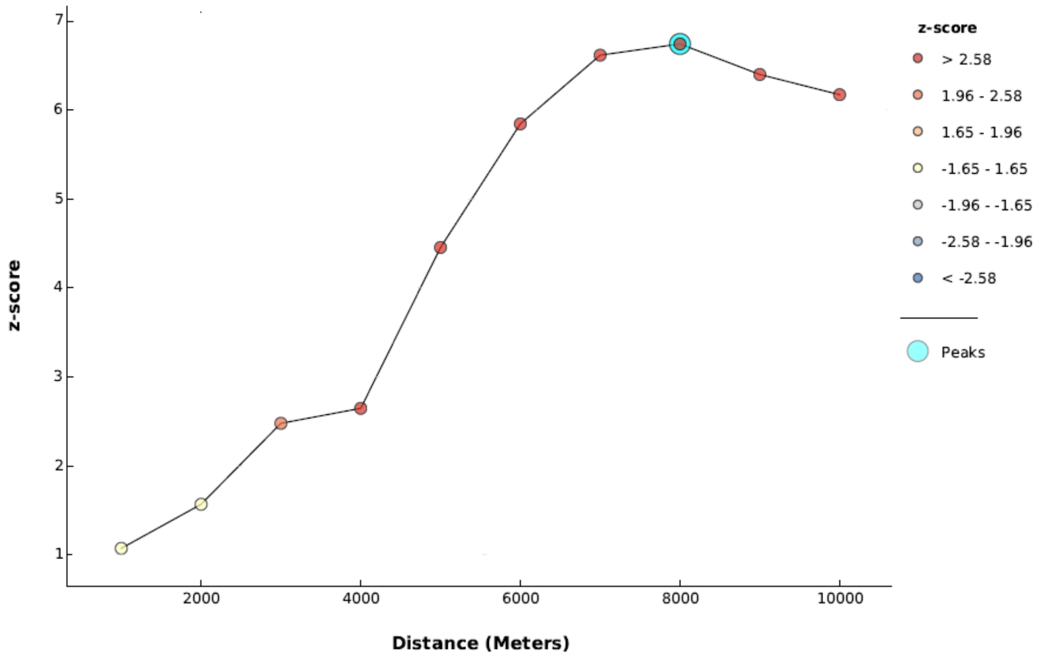

Figure. 2. Incremental spatial autocorrelation of elephant-carcass locations for the 2004–2012 period showing clustered elephant mortality pattern in the Tsavo Protected Area. The graph's peak at ~8 km indicates the distance of highest clustering of elephant carcasses.

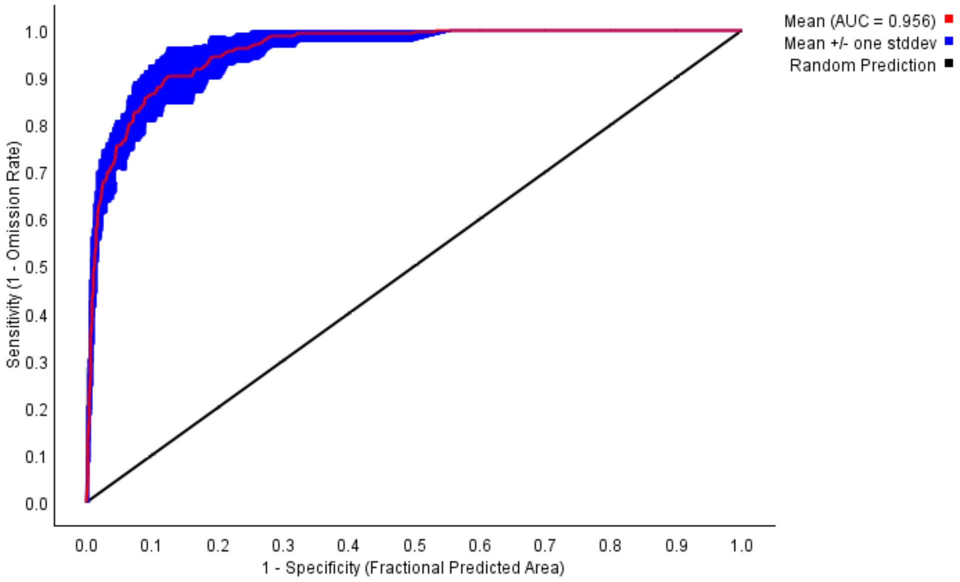

Figure. 3. The Area Under the Curve (AUC) of the best fitting model using MaxEnt to predict probability of natural elephant mortality in Tsavo Protected Area.

The four months cumulative precipitation prior to an elephant's death (41% contribution), NDVI (19% contribution) and the distance to nearest permanent rivers (6% contribution) negatively correlated with the mortality of elephant, whereas local elephant density (19% contribution) showed a small positive correlation with elephant mortality (Figure 4). Furthermore, with exception of the long wet season, all other seasons showed a high probability (>0.5) of elephant mortality (Fig. 5). Based on this analysis, the probability of finding an elephant carcass is not uniform in Tsavo Conservation Area (Fig. 6), and the highest mortality occurs around permanent water and at low NDVI values.

We tested for the change in NDVI values with an increase in distance from the Galana River (at 5 km interval from 1km to 50 km) for the driest recorded month of September 2009. NDVI was the lowest in this month and much lower than at the end of wet season. NDVI values were not significantly different with an increase in distance from the Galana river (ANOVA, F = 0.362, P = 0.90), suggesting that food availability was equally low close to the river compared to further away from the river.

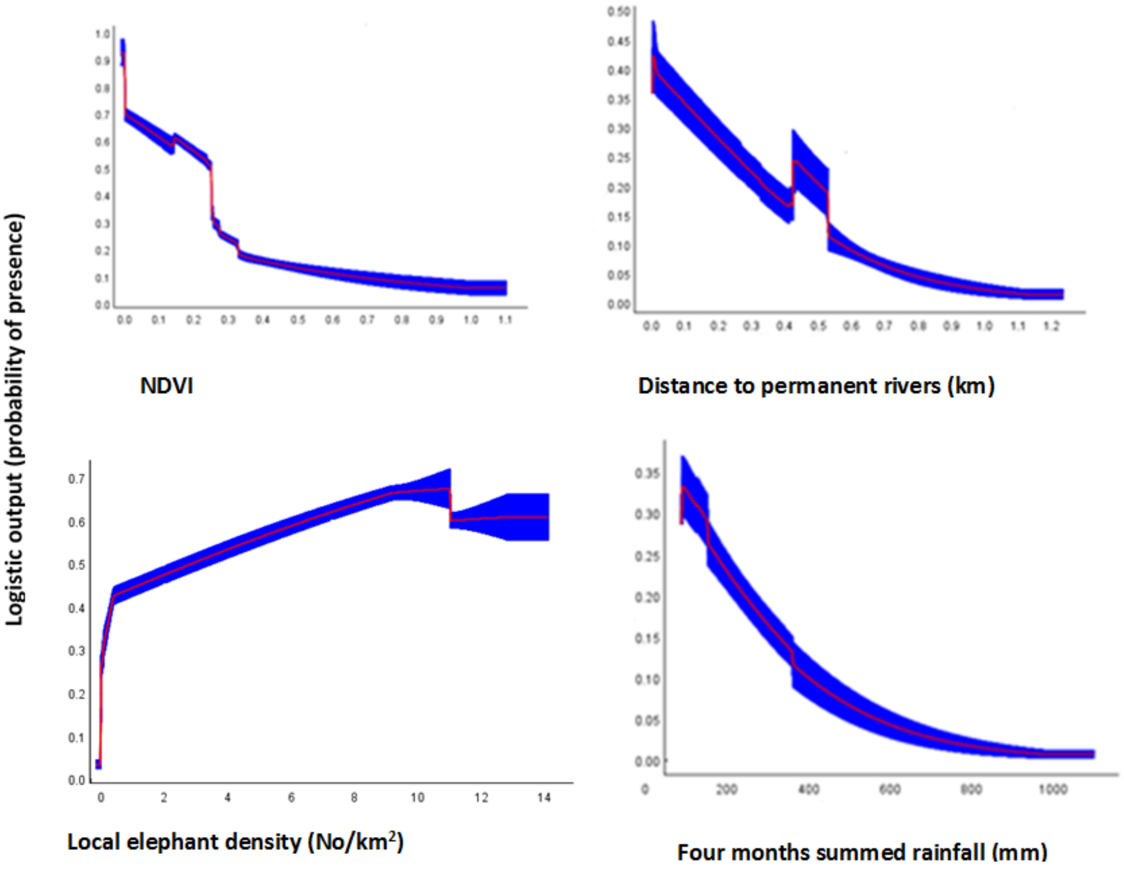

Figure. 4. The probability of elephant mortality in Tsavo as function of several environmental variables: (a) NDVI, (b) distance to permanent water, (c) local elephant density, and (d) cumulative precipitation for the past four months . For each panel, all environmental variables other than the one for which the effect is shown were kept at their average sample value in the MaxEnt model. The curves show the mean response of the 10 replicate MaxEnt runs and the mean ± one standard deviation (shades).

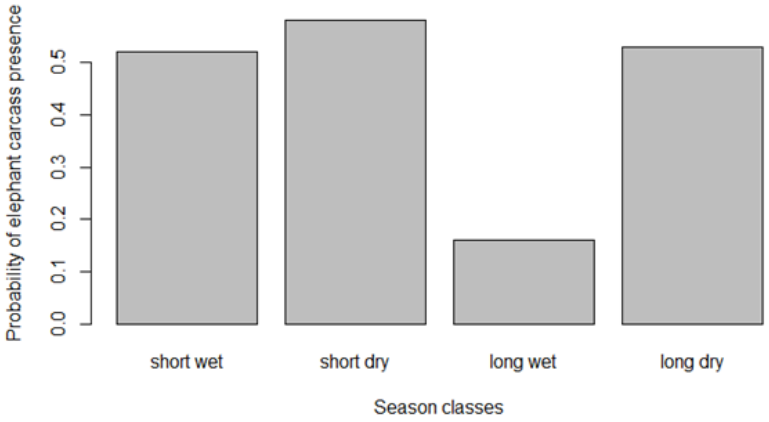

Figure. 5. Probability of elephant mortality for each of the four seasons in Tsavo Protected Area for the period 2004-2012.

Figure. 6. Predicted probability of elephant mortality in Tsavo Protected Area, based on the MaxEnt model. Dark shades represent high probability (close to permanent water, Figure 1D) and light shades representing low probability.

Discussion

Elephant are bulk feeders and require large amount of food to survive (Barnes, 1983, Jachmann and Bell, 1985, Jachmann, 1989, Osborn, 2004). They are also water dependent and must drink water frequently; mostly every two days (De Knegt et al., 2011, Skarpe et al., 2014). In arid and semi-arid savannas where both water and forage are deficient in the dry season, elephant are faced with two major challenges: starvation or dehydration. The results of this study show that elephant mortality was high during long drought periods, i.e., at least four consecutive months with low or no rainfall (< 150mm). Moreover, elephant carcasses were aggregated and elephant mortality was high in areas with high local elephant density, low NDVI and in close proximity to permanent rivers. With the predicted increasing frequency of droughts in (East) Africa (Collier et al., 2008, Yang et al., 2014), these findings are vital for effective conservation of the African elephant.

Although drought-related elephant mortality is frequently observed (Dudley et al., 2001, Foley et al., 2008, Moss et al., 2011), and short-term studies on the role of extrinsic (environmental) and intrinsic (density-dependent) factors exists (Young and Van Aarde, 2010), long-term studies focussing on adult elephant are rare. This has been a major issue in understanding the repercussions of the infamous Tsavo Elephant disaster of the 1970s which often has been interpreted solely as the outcome of 'overpopulation' and has been used as a proof of density dependency in elephant (Myers, 1973, Corfield, 1973). Our results support the role of high densities especially around permanent water during dry seasons. It has been observed that elephant aggregate in the proximity of rivers, particularly during the dry season (O'Connor et al., 2007, Young and Van Aarde, 2010). This 'crowding' effect can lead to depletion of local food resources (De Beer et al., 2006, Chamaillé-Jammes et al., 2008) and probably a high elephant mortality around water points. These observations corroborate with our finding that carcasses are aggregated and that mortality probability of elephant is higher closer to water.

In our study, permanent rivers, specifically the Galana and Tiva rivers, seem to be the determinants for the heterogeneous distribution of elephant in the Tsavo landscape with high densities consistently recorded in close proximity to these rivers during the dry season. Our results further suggest that elephant mortalities are not likely to be explained by dehydration as elephant aggregate around permanent water, but that elephant mortalities are likely due to starvation. Our data shows that NDVI is low during dry periods close to rivers and further away. Although NDVI does not give any information about plant species composition and availability of palatable plants, it has previously been used as a proxy measure of available forage (Rasmussen et al., 2006, Young et al., 2009, Young and Van Aarde, 2010). Our findings therefore support the hypothesis that forage limitation in prolonged drought may result in elephant starvation (Gough and Kerley, 2006, Young and Van Aarde, 2010), which appears to be intensified by local density. Effects of diseases and poaching are ruled out due to the selection of the carcasses.

We found a large effect of the cumulative precipitation of four months before an elephant's death. Similarly, Dudley et al. (2001) reported that it is the effective duration of the rainy season and not the total annual precipitation that determines elephant mortality during dry periods. A typical long dry season in Tsavo Conservation Area lasts for 5 months (June-October) (Omondi et al., 2008, Ngene et al., 2014). Rasmussen et al. (2006) showed that NDVI, which is a proxy measure of available browse, peaks at around 80 days after the onset of the rains. This implies that by the end of the long rainy season in May, there is probably sufficient forage and water for elephant, which may remain available up to about 3 months into the dry period (Rasmussen et al., 2006). Therefore, elephant have to cope with the remaining two dry months of declining food availability assuming that the short rains (November-December) come on time. Elephant is a coarse feeder and can survive for long on poor quality forage and during the long dry season when the fibre content of the grass is high, they switch to browse and herbs (Beekman and Prins, 1989, Moss et al., 2011). Sometimes the amount of rainfall in the long wet season may be too low to yield enough plant growth and fill the water points or the short rains may come late. Our results imply that, if the period of dry months extends beyond three months, it may lead to starvation of elephant, especially when local elephant density is high.

For the nine years that this study covered, each year had an annual rainfall of over 250 mm, which is the average minimum rainfall reported for the Tsavo Conservation Area (Ngene et al., 2014). However the highest cumulative elephant deaths occurred in October of the year 2009. This year had the lowest rainfall during the long wet season, yielding 69 mm of annual rainfall. Because aboveground net primary production in arid and semi-arid environments is closely related to the amount of precipitation (Rosenzweig, 1968, Rasmussen et al., 2006, Moss et al., 2011), the amount of rainfall during the long wet season in 2009 may not have been enough to produce sufficient woody browse to take elephant through the long dry season. This finding suggests that the long wet season determines the number of months that the forage will remain available in the long dry season before elephant succumb to starvation. Although we expected that the five months cumulative precipitation would show an even stronger correlation with elephant mortality, its effect was likely smaller than when considering four months cumulative precipitation: forage insufficiency did not last more than four months in the entire period that was covered by this study.

Although this study was conducted in Tsavo Conservation Area, the findings from this study can be generalized to other arid and semi-arid savannas where elephant occur. Because water is a key determinant of elephant distribution in these areas (Verlinden and Gavorv, 1998), it has long been used as management tool to manipulate impact of elephant on the vegetation, for example in Kruger National Park in South African (Smit and Grant, 2009, Smit and Ferreira, 2010, Hilbers et al., 2015). Although artificial water holes may lead to lower mortality, it is argued that the increase of water points is indirectly causing vegetation degradation by attracting and building up elephant densities around them (Smit and

Ferreira, 2010). The closure of artificial waterholes in Kruger National Park to induce spatial redistribution of elephant in the landscape have resulted in increased elephant densities around large perennial rivers and large seasonal rivers as compared to smaller streams and areas far removed from rivers (Smit and Ferreira, 2010). Because there are few artificial water holes in the Tsavo Conservation Area, the trends in elephant distribution show opposite patterns to Kruger National Park, with very high elephant densities and mortalities around the perennial rivers.

Even though prolonged droughts usually result in high elephant mortality, the resilience of these dry ecosystems may perhaps improve as a result of these deaths that release the vegetation from high browsing pressure and give it a window to regenerate. Our results suggest that elephant populations in arid and semi-arid savannas appear to be controlled by drought-induced mortalities, which may be the best way of controlling elephant numbers without having to cull. This implies that arid and semi-arid savannas may in fact be sustained by growth and crashes of herbivore populations, which is predicted by the non-equilibrium hypothesis for rangelands (e.g., Vetter, 2005): non-equilibrium rangelands are thought to be mainly determined by stochastic abiotic factors, especially variable rainfall, which result in highly variable and unpredictable primary production, and population sizes of large herbivores rarely reach equilibrium with their fluctuating resource base. Maintaining these system as natural as possible may therefore keep elephant populations in savannas sustained for posterity.

Chapter 4

Movement patterns of African elephant (*Loxodonta africana*) in dry savannas suggest that they have information on the location of the dispersed water sources.

Yussuf A. Wato, Ignas M.A. Heitkönig, Herbert H.T. Prins, Geoffrey Wahungu , Shadrack Ngene[2], Steve Njumbi & Frank van Langevelde

Abstract

The movement strategy of an animal determines its efficiency in exploiting heterogeneous resources in a landscape. Water is a scarce resource in semi-arid savannas where over half of the African elephant *(Loxodonta africana)* population occurs and may therefore influence their movement strategies. To maximise resource use efficiency, a random search is expected for an animal with no information on the location of the target resource. On other hand, a more direction-oriented ballistic walk is expected for an animal with information on the target resource. For elephant to survive in a dry savanna, they are likely to have information on the location of the few available water sources, especially in the dry season, and this will be reflected in their movement pattern. We therefore hypothesized that elephant movement patterns are ballistic and show a stronger directional-orientation towards water sources in the dry season compared to the wet season. We investigated the movement paths of four male and four female collared elephant with hourly GPS fixes in Tsavo National Park, Kenya in 2012-2013. Consistent with our predictions, the movement paths of elephant had longer step lengths, longer squared net displacement distances and were strongly directional towards water sources for both sexes in the dry season as compared to the wet season. We argue that African elephant have

information on the location of dispersed water resources, enabling them to survive with scarce resources in dry savannas. These results can be used in conservation and management of wildlife, through for instance, protection of preferred water sources.

Introduction

Animals' movement paths represent behavioural and ecological processes, such as navigation, migration, dispersal and food searching (Benhamou, 2004) and the distribution of the resources. For instance, the movement strategies used by an animal when foraging in a landscape with dispersed resources would be different from those of animals foraging in an area with clustered resources (Bartumeus, 2009). It is generally hypothesized that animals increase tortuosity of their movement paths in areas with high resource density (Bartumeus et al., 2005, Hengeveld, 2007, Bartumeus, 2009). Consequently, the net displacement of the animal decreases and the time spent in utilising these resources increases, leading to efficient resource use (Turchin, 1991). On the other hand, straight and less tortuous movement paths with high net displacement are more efficient in landscapes with dispersed resources (Turchin, 1998, De Knegt et al., 2007, Roshier et al., 2008). Therefore, analysis of animals' movement paths can give a useful insight on the relationship between the resource distribution and foraging efficiency.

Previous studies on movement path analysis were mostly carried out on insects, birds, and small mammals (Turchin, 1991, Viswanathan et al., 1996, Atkinson et al., 2002). However, recent advances in radio-telemetry have made it possible to collect vast quantities of movement data in space and time for both large terrestrial and marine mammals (Austin et al., 2004, Boyce et al., 2010). Although the movement parameters to be measured varies with the objectives of the study (Marsh and Jones, 1988), generally, parameters such as the distance covered between successive relocations, the turn angles, the directionality of the track and the relationship of the track with properties of the environment that the animal passes through form the basis of movement path analysis (Root and Kareiva, 1984, Marsh and Jones, 1988, Hengeveld, 2007, Dray et al., 2010, Calenge and Calenge, 2015). These movement patterns may in turn determine the frequency with which the animal will encounter the object of interest which may be forage, water, mates or escape from predation (Marsh and Jones, 1988). To increase resource use efficiency, a random search is expected for a forager with no information on the location of the target resource, whereas a more direction-oriented ballistic walk is expected for a forager with information on the target resource (Valeix et al., 2010). Knowledge on how animals move within their environment can give critical insight on animal's behaviour that may be used in the effective management and conservation of species under study.

Water is a scarce resource in semi-arid savanna, where over half of the African elephant *(Loxodonta africana)* population occurs, and may therefore influence the movement strategies used by elephant. Elephant are water dependent and they usually have to drink water every two to three days (Stokke and Du Toit, 2002, Redfern et al., 2005, Smit et al., 2007). To survive in dry savannas, it is therefore critical for elephant to be able to efficiently find the sparsely distributed water sources, especially during dry season. Based on the elephant's water requirements and the scarcity of water during the dry season, we expect that the movement pattern of the elephant will reflect these seasonal contrasts in water distribution. Although it is not in doubt that the distance to water is a primary environmental factor influencing habitat use by elephant (Verlinden and Gavorv, 1998, Smit et al., 2007, Chamaille-Jammes et al., 2007, Hilbers et al., 2015), it remains unclear how the behavioural responses of elephant change as a result of water scarcity(Chamaille-Jammes et al., 2008). Here, we analyse the movement paths of four male and four female elephants to address the hypothesis that elephant movement patterns are ballistic and show a stronger directional-orientation towards water sources in the dry season compared to the wet season. We predict that the movement path for the male and female elephant are less tortuous, have longer step lengths, longer displacement distances and smaller turning angles and will depict strong directionality towards water sources in the dry season than in the wet season. Past reports indicate that elephant remember and re-visit previously visited sites (De Beer and Van Aarde, 2008, Prins and Van Langevelde, 2008, De Knegt et al., 2011) and pass on the information of their historical migration routes through generation (Moss et al., 2011, McComb et al., 2001). Thus, longer step-lengths and higher directionality of elephant movement paths towards water sources in the dry season is an indication that elephants use information to travel to these water sources.

We used radio-telemetry data from GPS collared elephant in Tsavo Conservation Area to investigate the differences in elephant movement pattern between a wet and a dry season. During the wet season, there is abundant water for wildlife in the Tsavo ecosystem (Omondi et al., 2008, Mukeka, 2010). However, this area has sparsely distributed permanent water sources in the dry season when the only available water sources for wildlife are reduced to two perennial rivers, three boreholes, and a few water pools constantly refilled by the hoteliers and neighbouring community ranches (Ayeni, 1975). Water has been identified as key resource that affects elephant distribution and their spatial habitat use (Chamaille-Jammes et al., 2007, Harris et al., 2008, Smit and Grant, 2009). For instance, in drier environments, elephant take an average of 3 days to drink water and the duration of re-visiting water points differ between sexes (Stokke and Du Toit, 2002), with bull elephant drinking every 3–5 days while breeding herds every 2–4 days (Viljoen, 1989, Leggett, 2006). Furthermore, the breeding herds have been reported to forage close to the proximity of water sources in dry season compared to the male elephant (Harris et al., 2008).

Method

Study area

We conducted this study in the Tsavo Conservation Area in Kenya, a semi-arid ecosystem spanning an area of ~48,300 km^2, located at 2° - 4° S and 37.5° - 39.5° E in the southern part of Kenya (Omondi et al., 2008, Ngene et al., 2012). The area is characterized by a bi-modal rainfall with long rains in mid-March to May, short rains in November to December (Tyrrell and Coe, 1974) and a mean annual rainfall of 250 to 500 mm(Tyrrell and Coe, 1974, Prins and Loth, 1988). The two rainfall seasons are separated by a five months long dry season typically ranging from June through October (Tyrrell and Coe, 1974, Leuthold and Leuthold, 1978, Omondi et al., 2008). There are two permanent rivers in Tsavo (Galana and Tsavo) and several seasonal rivers, with Voi and Tiva rivers flowing for a short time in the rainy season (Ayeni, 1975). Other sources of water are the numerous natural waterholes which fill up with water during rainy season. Some of these waterholes can hold water throughout the short dry season (January-March) but all the natural waterholes dry up around July-August during the long dry season (June to October) (Ayeni, 1975, Mukeka, 2010). In addition, there are three wind pumped boreholes and a few water reservoirs located around tourist facilities and community owned ranches with constant water supply for animals in the peak of the dry months.

Elephant GPS data

We monitored four female and four male elephant fitted with satellite-linked GPS collars between March 2012 to June 2013 in the Tsavo National Park in Kenya. The individuals that were collared were randomly selected from five sectors in the Tsavo Conservation Area to represent elephant movement patterns across the entire Park. The procedure for fitting GPS collars are described in Ngene et al. (2012). The GPS collars transmitted hourly fixes and the data were automatically transmitted to a web-linked database at the Tsavo East Research Station in Kenya. The GPS had an error of ~10 meters for relocation fixes and some hours had missing values caused by obstruction of signals by, for instance, heavy cloud cover or dense tree canopies. In our analysis we considered only the successive time steps with GPS fixes.

We analysed elephant movement patterns for the males and the females in two seasons: the long dry season (June to October 2012) and the long wet season (March to May 2013). These two seasons are distinctly different in the amount of rainfall and would therefore show the relationship between the change in movement pattern related to water availability.

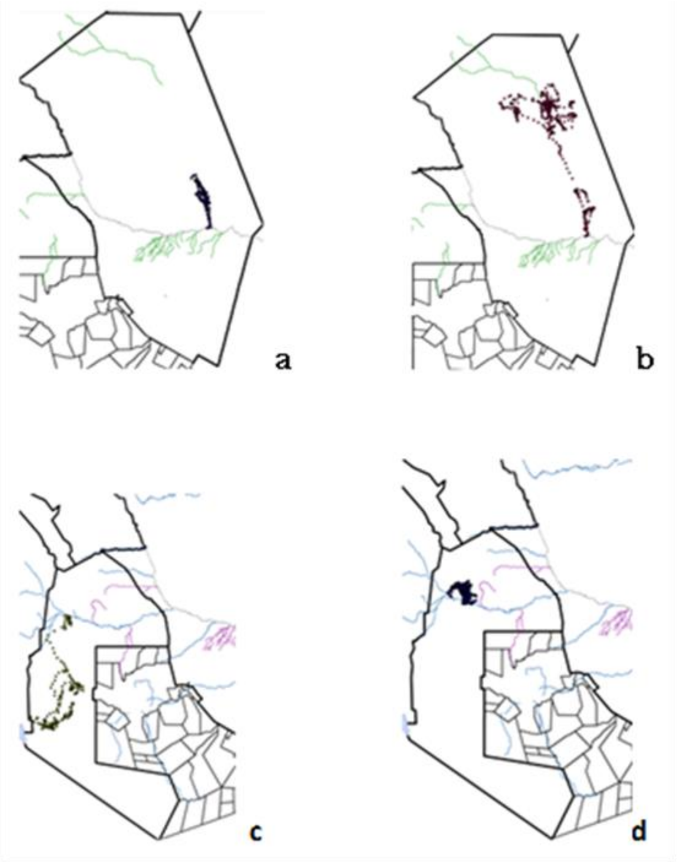

Figure 1: The black dots are hourly GPS fixes for a male elephant a) in the dry and b) the wet season; and for a female elephant c) in the wet and d) the dry season. In both sexes the individuals' movement paths seem to be tightly anchored on a river in the dry season.

Data analysis

We calculated the distance covered by each elephant per hour based on the hourly GPS fixes. We recorded the distance between successive hours to represent a single movement path (i.e., step-length) based on the methods described by (Root and Kareiva, 1984, Marsh and Jones, 1988, Hengeveld, 2007). We calculated the turn angle as a measure of the change of direction between successive steps with a zero degrees turn corresponding to locomotion on a straight line without change of direction, a negative angle representing a turn to the left and a positive angle representing a turn to the right (Calenge and Calenge, 2015). We then analysed the distribution of step lengths, turning angles and squared net displacement distances (NDD) for both sexes and seasons with AdehabitatLT animal movement analysis package in R (Calenge and Calenge, 2015). We calculated the parameters of turn angle distributions such as the mean resultant length and the mean direction using CircStats package Version 0.2-4 in R (Lund and Agostinelli, 2015). The mean direction vector represents the mean orientation of the turn angles while the mean resultant length shows the strength of directionality and the concentration of the angles distribution around the mean (R = 0 represents a dispersed turn angles distribution and R = 1 shows that all angles are equal to the mean direction vector) (Lund and Agostinelli, 2015). We only analysed the movement paths that were directed towards the nearest water source to focus on the effects of water on movement path. In order to establish whether the directionality changed with distance from the water source, or whether proximity had no effect, we also stratified our analysis to 5, 10 and 15 km from the water source. We analysed the effect of the fixed variables, season, sex and distance from the nearest water source, on elephant's movement pattern using linear mixed effects models (LMMs). We used the ID of the elephant as a random effect variable to account for variation due to individual differences. We also checked for the interaction effects between sex and season in our analysis. We performed this analyses using the R packages lme4 (Bates et al., 2013).

Results

The step-lengths per hour for the elephant were significantly longer in the dry season compared to the wet season (Table 1a). The step-lengths changed with distance from the nearest water point, with the step-lengths further from the water (15 km) being significantly shorter than those closer to water points (5 and 10 km) (Table 1a). Even though both male and female elephant have a longer step-lengths in the dry season as compared to the wet season, the results showed a significant interaction effect of sex and season (Figure 1a). The male elephant have a longer step-lengths than the females in the dry season. Similarly, the squared net displacement distance for the elephant were significantly longer in the dry season compared to the wet season (Table 1b). The squared net displacement distances were significantly longer further away from water (15 and 10 km) as compared to distance closer to the water (5 km) (Table 1b). Furthermore, the squared net displacement distance was also significantly affected by the interaction between the sex and the season with squared net displacement distances in the dry season being longer than the wet season. Moreover, squared net displacement distances of males were longer than the females in both the wet and the dry season (Figure 1b). However, the turn-angles for both sexes were large in both the wet and the dry season and did not show any significant difference between the seasons.

Table 1: Fixed effect variables with coefficients = β, CI = confidence interval and p-value = P from the LMM model. Main effect coefficients indicate the separate effects of sex, season and distance (km) from the nearest water source on the movement pattern of the male and the female elephant. Interaction coefficients show the combined effect of sex and season on the elephant movement pattern; the dependent variables; a) step-length b) net displacement distances.

a) Step-length

Variables	**β**	**SE**	**95% CI**		**t-value**	**P-value**
(Intercept)	0.7	0.2	0.4	1.0	4.41	0.002**
Dry Season	[***]					
Wet season	-0.2	0.1	-0.3	-0.1	-3.76	<0.001 ***
Female	[***]					
Male	1.2	0.2	0.7	1.6	5.40	<0.001 ***
Distance [5km]	[***]					
Distance (10 km)	0.1	0.04	0.04	0.2	2.89	<0.004 **
Distance (15 km)	-0.3	0.04	-0.3	-0.2	-6.51	<0.001 ***
Wet season:male	-1.2	0.1	-1.3	-1.1	-17.45	<0.001 ***

b) Net Displacement Distance

Variables	**β**	**SE**	**95% CI**		**t-value**	**P-value**
(Intercept)	874	432	28	1720	2.03	ns
Dry Season	[***]					
Wet season	-684	33	-750	-619	-20.43	<0.001 ***
Female	[***]					
Male	208	579	-927	1343	0.36	ns
Distance [5km]	[***]					
Distance (10 km)	310	28	254	365	10.94	<0.001 **
Distance (15 km)	311	29	255	367	10.89	<0.001 ***
Wet season:male	715	48	622	809	14.98	<0.001 ***

Significant codes: 0 '***' 0.001 '**' 0.01 '*' , [***] represents the reference variable

The mean resultant length of the turning angles for males showed strong directionality in the dry season compared to the wet season (Figure 2).

Similarly, the female elephant's turning angles showed strong directionality in the dry season compared to the wet season. The resultant mean length of the turning angles for females were in the same range with males in wet season but much lower than the males in the dry season, although not significantly different (Figure 2).

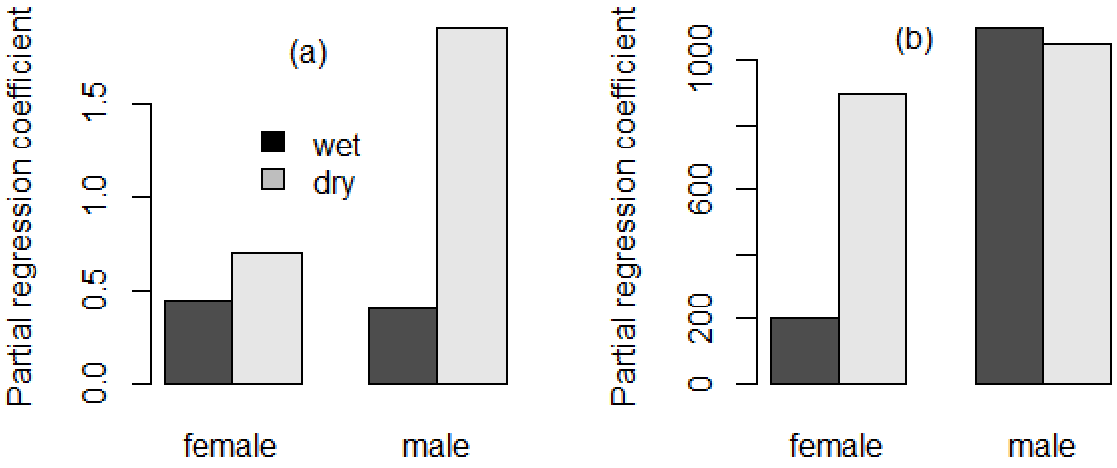

Figure 1: Partial regression coefficients for a) the step-length, and (b) squared net displacement distances for the male and the female elephant movement paths in the wet (black bars) and the dry (grey bars) season. The distance of the trajectories were in km.

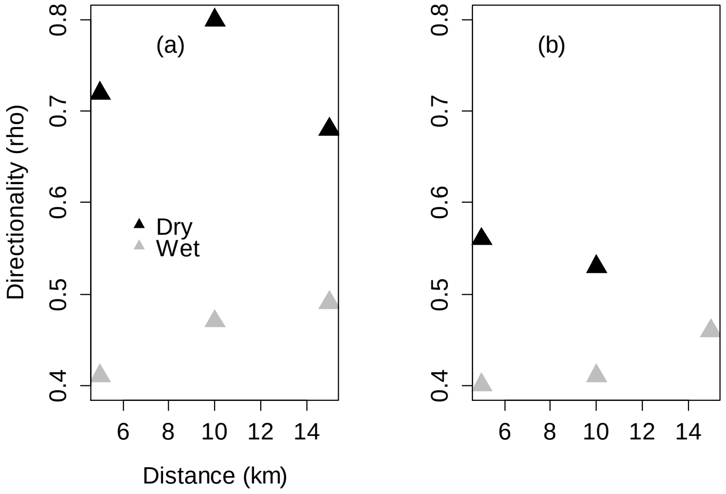

Figure 2: Directionality of the elephant movement pattern in the wet and dry season for a) males and b) females for different distances to water sources. Rho = 0 represents a dispersed turn angles distribution, hence indicates weak directionality, and R = 1 shows that all angles are equal to the mean direction vector, hence indicates strong directionality. Females were not recorded to be at 15 km from the nearest water point in the dry season (b).

The range of water re-visitation frequency was 1-4 days for the females and 2-5 days for the male elephant in the dry season

Discussion

The study of animal movement patterns in relation to resource distribution is one of the novel ways to link behaviour of individuals to the spatial distribution of resources (Schick et al., 2008, Giuggioli and Bartumeus, 2010). Resource distribution varies in space and time, and can occur in a spectrum ranging from over-dispersed, random, in patches or highly aggregated clusters (Prins and Van Langevelde, 2008, De Knegt et al., 2011). We examined the role of water distribution on the movement pattern of elephant. In this study, we show how elephant movement pattern changes as a result of seasonal changes in water distribution. The results support our predictions that both the male and the female elephants' movement paths are less tortuous resulting in longer step lengths, and longer net displacements distances in the dry season compared to the wet season. Furthermore, the mean length of the turning angle showed strong directionality towards water sources for both the sexes in the dry season.

Tsavo Conservation Area is an ecosystem experiencing pronounced scarcity of water and in the long dry season, two perennial rivers and three boreholes serve as the primary water source for wildlife. Most wildlife species, and particularly elephant, require regular water intake (Stokke & du Toit 2002; Redfern et al. 2005) and have to travel between the foraging sites and watering points to meet their energy and water requirements. For instance, in Kruger National Park, elephant drink water every two days during the dry season (Young, 1970), and other studies show that duration of water re-visitation is sex dependent (Viljoen, 1988; Leggett, 2006). Their movement paths are expected to be influenced by water distribution, and elephant appear to have information about the water locations. Therefore, regular re-visitation of watering points may explain the long step-lengths and net displacement distances and the strong directionality towards water sources in the dry season. The use of information about the location of the water sources is especially apparent when they show this behaviour at long distances from the water sources. A few studies have found a relationship between resource distribution and the movement patterns of other wildlife species (Prins, 1996, Loureiro et al., 2007, Valeix et al., 2010). For instance, in a study of lions in arid savannas, their step-lengths and net displacement distances were longer as they headed towards waterholes with high aggregation of prey species (Valeix et al., 2010). Similarly, the study of Eurasian badgers showed that their movement paths were less tortuous as they headed towards their dens and latrine sites (Loureiro et al., 2007).

During the wet season, there is abundant forage and water for wildlife in Tsavo ecosystem (Omondi et al., 2008, Mukeka, 2010). In addition to the perennial rivers that flow throughout the year, most of the natural waterholes across Tsavo ecosystem fill up with water during rainy season (Tyrrell and Coe, 1974, Ayeni, 1975). Some of these waterholes have water throughout the rainy season and may extend to the short dry season (January-March) (Ayeni, 1975), hence elephants are not water limited then. Thus, the step-lengths and net displacement distances can be shorter in the wet season. Similar movement patterns have been reported for foragers in sites of abundant resources. For instance, the movement paths of lions hunting close to a waterhole where there are high prey species congregation, had a short step-length and net-displacement distances and was more tortuous than when they are further away from a waterhole (Valeix et al., 2010).

Although water is limiting for both sexes in the dry season, female elephant rarely moved further than 10 km from the nearest water source to forage in the dry season while male elephant accessed forage sites beyond 15km. This agrees with other studies (O'Connor et al. 2007, Young and Van Aarde 2010). Furthermore, in the dry season, the directionality of movement path for male elephant was much stronger than the female elephant. This is in line with past studies that reported that breeding herds rarely roam far away from drinking water in drier environments (Viljoen, 1988; Leggett, 2006). In these mixed herds, the increased costs associated with moving long distances to far foraging sites may be especially stressful for infants and juveniles (Lee and Moss, 1986, Loveridge et al., 2006) and could lead to increased calf mortality (Foley et al., 2008, Loveridge et al., 2006, Young and Van Aarde, 2010). Our results support the hypothesis that elephant initially seek habitats closer to water in the dry season, regardless of the distribution of food (Illius, 2006, de Beer et al., 2006, Chamaille-Jammes et al., 2007, Evans and Harris, 2008). However, if there are many water sources, elephant choose those water sources with more vegetation and avoid those that are not associated with suitable vegetation (Harris et al., 2008).

The difference between male and female elephant movement patterns may be also be explained by elephants' social organization (Moss et al., 2011, Archie et al., 2011) and the difference in foraging strategy between the sexes (Lee et al., 2011a). The foraging range of a male elephant is larger than the females as they take more risks and disperse to unfamiliar habitats to seek for forage and mates (Lee et al., 2011a, Skarpe et al., 2014). This foraging behaviour may have advantages such as accessing far foraging grounds and water points in dry season (Lindsay, 2011, Lee et al., 2011a). Moreover, the mixed herd comprises of individuals of different ages and the group's movement is affected by, for instance, calves that may not be able to move fast and far from water sources like the adult elephant (Ngene et al 2010). The large herds also spread widely while foraging and probably, while heading to the water sources to drink. Conversely, the bulls move and forage alone or in a bachelor herd without calves to retard their speed (Ngene et al., 2010). Thus, bulls may travel far to forage but also walk in a less spread formation towards the watering point. The difference in foraging strategies among different sexes are common in other sex-dimorphic species like the red deer (Gordon, 1989), moose (Miquelle et al., 1992), among many others. Generally, the differences in foraging strategies in many species appears to be driven by factors such as energy need requirements, reproductive status of an individual, body sizes and the social context, all of which differ between sexes (Miquelle et al., 1992, Lindsay, 2011).

This study shows a positive correlation between water distribution and its consequences on the movement path of the elephant. It supports other studies and models that indicated that animals often adjust their movement pattern in relation to critical and scarce resources. Our findings reveal that elephants' movement paths are ballistic and show strong directionality in dry season driven by water distribution. We demonstrate that environmental variables can be used to predict general movement patterns of large herbivores and the findings can be used in conservation and management of wildlife, through for instance, protection of preferred water sources.

Chapter 5

Elephant in dry savannas choose a forage site with high forage biomass in the dry season and high nutrients in the wet season.

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Abstract

African elephant *(Loxodonta africana)* is generally considered to be a bulk feeder and thus non-selective. However, recent studies indicate that elephant is able to forage selectively, but the level at which it makes foraging decision is still debated. In this study, we investigated the effect of forage biomass and nutrient concentrations on forage site selection by elephant in a semi-arid ecosystem. We collared four female and four male elephant in Tsavo National Park, Kenya in 2013-2015. We then (i) mapped their seasonal activity ranges, (ii) determined areas of high and low use, and finally (iii) determined elephant forage site choice based on nutrient concentration in forage and biomass of the forage. The results show that elephant chose sites with high forage biomass in the dry season whereas forage nutrients, particularly the nitrogen concentration and the grass biomass, appear to determine forage site choice by elephant in the wet season. Comparing the sexes, female elephant chose sites with higher forage biomass whereas male elephant chose sites with high nutrients. The results of this study can be used to identify suitable land for the establishment of new protected areas and for zoning existing protected areas for elephant conservation.

Introduction

African elephant *(Loxodonta africana)* are the largest terrestrial mammals, and they are generally considered to be bulk feeders and thus, non-selective (Van Soest, 1981, Lindsay, 2011, Shrader et al., 2012). Over half of the free-ranging African elephant live in semi-arid savannas. These savanna ecosystems are characterised by diverse plants species with varying structure ranging from grasses, shrubs and trees (Scholes and Archer, 1997). In such ecosystems, forage resources to satisfy herbivore nutrient and energy requirements are rarely homogeneously distributed since there are many factors that affect the forage quality and quantity (Knox et al., 2012). These factors includes soil types (Heitkonig and Owen-Smith, 1998, Craine et al., 2009), geology (Grant and Scholes, 2006, De Knegt et al., 2011), slopes and catenas (De Knegt et al., 2011), amounts of rainfall (Prins and Van Langevelde, 2008) among other factors (e.g., (Olff et al., 2002). Thus, forage quality and quantity vary between seasons, plant species and different plant growth stages (Beekman and Prins, 1989, Knox et al., 2012). Consequently, herbivores have to search for and forage on different plant species, from different patches, and sometimes from different seasonal ranges to meet all of their requirements (Prins and Van Langevelde, 2008, Young and Van Aarde, 2010). Previous studies report that elephant initially choose a foraging area with high food availability irrespective of plant species composition (De Knegt et al., 2011, Shrader et al., 2012), and then selectively forage on more nutritious plants within the selected foraging site (Holdo, 2003, Pretorius et al., 2011). This explanation is invoked for heavy browsing on some plant species in a landscape (Babaasa, 2000).

Most of the dry savannas have typically a wet and dry season, and this seasonality appears to play an important role on elephant's forage site choice. For instance, elephant feed mostly on abundant and nutritious grass in the wet season (Beekman and Prins, 1989, Lindsay, 1994, Osborn, 2004, Cerling et al., 2007, Skarpe et al., 2014). During dry seasons, the grass becomes moribund and many plant species shed leaves to conserve water and reduce evapotranspiration (Osborn, 2004, Do et al., 2005). Hence, elephant shift their diet from a predominance of grass towards increasing amounts of woody browse to meet their energetic requirements (Lindsay, 1994, Moss et al., 2011, Kohi et al., 2011, Kos et al., 2012). Browse is sparsely distributed in a savanna landscape and therefore, elephant must spend more energy in searching for sites with sufficient browse (Young and Van Aarde, 2010). Consequently, to minimise this energy expenditure, elephant will probably choose a site with a high biomass of forage in the dry season (Prins and Van Langevelde, 2008, Ngene et al., 2010, De Knegt et al., 2011). In contrast, during the wet season, forage is abundant (Wittemyer et al., 2007, Ngene et al., 2010) and hence, elephant movements are less limited by the availability of forage (Chamaille-Jammes et al., 2007). Therefore, we expect elephant distribution to be influenced more by selection of forage sites with a higher plant quality that can satisfy their nutrient and energy requirements at minimal effort in the wet season.

The persistence of a large herbivore in an area is not only linked to forage abundance but also forage quality (Olff et al., 2002). While forage abundance increases linearly with rainfall, the leaf tissue nutrient content that indicates forage quality has been shown to increase at low rainfall as long as the plant-available nutrients is high (Olff et al., 2002). Since dry savannas have variable rainfall and plant-available nutrients, plants in some sites are often limited by nitrogen or phosphorous (Augustine et al., 2003, Cech et al., 2008, Pretorius et al., 2011). Therefore, a herbivore species in these ecosystem will choose a foraging site based on the availability of forage quality that meets its energetic needs (Olff et al., 2002). For instance, in an experiment of different nutrient additions in soils of a homogeneous tree stand, it was shown that elephant were able to choose nutrient-rich patches at the scale of 100 m^2 with the patch choice strongly correlated to nitrogen content in plants (Pretorius et al., 2011).

The use of telemetry has made it possible to describe the link between animal movement patterns and the distribution of key resources (forage and water) at a fine temporal and spatial scale (Douglas-Hamilton, 1987, Murwira et al., 2010, Ngene et al., 2010, Pittiglio et al., 2012). Most studies use remote sensing data as a proxy of forage availability (Mueller et al., 2008, Pettorelli et al., 2011) such as NDVI (Pettorelli et al., 2011, de Boer et al., 2013), to infer choice and selectivity of forage sites (Loarie et al., 2009). However, despite its popularity, NDVI is a poor proxy measurement of forage quality, particularly in semi-arid areas (Huete, 1988, Huete et al., 2002) and it neglects how plant species composition and their nutrient concentrations influence elephant distribution (Ferwerda et al., 2006, Skidmore et al., 2010). Therefore, measuring the biomass and nutrients concentrations of plants in the field yields a more robust representation of forage site choice by herbivores.

The foraging decisions of mammalian herbivores is influenced by their body size (Demment and Van Soest, 1985), with smaller herbivores being more selective than larger herbivores (Gordon and Illius, 1994). This difference also exists within conspecifics based on behavioural differences between the sexes and the age classes (Woolley et al., 2009). For instance, male elephant have prolonged growth (Moss et al., 2011), and have to incur additional energetic costs in the annual reproductive musth phase where they spend less time foraging and more time searching for the females, hence incurring energetic costs of contests and fights (Poole et al., 2011). Thus, the male elephant may need to consume more forage biomass than the female elephant to meet these additional energy cost (Lee et al., 2011). However, the energetic requirements for females are also high especially during the period of peak lactation (Moss and Lee, 2011). Because of these behavioural and social-organizational differences between male and female elephant (Lindsay, 2011), we tested the differences in forage site selection between the sexes.

In this study, we investigated the effect of forage biomass and leaf tissue nutrient contents on forage site choice by elephant in a semi-arid ecosystem. Specifically, we investigated (i) the seasonal activity ranges of 8 satellite-linked GPS collared elephant, (ii) areas of high and low use, and (iii) how they are linked to sites visited by these elephant that differ in quality and quantity of food over the seasons. We hypothesize that the choice of a foraging site by elephant is determined by: 1) forage quality during the wet season, 2) forage biomass during the dry season, and (iii) forage with higher nutrient concentration for female elephant and with higher biomass for male elephant.

Methods

We monitored eight elephant (4 females and 4 males) fitted with satellite-linked GPS collar in a wet and a dry season from 2012 to 2014 in Tsavo Conservation Area, Kenya. The procedure for fitting GPS collars is described in Ngene et al. (2012). The collars had a battery life of 24 months and were set to record elephant position every hour, with 24 fixes per elephant per day. The GPS signals were sometimes obstructed by weather condition such as cloud cover or thick vegetation canopy and failed to take the hourly coordinates (Hebblewhite et al., 2007). We used only those fixes which had GPS coordinates in our analysis with the mean number of fixes per elephant in the dry season (± standard deviation) being 3270±392 and in the wet season 2015±71.

Data were retrieved from collared elephant via a satellite link and uploaded automatically on online software provided by Africa Wildlife Tracking (AWT). We calculated the kernel density to visualize the intensity of forage site use for each elephant (Rodgers and Kie, 2010). A kernel density measures the density of GPS fixes within the foraging area of each elephant, and uses this to estimate which areas an individual uses most frequently. First, we mapped total foraging area of each GPS collared elephant where GPS fixes occurred 90% of the time irrespective of the frequencies of the fixes. Within the total foraging area, we then identified areas where GPS fixes occurred 50% of the time, referred to in this paper as “the high use area” (Figure 1). We sampled vegetation in the high-use areas of each of the 8 GPS collar-fitted elephant. We converted the high use area into a polygon (ESRI, 2011) and divided the polygon into equal grids measuring 20 X 20 meters (Figure

1). We then randomly selected 25 grids for each of the 8 collared elephant; hence we sampled a total of 400 grids (200 in the wet and 200 in the dry season).

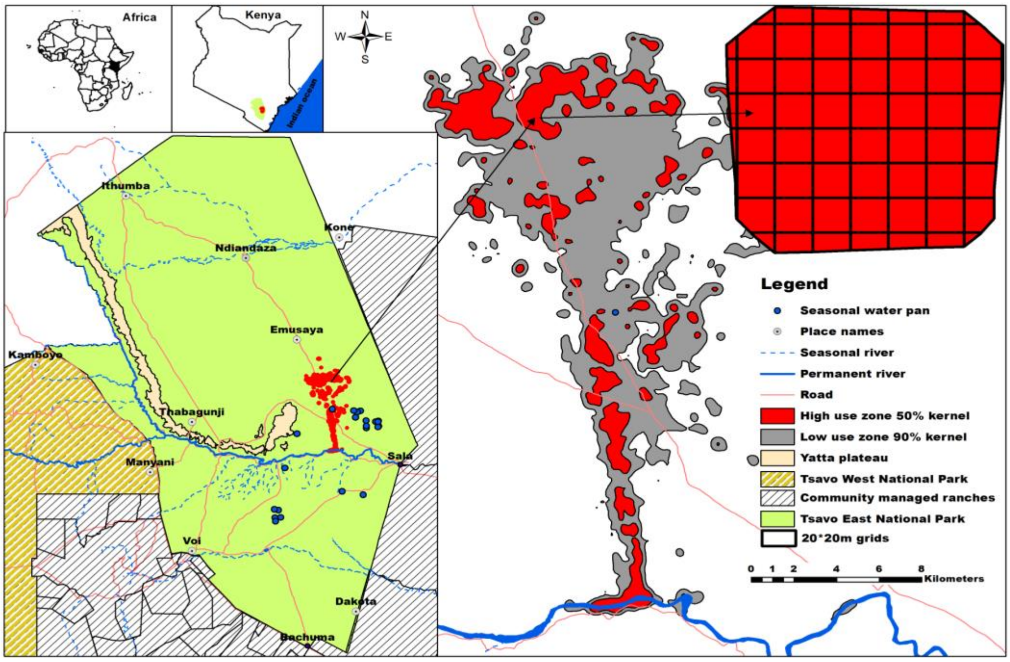

Figure 1: The foraging range of one of the collared elephant (Emusaya male) in the dry season showing the sampling protocol. The red polygons represents high-use area while the grey polygons represents the total foraging area. 25 grids of 20x20m were randomly selected for vegetation sampling.

Browse biomass estimation

We used the individual trees in the grids as a sampling unit. The mean number of trees (± standard deviation) sampled at sites of high use for each elephant was 692±334 in the dry season and 880±346 in the wet season and, we sampled a total of 114 plant species. Within each sampled grid, we recorded all the tree species and measured their browseable leaf biomass using the biomass estimate from the canopy volume (BECVOL; (Smit, 1996, Smit, 2014). To calculate browseable biomass for each individual tree, we measured the following parameters: tree height, height of maximum canopy diameter, height of first leaves or potential leaf bearing stems, maximum canopy diameter, and the base diameter of the foliage at height of first leaves or potential leaf bearing stems (Smit, 1996). To account for tree shape variation (Smit, 1996), we segmented the tree canopy into parts; as the top part is dome shaped, we calculated the volume using the formula for a half ellipsoid (Smit, 1996, Kohi et al., 2011). Depending on the lower shape of the canopy of each tree, we used a formula of a cone frustum or a cylinder to calculate its volume (Smit, 1996, Kohi et al., 2011). We then used Smit's (1996) generic equation for broad-leaved and microphyllous tree species to calculate the available browseable biomass per tree.

Leaf nutrient analysis

We hand-picked leaves from each of the sampled trees and stored them in paper bags, which we oven dried at 70°C for 48h. We then ground the dried leaves and sieved them through a 1mm sieve. Finally, we analysed the powdered leaves samples at the chemical laboratory of the Resource Ecology Group in Wageningen University, The Netherlands. We analysed the nitrogen (N) and phosphorous (P) concentrations of the leaves through digestion in a mixture of sulfuric acid, salicylic acid and selenium (Novozamsky et al., 1983). We then measured N and P with a Skalar San-plus autoanalyzer (Breda, The Netherlands) as described by Kohi et al. (2011

Grass biomass

To estimate available grass biomass, we randomly laid 100m transects in the high-use areas of the collared male and female elephant and divided each transect into six points at intervals of 20m. We then randomly selected two points from the six points on each transect and used a disc-pasture meter to estimate the grass biomass. We harvested the grass under the disc, air-dried, and stored them in paper bags. We then estimated the grass biomass in the Kenyatta University laboratory using the standard procedures described by 't Mannetje (2000). In total we laid 80 transects (40 in wet and 40 in dry season), from which we harvested a total of 160 grass samples. The transects where grass biomass was measured overlapped with 50 % of the grids where the tree biomass were measured.

Data analysis

We analysed whether browseable tree, and grass biomass and nutrient concentrations (nitrogen and phosphorous) determined elephant forage site selection using linear mixed effects models (LMMs). Partial regression coefficients were used to understand the differences between browseable tree biomass and grass biomass and nutrient concentrations between sites visited by the male and the female elephant during the wet and the dry season. We used sex and season as fixed effect variables, the individual elephant, the grids and tree species as random effect variables and browseable tree and grass biomass and nutrient concentrations in the forage as the dependent variables. We also checked for the interaction effects of sex and season in our analysis. We performed this analyses using R (Team, 2014) with the R packages lme4 (Bates et al., 2013).

Results

Generally, elephant chose areas with a higher amount of browseable tree biomass in the dry season compared to the wet season (Table 1a). Forage site choice by elephant was dependent on the interaction between the sex of the elephant and the season, with the female elephant choosing sites with a higher browseable tree biomass in the dry season compared to the sites selected by the male elephant (Figure 2a).

Table 1: Fixed effect variables with coefficients = β, Confidence interval = CI and p-value = P from the LMM model for a) browseable tree biomass, b) Nitrogen concentration in the browse, and c) grass biomass. Main effect coefficients indicate the separate effects of sex and season on the forage site choice by the male and the female elephant. Interaction coefficients show the combined effect of sex and season on the choice of forage site by elephant.

a) browseable tree biomass

Variables	**β**	**95% CI**		**t-value**	**P-value**
(Intercept)	0.3	0.08	0.5	2.75	<0.02 *
Dry season	[***]				
Wet season	-0.4	-0.5	-0.3	-8.21	<0.001 ***
Female elephants	[***]				
Male elephants	-0.4	-0.6	-0.2	-3.40	<0.01 **
Wet season : Male	0.4	0.2	0.5	4.90	<0.001 ***

b) Nitrogen

Variables	**β**	**95% CI**		**t-value**	**P-value**
(Intercept)	1771	1611	1931	21.747	<0.001 ***
Dry season	[***]				
Wet season	267	120	413	3.571	<0.001 ***
Female elephants	[***]				
Male elephants	-7	-243	229	-0.059	0.95
Wet season : Male	141	-186	468	0.845	0.40

c) grass biomass

Variables	**β**	**95% CI**		**t-value**	**P-value**
(Intercept)	32	13	51	3.243	0.07
Dry season	[***]				
Wet season	30	22	39	6.946	<0.001 ***
Female	[***]				
Male	2	-26	29	0.126	0.90
Wet season : Male	-19	-31	-7	-3.176	0.01**

Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ , [***] represents the reference variable

There was no significant difference in the nitrogen concentration of the forage in the sites chosen by the males and the female elephant (Table 1b). However, the sites chosen by both sexes had forage with significantly higher nitrogen concentration in the wet season compared to the dry season ($\beta = 267$, $t = 3.6$, $p < 0.001$) (Table 1b). Forage phosphorous concentration was not different in the sites chosen by the males and the female elephant in both wet and dry seasons.

Grass biomass was significantly higher in the sites selected by both the female and the male elephant in the wet season compared to the dry season ($\beta = 30$, $SE = 4.3$, $t = 7.0$, $p < 0.001$) (Table 1c). However the site selection was dependent on the interaction between the sex of the elephant and the season, with female elephant choosing areas with significantly more grass biomass compared to male elephant in the wet season ($\beta = -19$, $SE = 6.0$, $t = -3.2$, $p = 0.002$, Figure 2b).

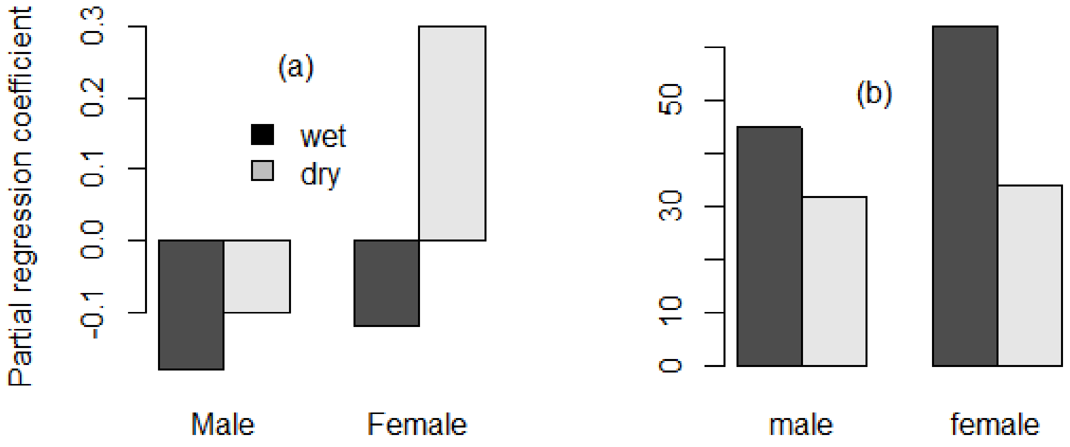

Figure 2: Partial regression coefficients for the a) browseable tree biomass and (b) grass biomass in the sites selected by the male and the female elephant in wet and dry season.

Discussion

The aim of this study was to understand what determines the forage site choice by free living elephant in the wet and dry season, and if the forage site choice was different between sexes. Our approach was to map areas that recorded low and high residence time for collared elephant and to sample the leaf nutrient contents and measure biomass of all trees and grass found in these foraging sites, hence eliminating the possibility of any bias of assumed plant preference by elephant. We found that there is a difference in forage site choice between male and female elephant in the wet and dry seasons. Although both the sexes chose sites with a higher tree biomass in the dry season and sites with a higher grass biomass and leaf nitrogen concentration in the wet season as expected, the results show an interaction between sex and season. In the dry season, female elephant chose sites with a higher amount of browse biomass as compared to the sites selected by male elephant. Similarly, in the wet season, female elephant selected forage sites with a higher grass biomass as compared to the sites selected by the male elephant. However, leaf nitrogen concentration determined forage site choice for male and female elephant in the wet season, thus it was not a discriminatory factor for explaining forage site choice between the sexes.

During the dry season, the availability and abundance of food and the nutrient content to satisfy the requirements for large herbivores like the elephant become scarce (Babaasa, 2000, Prins and Van Langevelde, 2008, Owen-Smith and Chafota, 2012). Therefore, in the dry period, the value of a plant to a herbivore is not only determined by the energy content in the plant but also the increased energy costs to find it (Pretorius et al., 2012). Our results show that female elephant chose forage sites with a high browseable biomass in the dry season, thus they appeared to maximise the energy gained from the browse while at the same time minimising energy that is expended to search for nutritious browse that is sparsely distributed. Previous studies reported that elephant reduce the energy costs incurred searching for the sparsely distributed nutritious food and increase their energy intake by consuming more of the most abundant but sometimes, less nutritious food (Pretorius et al., 2012). For female elephant that are in mixed herds of different age and sex, the strategy of moving less and feeding on more available food may be advantageous for the group (Ngene et al., 2010, Lindsay, 2011). However, male elephant can roam more and increase their chances of finding more nutritious forage even in the dry season as they are not slowed down by herd speed (Lindsay, 1994, Ngene et al., 2010, Lindsay, 2011).

In the wet season, the availability and abundance of nutritious plant species increases, hence reducing the energy demand required by elephant to search and feed on these plants (Loarie et al., 2009). However, the link between rainfall and availability of nutrients in forage is never linear, as leaf tissue nitrogen content decreases with plant available moisture and increases with plant-available nutrients (Olff et al., 2002). Rainfall amounts and soil fertility are heterogeneous in a savanna landscape, and so is the spatial distribution of forage quality (De Knegt et al., 2011, Pretorius et al., 2012). During the wet season, the demand for all nutrients increases as elephant replenish the deficient nutrients required for the biochemical reactions that drives their metabolism (Brown et al., 2004, Parker et al., 2009). Although trees are sparsely distributed compared to grasses, we found that both sexes of elephant chose sites with browse of a higher nitrogen content in the wet season. Elephant are hindgut fermenters and are less effecient at digesting their food, hence they incur high losses of nutrients in the faeces (Clauss et al., 2003). Thus, they chose sites with plant species that have high nutrient concentration (Jachmann and Bell, 1985, Pretorius et al., 2011, Pretorius et al., 2012). Consistent with our finding, Pretorius et al. (2012) found that elephant maximized their nitrogen intake in the wet season. Since plants consist of low nitrogen to fibre and carbohydrates ratio (White, 1978, Mattson, 1980), whereas animals need nitrogen to build structural proteins in their body, elephant need to spend more time foraging on these plants to get enough nitrogen to satisfy their requirements.

Compared to the males, the female elephant foraged more in areas with a higher grass biomass in the wet season (Osborn, 2004). Grass is abundant in the wet season and it has higher nutrient content and lower toxin and fibre content (Lindsay, 1994), hence it provides a higher return per unit foraging time than browse (Osborn, 2004). This result indicated that female elephant appear to choose a site based on forage biomass and availability. However, grass lacks certain essential nutrients and it becomes moribund and less nutritious quickly in the dry season. Although both grass and browse are abundant in the wet season, woody trees are sparsely distributed compared to grass. Despite that, browse has a higher and diverse nutrient content than grass and the nutrients remain available in the dry season (Jachmann, 1989). The male elephant consumed less grass as opposed to female elephant in the wet season suggesting that they foraged more on browse that is rich in nutrients. Our results are in line with Osborn (2004) who observed that the male elephant appeared to choose forage based on their nutrient content rather than the availability. Male elephant roam far and wide to forage as compared to females (Chiyo et al., 2011) and can therefore forage on sparsely distributed trees, and access browse on tall trees by pushing them over (Lindsay, 2011). Furthermore, male elephant have been reported to crop-raid in the transitional period between the wet and the dry season, perhaps to seek for more nutritious forage when grass begins to dry and drop in nutrient content (Osborn, 2004). The difference in forage decisions based on gender has been reported in other studies. For instance, Woolley et al. (2009) found that diet quality differed between elephant of different sexes, ages and body sizes.

We conclude that forage biomass is the primary determinant of forage site choice for elephant in the dry season whereas nutrients, particularly leaf tissue nitrogen concentration and grass biomass, determined forage site choice by elephant in the wet season. Comparing the sexes, female elephant are driven more by forage biomass as compared to male elephant where nutrients appear to be more important in forage site choice. In view of the current challenges of increased human-elephant conflicts and the reduction of space for wildlife as a result of competing alternative land-uses, the results of this study can be used to identify suitable land to establish new protected areas and to zone existing protected areas for elephant conservation. This could be done through regular assessments of forage quality and quantity within the landscapes based on elephant forage site preferences.

Chapter 6

Synthesis

African Elephant in a Cleft Stick

Choosing between starving or dying from thirst in arid savanna.

Elephant have been studied extensively as they are the largest extant terrestrial mammal, a charismatic species, have a high economic and ecological value, and a complex social behaviour (Scholes and Mennell, 2008, Moss et al., 2011). Studies on wildlife populations, especially on the African elephant, have attracted immense attention because of the long standing perception that an increase in elephant numbers have an adverse impact on vegetation (Glover and Sheldrick, 1964, Laws, 1970b, Myers, 1973, Ben-Shahar, 1993, de Beer et al., 2006, Guldemond and Aarde, 2008, Staub et al., 2013), and sometimes, on other species (Cumming et al., 1997, Kohi et al., 2011) through their foraging behaviour of pushing over, uprooting and snapping trees (Staub et al., 2013).

Consequently, elephant population management has been debated for decades with contradicting propositions on how it should be addressed (Laws, 1970b, Caughley, 1976, Myers, 1973, Barnes, 1983, Owen-Smith et al., 2006, Van Aarde and Jackson, 2007). Most rangeland and wildlife ecologists view arid and semi-arid savannas, where over half of the elephant population in Africa occur, to be governed by equilibrium dynamics (Sinclair, 2003, Gillson and Lindsay, 2003, Vetter, 2005, Junker et al., 2008). Based on the equilibrium view, it is assumed that the ecosystem has an ecological carrying capacity that can only support a certain maximum desirable number of elephants (Sinclair, 2003). Once this number is surpassed, elephant populations are perceived to cause undesirable habitat modification and significant loss of woody vegetation (Barnes, 1983, Calenge et al., 2002). Hence, management intervention such as provisioning of water supplies, culling or translocation is deemed necessary to keep elephant populations artificially close to the presumed “ecological carrying capacity” or to disperse and possibly reduce the perceived negative impacts (Van Aarde and Jackson, 2007). Conversely, in areas where elephant population are on the decline through various causes such as poaching (Douglas-Hamilton, 1987, Prins et al., 1994, Wittemyer, 2011, Chase et al., 2016), human-wildlife conflicts, disease outbreaks or natural causes such as drought (Dudley et al., 2001, Foley et al., 2008), the interest of wildlife managers is to reverse the trend. This is usually done through, for instance, reduction of elephant deaths by intensifying anti-poaching surveillance and disease control through veterinary services. However, the ecological carrying capacity is, in itself, difficult to determine in a natural ecosystem such as tropical savannas (Owen-Smith et al., 2006). Tropical savannas are characterized by a highly variable rainfall which deems ecological carrying capacity a doubtful basis for population control (Gillson and Lindsay, 2003).

While some causes of elephant mortality such as poaching can be managed, drought induced mortality is hard to control. The case studies invoked to indicate the adverse effects of severe droughts and the negative consequences of elephant overpopulation on vegetation include Tsavo National Park in Kenya (Corfield, 1973, Myers, 1973, Phillipson, 1975), Chobe National Park in Botswana (Skarpe et al., 2004), Hwange National Park in Zimbabwe (Dudley et al., 2001) and other tropical savannas (Foley et al., 2008). The “Tsavo Elephant Problem” where about 5000 drought induced mortality were reported in the 1960s and 1970s (Corfield, 1973), for instance, attracted immense global research interest. Most studies investigating Tsavo elephant mortality inclined towards the explanation that the cause of death was probably due to high elephant population that had little food to sustain it, basing their arguments on equilibrium view (Owen-Smith et al., 2006, Guldemond and Aarde, 2008). There is however, a contrary view that the mass elephant death could be a natural event that happens in such arid ecosystem whenever prolonged drought occurs, suggesting that tropical savannas are non-equilibrium systems (Caughley, 1976). Non-equilibrium dynamics predicts that plant composition and biomass in tropical savannas are primarily driven by rainfall and not by grazing pressure, that animal numbers are kept at low densities by frequent droughts, and that herbivory has little impact on vegetation change (Ellis and Swift, 1988, Illius and O'Connor, 1999, Sullivan and Rohde, 2002). The Tsavo debate was not concluded partly because it was based on only one drought incident, but also research interest slowed down as occurrence of severe droughts declined. However, elephant mortality continued to occur even during short droughts though not in the magnitude of the 1960s and 1970s, and the frequency of these droughts have been increasing and is predicted to increase into the future (Shrader et al., 2012, Yang et al., 2014), and that is the basis of my motivation to undertake this study.

The understanding of drought related elephant mortality and its impact on elephant population require a long term dataset of population change in relation to drought occurrences. I relied on the best existing data in Africa of wild elephant population that has been consistently monitored for over 40 years where life histories of over 3000 individual elephants are known, at Amboseli National Park in Kenya. Further, I also analysed geo-referenced elephant mortality data collected daily for 10 years from Tsavo ecosystem. In this thesis, I present four studies; two of these are based on the long-term data and focussed on the theme of spatial and temporal changes in elephant mortality in relation to drought length (months of dry season) and intensity (rainfall amount) in chapter 2 and 3. The other two studies are based on short-term data covering the movement response of African elephant to seasonal water and forage distribution in the landscape (chapters 4 and 5). First, I will discuss the themes of each chapter separately and synthesize the prominent issue that arises in each. Secondly, I will proceed to generalize the findings to a broader context of elephant population change in tropical savannas. Finally, I will draw conclusions and identify gaps and recommendations for further research.

Drought-related elephant mortality with respect to age and sex

The result of this study corroborates other past studies that calves (<2years) are more susceptible to drought caused mortality in elephant and the risk of dying decreased with age (Foley et al., 2008, Guldemond and Aarde, 2008, Lee et al., 2011a, Moss, 2001). Further to what is already known from the past studies, this study indicates that the effect of drought induced mortality for the adult elephant is sex and age dependent with males older than 25 years being less likely to die as compared to females of the same age (chapter 2). This is a new finding as past research suggested the effect of droughts on adult male and female elephant were insignificant (Moss, 2001, Lee et al., 2011a). This new finding may have arisen because of the resolution of the analysis of my study which focused on the length and severity of drought as opposed to past studies that restricted their analysis to seasonal and inter-annual differences in rainfall patterns (Lindsay, 1994, Moss, 2001, Lee et al., 2011a).

Drought and spatial elephant mortality

Based on a model from observed spatial elephant mortality in Tsavo Conservation Area for 10 years, the findings of chapter 3 indicate that elephant carcasses were aggregated and elephant mortality was negatively correlated with four months cumulative precipitation prior to death, forage availability and distance to water, while local elephant density showed a positive correlation. This finding rules out dehydration as the cause of elephant mortality in Tsavo ecosystem even during drought. Analysis of forage availability in areas near and further away from the permanent river in Tsavo Conservation area did not show significant difference in the driest season. This finding suggests that however far from the river the elephant would have foraged, there would be no gain in more forage, and perhaps, it may be more beneficial to forage close to the water source to minimise energy expended in foraging further away from the river. Hence, in a prolonged drought, elephant mortalities may have occurred as a result of the forage quality and quantity that may have dropped too low to meet their energetic requirements. However, elephant are known to migrate for long distances and it has also been suggested that they can remember and re-visit previously visited sites (De Beer and Van Aarde, 2008, Prins and Van Langevelde, 2008, De Knegt et al., 2011) and pass on the information of their historical migration routes through generation (Moss et al., 2011, McComb et al., 2001). It therefore still remains unclear from this investigation, why they remained near a water source with no sufficient forage and eventually starved to death. Perhaps, the fidelity to a watering point is too strong and it takes a long time for elephant to explore other watering points unknown to them, or it may be likely that elephant may avoid moving into the unknown area and instead adopt a strategy to stay close to water, conserve energy, and wait for the rain. It may also mean that the historical migratory routes that linked elephant to other areas with better forage have been blocked by other land uses such as farms and human settlements. Past studies have reported that some species exhibit site fidelity, such as breeding-site fidelity (Switzer, 1993).

Habitat utilization by elephants in relation to forage distribution

In a landscape where the water sources and rich foraging sites are few and far apart, hundreds of kilometres in the case of Tsavo ecosystem, the activity time budget for the elephant include movement between the water sources and the foraging sites. How far they go to forage from the water source will be determined by the distribution of forage relative to water sources and the amount of energy that the elephant is able to spend moving between the foraging and watering sites. Animals optimize their energy expenditure, hence, they will use the foraging site that are close enough to water so that they are able to re-visit the water source as frequently as they require. The questions that can be explored are; what is “a close enough” foraging site for elephant? and, what determines selection of a foraging site for elephant – is it the forage nutrient concentrations or forage biomass?

Allometric studies show that forage selection is inversely related to body size (Demment and Van Soest, 1985). Based on their large body size, it was generally believed that elephant can survive on a less nutritious but a high biomass forage (Shrader et al., 2010, Shrader et al., 2012), and are therefore, less susceptible to starvation. In Tsavo ecosystem and other tropical savannas, high elephant mortalities were recorded close to rivers during periods of prolonged droughts (Corfield, 1973, Dudley et al., 2001, Foley et al., 2008). In all these cases, other causes of deaths such as diseases and poaching were ruled out, thus the likely cause of these mortalities may be starvation.

The unanswered questions are: was there interspecific competition for forage due to high elephant density? Were there no better foraging sites these elephant could migrate to? Were the better foraging sites too far for the elephant to utilize and re-visit the few watering points? Was the vegetation already very low in nutrients or biomass, enough to meet elephant physiological requirements? Through analysis of seasonal elephant movement data, my study shows how available vegetation biomass and nutrients influenced elephant habitat utilization in tropical savannas. Whereas elephant selected foraging sites based on biomass available in the dry season, our findings showed that forage quality is important for the elephant in the wet season (chapter 4). Comparing the sexes, females selected areas with a higher forage biomass compared to the males. This result may be explained by the difference in social organisation and foraging strategies between the sexes (Lindsay, 2011). In human-elephant conflict incidences, for instance, male elephant raid crops more than mixed herd (Sitati et al., 2003). Therefore, the crop raiding incidences by the male elephant may be due to the search for quality forage, and these sites may be farms close to Tsavo Conservation Area. In addition, males foraged alone or in small bull groups except during the breeding season when they join mixed herds (van Aarde et al., 2008, Moss et al., 2011). This social behaviour allows male elephant to access far foraging sites because when foraging alone or in a small all-male groups they are not slowed down by calves as when they would be foraging in mixed herds.

Elephant movement pattern in relation to water

Movement strategy of an individual organism determines its chances to survive, as animals must move to forage (Stephens, 2007, De Knegt et al., 2011), provision (Stephens, 2007, Prins and Van Langevelde, 2008), disperse or migrate to favourable habitats (Kot et al., 1996, Wikelski et al., 2003). By determining the fate of an individual, movement ultimately affects population dynamics of animals (Turchin, 1991, Huisman, 2014). In chapter 5, I explored how water scarcity affect elephant seasonal movement patterns (in a peak wet and dry season). It is not in doubt that water is a major constraining factor for elephant in tropical savannas and to a large extent, influence elephant distribution and local elephant densities (Chamaille-Jammes et al., 2007, Chamaillé-Jammes et al., 2008, Smit et al., 2007, Smit and Grant, 2009, Young and Van Aarde, 2010). In dry seasons, large elephant congregations are found around the few water sources causing heavy browsing and creating "piospheres" around them (Smit and Ferreira, 2010, Chamaillé-Jammes et al., 2009, Shrader et al., 2010). To spread elephant distribution across landscapes, one prescription is water provisioning by sinking boreholes and digging water pans (Smit et al., 2007). Most protected areas in Africa, particularly, the southern African parks, have practiced this for decades and indeed succeeded in spreading elephant across landscapes. However, in the recent studies, water provisioning has been reported to cause homogenisation of landscapes which is not good for wildlife, and particularly, elephant (Hilbers et al., 2015). Moreover, utilization of water sources is uneven with some water sources heavily used than others, hence elephant impacts on vegetation differ around these watering points. For example, in Kruger National Park, permanent rivers attract higher elephant densities than smaller water pans (Smit and Ferreira, 2010). Although there is a general consensus that water influences elephant distribution and their survival, there are many questions that remain to be studied (Hilbers et al., 2015). For instance, how do elephant select which water source to visit? What mechanisms do they use to locate these water for re-visitation – is it back-tracking, using landmarks or dead reckoning? Do they have site fidelity where they prefer to drink water? Do they have information about their landscapes and watering points or do they randomly search for these water sources? The historical reports that elephant took over 50 years to colonize Kruger may perhaps, be something to do with how elephant slowly familiarize and discover water sources unknown to them in a new environment (Whyte et al., 2003).

The results from chapter 4 indicates that elephant have strong fidelity to a particular water source. Male elephant remained at a distance of about 20 km from the nearest water source while the female elephant foraged to a maximum of about 10 km way from the water and only moved further than this distances in the wet season. All the individuals re-visited only one particular water source. The strong directionality of elephant movement from a distance of 15km (rho > 0.5) as they re-visited their watering source in the peak dry season suggest that elephant have information on location of their water sources. Whether they use land marks, back-tracking or dead reckoning to find the water source was not investigated in this study. During wet seasons, the individual elephant I studied migrated as far as 100 km to forage and they used temporary water pans and seasonal rivers. They all returned back to a permanent water source just before the onset of the dry season. The timing to return to the permanent water source in the dry season was so precise and the whole trek happened in a span of two days with movement clearly directed to the river. Again, whether the same water pans are used during all the wet seasons or whether elephant randomly search for these water pans before they found them the first time is an area that require further research and outside the scope of my study.

Drought and elephant population change: Is non-equilibrium dynamics at play?

Elephant are bulk feeders and require large amount of food to survive (Barnes, 1983, Jachmann and Bell, 1985, Jachmann, 1989, Osborn, 2004). They are also water dependent and must drink water frequently; mostly every two days (De Knegt et al., 2011). Tropical savannas are deficient in both water and forage especially in dry seasons and therefore, elephant are faced with two major challenges; starvation or dehydration. However, elephant have existed in these dry ecosystems for a long time and this implies that they have probably adapted mechanisms to survive. The question is, how do they cope with scarcity of water and food although they require both in very high quantities?

Tropical savannas are characterized by variable rainfall (Huenneke and Noble, 1996, Prins, 1996), a typical characteristic of a non-equilibrium system. Although it is conceivable that as animal population increases, the resources they depend on would be limiting (Sinclair and Krebs, 2002), two aspects make density-dependent regulation difficult to observe in elephant populations in tropical savannas: First, elephant are the largest and long-lived terrestrial mammals (Moss et al., 2011), thus there is a long time lag before the effect of density on population occurs making negative feedback between population numbers and resources unlikely. Second, the frequent droughts in tropical savannas probably reduce elephant numbers before the population reaches a point where food could become limiting, hence there may be no opportunity for density dependent regulation to develop. This may explain why there are many reports of density dependent regulation in mammalian species, mostly from the stable temperate environments (Gaillard et al., 1993, Gaillard et al., 1998), and rare evidence of density dependent regulation in African elephant populations (Van Aarde et al., 1999, Sinclair, 2003, Junker et al., 2008). From these studies, water is the key resource that determines elephant distribution while food is secondary in habitat selection (de Boer et al., 2013). After a permanent water source is secured, then food quality and quantity becomes important for elephant habitat selection. Even so, forage biomass is the currency of choice in dry seasons and forage quality becomes important mostly in wet season.

Prolonged droughts usually result in high elephant mortality, but the resilience of these tropical savannas may perhaps be as a result of these deaths that release the system from high browse pressure and give it a window to regenerate (Prins and van der Jeugd, 1993). If that is the case, then drought induced elephant mortality may not be a bad thing. The findings from my studies strongly suggests that the tropical savannas may in fact be a non-equilibrium system sustained by growth and crashes of herbivore populations.

Recent studies have brought to the fore the failure of drought mitigation measures such as water provision, culling, fencing, translocation and others to address drought induced elephant mortality. In Tsavo Conservation Area where these studies were conducted, the drying of Voi river and the subsequent establishment of three boreholes to supply water for wildlife turned that part of Tsavo to a “desert” in complete contrast to northern section of the park where the system was let to be. The drying up of Voi river has also resulted to high elephant population on the only remaining Galana river and, consequently, increased elephant mortality around this river. We can argue that manipulation of ecosystems, may in some instances, lead to elephant mortality in the long-term. Therefore, dry ecosystems may better be managed as a *“laissez faire”.* This option is however, challenged by the anthropogenic factors that interfere with the natural ecosystem such as closing up of historical migratory corridors used by elephant to access dry season foraging sites or siltation and drying up of the rivers that lead to re-distribution of elephant populations across the landscape. Anthropogenic factors will keep changing tropical savannas, hence, some level of active management is indeed inevitable. I argue that these management efforts should be directed to try and revive human-altered ecosystems, such as, opening up corridors through land use planning and restoration of rivers, as opposed to opening up artificial water sources. Supporting initiatives to mitigate the negative effects of climate change such as planting of trees, reducing greenhouse gas emission and others may be a long-term global agenda for elephant and other wildlife species survival.

The modern day park managers have a daunting challenge to address issues such as mass elephant deaths in drought, increased human wildlife conflicts or changes in wildlife use of the landscape which may all be symptoms of wrong management interventions taken in the past or interference by anthropogenic factors that may have changed the natural functioning of a non-equilibrium system. Apart from field experience gained at work, park managers need to make evidence-based conservation decisions that rely on research results. Such investigations can be ecological, social sciences, economics studies or even historical investigations. This argument is clearly exemplified by the most recent severe drought in South Africa in 2016 that is raising a debate similar to the one in Tsavo 50 years ago - on whether to cull 2000 elephant or not? The pertinent question that arises is; what have we learnt after 50 years of Tsavo elephant mortality incident? The findings from these studies can be used to contribute to the direction that should be taken to address the long standing elephant management challenges in tropical savannas into the future (A copy of my response to address challenges of drought on mega-herbivores management in South African in 2016 based on this thesis is attached).

Finally, as Poole (1996) observed, " *Literally hundreds of studies on African elephant (Loxodonta africana) have been carried out across the African continent. We have learned more about elephant than, perhaps, any other large undomesticated African mammal, and yet we are just beginning to understand their complex lives*". Although this study has come up with important findings that will influence the management of African elephant population in tropical savannas, a lot of research questions remain unanswered as highlighted in the synthesis of each chapters and I recommend future follow-up studies. In conclusion, I argue that tropical savannas are non-equilibrium systems and should be managed as such. I further propose that maintaining tropical savannas as natural as possible is better for elephant populations to prosper for posterity as opposed to interventions such as culling or water provisioning.

My response to a proposal to cull 2000 elephants in South African Private Reserves to save other herbivores in the severe drought experienced in the year 2016

"THE HERBIVORE-DROUGHT PROBLEM" IN THE ASSOCIATION OF PRIVATE NATURE RESERVES (APNR), WITH A FOCUS ON ELEPHANT – MAY 2016.

Summary of the problem and the proposed solution as per the APNR report:

The APNR is presently faced with the challenge of maintaining herbivore biomass which is thought to be way above the threshold that can be supported by the reserve's available resources (especially food because there is enough water from artificial watering sources), and this is feared to cause rangeland degradation. The probable reason for the increased herbivore density (especially elephant) in APNR is the provision of excessive surface water and opening of the fence between the reserve and Kruger National Park, hence allowing free movement of the herbivores. The result is a decline in the spatial heterogeneity of the natural resources in the reserve and extensive grass mortality which is exacerbated by the current drought. To address this challenge, one of the proposed solution is to reduce elephant numbers because they are highly successful and competitive species and consequently, may result to increased mortalities of other herbivores, especially the endangered white rhinoceroses (*Cerathotherium simum*). The current conservation debate is to find options to reduce the elephant population. The favoured proposal is to cull at least 2000 elephant.

THE TSAVO EXPERIENCE

The effects of severe drought and the perceived negative consequences of elephant over-population on vegetation is best illustrated in the mass elephant die-offs that occurred in Tsavo Conservation Area in Kenya in the 1960s and 1970s. During the single drought event of the 1970s, called The

“Tsavo Elephant Problem”, over 5000 elephant died and this attracted immense global research interest. Most studies then inclined towards the explanation that the cause of mass elephant mortalities were probably due to high elephant population that had little forage resources to sustain it. Therefore, culling was recommended to reduce the population. However, culling did not happen. Part of my PhD thesis investigated the drought induced spatial mortality pattern of elephant in Tsavo to explore the role of elephant density (alongside other factors such as food availability and water) in explaining these mortality patterns.

The findings of my study indicate that elephant carcasses were aggregated and elephant mortality was negatively correlated with four months cumulative precipitation prior to death, forage availability and distance to water, while local elephant density showed a positive correlation. This particular finding rules out dehydration as the cause of elephant mortality in Tsavo because the mass elephant mortality occurred around one of the perennial rivers in the ecosystem. Analysis of forage availability close to or further away from the river did not show significant difference in the driest season. This finding suggests that however far from the river the elephant would have foraged, there would be no gain in more forage, and perhaps, it may be more beneficial to forage close to water source and minimise energy expenditure searching for a foraging site far removed, which is equally of poor quality. Hence, in a prolonged drought, it may be the forage quality and quantity that may have dropped too low to meet elephant food requirements. However, elephant are known to migrate for long distances and it has also been suggested that they can remember and re-visit previous ranging areas and pass on the information on their historical migration routes for generations. Why did the elephant not migrate then? One explanation is the historical migratory routes that linked elephant to other areas with better forage have been blocked by other land uses such as farms and human settlement, which is evident around Tsavo Conservation Area; Or may be all areas around Tsavo experienced severe drought.

Tsavo Conservation Area is different from Kruger and the reserves that surrounds it in terms of artificial water provision. Although there are several water pans (both natural and artificial) that spread across the 20,000 km^2 of Tsavo landscape, these water pans only hold water in the wet season and dry up before the onset of the dry season. A few boreholes (5 in total out of which only 3 are working currently in the whole of Tsavo) supply water throughout the year. In addition, there is one permanent dam that was dug over 50 years ago and is now completely covered with silt, hence hardly holds water in the dry season. Therefore, elephant distribution is restricted to the few rivers (2-permanent and 2-seasonal) and the 3-boreholes during the dry season with local elephant densities sometimes going to as high as 15 elephants per square kilometre around this water sources. The ranches surrounding Tsavo National Parks were mostly established for livestock farming but a few of them are slowly embracing wildlife conservation as an alternative land use. The ranchers provide artificial water supplies for their livestock and this attracts elephant as well during the dry seasons. Again, the density of elephant in this ranches have never been an issue because the water supplies are not many and also human disturbances, including wildlife poaching, is high in these ranches hence, deterring elephant numbers there. The important role these ranches play is to provide habitat connectivity between Tsavo National Parks (Tsavo East and Tsavo West) and Mkomanzi National Reserve at the border of Kenya and Tanzania.

In Tsavo, elephant have never been culled to control their numbers, even after the massive die-offs in the severe droughts of 1960s and 1970s. Like Kruger, Tsavo also hosts other species of herbivores such as Impalas, Buffaloes, Zebras, Giraffes, Eland and other meso-herbivores. Although the severity is low, Tsavo has experienced many short drought events since the 1970s, the latest being in the year 2009 where more than 300 elephant died. The population of elephant in Tsavo dropped to a low of 5,000 around the late 80s (because of droughts but also increased poaching). However, in 1989 to date, poaching of elephant has reduced significantly, and the population has grown to over 12,000 in the latest census done in 2013. This is despite the few short drought events the population has experienced in the past few years. The vegetation, especially woody trees, were negatively impacted on by high elephant density in the 1960s and 1970s, just before the drought. Today, the northern parts of Tsavo East National Park, which had the highest elephant population, and also experienced the greatest vegetation change due to high elephant density, has the thickest woody vegetation. This part has one of the permanent rivers which all wildlife species depends on, especially in the dry season. In contrast, the Southern part of Tsavo East National Park, where the three boreholes are still functional, has turned to an open grassland with hardly any trees and appears to be “a desert” within a park especially during dry season when all vegetation dry up and elephant (and other wildlife species) density increases around these boreholes.

Lessons Learnt

The tropical savannas are deficient in both water and forage especially in the dry season and therefore, elephant (and other wildlife species) are faced with two major challenges; starvation or dehydration. However, elephant (and other mega and meso-herbivores) have existed in these dry ecosystems for a long time and this implies that they have probably adapted mechanisms to survive. The question is how do they (elephants and other herbivores) cope with water and food scarcity and yet they require both in very high quantities?

Even though prolonged droughts usually result in high elephant mortality, the resilience of these dry ecosystems may perhaps be as a result of these deaths that release the system from high browse pressure and give it a window to regenerate. If that is the case, then drought induced elephant (and may be other herbivores) mortality may not be a bad thing. The trend strongly suggests that tropical savannas may in fact be a non-equilibrium system sustained by growth and crashes of herbivore population. Maintaining the system as natural as possible may therefore keep elephant (and other herbivores) populations in savannas sustained for posterity.

Manipulation of the wildlife numbers or their habitats by for instance, culling, translocation or water provisioning, may temporarily appear to solve the immediate symptoms of "wildlife over-population" as we perceive it, but it will eventually result to other problems in the long-term. The evidence is clear in the effect of water provisioning which is now resulting in declines of the spatial heterogeneity of landscape resources by attracting highly water dependent species to congregate in an area. One may argue that it's better to cull than to let wildlife species die of starvation, which is indeed a valid point. But again, the question is: Do we know which individuals will survive or succumb to starvation, so that we develop a criteria that selects only those individuals for culling? Probably the old, sick or weak individuals may be selected based on logic, but practically, identifying these individual animals in the field is not easy. In nature, those individuals that survive drought have traits that make them survive and it is best if those genes are passed on. Furthermore, if the forage quality and availability goes so low because of drought to the point that it cannot sustain herbivores' survival, culling of elephant may not solve drought induced mortality of those herbivores.

The challenge APNR faces today is similar to Tsavo 50 years ago, but APNR's case is complicated even more by management actions (such as water provision and opening up of fences) that is not easy to reverse quickly, yet the need for the solution to this challenge is urgent. The cost of saving rhinos (and other herbivores) will come at a cost of culling elephant, which may solve the current symptoms of perceived negative impact on vegetation and competition for forage by elephant. However, in the long term, droughts will occur and a similar challenge will recur again. I therefore propose a long term solution to this current drought related challenge than to cull elephant. I argue that maintaining these dry savannas as natural as possible is better for elephant and other herbivores to prosper for posterity compared to short-term interventions such as culling or water provisioning.

Bibliography

'T MANNETJE, L. 2000. Measuring biomass of grassland vegetation. *In:* 'T MANNETJE, L. & JONES, R. (eds.) *Field and laboratory methods for grassland and animal production research.* Wallingford, U.K.: CAB International.

AESG 2013. IUCN/SSC African Elephant Specialist Group, TRAFFIC International. 2013. *Status of African elephant populations and levels of illegal and the illegal trade in ivory: A report to the African Elephant Summit*.

ALBON, S., GUINNESS, F. & CLUTTON-BROCK, T. 1983. The influence of climatic variation on the birth weights of red deer (Cervus elaphus). *Journal of Zoology,* 200**,** 295-298.

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

ALTMANN, J., ALBERTS, S., ALTMANN, S. & ROY, S. 2002. Dramatic change in local climate patterns in the Amboseli basin, Kenya. *African Journal of Ecology,* 40**,** 248-251.

ANDERSON, D. R. & BURNHAM, K. P. 2002. Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management***,** 912-918.

ANDREWARTHA, H. & BIRCH, L. 1954. The distribution and abundance of animals. *University of Chicago*.

ARCHIE, E. A., MOSS, C. J. & ALBERTS, S. C. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society of London B: Biological Sciences,* 273**,** 513-522.

ARCHIE, E. A., MOSS, C. J. & ALBERTS, S. C. 2011. Friends and relations: Kinship and the nature of female elephant social relationships. University of Chicago Press: Chicago, IL, USA.

ATKINSON, R., RHODES, C., MACDONALD, D. & ANDERSON, R. 2002. Scale-free dynamics in the movement patterns of jackals. *Oikos,* 98**,** 134-140.

AUGUSTINE, D. J., MCNAUGHTON, S. J. & FRANK, D. A. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications,* 13**,** 1325-1337.

AUSTIN, D., BOWEN, W. & MCMILLAN, J. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos,* 105**,** 15-30.

AYENI, J. 1975. Utilization of waterholes in Tsavo National Park (east). *African Journal of Ecology,* 13**,** 305-323.

BABAASA, D. 2000. Habitat selection by elephants in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology,* 38**,** 116-122.

BARNES, R. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology***,** 521-539.

BARTUMEUS, F. 2009. Behavioral intermittence, Lévy patterns, and randomness in animal movement. *Oikos,* 118**,** 488-494.

BARTUMEUS, F., DA LUZ, M. G. E., VISWANATHAN, G. & CATALAN, J. 2005. Animal search strategies: a quantitative random-walk analysis. *Ecology,* 86**,** 3078-3087.

BATES, D., MAECHLER, M. & BOLKER, B. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. 2012. *URL: http://CRAN. R-project. org/package= lme4*.

BAX, P. N. & SHELDRICK, D. 1963. Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *African Journal of Ecology,* 1**,** 40-51.

BEEKMAN, J. & PRINS, H. 1989. Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, Syncerus coffer. *African Journal of Ecology,* 27**,** 129-147.

BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation,* 65**,** 249-256.

BENHAMOU, S. 2004. How to reliably estimate the tortuosity of an animal's path:: straightness, sinuosity, or fractal dimension? *Journal of theoretical biology,* 229**,** 209-220.

BEYER, H. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/tools [Verified 20th August 2015].

BLANC, J., BARNES, R., CRAIG, G., DUBLIN, H., THOULESS, C., DOUGLAS-HAMILTON, I. & HART, J. 2007. African Elephant Status Report 2007: an update from the African Elephant Database. *In:* OCCASIONAL PAPER SERIES OF THE IUCN SPECIES SURVIVAL COMMISSION, N. I. S. A. E. S. G. (ed.). Switzerland: IUCN, Gland.

BLANC, J. J., BARNES, R. F., CRAIG, G. C., DOUGLAS-HAMILTON, I., DUBLIN, H. T., HART, J. A. & THOULESS, C. R. 2005. Changes in elephant numbers in major savanna populations in eastern and southern Africa. *IUCN***,** 18.

BOTH, C. 1998. Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology,* 67**,** 667-674.

BOUCHÉ, P., DOUGLAS-HAMILTON, I., WITTEMYER, G., NIANOGO, A. J., DOUCET, J.-L., LEJEUNE, P. & VERMEULEN, C. 2011. Will elephants soon disappear from West African savannahs? *PLoS One,* 6**,** e20619.

BOUWHUIS, S., CHARMANTIER, A., VERHULST, S. & SHELDON, B. C. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. *Journal of Animal Ecology,* 79**,** 1251-1261.

BOYCE, M. S., PITT, J., NORTHRUP, J. M., MOREHOUSE, A. T., KNOPFF, K. H., CRISTESCU, B. & STENHOUSE, G. B. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 365**,** 2213-2219.

BRONIKOWSKI, A. & WEBB, C. 1996. Appendix: A critical examination of rainfall variability measures used in behavioral ecology studies. *Behavioral Ecology and Sociobiology,* 39**,** 27-30.

BROWN, J. H., GILLOOLY, J. F., ALLEN, A. P., SAVAGE, V. M. & WEST, G. B. 2004. Toward a metabolic theory of ecology. *Ecology,* 85**,** 1771-1789.

BURN, R. W., UNDERWOOD, F. M. & BLANC, J. 2011. Global trends and factors associated with the illegal killing of elephants: a hierarchical Bayesian analysis of carcass encounter data. *PLoS one,* 6**,** e24165.

CALENGE, C. & CALENGE, M. C. 2015. Package 'adehabitatLT'. R Foundation for Statistical Computing. Vienna, Austria.

CALENGE, C., MAILLARD, D., GAILLARD, J.-M., MERLOT, L. & PELTIER, R. 2002. Elephant damage to trees of wooded savanna in Zakouma National Park, Chad. *Journal of Tropical Ecology,* 18**,** 599-614.

CAMERON, A. C. & TRIVEDI, P. K. 1998. Regression analysis of count data Cambridge University Press. *Nueva York*.

CAUGHLEY, G. 1976. The elephant problem–an alternative hypothesis. *African Journal of Ecology,* 14**,** 265-283.

CECH, P. G., KUSTER, T., EDWARDS, P. J. & VENTERINK, H. O. 2008. Effects of herbivory, fire and N2-fixation on nutrient limitation in a humid African savanna. *Ecosystems,* 11**,** 991-1004.

CERLING, T. E., OMONDI, P. & MACHARIA, A. N. 2007. Diets of Kenyan elephants from stable isotopes and the origin of confiscated ivory in Kenya. *African Journal of Ecology,* 45**,** 614-623.

CHAMAILLE-JAMMES, S., FRITZ, H., VALEIX, M., MURINDAGOMO, F. & CLOBERT, J. 2008. Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *J Anim Ecol,* 77**,** 135-44.

CHAMAILLÉ-JAMMES, S., FRITZ, H. & MADZIKANDA, H. 2009. Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. *Ecography,* 32**,** 871-880.

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

CHAMAILLE-JAMMES, S., VALEIX, M. & FRITZ, H. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology,* 44**,** 625-633.

CHASE, SCHLOSSBERG S., GRIFFIN C. R., BOUCHÉ P. J.C. , DJENE S. W., ELKAN P. W. , FERREIRA S, GROSSMAN F, KOHI E. M , LANDEN K., OMONDI P., PELTIER A., SELIER S.A. J. & SUTCLIFFE R. 2016. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ***,** DOI 10.7717/peerj.2354.

CHIYO, P. I., ARCHIE, E. A., HOLLISTER-SMITH, J. A., LEE, P. C., POOLE, J. H., MOSS, C. J. & ALBERTS, S. C. 2011. Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. *Animal Behaviour,* 81**,** 1093-1099.

CLAUSS, M., FREY, R., KIEFER, B., LECHNER-DOLL, M., LOEHLEIN, W., POLSTER, C., RÖSSNER, G. & STREICH, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia,* 136**,** 14-27.

COBB, S. 1976. *The distribution and abundance of the large herbivore community of Tsavo National Park, Kenya.* University of Nairobi.

COLLIER, P., CONWAY, G. & VENABLES, T. 2008. Climate change and Africa. *Oxford Review of Economic Policy,* 24**,** 337-353.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science,* 199**,** 1302-1310.

COPPES, J. & BRAUNISCH, V. 2013. Managing visitors in nature areas: where do they leave the trails? A spatial model. *Wildlife Biology,* 19**,** 1-11.

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

COULSON, T., ROHANI, P. & PASCUAL, M. 2004. Skeletons, noise and population growth: the end of an old debate? *Trends in Ecology & Evolution,* 19**,** 359-364.

CROZE, H. & LINDSAY, W. 2011. The Amboseli ecosystem context: Past and present. *In:* MOSS, C., CROZE, H. & LEE, P. (eds.) *The Amboseli elephants.* Chicago & London: University of Chicago Press.

CUMMING, D. H., FENTON, M. B., RAUTENBACH, I. L., TAYLOR, R. D., CUMMING, G. S., CUMMING, M. S., DUNLOP, J. M., FORD, A. G., HOVORKA, M. D. & JOHNSTON, D. S. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science,* 93**,** 231-236.

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

DE BEER, Y. & VAN AARDE, R. 2008. Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments,* 72**,** 2017-2025.

DE BOER, W. F., VAN LANGEVELDE, F., PRINS, H. H., DE RUITER, P. C., BLANC, J., VIS, M. J., GASTON, K. J. & HAMILTON, I. D. 2013. Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biological Conservation,* 159**,** 468-476.

DE KNEGT, H., HENGEVELD, G., VAN LANGEVELDE, F., DE BOER, W. & KIRKMAN, K. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology,* 18**,** 1065-1072.

DE KNEGT, H. J., VAN LANGEVELDE, F., SKIDMORE, A. K., DELSINK, A., SLOTOW, R., HENLEY, S., BUCINI, G., DE BOER, W. F., COUGHENOUR, M. B. & GRANT, C. C. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology,* 80**,** 270-281.

DE LEEUW, P. N. & TOTHILL, J. C. 1993. The concept of rangeland carrying capacity in sub-Saharan Africa: Myth or reality. *In:* BEHNKE JR., R. H., SCOONES, I. & KERVEN., C. (eds.) *Range Ecology at Disequilibrium.* London: Overseas Development Institute.

DEMMENT, M. W. & VAN SOEST, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, 641-672.

DO, F. C., GOUDIABY, V. A., GIMENEZ, O., DIAGNE, A. L., DIOUF, M., ROCHETEAU, A. & AKPO, L. E. 2005. Environmental influence on canopy phenology in the dry tropics. *Forest Ecology and Management,* 215, 319-328.

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

DRAY, S., ROYER-CARENZI, M. & CALENGE, C. 2010. The exploratory analysis of autocorrelation in animal-movement studies. *Ecological Research,* 25, 673-681.

DUBLIN, H. T. 1991. Dynamics of the Serengeti-Mara woodlands: an historical perspective. *Forest & Conservation History,* 35, 169-178.

DUDLEY, J., CRIAG, G., GIBSON, D., HAYNES, G. & KLIMOWICZ, J. 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology,* 39, 187-194.

EBERHARDT, L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology,* 83, 2841-2854.

ELITH, J., PHILLIPS, S. J., HASTIE, T., DUDÍK, M., CHEE, Y. E. & YATES, C. J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and distributions,* 17, 43-57.

ELLIS, J. E. & SWIFT, D. M. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management Archives,* 41, 450-459.

ESRI 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute Redlands, CA.

EVANS, K. E. & HARRIS, S. 2008. Adolescence in male African elephants, Loxodonta africana, and the importance of sociality. *Animal Behaviour,* 76, 779-787.

FERWERDA, J., SKIDMORE, A., VAN WIEREN, S. & PRINS, H. 2006. Soil N and P affected reflectance signatures of individual Colophospermum mopane leaves. *Journal of spatial science,* 51, 103-113.

FISHER, R. A. 1930. *The genetical theory of natural selection: a complete variorum edition*, Oxford University Press.

FOLEY, C., PETTORELLI, N. & FOLEY, L. 2008. Severe drought and calf survival in elephants. *Biol Lett,* 4, 541-4.

FORCHHAMMER, M. C., CLUTTON-BROCK, T. H., LINDSTRÖM, J. & ALBON, S. D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology,* 70, 721-729.

GAILLARD, J.-M., DELORME, D., JEAN-MARIE, B., VAN LAERE, G., BOISAUBERT, B. & PRADEL, R. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology*, 778-791.

GAILLARD, J.-M., FESTA-BIANCHET, M., YOCCOZ, N., LOISON, A. & TOIGO, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 367-393.

GAILLARD, J.-M., FESTA-BIANCHET, M. & YOCCOZ, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution,* 13, 58-63.

GILLSON, L. 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity,* 1, 281-298.

GILLSON, L. & LINDSAY, K. 2003. Ivory and ecology—Changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy,* 6, 411-419.

GIUGGIOLI, L. & BARTUMEUS, F. 2010. Animal movement, search strategies and behavioural ecology: a cross-disciplinary way forward. *Journal of Animal Ecology,* 79, 906-909.

GLOVER, P. & SHELDRICK, D. 1964. An urgent research problem on the elephant and rhino populations of the Tsavo National Park in Kenya. *Bull. Epizoot. Dis. Afr,* 12, 33-38.

GORDON, I. 1989. Vegetation community selection by ungulates on the Isle of Rhum. II. Vegetation community selection. *Journal of Applied Ecology*, 53-64.

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

GRIFFITH, D. A. 1985. An evaluation of correction techniques for boundary effects in spatial statistical analysis: contemporary methods. *Geographical Analysis,* 17, 81-88.

GULDEMOND, R. & AARDE, R. 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *The Journal of Wildlife Management,* 72, 892-899.

HARRIS, G. M., RUSSELL, G. J., VAN AARDE, R. I. & PIMM, S. L. 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx,* 42.

HARTE, J. & NEWMAN, E. A. 2014. Maximum information entropy: a foundation for ecological theory. *Trends in ecology & evolution,* 29, 384-389.

HARVELL, C. D., MITCHELL, C. E., WARD, J. R., ALTIZER, S., DOBSON, A. P., OSTFELD, R. S. & SAMUEL, M. D. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science,* 296, 2158-2162.

HEBBLEWHITE, M., PERCY, M. & MERRILL, E. 2007. Are All Global Positioning System Collars Created Equal? Correcting Habitat-Induced Bias Using Three Brands in the Central Canadian Rockies. *The Journal of Wildlife Management,* 71, 2026-2033.

HENGEVELD, G. 2007. Moving to eat, optimal foraging and environmental heterogeneity. *Moving to eat: animal foraging movements in a heterogeneous environment*, 1-9.

HILBERS, J. P., VAN LANGEVELDE, F., PRINS, H. H., GRANT, C., PEEL, M. J., COUGHENOUR, M. B., DE KNEGT, H. J., SLOTOW, R., SMIT, I. P. & KIKER, G. A. 2015. Modeling elephant-mediated cascading effects of water point closure. *Ecological Applications,* 25, 402-415.

HOARE, R. E. & DU TOIT, J. T. 1999. Coexistence between people and elephants in African savannas. *Conservation Biology,* 13, 633-639.

HOLDO, R. M. 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology,* 19, 189-196.

HUENNEKE, L. & NOBLE, I. 1996. Ecosystem function of biodiversity in arid ecosystems. *Scope-Scientific Committee on Problems of the Environment International Council of Scientific Unions,* 55**,** 99-128.

HUETE, A., DIDAN, K., MIURA, T., RODRIGUEZ, E. P., GAO, X. & FERREIRA, L. G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote sensing of environment,* 83**,** 195-213.

HUETE, A. R. 1988. A soil-adjusted vegetation index (SAVI). *Remote sensing of environment,* 25**,** 295-309.

HUISMAN, T. J. 2014. *Search Performance and Spatial Resource Distribution.* PhD thesis, Wageningen University.

HUSO, M. M. 2011. An estimator of wildlife fatality from observed carcasses. *Environmetrics,* 22**,** 318-329.

ILLIUS, A. & O'CONNOR, T. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications,* 9**,** 798-813.

ILLIUS, A. W. 2006. Foraging and population dynamics. *In:* DANELL, K., BERGSTRÖM, R., DUNCAN, P. & PASTOR, J. (eds.) *Large herbivore ecology, ecosystem dynamics and conservation*

,Cambridge: Cambridge University Press.

JACHMANN, H. 1989. Food selection by elephants in the 'miombo'biome, in relation to leaf chemistry. *Biochemical Systematics and Ecology,* 17**,** 15-24.

JACHMANN, H. & BELL, R. 1985. Utilization by elephants of the Brachystegia woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology,* 23**,** 245-258.

JUNKER, J., VAN AARDE, R. J. & FERREIRA, S. M. 2008. Temporal trends in elephant Loxodonta africana numbers and densities in northern Botswana: is the population really increasing? *Oryx,* 42.

KAHINDI, O., WITTEMYER, G., KING, J., IHWAGI, F., OMONDI, P. & DOUGLAS-HAMILTON, I. 2010. Employing participatory surveys to monitor the illegal killing of elephants across diverse land uses in Laikipia–Samburu, Kenya. *African Journal of Ecology,* 48**,** 972-983.

KANGWANA, K. 1996. *Studying elephants,* Nairobi, Kenya, African Wildlife Foundation.

KERLEY, G. I. & LANDMAN, M. 2006. The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets. *South African Journal of Science,* 102**,** 395-402.

KNIGHT, M. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology,* 33**,** 377-394.

KOHI, E. M., DE BOER, W. F., PEEL, M. J., SLOTOW, R., VAN DER WAAL, C., HEITKÖNIG, I., SKIDMORE, A. & PRINS, H. H. 2011. African elephants Loxodonta africana amplify browse heterogeneity in African savanna. *Biotropica,* 43**,** 711-721.

KOS, M., HOETMER, A. J., PRETORIUS, Y., DE BOER, W. F., DE KNEGT, H., GRANT, C., KOHI, E., PAGE, B., PEEL, M. & SLOTOW, R. 2012. Seasonal diet changes in elephant and impala in mopane woodland. *European journal of wildlife research,* 58**,** 279-287.

KOT, M., LEWIS, M. A. & VAN DEN DRIESSCHE, P. 1996. Dispersal data and the spread of invading organisms. *Ecology,* 77**,** 2027-2042.

KREBS, C. J. 1995. Two paradigms of population regulation. *Wildlife Research,* 22**,** 1-10.

KREBS, C. J. 2002. Two complementary paradigms for analysing population dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 357**,** 1211-1219.

LAWS, R. 1970a. The Tsavo research project. *Oryx,* 10**,** 355-361.

LAWS, R. & PARKER, I. Recent studies on elephant populations in East Africa. Symp. Zool. Soc. Lond, 1968. 319-359.

LAWS, R. M. 1970b. Elephants as agents of habitat and landscape change in East Africa. *Oikos***,** 1-15.

LEE, P., LINDSAY, W. & MOSS, C. 2011a. Ecological patterns of variability in demographic rates. *In:* MOSS, C. J., HARVEY CROZE, AND PHYLLIS C. LEE. (ed.) *The Amboseli elephants.* Chicago, Illinois, USA: University of Chicago Press.

LEE, P. & MOSS, C. 2011. Calf development and maternal rearing strategies. *In:* C. J. MOSS, H. C., P. C. LEE (ed.) *The Amboseli elephants.* Chicago, IL:: U Chicago Press.

LEE, P., POOLE, J., NJIRAINI, N., SAYIALEL, C. & MOSS, C. 2011b. Male social dynamics: independence and beyond. *In:* MOSS, C. J., CROZE, H. & LEE, P. C. (eds.) *The Amboseli Elephants: A long-term perspective on a long-lived mammal.* Chicago and London: The University of Chicago Press.

LEE, P. C. 2011. Size and energetics of elephants. *In:* C. J. MOSS, H. C., P. C. LEE (ed.) *The Amboseli*

elephants. Chicago, IL: U Chicago Press.

LEE, P. C., BUSSIERE, L. F., WEBBER, C. E., POOLE, J. H. & MOSS, C. J. 2013. Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (Loxodonta africana). *Biol Lett,* 9**,** 20130011.

LEE, P. C. & MOSS, C. J. 1986. Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology,* 18**,** 353-361.

LEGGETT, K. E. 2006. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology,* 41**,** 17-36.

LEUTHOLD, B. M. & LEUTHOLD, W. 1978. Ecology of the giraffe in Tsavo East National Park, Kenya. *African Journal of Ecology,* 16**,** 1-20.

LEUTHOLD, W. & SALE, J. B. 1973. Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. *African Journal of Ecology,* 11**,** 369-384.

LINDSAY, K. 2011. Habitat use, diet choice and nutritional status in female and male Amboseli elephants. *In:* MOSS, C. J., CROZE, H. & LEE, P. C. (eds.) *The Amboseli Elephants: a long-term perspective on a long-lived mammal.* Chicago & London: University of Chicago Press.

LINDSAY, W. K. 1994. *Feeding ecology and population demography of African elephants in Amboseli, Kenya.* University of Cambridge.

LOISON, A., LANGVATN, R. & SOLBERG, E. J. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography,* 22**,** 20-30.

LOTKA, A. J. 1925. *Elements of physical biology,* Baltimore, Williams & Wilkins Company.

LOUREIRO, F., ROSALINO, L. M., MACDONALD, D. W. & SANTOS-REIS, M. 2007. Path tortuosity of Eurasian badgers (Meles meles) in a heterogeneous Mediterranean landscape. *Ecological Research,* 22**,** 837-844.

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

LUND, U. & AGOSTINELLI, C. 2015. Circstats: circular statistics, from "topics in circular statistics "(2001)". *S-plus original by Lund, U. R port by Agostinelli, C. R package version 0.2-4*.

MACKENZIE, D. I. & ROYLE, J. A. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology,* 42**,** 1105-1114.

MAINGI, J. K., MUKEKA, J. M., KYALE, D. M. & MUASYA, R. M. 2012. Spatiotemporal patterns of elephant poaching in south-eastern Kenya. *Wildlife Research,* 39**,** 234-249.

MARSH, L. & JONES, R. 1988. The form and consequences of random walk movement models. *Journal of Theoretical Biology,* 133**,** 113-131.

MATTSON, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics,* 11**,** 119-161.

MCCOMB, K., MOSS, C., DURANT, S. M., BAKER, L. & SAYIALEL, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science,* 292**,** 491-494.

MCNAUGHTON, S., RUESS, R. & SEAGLE, S. 1988. Large mammals and process dynamics in African ecosystems. *BioScience,* 38**,** 794-800.

MIQUELLE, D. G., PEEK, J. M. & VAN BALLENBERGHE, V. 1992. Sexual segregation in Alaskan moose. *Wildlife Monographs***,** 3-57.

MOSS, C. & LEE, P. 2011. Female social dynamics: fidelity and flexibility. University of Chicago Press: Chicago, IL, USA.

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

MOSS, C. J., CROZE, H. & LEE, P. C. 2011. *The Amboseli elephants: a long-term perspective on a long-lived mammal*, University of Chicago Press.

MUELLER, T., OLSON, K. A., FULLER, T. K., SCHALLER, G. B., MURRAY, M. G. & LEIMGRUBER, P. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology,* 45**,** 649-658.

MUKEKA, J. M. 2010. *Analyzing the distribution of the African elephant (Loxodonta africana) in Tsavo, Kenya.* Masters thesis, Miami University.

MUMBY, H. S., COURTIOL, A., MAR, K. U. & LUMMAA, V. 2013. Climatic variation and age-specific survival in Asian elephants from Myanmar. *Ecology*.

MURWIRA, A., SKIDMORE, A. K., HUIZING, H. & PRINS, H. H. 2010. Remote sensing of the link between arable field and elephant (Loxodonta africana) distribution change along a tsetse eradication gradient in the Zambezi valley, Zimbabwe. *International Journal of Applied Earth Observation and Geoinformation,* 12**,** S123-S130.

MYERS, N. 1973. Tsavo National Park, Kenya, and its elephants: an interim appraisal. *Biological Conservation,* 5**,** 123-132.

NGENE, S., IHWAGI, F., NZISA, M., MUKEKA, J., NJUMBI, S. & OMONDI, P. 2011. Total aerial census of elephants and other large mammals in the Tsalvo-Mkomazi ecosystem. *Nairobi, Kenya: Kenya Wildl. Serv,* 43**,** 5-56.

NGENE, S. M., NJUMBI, S., NGORU, B., NZISA, M., BITOK, E., POGHON, J., GOMBE, A., KOECH, E., SANGAWE, O., WAMBUA, D., OMONDI, C. & KORIR, W. 2012. Satellite-linked GPS collars deployed on elephants in Tsavo Ecosystem, Kenya. *In:* GARDINER, S. & OLSEN, K. P. (eds.) *Recent Advances in Satellite Research and Development.*: Nova Publishers.

NGENE, S. M., SKIDMORE, A., VAN GILS, H., MUTHONI, F. K., MUTERO, W. & OMONDI, P. 2014. Zero Tolerance: Evolving Wildlife Management in Kenya. *International Journal of Environmental Protection and Policy,* 1**,** 24.

NGENE, S. M., VAN GILS, H., VAN WIEREN, S. E., RASMUSSEN, H., SKIDMORE, A. K., PRINS, H. H., TOXOPEUS, A. G., OMONDI, P. & DOUGLAS-HAMILTON, I. 2010. The ranging patterns of elephants in Marsabit protected area, Kenya: the use of satellite-linked GPS collars. *African journal of ecology,* 48**,** 386-400.

NICHOLSON, A. J. & BAILEY, V. A. The Balance of Animal Populations.—Part I. Proceedings of the Zoological Society of London, 1935. Wiley Online Library, 551-598.

O'CONNOR, T. G., GOODMAN, P. S. & CLEGG, B. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation,* 136**,** 329-345.

OBA, G. 2001. The effect of multiple droughts on cattle in Obbu, Northern Kenya. *Journal of Arid Environments,* 49**,** 375-386.

OGUTU, J. O. & OWEN-SMITH, N. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters,* 6**,** 412-419.

OKELLO, M. M., KENANA, L., MUTETI, D., WARINWA, F., KIRINGE, J. W., SITATI, N. W., MALITI, H., KANGA, E., KIJA, H. & BAKARI, S. 2015. The status of key large mammals in the Kenya Tanzania borderland: A comparative analysis and conservation implications. *International Journal of Biodiversity and Conservation,* 7**,** 270-279.

OLFF, H., RITCHIE, M. E. & PRINS, H. H. 2002. Global environmental controls of diversity in large herbivores. *Nature,* 415**,** 901-904.

OMONDI, P., BITOK, E., MUKEKA, J., MAYIENDA, R. & LITOROH, M. 2008. Total aerial count of elephants and other large mammal species of Tsavo–Mkomazi ecosystem. *Kenya Wildlife Service Report. Nairobi, Kenya*.

OSBORN, F. 2004. Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe. *African Journal of Ecology,* 42**,** 322-327.

OWEN-SMITH, N. & CHAFOTA, J. 2012. Selective feeding by a megaherbivore, the African elephant (Loxodonta africana). *Journal of Mammalogy,* 93**,** 698-705.

OWEN-SMITH, N., KERLEY, G., PAGE, B., SLOTOW, R. & VAN AARDE, R. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African journal of science,* 102**,** 389-394.

PARKER, K. L., BARBOZA, P. S. & GILLINGHAM, M. P. 2009. Nutrition integrates environmental responses of ungulates. *Functional ecology,* 23**,** 57-69.

PEEL, M. & ANDERSON, J. 2016. Grazing situations and offtakes 2016: Association of Private Nature Reserves (APNR). . South Africa.

PEET, R., GLENN-LEWIN, D. & WOLF, J. W. 1983. Prediction of man's impact on plant species diversity. *In:* HOLZNER, W., WERGER, J. J. A. & IKUSIMA, I. (eds.) *Man's impact on vegetation.* Boston: Junk.

PETTORELLI, N., RYAN, S., MUELLER, T., BUNNEFELD, N., JĘDRZEJEWSKA, B., LIMA, M. & KAUSRUD, K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research,* 46**,** 15-27.

PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological modelling,* 190**,** 231-259.

PHILLIPS, S. J. & DUDÍK, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography,* 31**,** 161-175.

PHILLIPSON, J. 1975. Rainfall, primary production and 'carrying capacity'of Tsavo National Park (East), Kenya. *African Journal of Ecology,* 13**,** 171-201.

PICKETT, S. T., CADENASSO, M. L., BENNING, T. L., DU TOIT, J., ROGERS, K. & BIGGS, H. 2003. Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. *In:* J. DU TOIT, H. BIGGS & ROGERS, K. (eds.) *The Kruger Experience: ecology and management of savanna heterogeneity.* USA: Island Press, Washington, D.C.

PITTIGLIO, C., SKIDMORE, A. K., VAN GILS, H. A. & PRINS, H. H. 2012. Identifying transit corridors for elephant using a long time-series. *International journal of applied earth observation and geoinformation,* 14**,** 61-72.

POOLE, J. 1996. The African elephant. *In:* KANGWANA, K. (ed.) *Studying elephants. .* Kenya: African Wildlife Foundation Technical Handbook Series.

POOLE, J., LEE, P., NJIRAINI, N. & MOSS, C. 2011. Longevity, competition and musth: a long-term perspective on male reproductive strategies. *In:* MOSS, C. J., CROZE, H. & LEE, P. C. (eds.) *The Amboseli elephants: A long-term perspective on a long-lived species.* Chicago & London: The University of Chicago Press.

POOLE, J. H. & MOSS, C. J. 1981. Musth in the African elephant, Loxodonta africana. *Nature*.

PRETORIUS, Y., DE BOER, F. W., VAN DER WAAL, C., DE KNEGT, H. J., GRANT, R. C., KNOX, N. M., KOHI, E. M., MWAKIWA, E., PAGE, B. R. & PEEL, M. J. 2011. Soil nutrient status determines how elephant utilize trees and shape environments. *Journal of Animal Ecology,* 80**,** 875-883.

PRETORIUS, Y., STIGTER, J., DE BOER, W., VAN WIEREN, S., DE JONG, C., DE KNEGT, H., GRANT, C., HEITKÖNIG, I., KNOX, N. & KOHI, E. 2012. Diet selection of African elephant over time shows changing optimization currency. *Oikos,* 121**,** 2110-2120.

PRINS, H. 1987. Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai Ecosystem of northern Tanzania. *Biological Conservation,* 40**,** 141-161.

PRINS, H. 1996. *Ecology and behaviour of the African buffalo: social inequality and decision making*, Springer Science & Business Media.

PRINS, H. & LOTH, P. 1988. Rainfall patterns as background to plant phenology in northern Tanzania. *Journal of Biogeography***,** 451-463.

PRINS, H. H., JEUGD, H. P. & BEEKMAN, J. H. 1994. Elephant decline in Lake Manyara National Park, Tanzania. *African Journal of Ecology,* 32**,** 185-191.

PRINS, H. H. & VAN DER JEUGD, H. P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology***,** 305-314.

PRINS, H. H. & VAN LANGEVELDE, F. 2008. *Resource ecology: spatial and temporal dynamics of foraging*, Springer Science & Business Media.

RASMUSSEN, H. B., WITTEMYER, G. & DOUGLAS-HAMILTON, I. 2006. Predicting time-specific changes in demographic processes using remote-sensing data. *Journal of Applied Ecology,* 43**,** 366-376.

REDFERN, J., GRANT, C., GAYLARD, A. & GETZ, W. 2005. Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments,* 63**,** 406-424.

REICE, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia,* 67**,** 90-97.

REICE, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist,* 82**,** 424-435.

RODGERS, A. & KIE, J. 2010. HRT: Home Range Tools for ArcGIS®, version 1.1, 24.4. 2011.

ROOT, R. B. & KAREIVA, P. M. 1984. The search for resources by cabbage butterflies (Pieris rapae): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology***,** 147-165.

ROSENZWEIG, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist*, 67-74.

ROSHIER, D. A., DOERR, V. A. & DOERR, E. D. 2008. Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia,* 156**,** 465-477.

ROYALL, R. 1997. *Statistical evidence: a likelihood paradigm,* London, United Kingdom, Chapman & Hall.

SÆTHER, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution,* 12**,** 143-149.

SALE, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist*, 337-359.

SCHICK, R. S., LOARIE, S. R., COLCHERO, F., BEST, B. D., BOUSTANY, A., CONDE, D. A., HALPIN, P. N., JOPPA, L. N., MCCLELLAN, C. M. & CLARK, J. S. 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology letters,* 11**,** 1338-1350.

SCHOLES, R. & MENNELL, K. 2008. *Elephant management: a scientific assessment of South Africa*, Wits University Press.

SHANNON, G., PAGE, B. R., DUFFY, K. J. & SLOTOW, R. 2006. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia,* 150**,** 344-354.

SHRADER, A. M., BELL, C., BERTOLLI, L. & WARD, D. 2012. Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica,* 42**,** 3-10.

SHRADER, A. M., PIMM, S. L. & VAN AARDE, R. J. 2010. Elephant survival, rainfall and the confounding effects of water provision and fences. *Biodiversity and Conservation,* 19**,** 2235-2245.

SIBLY, R. M. & HONE, J. 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 357**,** 1153-1170.

SINCLAIR, A. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *Frontiers of population ecology*, 127-154.

SINCLAIR, A. & KREBS, C. J. 2002. Complex numerical responses to top–down and bottom–up processes in vertebrate populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 357**,** 1221-1231.

SINCLAIR, A. R. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. *Philos Trans R Soc Lond B Biol Sci,* 358**,** 1729-40.

SITATI, N. W., WALPOLE, M. J., SMITH, R. J. & LEADER-WILLIAMS, N. 2003. Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology,* 40**,** 667-677.

SKARPE, C., AARRESTAD, P. A., ANDREASSEN, H. P., DHILLION, S. S., DIMAKATSO, T., DU TOIT, J. T., HALLEY, D., J, HYTTEBORN, H., MAKHABU, S. & MARI, M. 2004. The return of the giants: ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment,* 33**,** 276-282.

SKARPE, C., DU TOIT, J. & MOE, S. R. 2014. *Elephants and savanna woodland ecosystems: a study from Chobe National Park, Botswana,* West Sussex, UK, John Wiley & Sons.

SKIDMORE, A. K., FERWERDA, J. G., MUTANGA, O., VAN WIEREN, S. E., PEEL, M., GRANT, R. C., PRINS, H. H., BALCIK, F. B. & VENUS, V. 2010. Forage quality of savannas—Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote sensing of environment,* 114**,** 64-72.

SMIT, G. 1996. *BECVOL: Biomass Estimates from Canopy VOLume (version 2): Users Guide*, University of the Free State.

SMIT, I. & GRANT, C. 2009. Managing surface-water in a large semi-arid savanna park: Effects on grazer distribution patterns. *Journal for Nature Conservation,* 17**,** 61-71.

SMIT, I. P. & FERREIRA, S. M. 2010. Management intervention affects river-bound spatial dynamics of elephants. *Biological Conservation,* 143**,** 2172-2181.

SMIT, I. P., GRANT, C. C. & DEVEREUX, B. J. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation,* 136**,** 85-99.

SMIT, N. 2014. BECVOL 3: an expansion of the aboveground biomass quantification model for trees and shrubs to include the wood component. *African Journal of Range & Forage Science,* 31**,** 179-186.

STAUB, C. G., BINFORD, M. W. & STEVENS, F. R. 2013. Elephant herbivory in Majete Wildlife Reserve, Malawi. *African Journal of Ecology,* 51**,** 536-543.

STEPHENS, D. W. 2007. Models of information use. *Foraging: Behavior and ecology*, 31-58.

STOKKE, S. & DU TOIT, J. T. 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology,* 40**,** 360-371.

SULLIVAN, S. & ROHDE, R. 2002. On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography,* 29**,** 1595-1618.

SWITZER, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology,* 7**,** 533-555.

TEAM, R. D. C. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, URL: http://www. R-project. org.

THUILLER, W., BROENNIMANN, O., HUGHES, G., ALKEMADE, J. R. M., MIDGLEY, G. F. & CORSI, F. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology,* 12**,** 424-440.

TRIMBLE, M., FERREIRA, S. & VAN AARDE, R. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology,* 279**,** 18-26.

TULJAPURKAR, S. & CASWELL, H. 2012. *Structured-population models in marine, terrestrial, and freshwater systems*, Springer Science & Business Media.

TURCHIN, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology,* 72**,** 1253-1266.

TURCHIN, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*, Sinauer Associates Sunderland.

TURCHIN, P. 1999. Population regulation: a synthetic view. *Oikos*, 153-159.

TYRRELL, J. & COE, M. 1974. The rainfall regime of Tsavo National Park, Kenya and its potential phenological significance. *Journal of Biogeography*, 187-192.

VALEIX, M., LOVERIDGE, A. J., DAVIDSON, Z., MADZIKANDA, H., FRITZ, H. & MACDONALD, D. W. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology,* 25**,** 337-351.

VAN AARDE, R., FERREIRA, S., JACKSON, T., PAGE, B., DE BEER, Y., GOUGH, K., GULDEMOND, R., JUNKER, J., OLIVIER, P. & OTT, T. 2008. Elephant Management-A scientific assessment for South Africa. Wits University Press Johannesburg, South Africa.

VAN AARDE, R., JACKSON, T. & FERREIRA, S. 2006. Conservation science and elephant management in southern Africa. *South African journal of science,* 102**,** 385.

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

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

VAN LANGEVELDE, F., VAN DE VIJVER, C. A., KUMAR, L., VAN DE KOPPEL, J., DE RIDDER, N., VAN ANDEL, J., SKIDMORE, A. K., HEARNE, J. W., STROOSNIJDER, L. & BOND, W. J. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology,* 84**,** 337-350.

VERLINDEN, A. & GAVORV, I. K. N. 1998. Satellite tracking of elephants in northern Botswana. *African Journal of Ecology,* 36**,** 105-116.

VETTER, S. 2005. Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments,* 62**,** 321-341.

VILJOEN, P. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology,* 27**,** 227-240.

VISWANATHAN, G. M., AFANASYEV, V., BULDYREV, S., MURPHY, E., PRINCE, P. & STANLEY, H. E. 1996. Lévy flight search patterns of wandering albatrosses. *Nature,* 381**,** 413-415.

VON WEHRDEN, H., HANSPACH, J., KACZENSKY, P., FISCHER, J. & WESCHE, K. 2012. Global assessment of the non-equilibrium concept in rangelands. *Ecological Applications,* 22**,** 393-399.

WALKER, B. 1989. Diversity and stability in ecosystem conservation. *In:* WESTERN, D. & PEARL, M. (eds.) *Conservation for the 21st Century.* Oxford: Oxford University Press.

WALKER, B. H., EMSLIE, R., OWEN-SMITH, R. & SCHOLES, R. 1987. To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology*, 381-401.

WALKER, B. H. & NOY-MEIR, I. 1982. Aspects of the stability and resilience of savanna ecosystems. *Ecology of tropical savannas.* Springer.

WALTERS, C. J. 1987. Nonstationarity of production relationships in exploited populations. *Canadian Journal of Fisheries and Aquatic Sciences,* 44**,** s156-s165.

WATO, Y. A., HEITKÖNIG, I. M. A., WIEREN, S. E. V., WAHUNGU, G., PRINS, H. H. T. & LANGEVELDE, F. V. 2016. Prolonged drought results in starvation of African elephant (*Loxodonta africana*). *Biological Conservation***,** Accepted.

WESTERN, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology,* 13**,** 265-286.

WHITE, K. S., PENDLETON, G. W., CROWLEY, D., GRIESE, H. J., HUNDERTMARK, K. J., MCDONOUGH, T., NICHOLS, L., ROBUS, M., SMITH, C. A. & SCHOEN, J. W. 2011. Mountain goat survival in coastal Alaska: effects of age, sex, and climate. *The Journal of Wildlife Management,* 75**,** 1731-1744.

WHITE, T. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia,* 33**,** 71-86.

WHYTE, I., VAN AARDE, R. & PIMM, S. L. 1998. Managing the elephants of Kruger national park. *Animal Conservation,* 1**,** 77-83.

WHYTE, I. J., VAN AARDE, R. J. & PIMM, S. L. 2003. Kruger's elephant population: its size and consequences for ecosystem heterogeneity. *In:* TOIT, J. T. D. & ROGERS, K. H. (eds.) *The Kruger experience: ecology and management of savanna heterogeneity. Island, Washington, DC.* Washington: Island Press.

WIKELSKI, M., TARLOW, E. M., RAIM, A., DIEHL, R. H., LARKIN, R. P. & VISSER, G. H. 2003. Avian metabolism: costs of migration in free-flying songbirds. *Nature,* 423**,** 704-704.

WISEMAN, R., PAGE, B. R. & O'CONNOR, T. G. 2004. Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research,* 34**,** 25-37.

WITTEMYER, G. 2011. Effects of economic downturns on mortality of wild African elephants. *Conservation Biology,* 25**,** 1002-1009.

WITTEMYER, G., DABALLEN, D., RASMUSSEN, H., KAHINDI, O. & DOUGLAS-HAMILTON, I. 2005. Demographic status of elephants in the Samburu and Buffalo Springs national reserves, Kenya. *African Journal of Ecology,* 43**,** 44-47.

WITTEMYER, G., GETZ, W., VOLLRATH, F. & DOUGLAS-HAMILTON, I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology,* 61**,** 1919-1931.

WITTEMYER, G., NORTHRUP, J. M., BLANC, J., DOUGLAS-HAMILTON, I., OMONDI, P. & BURNHAM, K. P. 2014. Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences,* 111**,** 13117-13121.

WONG, W. & LEE, J. 2005. *Statistical analysis of geographic information with ArcView GIS and ArcGIS*, John Wiley and Sons.

WOOLLEY, L. A., MILLSPAUGH, J. J., WOODS, R. J., RENSBURG, S. J., PAGE, B. R. & SLOTOW, R. 2009. Intraspecific strategic responses of African elephants to temporal variation in forage quality. *The Journal of Wildlife Management,* 73**,** 827-835.

YANG, W., SEAGER, R., CANE, M. A. & LYON, B. 2014. The East African long rains in observations and models. *Journal of Climate,* 27**,** 7185-7202.

YOUNG, E. 1970. *Water as a factor in the ecology of game in the Kruger National Park.* Ph.D. thesis University of Pretoria.

YOUNG, K., FERREIRA, S. & VAN AARDE, R. 2009. Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology,* 278**,** 189-205.

YOUNG, K. & VAN AARDE, R. 2010. Density as an explanatory variable of movements and calf survival in savanna elephants across southern Africa. *Journal of Animal Ecology,* 79**,** 662-673.

ZUUR, A. F., IENO, E. N. & ELPHICK, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* 1**,** 3-14.

Summary

Elephant population studies have become important especially because of the long standing perception that high elephant densities have negative impact on vegetation and other wildlife species. Thus, in areas of high elephant density, managers attempt to re-distribute them or keep their numbers low through provision of water, translocation or culling. These approaches are thought to keep the population within the limits that can be sustained by the ecosystem, termed "the ecological carrying capacity", a management option hinged on equilibrium theory. Equilibrium systems are considered stable, with resources and the animals that depend on them being at balance with each other. This stability is rarely the case in tropical savannas where the rule appears to be "a flux of nature" rather than "a balance of nature".

Tropical savannas, where over half of the African elephant live, are prone to constant environmental fluctuations, especially prolonged droughts, and hence there is a growing understanding that populations of wildlife species and their communities are rarely at equilibrium. Therefore, it is critical to understand how the constant environmental flux in this system affects wildlife populations and the implication for their management. In this thesis, the central focus is to investigate the role of drought occurrences on elephant population dynamics in tropical savannas. To address this question, it is important to have a good understanding of the historical changes of elephant population in relation to drought events and the ecology of elephant in semi-arid savannas - their distribution and density, their movements and behaviour. For the historical data, I analysed the best existing long-term data in Africa of wild elephant population that has been consistently monitored for over 40 years where life histories of over 3000 wild individual elephant are known, at Amboseli National Park in Kenya. In addition, I also analysed geo-referenced elephant mortality data collected daily for 10 years from Tsavo Conservation Area. Further, I analysed 2 years data from 8 GPS collared African elephant to investigate their movement response to seasonal water and forage distribution in Tsavo Ecosystem.

First, I investigated the temporal effects of drought duration (number of consecutive dry months) and intensity (amount of rainfall) on elephant population structure in Amboseli National Park, Kenya. The result corroborates findings from past studies that calves (<2years) are more susceptible to drought caused mortality and the risk of dying decreased with age. A new finding in this study reveals that the effect of drought induced mortality for the adult elephant is sex and age dependent, with males older than 25 years being less likely to die as compared to females of the same age. This new result is because of the resolution of analysis in this study which focused on the length and severity of drought as opposed to past studies that restricted their analysis to seasonal and inter-annual differences in rainfall pattern. As they grow older and sexually mature, the foraging range of male elephant increase and they begin to take more risks and disperse to unfamiliar habitats to seek for quality forage and mates. Generally, foraging strategies between sexes in many species are more pronounced during periods of food scarcity, and the driving force in the differences appears to be driven by energy need requirements, reproductive status of an individual, body sizes and the social context, all of which differ between sexes.

In the next study, I investigated the spatial pattern of elephant mortality in relation to drought occurrences in Tsavo National Park using MaxEnt. The results shows that elephant carcasses were aggregated and elephant mortality was negatively correlated with four months cumulative precipitation prior to death, forage availability and distance to water, while local elephant density showed a positive correlation. This finding rules out dehydration as the cause of elephant mortality in Tsavo as the river where the carcasses were aggregated is perennial. Furthermore, forage availability was low close to water sources and did not show a significant difference close to or further away from the river despite high elephant density around the river. Hence, these elephant mortalities may have occurred as a result of starvation.

I went further to focus on two main limiting resources for elephants, namely forage and water, and their effect on elephant-habitat utilization in semi-arid savannas. I first investigated how water source distribution affect elephants' seasonal movement patterns. Results indicate that male elephant moved maximally 20 km away from the nearest water source in the dry season while the female elephant foraged to a maximum of about 10 km and only moved further than this distances in the wet season. The strong directionality of elephant movement from a distance of 15km towards water sources (rho > 0.5) as they re-visited their watering source in the dry season suggest that elephant have information on location of the water sources.

Next, I investigated the factors that determine selection of a foraging site for elephant with a focus on forage nutrients or biomass. Because of their large body size, it is thought that elephant can survive on a less nutritious but high biomass of forage. The results from this study shows that elephant selected foraging site based on forage biomass in dry seasons, whereas they selected areas with higher nutrients in the wet season. Moreover, females selected sites with a higher forage biomass as compared to males. This result may be explained by the difference in social organisation and foraging strategies between the sexes. In the previous studies on human-elephant conflict, for instance, male elephant raided crops more than the mixed herd, perhaps to seek for high quality forage.

Together, the four studies in this thesis strongly suggest that elephant starve to death in prolonged drought contrary to the past studies that reported that adult elephant are less affected by drought. Even though prolonged droughts usually result in higher elephant mortalities, the resilience of semi-arid savannas may perhaps be as a result of these deaths that release the system from high browsing pressure and give it a window to regenerate. If that is the case, then drought induced elephant mortality may be a better way to regulate elephant numbers than culling. This finding strongly suggests that semi-arid savannas may in fact be a non-equilibrium system sustained by growth and crashes of herbivore populations. Maintaining the system as natural as possible may therefore keep elephant populations in savannas sustained for posterity. The modern day park managers have daunting challenges such as mass elephant deaths in drought, increased human-wildlife conflicts or changes in wildlife use of the landscape which may all be symptoms of wrong management interventions taken in the past or negative impacts of anthropogenic activities that have tipped the natural functioning of a non-equilibrium system. Therefore, park managers should undergo regular trainings on new conservation techniques and they should apply evidence-based science to make informed long term decision.

Muhtasari

Tafiti za idadi na wingi wa tembo zimekuwa za msingi sana hasa kwa sababu kumekuwa na mtizamo wa muda mrefu kwamba wingi wa tembo kwa eneo una matokeo hasi kwenye uoto wa asili na aina nyingine za wanyama. Hivyo wahifadhi wengi hujaribu kuwatawanya tembo au kupunguza idadi yao kwa kuwahamisha, kuuwa baadhi ya makundi au kuweka maji maeneo mengine.

Mbinu hizi zinatazamiwa kuthibiti ongezeko la idadi ya tembo ukilinganisha na uwezo wa eneo la kuwahifadhi kiikolojia. Huu ni usimamizi unaolenga sheria ya usawa au usawazo. Mbinu hii ya usawazo ndio inakisiwa kuwa nafuu na yenye msimamo mzuri kwa rasilimali na wanyama wanayoitegemea katika hali ya usawa. Lakini usawa huu hauonekana maeneo ya tropika savanna ambapo muono wa sheria ni ule wa badiliko la asili na sio usawazo wa asili.

Uwanda wa tropika savana ambao una zaidi ya nusu ya idadi ya tembo waliopo barani Afrika, unakabiliwa na mabadiliko ya tabia nchi, haswa ya muda mrefu wa ukame. Hivyo basi ni muhimu kuelewa ni vipi mabadiliko haya ya asili yanaathiri idadi ya wanyama pori na athari zake juu ya usimamizi wa wanyama. Lengo langu kuu ni kutafiti ni vipi ukame unaathiri idadi ya tembo katika uwanda wa tropika barani Africa. Ili kuweza kushughulikia hili swala, ni muhimu kuwa na ufahamu wa mabadiliko ya kihistoria ya idadi ya tembo, uhusiano wake na ukame na pia ikolojia ya tembo katika sehemu kame za savanna – wingi na mtawanyiko wake, na mwenendo wao. Nilichambua madhara ya ukame kwa tembo nikitumia takwimu za zamani za tembo waliofanyiwa utafiti kwa takriban zaidi ya miaka arobaini ambapo historia ya zaidi ya tembo elfu tatu zajulikana katika mbuga ya Amboseli nchini Kenya. Vilevile, nilifanya uchambuzi wa mizoga ya tembo zilizokuwa zinajulikana kijiografia (geo-referenced) na takwimu za hiyo mizoga zilikusanywa kila siku kwa muda wa miaka kumi kwa mbuga ya Tsavo. Halikadhalika, nilifanya uchambuzi zaidi wa takwimu za tembo

kupitia kifaa cha GPS kwa takribani miaka mbili ili kuweza kutafiti harakati ya tembo kutokana na maji ya misimu na liishe katika mbuga ya Tsavo.

Kwanza nilifanya uchambuzi ya uhusiano wa muda (miezi iliyofuatana ya ukame) na kiwango ya mvua kwa idadi ya tembo nikitumia takwimu zilizokusanywa kwa zaidi ya miaka arobaini ya ndovu kutoka mbuga ya Amboseli. Matokeo yanalingana na utafiti uliofanywa tangu awali kwamba watoto wa tembo chini ya miaka miwili ndio wanaoathiriwa zaidi na ukame na wengi wao wanakufa. Vifo vya watoto wa tembo vinapungua pindi wanapozidi kukuwa. Utafiti mpya unaonyesha kwamba chanzo cha vifo vya tembo aliyepevuka kutokana na ukame unategemea jinsia na umri wa ndovu. Tembo jike wanaathriwa zaidi na vifo vinavyosababishwa na ukame wakilinganishwa na tembo dume wa umri sawa. Matokeo haya mapya umetokana na mbinu yetu ya utafiti uliyolenga urefu na ukali wa ukame kinyume na matokeo ya hapo awali ambayo imeweka vikwazo uchambuzi wake kwa mvua ya misimu na ile ya baina ya miaka. Pindi ndovu wanapokuwa kiumri na kubaleghe, jinsia ya kiume hutawanyika katika makazi mapya ili kupata liishe bora na pia wenzi. Kwa jumla, mikakati ya kuchagua eneo la liishe baina ya jinsia ya wanyama pori hujitokeza zaidi wakati wa upungufu wa chakula, na tofauti hizi hutokana na mahitaji ya nguvu, hadhi ya uzazi, ukubwa wa mwili na mazingira ya kijamii.

Katika utafiti wangu mwingine, nilifanya uchambuzi wa madhara ya ukame kwa tembo katika mbuga ya Tsavo kwa kutumia hisabati aina ya MaxEnt. Matokeo yameonyesha kuwa idadi kubwa ya mizoga ya tembo ilikusanyika kwenye maeneo yenywe madimbwi vya maji. Vilevile, kuna uhusiano wa vifo vya ndovu na upungufu wa mvua hasa katika miezi minne kabla ya vifo vyao, kuwepo kwa liishe bora na umbali wa dimbwi la maji. Vifo vya tembo vilikuwa vingi kwa eneo lililokuwa na idadi kubwa ya tembo. Matokeo yanaonyesha thahiri ya kwamba ukosefu wa maji sio sababu kuu ya vifo vya tembo katika mbuga ya Tsavo kwa kuwa mizoga mingi ilipatikana karibu na sehemu ambapo ina mito ya kudumu. Ama chakula kilichopo karibu na madimbwi ya maji ya kudumu hakikuonyesha tofauti kuu na chakula kilicho mbali na madimbwi. Hivyo basi, kuna uwezekano kwamba vifo vya tembo vilisababishwa na njaa.

Niliangazia kwa undani, rasilimali mbili muhimu zinazoathiri mnyama tembo katika sehemu kame za uwanda wa savanna, nazo ni chakula na maji. Kwanza nilifanya utafiti jinsi chimbuko la maji na mgawanyiko wake unavyoathiri harakati ya mnyama tembo. Matokeo yaliashiria kwamba tembo wa jinsia ya kiume hawaendi zaidi ya umbali wa kilometa ishirini kutoka kwa dimbwi la maji lililoko karibu yao kutafuta chakula wakati wa ukame ilhali wenzao wa jinsia ya kike walifuata chakula kwa umbali wa kilometa kumi pekee wakati wa msimu wa ukame. Mwelekezo dhabiti wa harakati ya mnyama ndovu kutoka umbali wa kilomita kumi na tano kutoka kwenye dimdwi la maji (rho >0.5) na wanavyozuru sehemu zilizo na madimbwi wakati wa ukame ni ishara mwafaka kwamba mnyama ndovu anazo hisia kuhusu ni wapi maji yanapopatikana.

Aidha, nilifanya upelelezi sababu zinazoelekeza uchaguzi wa sehemu za chakula kwa tembo nikilenga virutubisho vya lishe na majani. Imedhaniwa ya kwamba mnyama tembo anaweza kuishi na lishe pungufu mradi apate majani yawe mengi. Utafiti huu unaonyesha kwamba mnyama tembo huchagua sehemu za majani mengi wakati wa misimu kame ilhali wanachagua sehemu zilizo na wingi wa madini lishe za majani wakati wa misimu ya mvua. Halikadhalika, kuna tofauti ya tembo wa kike na wa kiume kwa taratibu wanavyotumia kuchagua sehemu za liishe. Tembo wa kike huchagua sehemu za majani mengi na wale wa kiume huchagua sehemu zenye madini bora. Utafiti wa hapo awali unaolenga mizozano baina ya tembo na binadamu, inaonyesha kwamba tembo wa jinsia ya kiume walionekana wanavamia mimea zaidi, ili waweze kupata lishe bora.

Kwa pamoja, tafiti hizi nne zinaashiria kwamba mnyama tembo hufa njaa nyakati za kiangazi tofauti na tafiti za awali zinazoarifu kwamba tembo zilizo balehe haziathiriwi na ukame. Ingawa ukame wa muda mrefu huathiri sana, tembo na hata kusababisha vifo, usajiri wa savanna kame unatokana na vifo hivi ambavyo hukomboa mfumo shinikizo na kuipa fursa mpya ya kuzalisha. Utafiti huu unaashiria kwamba mfumo ya vifo vya tembo wakati wa ukame umewezesha savanna kuthabiti tembo kwa miaka mingi. Wasimamizi wa wanyama pori wa savanna wako na changamoto chungu nzima kubadili mbinu ya kulinda na kuhifadhi mnyama tembo kulingana na matokeo ya utafiti huu mpya ili kufanya uamuzi wa kudumu.

Samenvatting

Onderzoek naar olifantenpopulaties is steeds belangrijker geworden, vooral vanwege de langdurige perceptie dat een hoge olifantendichtheid een negatieve invloed heeft op de vegetatie en andere wilde diersoorten. In gebieden waar veel olifanten voorkomen proberen beheerders ze daarom te herverdelen of hun aantallen laag te houden door middel van overplaatsing, jacht, of het voorzien in drinkwaterplaatsen. Deze aanpak zou olifantenpopulaties binnen de grenzen moeten houden van wat het ecosysteem aankan, de zogenaamde “ecologische draagkracht”, een beheermethode die stoelt op de evenwichtstheorie. Volgens deze theorie is een systeem in evenwicht stabiel, omdat de bestaansmiddelen en de dieren die hiervan afhankelijk zijn in balans zijn met elkaar. Zulke stabiliteit is echter zeldzaam in tropische savannes, waar continue verandering eerder regel is, en natuurlijk evenwicht een uitzondering.

Tropische savannes herbergen meer dan de helft van alle Afrikaanse olifanten, maar zijn gevoelig voor continue ecologische schommelingen, vooral langdurige droogte. Er is een toenemend bewustzijn dat populaties wilde dieren en hun gemeenschappen zelden in evenwicht zijn, en het is daarom essentieel om te begrijpen hoe de constante ecologische veranderingen in savanne ecosystemen van invloed zijn op populaties wilde dieren en wat de implicaties zijn voor wildbeheer. In dit proefschrift staat de rol van droogte in de populatiedynamica van olifanten in tropische savannes centraal. Om deze rol te begrijpen, is een goed inzicht vereist in de historische veranderingen in olifantenpopulaties in relatie tot droogte, maar ook kennis van de ecologie van olifanten in halfdroge savannes, zoals hun distributie, dichtheid, migratiepatronen, en gedrag. Voor de historische data heb ik de beste langdurige dataset van wilde olifantenpopulaties in Afrika gebruikt. Deze dataset omvat de levensgeschiedenis van meer dan 3000 individuele wilde olifanten uit Amboseli National Park, Kenia, die over een periode van ruim 40 jaar consequent gevolgd zijn. Ook heb ik gegevens geanalyseerd over de vindplaatsen van olifantenkarkassen die de afgelopen 10 jaar dagelijks zijn gedocumenteerd in het Tsavo Conservation Area.

Daarnaast heb ik data geanalyseerd van 8 olifanten uit Tsavo die, uitgerust met een GPS zender, 2 jaar lang gevolgd zijn om te begrijpen hoe hun migratiepatronen afhangen van de seizoensgebonden distributie van water en voedsel.

In het eerste hoofdstuk onderzocht ik de temporele effecten van droogte (het aantal opeenvolgende droge maanden) en de intensiteit van droogte (hoeveelheid neerslag) op de structuur van olifantenpopulaties in Amboseli National Park, Kenia. De resultaten bevestigen die van eerdere studies: kalveren (<2 jaar oud) zijn vatbaarder voor sterfte veroorzaakt door droogte en dit risico wordt kleiner naarmate de dieren ouder zijn. Een nieuwe bevinding uit mijn studie is dat sterfte door droogte bij volwassen olifanten afhankelijk is van geslacht en leeftijd, waarbij mannetjes van meer dan 25 jaar oud een minder grote kans hebben om te overlijden aan de gevolgen van droogte dan vrouwtjes van dezelfde leeftijd. Deze resultaten konden worden gevonden dankzij de hoge resolutie van mijn analyse, waarbij ik me concentreerde op zowel de lengte als intensiteit van droogte, in tegenstelling tot eerdere studies die hun analyse beperkten tot seizoensgebonden en jaarlijkse schommelingen in neerslag. Wanneer mannelijke olifanten ouder worden en geslachtsrijp, wordt hun foerageergebied groter en nemen ze meer risico's door te verspreiden naar onbekende leefgebieden om te zoeken naar kwaliteitsvoer en partners. In het algemeen geldt voor veel diersoorten dat de verschillen in foerageerstrategieën tussen mannelijke en vrouwelijke dieren sterker zijn tijdens periodes van voedselschaarste. Deze verschillen lijken te worden gedreven door de energiebehoefte, voortplantingsstatus, lichaamsgrootte en sociale context, welke verschillen tussen geslachten.

In de tweede studie heb ik MaxEnt gebruikt om de relatie tussen droogte en de ruimtelijke patronen van olifantensterfte in Tsavo National Park te onderzoeken. De resultaten tonen aan dat olifantenkarkassen geaggregeerd waren en dat mortaliteit negatief gecorreleerd was met vier maanden cumulatieve neerslag voorafgaand aan sterfte, voedselbeschikbaarheid en afstand tot water, in tegenstelling tot lokale olifantendichtheid, welke een positieve relatie had met deze variabelen. Deze bevindingen sluit uitdroging uit als de voornaamste oorzaak van olifantensterfte in Tsavo omdat de rivier waar de karkassen geaggregeerd waren het hele jaar door water heeft. Bovendien was voedselbeschikbaarheid laag zowel dichtbij waterbronnen als verder weg, ondanks hoge olifantendichtheden rondom rivieren. Dit suggereert dat de geanalyseerde olifantensterfte het gevolg was van uithongering.

Vervolgens spitste ik me toe op twee belangrijke maar limiterende hulpbronnen van olifanten, namelijk voedsel en water, en hun effect op het habitatgebruik van olifanten in halfdroge savannes. Eerst heb ik onderzocht hoe de distributie van waterbronnen de seizoensgebonden migratiepatronen van olifanten beïnvloedt. De resultaten laten zien dat mannelijke olifanten zich maximaal 20 km verwijderden van waterbronnen tijdens het droge seizoen, terwijl vrouwelijke olifanten maximaal 10 km van de dichtstbijzijnde waterbron foerageerden en deze afstand alleen vergrootten tijdens het natte seizoen. De sterke gerichtheid waarmee olifanten zich binnen 15 km naar een waterbron begaven (rho > 0.5) tijdens het droge seizoen suggereert dat olifanten informatie hebben over de exacte locatie van deze waterbronnen.

Vervolgens heb ik onderzoek gedaan naar de factoren die de keuze voor een foerageergebied bepalen, met een focus op nutriënten en biomassa. Men denkt dat olifanten vanwege hun grootte, en daarmee hun grote voeropnamecapaciteit, in staat zijn op een minder nutriëntenrijk dieet te leven. De resultaten van deze studie laten zien dat olifanten in het droge seizoen foerageergebieden selecteerden die een hoge biomassa hebben, terwijl ze in het natte seizoen foerageergebieden selecteerden die een hoge nutritionele waarde hebben. Bovendien selecteerden vrouwelijke olifanten gebieden met een hogere biomassa dan mannelijke olifanten, waarschijnlijk vanwege verschillen in sociale organisatie en foerageerstrategieën. Uit studies naar conflicten tussen olifanten en mensen bleek bijvoorbeeld dat het vooral de mannelijke olifanten waren die gewassen beschadigden, wellicht op zoek naar voedsel met een hoge nutritionele waarde.

Bij elkaar laten de vier studies uit dit proefschrift zien dat olifanten sterven van uithongering tijdens droogte, in tegenstelling tot eerdere studies die suggereerden dat volwassen olifanten minder gevoelig zijn voor droogte. Hoewel langdurige droogte normaliter in hoge olifantensterfte resulteert, is de veerkracht van halfdroge savannes wellicht te danken aan deze sterfte doordat het systeem hierdoor minder belast wordt door overbegrazing en kans krijgt om te regenereren. Als dat het geval is, dan zou olifantensterfte door droogte een betere beheermethode zijn dan jacht. De bevindingen uit deze studie zijn een sterke aanwijzing dat halfdroge savannes een systeem vormen dat niet in evenwicht is en wordt gekarakteriseerd door snelle groei en dramatische afnames van populaties herbivoren. Het zo natuurlijk mogelijk houden van halfdroge savannes kan daarom bijdragen aan het behouden van olifantenpopulaties voor toekomstige generaties. Huidige beheerders worden geconfronteerd met enorme uitdagingen, zoals massale olifantensterfte tijdens droogte, toegenomen conflicten tussen mensen en wilde dieren, en veranderingen in de manier waarop wilde dieren hun natuurlijke leefgebied gebruiken. Dit kunnen symptomen zijn van verkeerd beheer uit het verleden of negatieve gevolgen van menselijke activiteiten die de natuurlijke werking van een niet-evenwichtssysteem hebben doen kantelen. Beheerders zouden daarom regelmatige trainingen moeten volgen over nieuwe natuurbeschermingsmaatregelen en gebruik moeten maken van empirisch onderbouwde studies om gefundeerde lange termijn beslissingen te nemen.

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Acknowledgements

The production of this thesis has been made possible by a scholarship from the Government of The Netherlands (NUFFIC), generously supplemented by a grant from the International Funds for Animal Welfare (IFAW) and the Kenya Wildlife Services (KWS). I want to particularly single out Mr. Julius Kipngetich, the former director of KWS, and Mr. Julius Kimani, who was then the Assistant Director of Tsavo Conservation Area, for not only granting me study leave but also for encouraging me and extending to me their total support throughout my PhD journey. I also sincerely thank the two KWS directors Mr. William Kiprono (former director KWS), and Mr. Kitili Mbathi (the current director KWS) for allowing me to continue with this study to completion.

At the beginning of my study, my initial concepts and proposal benefitted greatly from the input of Prof. Dr Herbert Prins and Sip Wieren, both of whom were also instrumental in encouraging me to join Wageningen University when we first met in Tsavo on their trip to supervise another Wageningen PhD student, Ben Okita. Our stimulating discussion on the long standing yet unresolved "*Tsavo Elephant Problem*" became my starting point for developing a concept. This idea eventually drifted and underwent many phases of metamorphosis as other interesting thoughts came along the way in my four years academic journey that culminated to this thesis. Thank you Herbert and Sip for believing in me and guiding me throughout my study. My gratitude goes to Ignas Heitkönig and Frank Langevelde who accepted to join my supervision team later in my study, and Geoffrey Wahungu, my local supervisor in Kenya. Ignas and Frank engaged me meticulously and continuously and ensured that I stayed on course as per the schedule we mutually agreed. They critically reviewed my work and gave me feedback on time every time. They were available for me anytime I needed to consult with them and maintained an open door policy. I owe the completion of this thesis to you! Other staff from Resource Ecology Group were always willing to review my work whenever I called upon them and in our weekly PhD lab meetings, their comments enriched and improved my thesis a great deal; to Fred, Pim, Patrick, Milena, Kevin, Ron, Herman, Henjo - I thank you all. Hassan Wario and Dr. Edward Kohi assisted me in translating the summary of this thesis to Swahili and Helen Esser and Jente did the Dutch translation in record time – You all deserve my sincere appreciation. Claudius Vijver and Lennart Suselbeek are my two heroes who not only mentored me but made me believe that graduating with PhD while still maintaining sanity is possible. They taught me all the tricks under the sun to smoothly wade through the challenges that come with PhD study in the many PE&RC meetings they organised!

My gratitude goes to Ben Okita and Shadrack Ngene for introducing me to Wageningen University and for being always available for consultation as I was writing this thesis. The Amboseli Elephant trust team led by Cynthia Moss and Phyllis Lee generously shared their long time series elephant data spanning for over 40 years and proof read some of my manuscripts. My sincere gratitude goes to you and your field team Vicky, Katitu and Norah for introducing me to the techniques of aging and sexing elephant in the field with precision. Thanks to Steve Njumbi, Dr Ngene and Dr Edward Kohi for guiding me with research design, data analysis and proof reading my manuscripts and the Rukinga research team led by Dr. Mwangi for valuable comments on my research design.

Patricia was always handy in organising my travel back to the Netherlands and provided me with all the assistance I needed and ensured I'm comfortable during my frequent visits to Resource Ecology Group – from providing office space to stationary and answering to any query I had on university procedures. Gerda sorted my finances in record time. My travels, insurance and registration processes were seamlessly handled by Marion. To all of you, I say thank you.

I cherish the stimulating discussions we had with all my colleagues and friends in Resource Ecology Group both formally in organised seminars and informally outside work-time. You were always available for consultations and you introduced me to R statistical software for the first time (particularly Joost and Tim), which I was later able to use when I was writing this thesis. My gratitude goes to all the REG colleagues - Jente, Yin, Audrey (My officemates), Hellen, Tim, Joost, Martyn, Mikhail, Iris, Sintayehu (We had great time exploring R together and "dredging"), Yingying, Gin and Mina.

I sincerely thank the Kenyan community in Wageningen University who made me feel at home away from home; Martin, Kariuki, Faith, Agogo, Mench, Dan Wakiri, Dan Machari, Moses Sila, Hellen, Collins Mweresa, Tabitha Hilam, Tabitha Mugo, Omare, Winnie, Jackie, Cyrus, Mungai, Irene, Ruth, Betsheba, Sophie, Rita, Juma, Olwith, Eunice, Jasper, Chepkwony. The many meet-and-greet sessions, barbeques, swimming, running and exploring the Netherlands together made my stay in Wageningen a lot more fun.

Special thanks are due to my field work crew who worked tirelessly with me for two years during data collection: Isack, the "senior driver" who was able to navigate the Tsavo jungle that appeared impossible to conquer; driving on rocks, in valleys, craters and thick bushes, with minimum mechanical problems was not easy but you did it; Alex, the research team leader whose motivation and energy was constantly high and his knowledge of plants and animals in Tsavo ecosystem was exemplary. His characteristic laughter, jokes and random song kept the team solid and focused. Other field research team like Kyalo, Ranger Komora, Venic, Mwaniki, Juma and all the security rangers, Nick & Franka (Wageningen MSc students), Geraldine, Fridah were always motivated and made fun of the hardest situations we encountered in the field. Jargon such as "stand alone" and "coppiced" referring to open woodland savanna and thickets respectively, during vegetation sampling exercise put smile on everyone's face. Charging through the thickets like irritated buffaloes made vegetation sampling a sport all of us looked forward to despite the boring exercise of measuring thousands of trees and plucking leaves from sometimes thorny acacia plants christened "wait-a-bit" for its ferocious and unforgiving thorns. To Jan van Walsem who assisted with leaves nutrients analysis in Wageningen lab and Makhoha, Prof. Kiringe and Prof. Okello for assisting with grass biomass analysis – I thank you all.

I sincerely thank my colleagues from Tsavo; Fredrick Lala and Martha for the logistical support and office space during my field work; Assistant Director Robert Obrien, Commander Arap Tanui, Oyugi, Mwakangalu, Grace, Wekesa, Luka Narisha, Isa, Cpl Oyugi, Hussein Sode, Cpt Ochieng, all security rangers in Tsavo East and West and the entire Tsavo Conservation Area staff for all their assistance and moral support during my study. Many colleagues at KWS played a very critical role in my PhD journey; I want to single out Karanja for assisting me with critical secondary data, Kenana with whom we did several trial statistical analysis and discussions of results, Mukeka for being the focal GIS consultant, Wambua and Esiromo for in depth discussion on my research and many other colleagues, particularly, Mr. Njue and Flora who stepped in for me and ensured that I had time to work on my thesis without jeopardising my work at KWS and all the MTs of 2001 for your support and encouragement throughout my 4 years PhD journey. Abj, Jikate, Saru, Budha and Boru Golicha - many thanks for your support and encouragement.

As I grew up, I was inspired to pursue a career in wildlife management by my father in-law, Dr. Hussein Isaack, who was then studying honey guide for a PhD degree at Oxford University and was popularly known as "Abba Simpirre", meaning the father of birds. At that time, I believed he could communicate with birds and I thought that was really cool. This belief stimulated my interest to study wildlife management in the hope that I could communicate with other wildlife species, a fact I later came to learn was not possible. However, I was not disappointed with my career path and I thoroughly enjoyed learning about a few wildlife species through studying their behavioural ecology. Later, Dr. Hussein constantly encouraged me to pursue a PhD study and we always had in-depth discussion about my work. My mother in-law, Habiba supported me throughout the 4 years of my study and also offered severally to baby-sit her grandson when I was away in the Netherlands and on occasions where my wife had to travel for work. My sisters, brother and my entire extended family and friends provided unwavering support and constantly kept tab of my progress. To all I say, thank you.

To my Dad, Adan Wato and Mom, Mariam Kame, special thanks go to you for taking me to school even though you never attended one, and consistently supporting me throughout my academic life, wondering whether this schooling will ever end. Your unwavering support not only gave me the energy to work hard but also the necessary pressure to focus and I'm happy to report the end of my PhD journey to you.

Special thanks go to my dear wife Simpirre for standing beside me throughout the 4 years of PhD journey and more importantly, for taking care of our son Jibril who was born just when I was leaving for Wageningen. She constantly motivated me to focus on my study and ensured that all family errands are fully taken care of while still maintaining her full time job in a challenging corporate business. Despite that, she still found time to proof-read my entire thesis and enrol in a master course in business administration. Her sacrifice to stay late for the skype calls made it easy for me to constantly stay connected with my family and share in the joy as I watched our son grow. I also thank my wonderful son Jibril for always making me smile by asking ingenious questions when I was writing this book instead of playing games with him on my computer. I hope that one day he can read this book and understand why I spent so much time in front of my computer.

Finally, for those whom I may not have mentioned here but who contributed in one way or another, I'm grateful to you all because without you, this thesis would not have become a reality.

Curriculum Vitae

Yussuf Adan Wato was born on 10th June 1976, in Marsabit, Kenya. He is happily married with a 4 year old son. In 2000 he obtained a BSc. Degree in Wildlife Management from Moi University in Kenya. The same year, he joined Kenya Wildlife Service (KWS) as a management trainee and after one year of training in the department of Wildlife Security, Community Wildlife Service, Park Management and Tourism, he got a full-time employment with KWS as a National Park Manager. He has since managed various marine and terrestrial Parks in Kenya for over 10 years, including the largest Park in Kenya; The Tsavo East National Park. In September 2003, he enrolled for a sandwich MSc Program in Applied Ecology & Conservation Biology jointly offered by Linkoping University in Sweden and Moi University in Kenya where he graduated in 2006. He has studied various short professional courses such as: Sustainable Environmental Conservation at Canadian School of Field Studies in Africa (CFSIA) by McGill University, Canada in 2007; Environmental Education for Conservation of Coastal Ecosystem in Okinawa, Japan in 2007; Biodiversity Conservation and Ecology Management in Yunan University, China in 2009; GIS and Spatial Analysis in Geodata Systems Technologies, Pasig, Philippines in 2011 among others. He joined Resource Ecology Group in Wageningen University for a PhD study in 2012 through NUFFIC and KWS Scholarship. His study focussed on the effect of droughts on elephant population dynamics. The results of this research culminated to this Thesis. Yussuf is currently a Senior Manager in the department of Wildlife Industry Governance & External Linkages at Kenya Wildlife Service coordinating programmes that are jointly implemented between various conservation partners and the Kenya Wildlife Service.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- The long term impact of a keystone species on savannas: the Tsavo (Kenya) elephant population crash re-visited (2012)

Writing of project proposal (4.5 ECTS)

- Elephant population dynamics in semi-arid ecosystems

Post-graduate courses (7.1 ECTS)

- Desk top GIS 1 & 2; Geodata Systems technologies, Pasig, Philipines (2011)
- Remote sensing course; Regional Center for Mapping of Resources for Development, Nairobi, Kenya (2013)
- GIS spatial analysis course; Regional Center for Mapping of Resources for Development, Nairobi, Kenya (2014)
- Course; PE&RC (2014)

Laboratory training and working visits (3 ECTS)

- Elephant collaring, GPS tracking techniques & data management; International Fund for Animal Welfare & Kenya Wildlife Service (2012)
- Training on the techniques of elephant monitoring – demography and social organization; Amboseli Elephant Research Center (2014)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Oryx – The International Journal of Conservation: spatial distribution of snares in Ruma National Park with implications for management of roan antelope and other wildlife (2012)

Deficiency, refresh, brush-up courses (5 ECTS)

- Ecological methods; PE&RC (2014)

Competence strengthening / skills courses (1.5 ECTS)

- Essentials of scientific writing; WGS (2015)
- PE&RC PhD Workshop carousel (2015)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.1 ECTS)

- PE&RC Weekend (2012)
- PE&RC Symposium – exploring life in the extremes and the extremes in life (2012)
- PE&RC Day (2014)
- PE&RC Midterm PhD weekend (2014)

Discussion groups / local seminars / other scientific meetings (4.2 ECTS)

- PE&RC Symposium: trait as a link between systematics and ecology (2012)
- Ecological theory and application group (2012-2015)
- Tsavo Ecological Research & Wildlife Monitoring seminars (2012-2015)
- R Group (2013-2015)
- Workshop to discuss the preliminary results for the Tsavo-Mkomanzi elephant samples census (2014)
- National Elephant Conference; Kenya (2015)

International symposia, workshops and conferences (7.6 ECTS)

- Twelfth Kenya Meteorological Society International Conference; Kisumu Hotel, Kisumu, Kenya (2015)
- 5th International Eco-summit: ecological sustainability conference ; Montpellier, France (2016)
- United Nations Conference on Space Technology and Applications for Wildlife Management and Protecting Biodiversity; poster presentation; Nairobi, Kenya (2016)
- 15th International Elephant and Rhino Conservation and Research Symposium; Singapore (2016)

Lecturing / supervision of practicals / tutorials (0.6 ECTS)

- Guest lecture in wildlife resource management course (2012)

Supervision of a MSc student (3.5 ECTS)

- How does the spatiotemporal availability of surface water affect elephant mortality and elephant home range size?
- Effect of soil salinity on vegetation in Tsavo conservation area, Kenya

The research described in this thesis was financially supported by NUFFIC, IFAW and KWS

Printed by Digiforce B.V.

Cover designed by Print Experts

Photos are from Peter Beard's book, ***“The End of the Game, Last Word from Paradise”*** (c) Peter Beard, Courtesy of Peter Beard Studio, <http://www.peterbeard.com>; The pictures were shot in Tsavo East during the severe drought of 1970.