The population status, habitat use and seasonal diet of African elephant (*Loxodonta africana*) in Majete Wildlife Reserve, Malawi

By

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Declaration

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Abstract

The African elephant (*Loxodonta africana*) is classified as a keystone species as it is critical to the integrity of the ecosystems it occupies. It influences a variety of factors in these ecosystems that include, but are not limited to, canopy cover, seed dispersal and various plant and animal species distributions. In addition to being classified as mixed feeders, elephants are water-dependent and the location and availability of water affects the extent and intensity at which elephants make use of vegetation. Confinement through the fencing of many elephant populations, particularly in Southern Africa, has adversely affected the management of this species. Population numbers tend to rapidly increase due to improved protection and supplementation of resources, intensifying the species negative effects on other herbivore species. Majete Wildlife Reserve, located in Malawi, was almost entirely devoid of wildlife but was revived by African Parks in 2003. The reserve was fenced, artificial waterholes were installed and an abundance of wildlife was reintroduced, including 213 elephants. Five years post reintroduction, elephant numbers have dramatically increased and concern has been raised regarding the potential impact of this species on the vegetation and other herbivore species in the reserve. In this study, a review of all relevant literature was reported and two field studies were conducted on the population status, habitat use and diet of elephants in the reserve.

The population status of the elephants was assessed with aerial survey data and individual identification techniques. The population has increased to an estimated 389 individuals, of which 366 were positively identified. Results revealed a sex ratio of 1:1 and a population growth rate of 13.8% per annum. Additionally, habitat use of the elephants was investigated using camera trap gridlines throughout the reserve. It was determined that a higher number of elephant frequented habitat near perennial water sources and at lower altitudes. Furthermore, waterhole usage was determined using camera traps placed at artificial water sources in Majete. Results suggested that fewer elephants utilised artificial waterholes during the wet season and that family herds tended to dominate the use of the majority of the artificial waterholes. Lastly, it was determined that the use of artificial waterholes was increasingly homogenous in the dry season. The increasing elephant population resulted in dispersal to less preferred areas, namely that of higher altitude miombo woodland as lower altitude regions were potentially becoming too densely populated.

Diet of the elephants was investigated using stable isotope analysis of faecal samples to determine seasonal grass and browse composition. Elephants' diets displayed a clear seasonal difference in the proportion of C3 browse consumed. In the dry season the diet contained 98% C3 browse but decreased to 59% in the early wet season and to 65% in the late wet season. This indicates that a greater proportion of C4 grass was consumed in the wetter seasons, typical of other elephant populations.

The results from this study will contribute towards the compilation of an elephant management plan that will be provided to African Parks, Majete, for further implementation.

Opsomming

Die Afrika-olifant (*Loxodonta africana*) word geklassifiseer as ’n hoeksteenspesie omdat dit van kritiese belang is vir die integriteit van die ekosisteme waarin dit voorkom. Dit beïnvloed ’n verskeidenheid faktore in hierdie ekosisteme, insluitend, maar nie beperk tot, lowerdekking, saadverspreiding en die verspreiding van verskeie plant- en dierspesies. Buiten dat hulle as gemengde vreters geklassifiseer word, is olifante afhanklik van water en die ligging en beskikbaarheid van water beïnvloed die mate en intensiteit waartoe olifante van plantegroei gebruik maak. Die inperking van baie olifantbevolkings deur heinings, veral in Suidelike Afrika, het ’n negatiewe effek op die bestuur van die spesie gehad. Bevolkingsgetalle neig om vinnig toe te neem as gevolg van verhoogde beskerming en die aanvulling van hulpbronne, wat die spesies se negatiewe effekte op ander herbivore versterk. Die Majete Wildreservaat, wat in Malawi geleë is, was feitlik gestroop van alle wild, maar is in 2003 deur African Parks herleef. Die reservaat is omhein, kunsmatige watergate is geïnstalleer en ’n oorvloed wild is hervestig, insluitend 213 olifante. Vyf jaar ná die hervestiging het olifantgetalle dramaties toegeneem en kommer is uitgespreek oor die potensiële impak van hierdie spesie op die plantegroei en ander herbivoorspesies in die reservaat. In hierdie studie word verslag gedoen oor die relevante literatuur, asook van twee veldstudies wat onderneem is om die bevolkingstatus, habitatgebruik en dieet van die olifante in die reservaat te ondersoek.

Die bevolkingstatus van die olifante is geassesseer deur gebruik te maak van data afkomstig van lugopnames en individuele identifikasietegnieke. Die bevolking het toegeneem tot ’n geskatte 389 individue, waarvan 366 positief geïdentifiseer is. Die resultate toon ’n geslagsverhouding van 1:1 en ’n bevolkingsgroeikoers van 13.8% per jaar. Daarbenewens is die habitatgebruik van die olifante ondersoek met behulp van kamerastrikke op ruitlyne in verskeie plekke in die reservaat. Daar is bepaal dat ’n groter getal olifante die habitat in die nabyheid van standhoudende waterbronne en op laer hoogtes bo seespieël meer dikwels besoek het. Die gebruik van watergate is verder ondersoek met behulp van kamerastrikke in die nabyheid van die kunsmatige waterbronne in Majete. Die resultate stel voor dat minder olifante die kunsmatige waterbronne tydens die nat seisoen gebruik het en dat familietroppe geneig het om die gebruik van die meerderheid kunsmatige watergate te domineer. Laastens is daar bepaal dat die gebruik van kunsmatige watergate toenemend homogeen was in die droë seisoen. Die groeiende olifantbevolking het gelei tot verspreiding na minder gunstige gebiede, veral na die hoërliggende miombo bosland soos die laer geleë streke potensieel te dig bevolk geraak het.

Die olifante se dieet is ondersoek met stabiele isotoop analise van mismonsters om die samestelling van seisoenale gras en takvoer te bepaal. Die olifante se diëte het ’n duidelike seisoenale verskil

getoon in die proporsie C3 takvoer wat gevreet is. In die droë seisoen het die dieet 98% C3 takvoer bevat, maar dit het afgeneem tot 59% in die vroeë nat seisoen en tot 65% in die laat nat seisoen. Dit dui daarop dat ’n groter proporsie van C4 gras in die natter seisoene gevreet is, wat tipies is van ander olifantbevolkings.

Die resultate van hierdie studie sal bydra tot die samestelling van ’n olifantbestuursplan wat aan African Parks, Majete verskaf sal word vir verdere implementering.

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List of Abbreviations

AENP	Addo Elephant National Park
ANP	Amboseli National Park
DNPW	Department of National Parks and Wildife, Malawi
KNP	Kruger National Park
MWR	Majete Wildlife Reserve
SNR	Samburu National Reserve
TENP	Tsavo East National Park

Chapter One

Thesis Introduction and Outline

Introduction

Wildlife management is an extremely intricate yet adaptable discipline. Its foundation is based on the combination of scientific research, its practical application and the manipulation of natural systems that all constantly adjust according to the management objectives of management teams for various species and the status of their populations. One such species that requires adaptive forms of management is the African elephant (*Loxodonta africana*) (Whyte *et al.* 2003; van Aarde & Jackson 2007). It is one of the most intensively studied species on the African continent, both biologically and ecologically, and this is mainly attributed to the keystone role it plays in the numerous habitats it occupies (Short 1966; Hanks 1969; Laws 1970; Croze 1972; Barnes 1983; Koch *et al*. 1995; van Aarde *et al.* 1999; Whitehouse & Schoeman 2002; Shannon *et al*. 2006; Loarie *et al.* 2009; Shrader *et al*. 2012; Kioko *et al*. 2013; Wittemyer *et al.* 2013). The elephant is well known for structuring both plant and animal communities and although its effect can be beneficial it can also be detrimental when elephant densities increase in confined areas (Whyte *et al.* 2003; Skarpe *et al*. 2004; Western & Maitumo 2004; de Beer *et al*. 2006). Therefore, the potential impact of the species and its population status is critical to the integrity of the ecosystems it inhabits and so raises many management questions for the protected and non-protected areas it occupies.

The management of the African elephant is further complicated by virtue of the fact that the status of the species varies greatly across its range states as it is more threatened in some countries compared to others (Blanc *et al*. 2007; Bouche *et al*. 2011). This is supported by the fact that there have been recent eradications of the species in central and western Africa and yet nearly a third of the entire population occurs in Southern Africa (Blanc *et al*. 2007). However, only 9% of the entire African continent has been declared as formally protected areas and only 31% of the entire elephant population ranges within these protected areas (Blanc *et al*. 2007). Coincidently, many elephants still occur outside of protected areas which lends to an additional challenge for wildlife management. In particular, human-elephant conflict runs rife in many parts of Africa, especially when human-agricultural expansion moves into undeveloped land or infringes on protected area boundaries (Hoare & Du Toit 1999; Osborn & Parker 2003; Sitati *et al.* 2005). Broadly speaking, the primary issues that impede the survival of African elephant populations are habitat loss and fragmentation, human-elephant conflict, poaching for meat and ivory and the negative local impacts of elephant on their habitats (Gillson & Lindsay 2003; Osborn & Parker 2003; Stiles 2004; Blanc *et al.* 2007; van Aarde & Ferreira 2009). These issues are exacerbated by an ever-increasing human population throughout Southern Africa as well as other anthropogenic activities such as economic expansion, poverty and social and environmental human displacement that infringe on remaining wilderness areas (Newmark 2008). Therefore, in order to try and mitigate some of these pressures on the remaining wilderness areas as well as elephant populations there is a great need for clear wildlife management objectives for both protected and unprotected areas throughout the African continent.

In order for wildlife management to minimise the impact of many of these issues faced, not only by the African elephant but many other species as well, an increasing number of reserves, particularly in Southern Africa, are being fenced (Newmark 2008; Hayward & Kerley 2009). Fencing protected areas is beneficial in terms of reducing human wildlife conflict but it essentially increases the isolation of protected areas by creating an artificially closed ecosystem where food, water and space are limited and wildlife is unable to migrate to and from the area (Boone & Hobbs 2004; Hayward & Kerley 2009). Elephants, in particular, are a mixed feeding and water dependent species that naturally shifts its ranges on a seasonal basis (Codron *et al*. 2006; Chamaille-Jammes *et al.* 2007; van Aarde & Jackson 2007; Loarie *et al.* 2009; Codron *et al*. 2011). The combination of confining an elephant population and preventing its natural seasonal migration, as well as supplementing its resources in the form of artificial waterholes and providing protection from poaching, can rapidly enhance the population growth rate (Boone & Hobbs 2004; van Aarde & Jackson 2007; Shrader *et al.* 2010). As a result, this increases the foraging pressure of elephant on the vegetation within fenced protected areas that can have large impacts on the woody vegetation structure and its diversity, ultimately causing a loss of vegetation cover and negatively affecting other herbivore species (Duffy *et al*. 2002; van Aarde & Jackson 2007; Loarie *et al.* 2009; Mapaure & Moe 2009). Therefore, closed systems such as fenced reserves require wildlife managers to know the status of their elephant populations, whether they are increasing or decreasing and whether numbers should be regulated as the intensive management of the species is fundamental to the mitigation of habitat degradation and additional effects on other biodiversity.

The management of elephants in closed systems is one of the greatest challenges for wildlife management not only because of the potential impact of the species on the biodiversity of the protected area but because to date there is very little understanding of what limits their population numbers (Skarpe *et al*. 2004; Owen-Smith *et al*. 2006; van Aarde & Jackson 2007). The African elephant is a long-lived mammal, with a long period of sexual maturity and the longest mammalian gestation period (Moss 2001; Wittemyer *et al.* 2013). What is understood is that survival of the adults is high, the survival of the sub adults (<10 years) is less so and poaching and droughts are two of the main variables that limit elephant numbers (Dudley *et al.* 2001; Owen-Smith *et al.* 2005; van Aarde & Jackson 2007). However, the protection and resources provided in protected areas enhance population growth (Boone & Hobbs 2004; Hayward & Kerley 2009). Due to this, many fenced protected areas particularly in Southern Africa, face the challenge of elephant populations rapidly increasing to the point where management needs to implement a form of population regulation such as, translocation, contraception or culling (Cumming *et al.* 1997; van Aarde *et al.* 1999; Pimm & van Aarde 2001; Slotow *et al*. 2005). Therefore, although we do not have a clear understanding of what limits elephant populations in natural systems, wildlife managers have a duty to regulate population numbers due to the artificial nature of fenced protected areas and to ensure the perseverance of other biodiversity in the area.

In order to regulate elephant population numbers in fenced reserves, wildlife managers require an understanding of the variables that contribute towards population growth such as demographics, waterhole use and diet. The diet of elephant, in particular, can be quantified using stable carbon isotope ecology as it addresses the proportion of grass and browse consumed by individuals. Stable carbon isotope ratios are distinct between plants using the C_3 photosynthetic pathway (trees, shrubs and forbs) and plants that make use of the C_4 photosynthetic pathway (grasses) (Cerling *et al.* 1999). Once herbivores consume either C_3 or C_4 vegetation the carbon from the food is incorporated into the animal body tissues (Codron *et al.* 2007). Materials such as bone or hair and even the excreted, undigested portion of the diet, the faeces, reflect the herbivore $^{13}C/^{12}C$ ratios and consequently the proportions of grass and browse consumed (Cerling *et al.* 1999; Sponheimer et al. 2003; Codron et al. 2005; Codron *et al.* 2007). Therefore, a greater understanding of such variables will aid in the development of efficient elephant management plans on reserves that will facilitate better population management.

The management conundrum of elephants is so topical for many protected areas throughout Africa, that management organisations such as African Parks (Pty) Ltd. are investigating these very challenges in their own reserves. African Parks (Pty) Ltd., is a non-profit organisation that focuses in developing wildlife parks to be socially and economically viable, especially to the advantage of the local communities. They work in partnerships with governments and local communities and get their primary source of funding from private donors who value the protection and sound management of Africa's protected areas. The first rehabilitation project taken on by African Parks (Pty) Ltd. was Majete Wildlife Reserve (MWR, hereafter) which is the primary study site for this specific study where African Parks (Pty) Ltd. requested that a population study be conducted on its elephants (Figure 1.1.). MWR is located in the lower Shire valley region of southern Malawi (S15° 54'26.6"; E034°44'24.3") (Figure 1.1.). It is a 700km^2 fenced reserve with the northern and eastern boundaries boarded by two perennial rivers, the Mkhulumadzi and the Shire. MWR has two distinct seasons, the wet season that occurs from December to May and the dry season from June to November. The annual precipitation on the reserve is between 680-800mm in the eastern lowlands and 700-1000mm in the western highlands (Wienand 2013). Water availability is affected by season but there are approximately five perennial springs, along with ten artificial waterholes in the reserve.

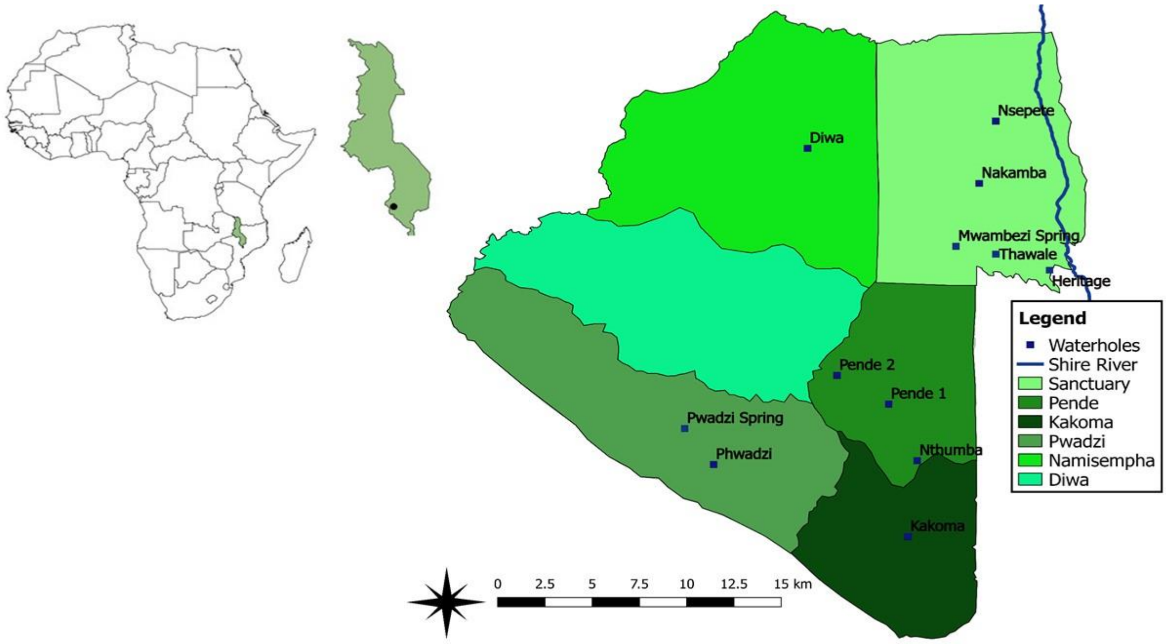

Figure 1.1. The location of Malawi in the African continent and the position of Majete Wildlife Reserve in Malawi. The various regions and perennial water sources that occur within the reserve are also shown. (Shapefiles per comms. African Parks (Pty) Ltd.)

The vegetation on the reserve is primarily woodland which varies according to altitude. The vegetation types include: high altitude miombo woodland, medium altitude mixed woodland, low altitude mixed woodland and savanna. MWR was gazetted in 1955 but by 2003 most of its large game had been decimated due to poaching and poor management. In 2003, MWR underwent one of Africa's greatest reintroduction programmes, after a Public Private Partnership (PPP) agreement was made between African Parks, Majete (Pty) Ltd. and the Malawian government. Wildlife reintroductions to MWR were undertaken in stages as the reserve was not yet fenced. The first stage involved fencing a smaller area of 140km^2 in the north-eastern region of the reserve, known as the Sanctuary, purely for reintroduction purposes in 2003. In the second stage the remaining boundary of the reserve was fenced and was completed in 2008, after which the sanctuary fence line was removed in 2011 and wildlife was able to roam into the greater reserve. In total over 2550 individual animals of 14 different species were reintroduced into MWR. Species reintroduced into the reserve included elephant, black rhino, buffalo, sable, Lichtenstein hartebeest and numerous other antelope species. Details of the reintroduction can be found in Appendix 1.

The reintroduction of wildlife species into an area where they were previously extinct due to anthropogenic pressures, is an effective tool in wildlife management (Muths & Dreitz 2008). The success of a reintroduction program is measured by the successful release of animals followed by their ability to reproduce and form self-sustaining populations in an area (Seddon *et al.* 2007; Muths & Dreitz 2008). Since the reintroduction a total of 213 elephants into the reserve in 2006, 2008 and 2010, respectively, populations have increased dramatically and apart from periodic aerial surveys (2010, 2012 and 2015), which recently counted 389 individuals in the reserve, there has been no other formal study on the status of the population. Currently, MWR has a no hunting and no culling policy with the intention to relocate surplus animals to restock other protected areas within Malawi. Therefore, it is of high importance to monitor and actively manage the current elephant population on MWR so as to establish a minimum viable population that must remain on the reserve in order to maintain a healthy ecosystem and to determine the number of individuals that will eventually be translocated.

The African elephant population on MWR was selected for this thesis as the population was increasing dramatically which could possibly lead to resource competition with other herbivores. Additionally, the combined biomass of the elephant population could have a detrimental effect of the reserves vegetation if left unchecked. It is important to know how animals utilise natural resources and more specifically to know the minimum and maximum viable populations for an area in order to maintain a healthy mammal population. The findings from this thesis may help to improve other reintroduction programmes and provide a better understanding of how pioneer populations successfully establish themselves in new territories.

Research Question

What is the current population status, habitat use and seasonal diet of Majete Wildlife Reserve's elephants, five years post reintroduction?

Research Statement

This study presents findings of the demographic changes to MWR's elephant population and their habitat use and seasonal dietary requirements, five years post reintroduction into the reserve. An assessment was conducted on the population structure, including gender ratio, in 2015/2016.

Additionally, habitat use of the elephants on MWR was investigated to determine which areas of the reserve they frequented and which water sources were preferred on a seasonal basis. Lastly, seasonal dietary changes were also investigated to determine whether there was a change in the browse and grass content between seasons. Data gathered in this study will aid MWR in the development of sound management strategies that will determine the future course of action in order to maintain and control the elephant population without negatively impacting MWR's remaining biodiversity.

Hypotheses

Alternative Hypothesis

a) Five years post reintroduction, MWRs' elephant population is steadily increasing: the sex ratio is skewed towards females, calves and juveniles form the largest proportion of the population, whereas the adults form the smallest.

b) Elephants prefer lower altitudinal areas of the reserve in both the dry and wet seasons. In the dry season the elephant's habitat use is focused around the water sources. However, in the wet season, when water is readily available throughout the reserve in the form of ephemeral pools, elephants increase home ranges and so habitat use is more homogenous and perennial water sources are less frequented.

c) Seasonal diet shifts from mixed feeding (both grass and browse) in the wet season to predominantly browse in the dry season.

Null Hypothesis

a) Five years post reintroduction MWRs' elephant population has not dramatically increased, the sex ratio is not skewed and there has been no change in the age structure.

b) Habitat use by elephants does not change on a seasonal basis and their use of perennial water sources is consistent throughout the year.

c) The seasonal diet of the elephants does not shift on a seasonal basis and remains very much the same throughout the year.

Research Goals

The main research goal is to provide MWR with baseline information and guidelines for the development of a sound management plan for the elephant population that currently inhabits the reserve. The guidelines, based on scientific and ecologically sound research, will aim to address the future course of action needed to maintain a viable elephant population on the reserve, to preserve spatial heterogeneity and to prevent loss of biodiversity.

Research Objectives and Research Questions

The first objective is to determine how the demographics of MWRs' elephants has changed five years post reintroduction and to identify whether population changes are associated with environmental variables, such as vegetation and water availability.

a) What is the elephant population size in MWR?
b) What is the population's age/size class structure? (number of males and females, number of adults, juveniles and calves)
c) How many elephant herds are there in the reserve?
d) What environmental variables in MWR can be associated with the change in population structure?

The second objective is to determine seasonal changes in habitat use, with a focus on which regions of the reserve are regularly frequented by elephants and which perennial water sources are favoured.

a) Does the presence of elephants within MWR differ on a seasonal and yearly basis?
b) Which regions of the reserve have the highest and lowest presence of elephants on a seasonal basis?
c) Does the use of perennial water sources by elephant change on a seasonal and yearly basis?
d) Which perennial water sources are frequented most in the wet and dry seasons?

The third objective is to determine the change in the seasonal diet of MWRs' elephant population, more specifically to determine the difference in the browse and grass content of the elephant's diet in the early wet, late wet, early dry and late dry seasons.

a) What is the isotopic composition of C_3 and C_4 biomass in the elephant's diets?
b) Is there a seasonal (i.e. early wet, late wet, early dry and late dry) change in the C_3 and C_4 biomass in the elephant's diet?

Significance of Research

African Elephants are a keystone species and the potential impact they may have on their habitat and other herbivore species raises management questions in both protected and unprotected areas (Short 1966; Hanks 1969; Laws 1970; Croze 1972; Barnes 1983; Koch *et al.* 1995; van Aarde *et al.* 1999;

Whitehouse & Schoeman 2002; Shannon *et al*. 2006; Loarie *et al*. 2009; Shrader *et al*. 2012; Kioko *et al.* 2013; Wittemyer *et al.* 2013). In order to maintain healthy ecosystems it is important to manage any enclosed elephant population, where fencing prevents the seasonal migration of the species (Newmark 2008; Boone & Thompson Hobbs 2004; Hayward & Kerley 2009). The combination of fencing and the installation of artificial waterholes in many of these fenced reserves intensifies the impact of elephants on vegetation due to increased elephant densities and improved foraging opportunities in the drier seasons (Chamaille-Jammes *et al.* 2007; Shannon *et al*. 2006). Therefore, it is important for reserve management to have access to all relevant information concerning the status of their elephant populations and the animal's habitat use in order to compile management plans that will help maintain healthy ecosystems within the protected area.

It is not just the keystone status of the African elephant that reflects the importance of their management. They are a species of high economic value in terms of tourism, where they are featured as a flagship species, and the ivory trade (Gillson & Lindsay 2003; Osborn & Parker 2003; Stiles 2004; Blanc *et al*. 2007; van Aarde & Ferreira 2009; Wittemeyer *et al.* 2013). The African elephant was listed in Appendix I in 1997, which banned all international trade of elephants and their parts. The listing was done by CITES (Convention on International Trade in Endangered Species of wild fauna and flora), an organisation that regulates the trade in species and their products (van Aarde & Ferriera 2009; Stiles 2004). The aim of this listing was to attempt to stop the trade in ivory, which was rapidly decreasing elephant numbers in parts of Africa (van Aarde & Ferriera 2009). It was not entirely effective as the number of elephants continued to decline in Central and Western Africa, and increased in Southern and Eastern Africa (Stiles 2004; Blanc *et al.* 2007). This suggests that there are factors, other than the illegal ivory trade, that can cause elephant population changes such as political and economic factors, government investment in wildlife, the bush meat trade and the commercial use of elephant by-products (Stiles 2004; van Aarde & Ferriera 2009). The status of the African elephant therefore varies across the continent, so much so that it is essential that we aim to conserve as many populations as possible by creating clear management objectives for both protected and unprotected areas by using sound scientific and ecological research.

Lastly, since the reintroduction of elephants into MWR only three ecological studies have been conducted. The first was conducted in 2012 and focused on the effects of elephant browsing on woody trees (Staub *et al*. 2013). The study found that elephants mostly favoured riparian woodlands and that browsing was negatively related to the distance from water sources (Staub *et al.* 2013). The second study was conducted in 2013 and investigated changes in the historic woody vegetation cover from 1985 – 2010, as well as elephant water point usage (Wienand 2013). The study found a high loss of woody vegetation between 2000 and 2010 which was mainly attributed to the synergistic effects of drought, fire and herbivory (Wienand 2013). Elephant water point use was effected by season, water point altitude and the surrounding vegetation type (Wienand 2013). The third study was conducted in 2013 and investigated the browsing impact of elephant on the woody tree species in MWR (Komoto 2013). The study found that elephants had a negative impact on woody species and the highest impacts occurred in the Sanctuary which is dominated by *Acacia/Sclerocarya* woodland (Komoto 2013). However, to date there has not been a study that has focused on the elephant population structure and status and how it has responded since the reintroductions. Neither of the two previous studies considered elephant diet specifically and how it changes on a seasonal basis. Therefore, this study, in combination with previous studies conducted on elephants in MWR (Staub *et al*. 2013; Weinand 2013) will provide the necessary data to compile a long term management plan for the elephants in the reserve. Findings of this research will be used to improve similar reintroduction programmes and provide a better understanding of how elephant populations establish in new environments.

Scope of Limitations

In this project four main limitations were identified and considered.

The first limitation to the research conducted in MWR is that African elephants are a particularly long-lived species (Wittemyer *et al.* 2013). They have the longest mammalian reproductive life as well as gestation period but have a slow rate of reproduction (Moss 2001; Wittemyer *et al.* 2013). This presents various problems in research conducted on the population dynamics of African elephants, as there is a large constraint in collecting longitudinal data on the demography of a population (Moss 2001). It could take up to 60 years to determine the complete life history of a herd (Moss 2001). Therefore, due to the fact that the reintroduction of the species into MWR was only completed five years ago and because of time constraints, this study this study was unable to investigate the complete life history and demographics of the population. The study did, however, manage to obtain a cross section of the population status of the elephants for the years 2015/2016, thus providing important baseline data that can be used for future research.

The second limitation to this study was the condition of the roads. The road network in the reserve is fairly limited and is only passable by 4x4 vehicles in the majority of the park. For this reason little time was spent in certain sections of the reserve and daily or even weekly transects of all the roads in the reserve were impossible to conduct. Additionally, in the wet season in particular, the vegetation on the reserve is mainly dense woodland with a few small savanna areas that are located in the south.

Visibility was thus reduced and this combined with the fact that the majority of the elephants in the reserve are not habituated towards cars or humans made it difficult to collect demographic data in certain areas. In order to overcome this limitation the project made use of camera traps that were placed at artificial waterholes throughout the reserve as well as at a few natural springs. Therefore, data could still be collected in a non-invasive manner and on a continuous basis.

The third limitation to the study was that there was little or no demographic data available from when the elephants were first reintroduced into the reserve in 2006, 2008 and 2010 except for total numbers. So results could not be compared with regards to how the population has changed over time, specifically referring to sex ratios and age groups.

The fourth limitation to the study was that the elephant faeces collected for the seasonal diet study was only collected from main road networks and around artificial waterholes on the reserve. Although the road network is limited with little access to the interior areas of MWR it does have access to all vegetation types. Therefore, in order to ensure that all possible habitat types are included, it is imperative that sampling of elephant faeces is conducted throughout the reserve.

Assumptions

a) Individuals that were captured on camera in a continuous sequence of photographs in a short time period, between 10 to 60 min, were assumed to be from the same herd.

b) Once an extended period of time, longer than 60 min, had passed between photographs, individuals we assumed to be from a different herd.

c) Bulls of the age categories, small, medium and large adults, were assumed to have left their original family herds (size classes were derived from the following literature: Moss 1996; Whitehouse & Hall-Martin 2000; Moss 2001). Bulls tend to leave their family herds between the ages of 11 and 13 years (Moss 1996; Whitehouse & Hall-Martin 2000; Moss 2001). If an individual was captured on photograph with the same family herd multiple times, the individual was assumed to still belong to the herd. However, if an individual male estimated to be a small adult appeared alone or with different family herds in photographs, notes were taken but the individual was assumed to range alone.

d) If more than one family herd was recorded while feeding or at waterholes, notes were taken as separate herds may be part of a larger family group and so could possibly be related.

Brief Chapter Overview

This master's thesis is composed of five chapters. Chapter One is a basic introduction to the subject matter by providing some background information about the importance of sound elephant management in protected areas, the research question and statement, the hypotheses, the goals of the study, the objectives, significance of the research and the assumptions and limitations of the study. Chapters Two, Three and Four have been compiled as stand-alone manuscripts to enable publication in peer-reviewed journals. Due to this there is some repetition between chapters. Chapter Five serves as both a discussion chapter for the thesis as well as a management recommendation document for African Parks Majete (Pty) Ltd. Therefore, the literature review is not discussed in Chapter Five.

Chapter Two presents a literature review that provides comprehensive background information on the influence of population demographics, resource use and range distribution on the management of the African elephant in protected areas.

Chapter Three describes how the population structure and demographics of MWRs' elephants has changed five years post reintroduction onto the reserve. The population age structure and sex ratio were determined for 2015/2016 and the changes since reintroduction were discussed. Additionally, it was determined whether there was a seasonal change in habitat use by the elephants and this was discussed in terms of presence/absence around the reserve and perennial water source usage.

Chapter Four describes the change in the seasonal diet of MWRs' elephant population. The effects of the different seasons (early wet, late wet, early dry and late dry) on elephant diet was analysed using the C_3 and C_4 values in elephant faeces and thus the difference in the browse and graze content of the diet was observed. The results and their implications towards elephant management were then discussed and compared to other dietary studies conducted on the African elephant.

Chapter Five summarises the main research findings of this thesis in terms of population structure and diet and proposes recommendations for the future management of MWR's elephants.

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Chapter 2

African elephant (*Loxodonta africana*) population demographics and resource use in protected areas: A review

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Abstract

African elephants (*Loxodonta africana*) are facing a continental wide decrease in numbers as populations are becoming increasingly isolated in remaining wilderness areas. Many protected areas, particularly in Southern Africa, are however experiencing an increase in elephant population growth rates. This has mainly been credited to two factors: fencing and water supplementation. Fencing limits elephant's migration and intensifies the species' impact on the vegetation in an area, potentially resulting in woody species degradation or loss. Water supplementation, concurrently, affords elephants the opportunity to expand their dry season ranging, allowing them to access areas that would normally be unreachable due to lack of water. The high population growth rates caused by the combination of these two factors necessitates that elephant numbers be carefully managed in these protected areas in order to maintain biodiversity and ecosystem functions. Therefore, it is essential that reserve managers understand the primary factors that affect demographic vital rates of elephants and how these can be manipulated to control population growth. In addition, it is important to understand the species' basic nutritional requirements/diet and investigate their movement and habitat use in an area in order to implement effective management strategies. In this review, research findings of peer-reviewed literature studying elephant population demographics, habitat use and diet were synthesised. The review discussed two core areas i) Elephant demographic vital rates and population growth and ii) Elephant resource use and range distribution in protected areas.

Key Words: African Elephants, demographic vital rates, diet, habitat use, *Loxodonta africana*.

Introduction

The African elephant (*Loxodonta africana*), a large pachyderm, ranges over 22% of the African continent but its status varies significantly across its range states as the long term survival of some national populations are more threatened than others (Blanc *et al*. 2007). Overall, total African elephant population numbers are declining and in the last century this was attributed to the commercial pursuit of ivory, safari hunting and the expansion of human populations (Milner-Gulland & Beddington 1993; Hoare & du Toit 1999; Skarpe *et al.* 2004). As a result CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) has given the species dual status (Stiles 2004; Lovett 2009; Jones 2016). The majority of elephant populations throughout Africa are listed under Appendix I, banning international trade (Stiles 2004; Lovett 2009; Jones 2016). However, in Botswana, Namibia, South Africa and Zimbabwe elephants are listed under Appendix II, permitting international trade due to well managed and generally increasing population numbers (Stiles 2004; Lovett 2009; Jones 2016). There are three subspecies of elephant on the African continent: the savanna elephant (*Loxodonta africana africana*) which occurs in Eastern and Southern Africa, the forest elephant (*Loxodonta africana cyclotis*) which primarily occurs in the Congo basin and Central Africa and lastly, the West African elephant which occurs in both forest and savanna systems but are taxonomically uncertain (Blake & Hedges 2004; Blanc *et al.* 2007). In the interest of this review, only the savanna elephants (*Loxodonta africana africana*) will be discussed.

Southern Africa accounts for 39% of the savannah elephant's range area and contains the largest known number of elephants relative to any other region on the continent (Blanc *et al.* 2007). Despite this, elephant populations have become progressively fragmented as their habitat range has decreased in response to an increasing human population (Newmark 2008; Hayward & Kerley 2009). In sub Saharan Africa the human population more than doubled from 1975-2001, which has led to an increase in the development of rural settlements, subsistence agriculture, deforestation and unsustainable hunting of wildlife (Newmark 2008; Hayward & Kerley 2009). The isolation and fragmentation of wilderness areas has progressed to the point where governmental or private protected areas are all that is left of the once vast expanses of undeveloped land (Newmark 2008; Hayward & Kerley 2009). Additional factors that promoted the isolation of protected areas include: fences, roads, over hunting and disease (Newmark 2008). Fencing, in particular, prevents the migration of elephants into and out of reserves, limiting elephants from accessing patches of higher quality food beyond protected area boundaries, but drastically reducing human-wildlife conflict (Osborn & Parker 2003; Boone & Hobbs 2004; Sitati *et al*. 2005; Guldemond & Van Aarde 2008, Loarie *et al.* 2009a).

Elephants are mixed feeders and their large body size and robust feeding allows them to feed on a variety of plants and specific plant parts such as bark, fruit and bulbs (Kerley & Landman 2006; Owen-Smith & Chapota 2012). In Addo Elephant National Park (AENP), South Africa, elephants fed on 146 different plant species throughout the year and in Chobe National Park, Botswana, 94% of the elephant's dry season diet was composed of stems, bark and roots from various plant species (Lombard *et al.* 2001; Kerley & Landman 2006; Owen-Smith & Chapota 2012). Additionally, elephants are a water dependent species and so need to remain within a few kilometres of water sources in the dry season (Stokke & du Toit 2002; Chamille-Jammes *et al.* 2008). The annual rainfall across the African continent strongly correlates with the historic distribution of elephants in terms of occurrence (de Boer *et al*. 2013). The species would migrate on a seasonal basis in search of resources that would reduce foraging pressure on any one particular area (de Boer *et al.* 2013). Presently, elephants are unable to migrate as they once did and so with water supplementation in many protected areas, elephant numbers and vegetation damage increase, promoting the principle known as the 'elephant problem' (Barnes 1983; Whyte *et al.* 2003; van Aarde & Jackson 2007).

Elephants are a keystone species, as they structure both plant and animal communities (Caughley 1976). The fencing of reserves results in elephants having large impacts on woody vegetation (Caughley 1976; Cumming *et al.* 1997; Boone & Hobbs 2004). The 'elephant problem' is where the vegetation/habitat of an area changes due to high elephant densities (Napier Bax & Sheldrick 1963; Duffy *et al.* 2002; Cerling *et al*. 2004; Guldemond & van Aarde 2007; van Aarde & Jackson 2007). Evidence of this was presented in Cumming *et al.* (1997) who found that an increasing elephant population led to a rise in tree felling in Zimbabwe. Additionally, Mapaure and Moe (2009) found that the presence of elephants altered the composition of miombo woodland, decreasing abundances of high preference species such as *Brachystegia boehmii*. The 'elephant problem' is not only limited to fencing but the combination of fencing and the increasing complexity of the surrounding matrix of protected areas prevents elephant populations from migrating across landscapes, resulting in high population numbers in protected areas and subsequent vegetation damage (Boone & Hobbs 2004, Van Aarde & Jackson 2007).

There may be a continental wide decrease in elephant numbers but well protected areas, particularly in Southern Africa, are experiencing an increase in elephant population growth rates (Slotow *et al*. 2005; Blanc *et al.* 2007). This can be credited to an increasing number of such areas being fenced as well as the supplementation of resources in the form of artificial waterholes (Chamaille-Jammes *et al*. 2007). Reserve managers face the challenge of managing high elephant population densities while attempting to maintain biodiversity and ecosystem function (Chamaille-Jammes *et al*. 2007; Loarie *et al.* 2009b; Gillson & Lindsay 2003). Thus, the knowledge of mechanisms that limit or regulate large herbivore populations is important, not only to theoretical understanding of populations, community and ecological patterns but also to our ability to effectively maintain assemblages of these organisms and the ecological processes they facilitate. This review synthesizes the findings of peer-review literature on elephant populations and focuses on two core areas i) Elephant demographic vital rates and population growth and ii) Elephant resource use and range distribution in protected areas.

Elephant Demographic Vital Rates and Population Growth

The central question behind the theory of population dynamics is to identify the stabilising mechanisms of species vital rates that have the potential to lead to population regulation (Murdoch 1994). The vital rates of a species are defined as the rates of survival, development and reproduction and they usually depend on the age, size and development stages of individuals within populations (Neubert & Caswell 2000). In order to estimate the vital rates of a population the relative contribution of each vital rate to the variability in population growth, the elasticity, as well as the amount of temporal variability in each vital rate, the sensitivity, needs to be addressed (de Kroon *et al.* 2000; Tuljapurkar *et al.* 2003). The elasticity of African elephants is fairly well understood and developed in the form of the life history traits of the species (Moss 2001). They are characteristic of large ungulates, being strongly iteroparous with low annual fecundity and high annual adult survivorship; they produce only one offspring per reproductive bout and have long gestation periods (de Kroon *et al*. 2000; Moss 2001; Tuljapurkar *et al.* 2003; Wittemyer *et al*. 2007b). However, elephants also exhibit unique life history traits, namely sensitivity of vital rates, that improves their ability to respond to temporal variability in ecological conditions or other factors, such as poaching, governmental corruption and conflict that influence population demographic fluctuations (Osborn & Parker 2003; Boone & Hobbs 2004; Guldemond *et al*. 2005; Guldemond & Van Aarde 2008; Wittemyer *et al.* 2007b; Chamaille-Jammes *et al.* 2008; de Boer *et al.* 2013). These unique traits include, the longest gestation period of all terrestrial mammals (22 months), an extended period of parental care of young in which weaning typically occurs over 2 years, an overlap of dependant offspring and lastly elephants necessitate extensive, long term energy investment in offspring (Whitehouse & Hall-Martin 2000; Moss 2001; Wittemyer *et al.* 2007b; Wittemyer *et al.* 2013). Therefore, the elasticity or the analysis of life history traits of long lived herbivores, such as elephant, indicate that the population growth rate is most sensitive to the change in adult female survival and the fecundity of prime age individuals, whereas the sensitivity of the population to temporal variation is most affected by juvenile survival (de Kroon *et al.* 2000; Gaillard *et al.* 2000; Eberhardt 2002; Tuljapurkar *et al.* 2003).

The elasticity and the sensitivity of an elephant population are interdependent and both are strongly influenced by environmental and anthropogenic factors. The reproductive phenology of the African elephant is a prime example of the interdependent relationship between the elasticity and sensitivity of a population as it is influenced by both ecological factors as well as life history constraints (Clutton-Brock 2002). As a consequence of their 22 month gestation period, elephants optimise the timing onset of reproduction so as to maximise the use of known and future resources to coincide with the energetic investment in reproduction (Wittemyer *et al*. 2007b; Trimble *et al.* 2009; Shrader *et al*. 2010). The initiation of the female reproductive bout is dependent on the conditions during the season of conception but is timed so parturition occurs during the most likely period of high vegetation primary productivity 22 months later (Gough & Kerley 2006; Wittemyer *et al*. 2007b). More specifically, there is an ecological control on elephant reproductive rates as the onset of the rainy season, when primary productivity and food quality increase, triggers an increase in progestin hormone levels and so the onset of reproductive activity (Wittemyer *et al.* 2007b). Therefore, the progestin levels in pregnant and non-pregnant females is closely correlated with the quality of available food resources and are impacted by age, decreasing the older the individual is, and inter-pregnancy interval (Wittemyer *et al.* 2007b). This gives a physiological basis for condition dependant oestrus and its influence on general population demographic fluctuations in reaction to climate variability.

The African elephant is a species of high conservation concern and so a clear understanding of any population's elasticity and sensitivity is essential to preserve the integrity of the ecosystems elephants inhabit and for protected area management. The majority of the existing data on elephant demographic parameters has been compiled from well protected populations that were stable or increasing at the time of the study (Moss 2001; Gough & Kerley 2006). However, in order to determine how the vital rates of different elephant populations vary it is necessary to discuss both populations that are well protected and those that are less protected and face pressures such as poaching. The following section will discuss the primary demographic vital rates that have the greatest influence on population growth. These include calving interval, average age of females at first calving, annual mortality, and density in order to observe the differences between four existing elephant populations with varying population histories, two from fenced reserves (Kruger National Park (KNP) and Addo Elephant National Park (AENP)) and two from unfenced reserves (Amboseli National Park (ANP) and Samburu National Reserve (SNP) (Table 2.1.).

Table 2.1. African elephant demographic parameters for four different populations collected through individual recognition, radio tracking or culling.

Location	Protection Status	Calving Interval (Years)	Age of first calf (years)	Annual Mortality (%)	Density (per km²)	Annual population growth rate (%)	Yearly Rainfall (mm)	References
Addo N.P. South Africa	Fenced	3.3	12.5	1.4	4	5.8	392	Gough & Kerley 2006
Kruger N.P South Africa	Fenced	3.8	13	3.2	0.52	-	450-700	Whyte *et al.* 1998; Freedman *et al.* 2009
Amboseli N.P. Kenya	Unfenced	4.5	12	4.15	0.36	2.2	341	Moss 2001
Samburu N.R. Kenya	Unfenced	4.0	11.34	4.7	0.27	0.17	350	Wittemyer *et al.* 2005; Wittemyer *et al.* 2013

Mean calving interval is considered the single most important factor that influences the population growth rate of elephants and it is dependent on the density of the population as well as the resources available (Moss 2001). The mean calving interval of African elephants can range from 2.9 years to 9.1 years, as derived from culled samples from several different populations throughout Africa (Eltringham 1982, as cited in Moss 2001; Freeman *et al.* 2008). The length of average calving intervals will increase in resource limited, high density or nutritionally stressed populations and this has the potential to slow population growth as individuals give birth less frequently (Wittemyer *et al.* 2013). The mean calving interval for the unfenced protected areas of ANP and SNR is 4.5 years and 4.0 years respectively (Table 2.1.). These mean calving intervals are longer than both fenced reserves, AENP and the KNP (Table 2.1.). The rainfall at the time these studies were undertaken was higher in both fenced reserves compared to the unfenced reserves (Table 2.1.), indicating that the populations of SNR and ANP were stressed and the pressures of poaching, resource competition with surrounding human settlements and limited rainfall increased the calving interval of these populations (Moss 2001; Wittemyer *et al.* 2005; Wittemyer *et al.* 2013). The mean calving interval of populations is, however, is a result of a number of variables and in fenced reserves, where resources are supplemented and human-elephant conflict is minimal, the mean calving interval is likely to be an outcome of high population density.

Density dependent effects is a management approach that has the potential to limit elephant populations in protected areas without resorting to extreme measures such as culling (Laws 1970a; van Aarde *et al.* 1999). In general, the evidence for density dependence in large mammal populations, such as elephant, indicates that the vital rates, mainly fecundity and mortality, change according to food resources available (Fowler 1987, as cited in Gough and Kerley 2006). More specifically, as population density increases to its highest levels there is a series of changes in demographic vital rates of populations. Firstly, an increase in juvenile mortality rate; secondly, an increase in the age of first reproduction; thirdly, a decrease in adult female reproductive rate and lastly, an increase in adult mortality rate (Gaillard *et al.* 2000; Eberhardt 2002; Gough & Kerley 2006). The reason as to why juvenile survival rate is more sensitive to density dependence compared to adult survival rate is because adult survival rate has a higher elasticity and is buffered by temporal variation (Gaillard *et al*. 1998; Gaillard *et al.* 2000; Gough & Kerley 2006). These changes in demographic vital rates of populations of large mammals have been recorded in a number of different species including red deer, *Cervus elephus* (Clutton-Brock *et al*. 1987).

Very little density dependence effects were recorded in the ANP elephant population. It is the only population that has been studied for the extended period of time of 27 years (Moss 2001; Wittemyer *et al.* 2013). The elephant population has not been disrupted in terms of age and sex structure because there has been no poaching for ivory, no culling and no fencing restricting movements (Moss 2001). Thus, the slower reproduction rate (calving interval) displayed in ANP when compared to SNR and KNP is due to the older age structure of the population and not density (Moss 2001; Wittemyer *et al.* 2013). Similarly, no density dependence was found in AENP, the population periodically reached high densities but the impacts were mitigated through the expansion of the park and resource provisioning that dampened the ecological processes that influence elephant populations (Whitehouse & Hall-Martin 2000; Gough & Kerley 2006; Wittemyer *et al*. 2013). Additionally, the vegetation type known as “thicket” is evergreen and highly nutritious and is able to support higher densities of elephants in smaller areas compared to the savanna found in KNP, ANP and SNR (Whitehouse & Hall-Martin 2000; Gough & Kerley 2006).

The average age of a female when she has her first calf or the average primiparous age, is another important factor that can influence a population’s growth rate (Whyte *et al.* 1998; Moss 2001). The younger the primiparous age of a female elephant the longer her reproductive life span, and as female elephants remain fertile well into their fifties, they have the longest reproductive life span of all mammals, therefore greatly contributing towards population growth (Moss 2001). Modelling the KNP population shows that if about 300 females are culled or sterilised just prior to their first pregnancy the population could be driven to extinction (Whyte *et al*. 1998). The average age of first calving was 12 years for ANP and 11.34 years for SNR (Table 2.1.). Whereas the average age of first calving was 13 years for the KNP and 12.5 years for AENP (Table 2.1.). Wittemyer *et al*. (2013), suggest that the age of first reproduction is positively correlated with rainfall and density (t=2.80, p=0.021). Similarly, Shrader *et al.* (2010) found that elephants born in high rainfall years were most likely to survive compared to elephants born in low rainfall years (Rainfall in year of birth: t=2.50, p=0.014). Table 2.1. shows that despite the high density of elephants in AENP the age of first calving is only marginally higher than SNR and ANP but not as high as KNP. This indicates that the variation in the age of first reproduction is a complex function of a female's early growth, nutrition, individual variation in condition and size when close to average age of reproduction, social and ecological conditions at the time and not just density and rainfall (Moss 2001). This is a life history trait that trades off between starting reproduction and maintaining individual condition and growth and is reflected in the observation that the calves of youngest females had a 50% probability of mortality whereas calves of older females had a 24% probability of mortality (Moss 2001).

The annual mortality within populations is a reflection of resource availability, age structure of a population as well as anthropogenic factors such as poaching. The elephant population at SNR was subject to consistent human pressure and predation throughout the study period and so the life expectancy of males (18.9 years) and females (21.8 years) (Wittemyer *et al.* 2005; Wittemyer *et al.* 2013) was much lower than the life expectancy of males (24 years) and females (40 years) at ANP (Moss 2001) (Table 2.1.). Furthermore, the reproductive effort of the elephants in SNR was greater than ANP as they had an earlier age of first reproduction and shorter calving interval, this is similar to other populations with human impacts or that are recovering (Lewis 1984; Moss 2001; Kioko *et al.* 2013; Wittemyer *et al.* 2013). Similar to the SNR population, the elephants of the KNP once suffered from high human impacts in the form of culling, the population has since recovered through great reproductive effort in the form of an even lower calving interval and a lower age of first calf (Whyte *et al.* 1998). It is therefore evident that past management methods of protected areas, location, political and environmental factors influenced the demographic vital rates of elephant populations (Lewis 1984; Moss 2001; de Boer *et al.* 2013; Kioko *et al.* 2013; Wittemyer *et al.* 2013).

Elephant resource use and range distribution in protected areas

Animal population ecology is strongly influenced by variation in the temporal and spatial quality of resources and their abundance (Brown 1984). The seasonal changes in resources, such as plant species composition and abundance, can have a strong effect on herbivore diet, essentially effecting the community dynamics and life history strategies of species (Ostfeld & Keesing 2000; Yang *et al.* 2008). The African elephant is a water-dependent species and so its movement and presence in an area is strongly influenced by the availability and quality of surface water sources (de Boer *et al.* 2000; Chamaille-Jammes *et al.* 2007; Martin *et al*. 2010). African elephants are also classified as mixed feeders as they consume large amounts of grass and browse (Wing & Buss 1970; van der Merwe *et al.* 1988). At great densities the species has been known to modify woody vegetation in protected areas (Wing & Buss 1970; van der Merwe *et al.* 1988; Jacobs & Biggs 2002; O'Connor *et al.* 2007; Mapaure & Moe 2009). The ratio of browse: grass consumed by elephants varies widely across seasons and habitats, some elephant populations have been classified as near pure browsers whereas others have been classified as near pure grazers (Wing & Buss 1970; Guy 1976; van der Merwe *et al*. 1988). Therefore, elephant populations and their distribution are strongly influenced by the resources available to them.

Rainfall patterns not only drive the availability of natural surface water but also the vegetation productivity in an area and both these resources affect the distribution and densities of elephant populations (Loarie *et al.* 2009b; Martin *et al.* 2010; de Boer *et al*. 2013). The diet of elephants is influenced by the species' large body size which requires them to bulk feed on many different trees, shrubs and grasses (Clauss *et al*. 2007; Kerley & Landman 2006). Their wide diet breadth enables them to tolerate foods of low nutritional value and while elephants do not display selective feeding behaviour they are still able to obtain their daily nutritional requirements (Kerley & Landman 2006; Shrader *et al.* 2012). Elephants prefer feeding on grass as it tends to have a greater palatability, holds a higher nutritional value and is generally lower in tannin concentrations compared to browse species (Guy 1976; Cooper & Owen-Smith 1985; de Boer *et al*. 2000; Shoshani *et al.* 2004 Codron *et al.* 2006). Due to the associated constraints of bulk feeding, elephant's diets tend toward a frequency dependent strategy, whereby they select habitats and utilise resources or plant species in proportion to their respective abundances within the habitat (Laws 1970b; de Boer *et al.* 2000; Shrader *et al.* 2012). As a result, elephants tend to predominantly graze in wetter seasons and predominantly browse in drier seasons (Cerling *et al*. 1999; de Boer *et al.* 2000; Cerling *et al.* 2004; Cerling *et al.* 2006; Codron *et al*. 2006; Codron *et al*. 2011).

There is little consensus regarding the African elephant's feeding strategy as several authors have argued that elephants diets do not reflect the relative availabilities of browse and grass species, rather elephants strategize their feeding habits to maximise their nutrient uptake and so focus on plants and habitats that have a higher nutritional value (Wing & Buss 1970; Shoshani *et al*. 2007; Codron *et al.* 2006; Loarie *et al.* 2009a; Owen-Smith & Chapota 2012). Studies have demonstrated that when feeding, elephants do display preferences for certain tree species and growth forms, such as tree height, and suggest that this could be due to the differences in nutritional content and/or plant defence mechanisms (Barnes 1982; Jachmen & Bell 1985; Stokke & du Toit 2000; Styles & Skinner 2000). There are a limited number of studies that investigate the diet of elephants in relation to food availability and so despite numerous dietary studies, our current understanding of elephant foraging decisions is still theoretical (Jachmen & Bell 1985; O'Conner *et al.* 2007). This is partly due to the comparison of data from different studies within different habitats and different time periods which can lead to multiple sources of error (Field 1972; Cerling *et al*. 2009).

Due to the theoretical nature of our understanding of elephant foraging strategies there is still some controversy as to whether elephants are principally browsers or grazers. A few authors have suggested that savanna elephants are predominantly grazers as certain populations had a high component of grass in their diets at the time of study (Laws 1970a; Laws 1970b; Wing & Buss 1970; Cerling *et al.* 2004). Other authors have found savanna elephants to have a high proportion of browse and very little grass in their diet (Cerling *et al*. 1999; Cerling *et al.* 2004; Cerling *et al.* 2006; Cerling *et al*. 2009; Codron *et al.* 2011). Traditional methods of analysing elephant's diet consisted of field observations or microhistological examination of gut and faecal contents (de Boer et al. 2000). These methods were deemed to be too time consuming to facilitate interregional or interhabitat comparisons of diet and so did little to solve the controversy (de Boer *et al.* 2000). A newer method that has become a common tool for studying the nutritional ecology of wildlife is stable isotope analysis and is based on knowledge of fractionation occurring in metabolic processes of plants and animals (van der Merwe *et al.* 1988; Codron *et al.* 2005). Stable carbon isotope analysis provides a means to quantify the consumption of browse and grass by savanna herbivores across multiple space and time scales (Codron *et al*. 2006). Stable carbon isotope ratios are distinct to plants that employ a C_3 photosynthetic pathway (trees, shrubs and forbs) and plants that employ a C_4 photosynthetic pathway (grasses) (Smith & Epstein 1971; Vogel *et al.* 1990). The consumer's tissues and excreta reflect the carbon from the food and so herbivore $_{13}C/_{12}C$ ratios reflect the proportions of browse and grass in diet (Vogel *et al.* 1990; Cerling *et al*. 1999; Codron *et al*. 2005; Codron *et al.* 2006). Although stable isotope analysis lacks the finer detail of microhistological techniques, the approach is a standardised method that produces data sets that are easily comparable with other studies across the continent. Stable isotope studies across Africa have shown that elephants are primarily browsers (<15% grass in diets) (van der Merwe *et al.* 1988; Tiezen *et al*. 1989; Vogel *et al.* 1990; Cerling *et al*. 1999) but moderate amounts of grass are consumed by some populations, such as the Tsavo (hereafter, TENP) and ANP elephant populations isotopically analysed by Koch *et al.* (1995) and Cerling *et al.* (1999).

Although elephants may currently be primarily browsers that substitute their diet with grass, their phylogenetic lineage suggests that modern elephants have ancestors that shifted between grazing and browsing (Cerling *et al*. 1999). From the late Miocene era to the Pleistocene era elephant's predominantly grazed but a dietary shift occurred less than one million years ago where elephants switched to browsing (Cerling *et al.* 1999). Like their ancestors, modern African elephants are large bodied, generalist herbivores that are capable of feeding on both browse (C_3 biomass) and grass (C_4 biomass) although the proportions of browse: grass consumed will vary according to factors that include geographic variability, rainfall and season, resource availability and quality, gender and proximity to permanent water sources (van der Merwe *et al.* 1988; Codron *et al.* 2006; Codron *et al.* 2011; Shrader *et al*. 2012).

Geographic Variability

Carbon from the vegetation consumed by herbivores is incorporated into animal body tissues and so the stable isotope analysis of elephants bone collagen reflects the $^{13}C/^{12}C$ ratios of the proportion of grass to browse consumed by an individual (Cerling *et al.* 1999). The analysis of a number of different bone samples collected from around the Africa revealed that savanna elephants from Namibia, South Africa, Botswana, Zambia and Malawi have a near pure C_3 diet with very little C_4 intake (van der Merwe *et al.* 1988). There were two exceptions to this; the first was AENP, South Africa, where elephants have a relatively low C_3 diet due to the CAM plants that make up to 40% of plant cover in the area (van der Merwe *et al*. 1988; Kerley & Landman 2006). The second was the TENP and ANP populations in Kenya, where elephants had a significantly large proportion of C_4 grass in their diet (van der Merwe *et al.* 1988). In TENP, this was attributed to a high elephant density that transformed the woodlands into grassland (Napier Bax & Sheldrick 1963, van der Merwe *et al.* 1988; Cerling *et al*. 2004).

The isotopic analysis of bone collagen tends to under represent the grass component of the diet due to the inefficiency of the elephant's digestive system at extracting inaccessible proteins from C_4 grasses (van der Merwe *et al.* 1988; Codron *et al*. 2005; Codron *et al*. 2006). Despite representing the excreted and undigested portion of the diet, the carbon isotopic composition of faeces has shown to be consistent with dietary values during both experimental and field studies and enables a finer scale of comparison between location and time (Tieszen *et al.* 1989; Sponheimer *et al.* 2003; Codron *et al.* 2005; Codron *et al.* 2006). The use of faecal carbon in isotopic studies suggests that elephants chiefly browse on C_3 woody vegetation in the dry season and graze on C_4 grasses in the wet season (Cerling *et al.* 2004; Cerling *et al.* 2006; Cerling *et al.* 2008). A dietary study conducted in the KNP using faecal carbon indicated that elephants inhabiting the northern areas of the park consumed significantly more grass (>30% more) compared to southern elephants, in the dry season (Codron *et al*. 2006). The difference in grass consumed was a result of the northern elephants consuming more grass as an alternative resource to a homogenous mopane-dominated landscape, whereas southern elephant populations had a higher tree diversity and so a greater dietary variety (Codron *et al*. 2006). The use of faecal samples in isotopic analysis has demonstrated that location does affect the proportion of browse: grass consumed and is linked to climate and resource availability (van der Merwe *et al*. 1988; Cerling *et al*. 1999; Shrader *et al*. 2012).

Seasonal Rainfall and Habitat Selection

The quality of the Savanna elephant's diet fluctuates with the seasonal variation of resources. In the dry season, diet quality decreases for elephant populations due to limited availability and poor quality of resources (de Boer *et al.* 2000; Woolley *et al.* 2008; Gaugris *et al.* 2009). In the wet season, however, the quality and quantity of resources increases and so elephants selectively feed on vegetation that is higher in nutritional value, this constitutes an increase in the consumption of C_4 grass by a mixed-feeder that is normally dominated by browse (Barnes 1982; de Boer *et al.* 2000; Cerling *et al.* 2004; Cerling *et al.* 2006; Codron *et al.* 2006; Cerling *et al.* 2009; Kos *et al.* 2012; Shrader *et al*. 2012). Owen-Smith & Chapota (2012) found that elephants only browsed on 30% of 27 common woody species during the wet season but this increased to 50% of the same species in the dry season. This indicates that elephants prefer high quality forage and so they select woody species based on nutritional quality and not availability (Owen-Smith & Chapota 2012). The elephants also shift the plant parts browsed on from just leaves and shoots in the wet season to stem bark and roots in the dry season (Owen-Smith & Chapota 2012).

Season influences the quality and availability of forage so with the change in season elephants must adapt their foraging strategy (Loarie *et al.* 2009a; Owen-Smith & Chapota 2012; Shrader *et al.* 2012). However, elephants select habitats independent of season as they consistently seek out vegetation that is greener than expected throughout the year (Skarpe *et al*. 2004; Loarie *et al.* 2009a; Codron *et al.* 2011; Shrader *et al.* 2012; Okello *et al*. 2015). In the wet season elephants select seasonally variable landscapes, which only contain high quality forage for a few months a year such as shrub lands, grasslands and dambos (flooded grasslands) (Loarie *et al*. 2009a). In the dry season landscapes become less variable as vegetation quality decreases and is interspersed with bare ground and so elephants prefer landscapes of good quality, such as well wooded areas and closed woodlands (Loarie *et al.* 2009a; Shrader *et al.* 2012). Thus, elephants initially focus their feeding on large spatial scales, preferring landscapes of higher quality (Loarie *et al*. 2009a). Yet the dependence of elephant on woody species in the dry season and the narrowed selection of woody species in the wet season suggests that elephants do adjust their foraging strategy on a seasonal basis (Loarie *et al*. 2009a; Codron *et al.* 2011; Owen-Smith & Chapota 2012; Shrader *et al.* 2012).

Sexual and spatial segregation in habitat use

In order to optimise nutritional trade-offs against limitations imposed by body size, nutritional requirements, digestive anatomy, physiology and food resources, mammalian herbivores adopt foraging strategies. Due to their large body size elephants have adopted sexual segregation as a form of foraging strategy (Stokke & du Toit 2000). This is often referred to as the Body Size Hypothesis whereby larger ungulates can tolerate a wider range in diet quality (digestibility) compared to smaller ungulates (Stokke & du Toit 2000). According to the hypothesis, elephant bulls and cows should utilise different browse resources in response to different metabolic demands (Stokke & du Toit 2000; Shannon *et al*. 2006a; Woolley *et al.* 2008). Females are expected to feed more selectively on higher quality forage whereas males are expected to feed less selectively on abundant forage of lower quality (Stokke & du Toit 2000; Shannon *et al.* 2006a; Woolley *et al*. 2008).

The Body Size Hypothesis proposes that bulls have higher ingestion rates and thus have a greater digestion efficiency than cows (Stokke & du Toit 2000; Shannon *et al.* 2006b; Woolley et al. 2008). Bulls have a less diverse diet in terms of woody plant species and they consume more plant parts than cows and family units (Stokke & du Toit 2000; Shannon *et al*. 2006b; Woolley *et al.* 2008). Additionally, bulls spend more time foraging on each woody plant, ingesting greater quantities of forage at each feeding bout and displaying destructive behaviour by engaging in tree felling (Guy 1976; Barnes 1982; Stokke & du Toit 2000; Shannon *et al.* 2006b; Woolley *et al.* 2008). Smaller bodied cows, specifically breeding individuals, have higher mass specific nutritional demands due to gestation and lactation and so feed more selectively on higher quality forage than bulls (Stokke & du Toit 2000; Shannon *et al*. 2006b; Woolley *et al*. 2008). In general, cows tend to have a more diverse diet in terms of woody plant species, are more selective for higher quality plant parts and exhibit shorter feeding bouts due to the social constraints of family units compared to bulls (Guy 1976; Barnes 1982; Stokke & du Toit 2000; Shannon *et al*. 2006b; Woolley *et al*. 2008).

The ranging behaviour of bulls and family units differs depending on the season. In a study focusing on the sexual segregation in habitat use of elephant in Botswana, Stokke and du Toit (2002) reported in the dry season bulls frequented more habitat types compared to family units and roamed widely (>10km) from perennial drinking water (Stokke & du Toit 2002). Larger bodied male elephants are consistently able to adapt their movement behaviour according to forage quality and abundance (Ntumi *et al.* 2005; Shannon *et al.* 2006b; de Knegt *et al.* 2011), whereas the smaller bodied females are unable to exhibit the same flexibility in ranging behaviour because of their higher nutritional demands, lower tolerance to fibrous forage and the social and energetic constraints of group living with juveniles and calves (Stokke & du Toit 2000; Shannon *et al.* 2006b; Woolley *et al*. 2008; de Knegt *et al.* 2011). Due to body size constraints and group living, elephants adopt a selective strategy that maximises the rate of nutritional intake by targeting abundant but often lower quality foraging opportunities through the expansion of home ranges during years when rainfall is below average (Shannon *et al.* 2006b; Kinahan *et al.* 2007; Smit *et al.* 2007; de Knegt *et al.* 2011). This indicates that home range size is primarily dictated by abiotic factors at a landscape scale, more specifically though home range size is influenced by vegetation productivity only during the wet season as elephants are less restricted by water compared to the dry season (Leggett 2006; Shannon *et al*. 2006b; Chamaille-Jammes *et al.* 2007; Harris *et al*. 2008; Roux & Bernard 2007; Young *et al*. 2009a).

Habitat Use and proximity to water resources

African elephant movement is complex and seasonally variable but in general habitat use tends to increase with proximity to water sources (Harris *et al.* 2008; Staub *et al.* 2013). The distance travelled by elephants within seasons varies greatly depending on the resources available (Grainger *et al.* 2005; Chamaille-Jammes *et al.* 2007). When essential resources occur locally elephants will travel less than a few kilometres from day to day (Chamaille-Jammes *et al.* 2007; Harris *et al.* 2008). Elephant ranging behaviour also depends on the season: in the dry season elephants are limited to areas surrounding permanent water sources whereas in the wet season ephemeral pools allow elephants to expand their movement across more of the landscape (Bhima & Dudley 1997; Dudley *et al.* 2001; Galanti *et al.* 2006; Leggett 2006; Chamaille-Jammes *et al*. 2007; Kinahan *et al.* 2007; de Beer & van Aarde 2008; Harris *et al.* 2008; Loarie *et al.* 2009a; Young *et al*. 2009b). However, this is not always the case as in Etosha National Park for example, the vegetation is much sparser, low in productivity and species poor, so elephants must travel greater distances between vegetation and water sources (Verliden & Gavor 1998; de Beer *et al.* 2006; Harris *et al.* 2008). A similar example of this is in Pongola Reserve, South Africa, where elephants displayed smaller ranges in the wet season compared to the dry season due to abundant vegetation that proved it unnecessary for elephants to increase the size of their home range (Shannon *et al*. 2010). This indicates that elephant home ranges are dependent upon the season, the vegetation available and the distance to water sources (Whitehouse & Schoeman 2002; Leggett 2006; Chamaille-Jammes *et al.* 2007; Roux & Bernard 2007; Harris *et al.* 2008).

Conclusion

Across Africa elephant numbers are decreasing due to habitat loss and fragmentation, human-elephant conflict, poaching for meat and ivory and the negative localised impacts of elephants on their habitat (Blanc *et al*. 2002; Blanc *et al.* 2007). In Southern Africa, a growing number of reserves are being fenced, essentially creating ecological islands in the form of artificially closed systems (Boone & Thompson Hobbs 2004). Fences have multiple effects on ecological processes within protected areas including limiting wildlife dispersal and the resources available to wildlife populations (Newmark

2008). Many elephant populations are increasing in these fenced, protected areas due to increased protection, limited migration and the provision of resources in the form of artificial waterholes (Laws 1970b; van Aarde & Jackson 2007). This complicates the management of these structured systems as the vegetation is exposed to increased foraging pressure that potentially leads to loss of woody vegetation cover (Duffy *et al*. 2002; van Aarde & Jackson 2007; Loarie *et al*. 2009a; Mapaure & Moe 2009). In order to maintain the balance between healthy elephant populations and the integrity of the ecosystems they occupy it has become a necessity for reserve managers to understand the primary factors affecting the demographic vital rates of elephant populations and how these can be manipulated to control population growth (Moss 2001; Wittemyer *et al.* 2005; Gough & Kerley 2006; Wittemyer *et al.* 2014). The vital rates of populations are primarily affected by factors such as resource quality and availability and so it is important to investigate the species dependence on the resources and their basic nutritional requirements, such as diet, in order to compile an effective management plan.

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Chapter 3

The population structure and habitat use of the African elephant (*Loxodonta africana*) in Majete Wildlife reserve, Malawi

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Abstract

African elephants are a species of high conservation concern. Due to elephant's status as a keystone species, their economic value and the threat of habitat loss they are the focus of numerous studies across various disciplines. The aim of this study was to firstly determine, with the use of individual identification techniques, the size, sex and age structure of the elephant population in Majete Wildlife Reserve, Malawi. Secondly, this study aimed to determine habitat use and movement of the population over time. An aerial survey conducted in late 2015 counted a total of 389 elephants in the reserve. The present study was able to formally identify 366 of these individuals, consisting of 47 different family herds, 91 solitary bulls and a sex ratio of 1:1. The largest age classes in the population were the medium sized adults (26.8%) and calves (23.8%). In the absence of migration and heavy poaching, the population has an estimated growth rate of 13.8%. In the dry seasons elephants appeared to remain close to perennial water sources such as the rivers, waterholes and springs situated on the eastern side of the reserve. Elephants tended to utilise the water points more in the dry season compared to the wet season and preferred areas of lower altitude mixed woodland. The population has an extremely high growth rate and it is postulated that it is operating under optimal conditions and has not yet begun to stabilise. Due to an increasing density of elephants, their home ranges are now expanding into the least preferred vegetation types, such as *Brachystegia* dominated woodland, and higher altitude regions in the reserve.

Key words: African elephant, camera traps, demography, habitat use, Malawi

Introduction

Detailed demographic data is only available for a small number of species, which are typically of high economic or conservation value (Gaillard *et al.* 1998). Furthermore, demographic data that has been compiled for these species has been generated from a single population and so data regarding multiple populations is generally not available (Gaillard *et al*. 2000). This essentially limits the ability to monitor a species' demographic responses to anthropogenic and ecological pressures as there is a lack of information on life history strategies across biological systems (Stockwell *et al.* 2003; Owen-Smith *et al.* 2005). Therefore, in order to manage and conserve species in the future it is of the utmost importance that species specific responses are understood, particularly for those species that are threatened or are economically prominent to their range states.

One of the better studied species in terms of detailed demographic data is the African elephant (*Loxodonta africana*). To date multiple studies have been conducted using individual based monitoring programs or culling data to provide demographic parameters for various populations (Wittemyer *et al*. 2014). African elephants are a keystone species and the state of their populations are critical to the ecosystems they occupy (Power *et al*. 1996). The species plays a pivotal role in ecological systems by influencing factors such as canopy cover (Dublin *et al.* 1990), species diversity and distributions (Pringle 2008) and seed dispersal (Spanbauer & Adler 2015). Although the majority of studies conducted suggest that elephants can have a detrimental effect on their environment as they are capable of transforming habitats, elephants can also be largely beneficial (Gough & Kerley 2006; Morrison *et al.* 2016). The impact this species has on its environment is determined by a number of factors that include location, available resources, the confinement of a population and population density (Skarpe *et al.* 2004; Kerley & Landman 2006; Chamaille-Jammes *et al.* 2008; Loarie *et al.* 2009). In order to understand what particular factors contribute to the influence an elephant population has on its environment, the demographic responses of the population need to be determined and these data are invaluable for both theoretical and management applications.

The African elephant is a flagship species that is of high economic value, especially in the commercial trade for ivory and ecotourism (Douglas-Hamilton 1987; Owen-Smith *et al*. 2006; Wittemyer *et al.* 2014). The species conservation status varies across the African continent, for example nearly a quarter of the total population of elephants inhabits one region in Botswana whereas the species has gone locally extinct in Central and Western Africa (Blanc *et al.* 2007; Bouche *et al.* 2011). Concurrently, the African elephant has an extreme life history strategy with long periods of sexual reproduction, sexual immaturity, the longest mammalian gestation period and a very slow rate of reproduction (Moss 2001; Wittemyer *et al.* 2014). Thus, the study of the population dynamics of such a species is limited by the collection of longitudinal data on demography as it would take up to 60 years to gain the complete life history of a single population (Moss 2001). However, due to the high economic value and conservation significance of the African elephant this limitation has not prevented multiple studies of the species being undertaken over the years.

A few of the earliest demographic studies of African mammals focused on elephants and the majority of these studies were conducted in Eastern and Southern Africa (Buss & Smith 1966, Laws 1966, Short 1966, Hanks 1969, Hanks 1972, Williamson 1976). Most of these earlier studies employed the method of carcass examination whereby the carcasses of individuals killed from culling operations were analysed, representing a cross section of a population from a single point in time (Whyte & Grobler 1998; Moss 2001; Whyte *et al.* 2003). In reserves that employed regular culling as a standard measure to control elephant populations, studies were able to model the demographic data of populations at successive points in time (Whyte & Grobler 1998; Moss 2001; Whyte *et al.* 2003). However, the current methods used to estimate the size of elephant populations are less invasive and include aerial surveys, faecal counts, direct counts using line transect sampling or stratification, and intensive ground based surveys providing total counts by means of registration of individual known animals (Douglas-Hamilton 1996, Mbugva 1996, Jackman 1996, Barns 1996, Whitehouse & Hall-Martin 2001). Techniques used to determine the age structure of populations involve ground and aerial surveys which rely on methods such as the measurement of shoulder height, back length, foot print length and visual assessments based on visual estimates (Croze 1972, Leuthold 1976, Jachman & Bell 1984, Lindeque 1991). Culling has been eliminated as a standard form of management in many Southern African reserves since the mid 1990's and so current methods used to gauge the demographic status of a population rely on assumptions and predictions to describe a population's history and project its future trends.

To date very few studies have followed elephant populations in detail over time. One particular study conducted in Addo Elephant National Park (AENP) recorded the precise population numbers and reconstructed each individual's life history since the park was fenced in 1931 (Whitehouse & Hall-Martin 2000). Apart from a brief population study conducted in the Luangwa Valley, Zambia, (Lewis 1984) the Amboseli National Park (hereafter, ANP) elephant study in Kenya remains the only other long term study of individually known free ranging elephants (Moss 2001). However, several other studies have employed the same mark-recapture methods used in these long term studies as a management tool to determine the demographic structure of confined elephant populations (Whitehouse & Hall-Martin 2000; Morley & van Aarde 2007; Trimble *et al*. 2009).

In Majete Wildlife Reserve (MWR hereafter), Malawi, a total of 213 individual elephants were reintroduced into the park by 2010. Since the reintroduction, aerial counts have suggested an increasing elephant population but no detailed demographic data has ever been recorded. Thus, reserve management is lacking the vital information it needs to decide a future course of action for this population.

The primary aim of this study was to characterise the demographic status of the Majete elephant population. More specifically the study aimed to firstly, use individual identification techniques to determine population size, age and sex structure. Secondly, to compare the populations current demographic parameters with those from initial reintroductions. Thirdly, this study aimed to determine the habitat use and movement of the elephants throughout MWR.

Techniques used to estimate the population size or densities of large mammals living in wooded areas are poorly developed and methods such as faecal counts and aerial surveys are inadequate for a reserve, such as MWR, where the majority of the vegetation is woodland (Caro 1999; Walsh *et al.* 2001; Whitehouse *et al.* 2001; Payne *et al.* 2003). Although aerial survey methods are well developed for open habitats, they tend to underestimate the number of individuals in small populations, below 250 individuals, in dense habitats and this error increases with increasing population size (Whitehouse *et al.* 2001, Morely & van Aarde 2007). Mark-recapture methods were therefore employed to study the demographics of the Majete elephant population through on-the-ground visual assessments and camera trapping. Results were used to determine the response of the population post reintroduction, providing a deeper understanding of reintroduction biology and thus contributing towards reserve management strategies.

Methods and Materials

Study Area

Majete Wildlife Reserve is located at the southern tip of the Great Rift Valley in the lower Shire Valley region of southern Malawi (S15° 54’26.6”; E034°44’24.3”) (Figure 3.1.). It is a 700km^2 reserve with northern and eastern boundaries defined by two perennial rivers, the Mkulumadzi and the Shire. The altitudinal gradient of the reserve varies, it is highest in the western region, Namisempha, where steeply undulating hills are distorted by river valleys and gradually decreases towards the eastern region of the reserve, the Sanctuary, where the terrain flattens towards the Shire River. Majete has two distinct seasons, the wet season (December to May) and the dry season (June to November). The expected annual precipitation in the reserve is between 680-800mm in the eastern lowlands and 700-1000mm in the western highlands (Wienand 2013). Water availability is dependent on seasonal rainfall, however, MWR has a number of perennial springs along with ten borehole-fed artificial waterholes. The vegetation is primarily woodland and it varies from low to high altitudes. The vegetation types are high altitude (410-770m) miombo woodland (*Brachystegia boehmii, Burkea africana* and *Pterocarpus*), medium altitude (230-410m) mixed woodland (*Brachystegia boehmii, Diiospyrus kirkii* and *Combretum* species), low altitude (205-280m) mixed woodland (*Acacia* species and *Steculia*) and savanna (*Combretum* species*, Acacia* species and *Panicum* species) (Patel, H. Unpub.).

Majete Wildlife Reserve was gazetted in 1955 but by 2003 most of its large game had been decimated due to poaching and poor management. In 2003, MWR underwent one of Africa's greatest reintroduction programmes, after a Public Private Partnership (PPP) agreement was made between African Parks, Majete (Pty) Ltd. and the Malawian Department of National Parks and Wildlife (DNPW). Wildlife reintroductions to MWR were undertaken in stages as the reserve was not initially fenced in its entirety. The first stage involved fencing a smaller area of 140km^2 in the north-eastern region, the Sanctuary, for reintroduction purposes in 2003. The second stage involved fencing the remaining boundary of the reserve and was completed in 2008, after which the sanctuary fence line was removed in 2011 and wildlife was able to roam into the greater reserve. In total over 2550 individual animals of 14 different species were reintroduced into MWR. Species reintroduced included elephant, black rhino, buffalo, sable, hartebeest and numerous other antelope species.

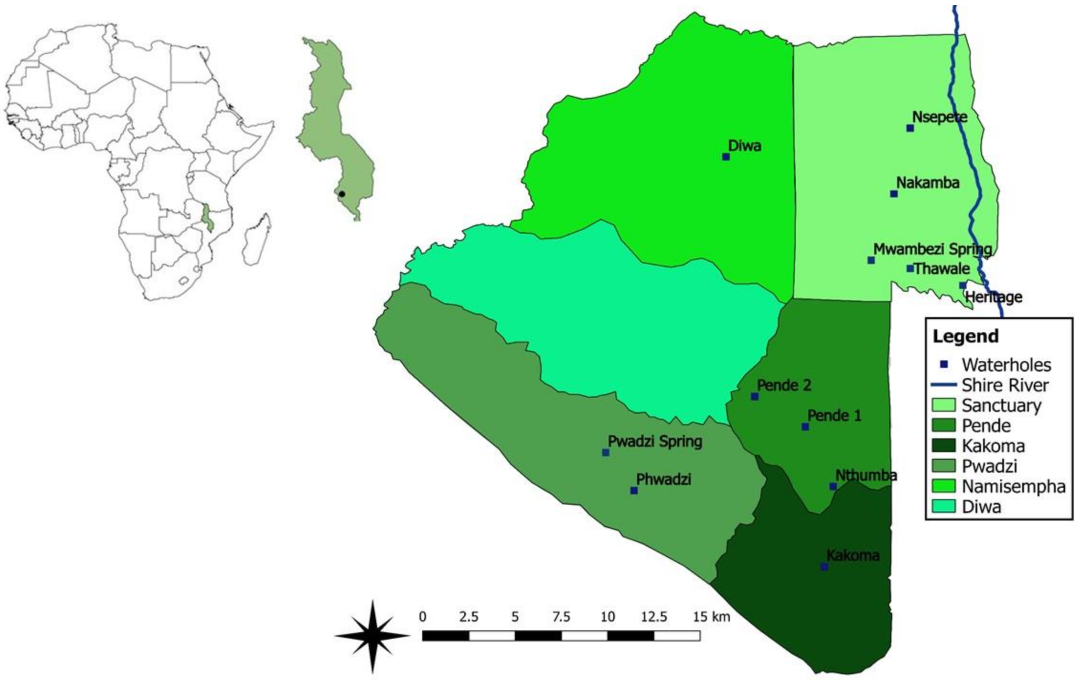


Figure 3.1. The location of Malawi on the African continent and the position of Majete Wildlife Reserve in Malawi. The various regions and perennial water sources that occur within the reserve are also shown. (Shapefiles per comms. African Parks (Pty) Ltd.)

Methods

Defining the population size, age and sex structure

In order to determine the size, age structure and sex ratio of the elephant population in MWR the majority of individuals needed to be identified and so this study modified the methods used by Moss (1996), Whitehouse and Hall-Martin (2000), Moss (2001) and Morley and van Aarde (2007) to identify individuals and record their gender, age and other unique characteristics. Sampling was conducted using two methods. The first was field observations which comprised of randomised distance sampling and waterhole counts. The second was camera traps which recorded images of individuals and herds, where cameras were placed at various artificial waterholes and springs and along the road network in grids. In this particular section of the overall study, the population status was determined for 2015 and early 2016 and so field observations commenced in April 2015 and ended in April 2016 and camera trap images were recorded from January 2015 to January 2016.

a) Individual Identification Techniques

Using mark and re-sight methods, upon observation in the field photographs were immediately taken of elephants and individuals were 'marked' by recording various characteristics and unique markings which can be used to facilitate individual identification. These characteristics included for example: age, sex, body size, ear shape, any notches or holes present in the ears, patterns of blood vessels in the ears, wrinkles on the face, tusk size and configuration, lumps or scars on the body and kinks or baldness of the tail. Also recorded was the total number of individuals, GPS locations and numerous photographs of each individual were taken.

Elephants were later positively identified as 'marked' or 'unmarked' using a customised database, developed by the author (Appendix 2.1. & 2.2.). The database aided the identification of individual elephants as it contained photographs and profiles of all encountered individuals and herds, and information such as estimated age of individuals, sex and other identifying characteristics mentioned above were recorded. When an unknown animal was encountered it was given an identification code, it was sexed and aged and any unique characteristics were recorded, after which it was added to the 'known' population database (Appendix 2.3). After 13 months of sampling the majority of the elephants in the population were sexed and approximate ages estimated, based on size and developmental state. Since elephants grow throughout their lifetime, individuals were aged according to the following size categories (Moss 1996):

Infant (0-0.9 years):	Infant's shoulder was taller than the breast level of mother, reaching wrinkles above elbow.

Calf (1-4.9 years):	Top of calf's shoulder above mother's armpit, back was level with anal flap and reached lower quarter of mother's ear. Tusks 5-7cm.
Juvenile (5-9.9 years):	Overall size of juvenile was about three quarters of adult female. Tusks splayed and 25-30cm in length.
Small Adult Female (10-19.9 years):	Same size as other adult females. Tusks had adult configuration (convergent, straight or asymmetrical). Body was square in shape compared to older females who were more rectangular.
Small Adult Male (10-19.9 years):	Same size or slightly taller than adult females. Head shape (sloping rather than angular) was more noticeable, tusk circumference was thicker than females of same age.
Medium Adult Female (20-34.9 years):	Circumference of tusks at base was distinctly bigger than small adult females. Bodies became more rectangular.
Medium Adult Male (20-34.9 years):	Taller than all adult females, head began to thicken and change into an hour glass shape, wide at the eyes and the base of the tusks.
Large Adult Females (>35 years):	Tusks marginally thicker, back lengthened so animal appeared long in body. Older females hollowed above the eyes, ears held lower, longer back length.
Large Adult Males (>35 years):	Very big, towered over largest females. Neck thick, overall body heavy set, tusk circumference at lip greater than younger males.

b) Distance Sampling

Established roads were used to conduct drive transects throughout MWR. Sampling in the Sanctuary was conducted on a weekly basis and sampling in the remainder of the reserve was conducted on a monthly basis due to logistics. Sampling generally began just before dawn and continued until after sunset, with a rest period during the hottest part of the day. The majority of sampling was conducted by a single observer, however, from June to December 2015 volunteers assisted in the observation and recording of data during counts. An average cruising speed of 15 kilometres per hour was maintained when searching for animals and due to the dense nature of the vegetation in the reserve, visibility of elephant was generally less than 150m. Elephants were initially sighted with the naked eye and binoculars were used when necessary to determine age, sex and observe other unique characteristics. Data recorded for distance sampling included: date, time of observation, GPS position of observer, total number of elephant seen, number of males and females and the respective age classes of individuals (infant, calf, juvenile, small adult, medium adult and large adult). Additionally, photographs were taken at each observation using a Nikon D40x DSLR camera. Images were later analysed and added to the database. Images recorded from distance sampling were analysed using the same method as described above.

c) Waterhole Counts

MWR has ten borehole-fed artificial water points and the majority of these water points were powered by solar energy. Counts were conducted at four artificial water points in the Sanctuary (Nsepete, Nakamba, Thawale and the Heritage) and one artificial water point in the Pende region (Nthumba) from June to December 2015. Counts were conducted for 12 hour periods and commenced at 06h00 and ended at 18h00. In the Sanctuary, three to four observers were stationed on a viewing platform or in an elevated hide from which elephants were monitored at the waterhole. Data recorded included the weather conditions (cloud cover, temperature), total number of elephants sighted, time of observation of individual or herd, the gender and ages of each individual and several behavioural observations (interspecific or intraspecific interactions). Additionally, photographs of each sighting were taken with a Nikon D40x DSLR camera and later added to the database.

d) Camera Trapping

Camera trapping, a non-invasive research technique, has been used in a number of studies to determine the relative abundance of certain species across a specific area. In MWR camera traps were a useful form of sampling as they increased the sampling area and allowed for continued monitoring of sites that, due to time constraints, could not be accessed more than once a month. In this study, Cuddeback™ Ambush© Black Flash© camera traps were stationed at specific artificial waterholes throughout the reserve for one dry season (June 2015 - November 2015) and one wet season (December 2015 - April 2016). Cameras were placed at seven of the artificial waterholes and at one perennial spring (Pwadzi Spring) due to the ease of access of these water points. Due to maintenance and technical issues at two waterholes (Pende 1 and Nthumba) only data from five water points (Nsepete, Nakamba, Diwa, Pende 2 and Pwadzi spring) was used in this study. Each camera was placed at each station for a period of 30 days after which SD cards and batteries were changed. Once images were downloaded from SD cards they were sorted, according to date and location, and saved into the appropriate files on an external hard drive.

In order to identify elephant individuals and herds in MWR individual identification techniques (as mentioned above). All data recorded from images was entered into Microsoft Excel 2013 and the customised database. In terms of analysing the camera trap images the following assumptions applied: firstly a single image containing elephants (bulls or family herds) was considered a single observation if no other photographs were taken. Secondly, if individuals were captured on camera in a continuous sequence of photographs in a short period of time (approximately 20 min) on the same day they were assumed to be from the same herd. Thirdly, when family herds were confirmed the sequence of photographs captured of the herd within 60 min was considered a single observation for that specific herd. Fourthly, once an extended period of time, longer than 60 min, had passed between photographs and new individuals had been confirmed they were assumed to be from a different herd. Lastly, small, medium and large adult bulls were assumed to have left their original family herds. This is as bulls tend to leave their family herds between the ages of 11 and 13 years. If an individual bull was captured on a photograph with a family herd, notes were taken but the individual was assumed to range alone.

e) Aerial census

In order for MWR management to determine the total size of the elephant population in the reserve aerial counts were conducted in 2010, 2012 and 2015. All aerial count data was provided by African Parks (Pty) Ltd. Exact methods and aerial count teams differed over the years, however, the basic procedure was the same. All aerial counts were conducted in the dry season and each aerial count consisted of a pilot and 1-3 observers. Counts were flown in transects, the calibrated strip width of each transect was 500m and flight paths were orientated in an east to west direction. Due to the size of MWR counting blocks were established (blocks varied in size and location per aerial count), each block in the reserve was counted on a separate day and all blocks were counted on consecutive days. When animals were sighted data recorded included the GPS track log of all transects, game species and number of individuals, and any significant waypoints were also marked using a GPS.

Comparing the current population with populations from the initial reintroductions

In order to determine how much the current elephant population has changed demographically since the reintroductions into MWR in 2006, 2008 and 2010, the data gathered from this study were compared to the capture records from the three translocation phases. All data regarding the capture records were acquired from the DNPW. However, the capture records from the 2006 and 2008 translocations were missing, so as a result only the 2010 capture data were utilised in this study. The capture records contained information such as the total number of individuals and the gender and ages of each individual translocated to Majete from Liwonde National Park and Pirilongwe Forest Reserve.

Habitat use and movement

The primary method used to determine the elephants' habitat use and movement in MWR was camera trapping. Sampling employed the same camera trap method mentioned above, where by camera traps were placed at certain perennial water points in MWR. Unlike in the previous section, this study required data from a number of different years in order to observe how habitat use and movement possibly changed over time. Thus, camera traps were placed at perennial water sources in

2014, 2015 and 2016. To sample elephant's waterhole use in different habitats and at different altitudes camera traps were stationed at Nakamba, Nsepete, Pende 2, Diwa and Pwazi spring (Figure 3.1). SD cards and batteries were changed on a monthly basis and all images were analysed using Timelapse Image Analyser 2.0 (Greenberg Consulting Inc. 2016).

Camera trap gridlines were established in MWR to determine elephant movement over time and to observe whether elephants influence the presence of other species. The camera trap grid delineated the 700km^2 reserve into four grid lines running from north to south. Sampling took place in the wet (January - May) and the dry (June - October) seasons in 2014 and 2015. All grid lines were designed according to the road network in MWR and covered the four different vegetation types, namely, high altitude woodland, medium altitude woodland, low altitude woodland and savanna. Only one of the grid lines was placed out in the field at any given time for a period of 30 days and once one grid was retrieved the next grid was immediately positioned. Each grid line consisted of eight stations and each station had a single Cuddeback™ Ambush© Black Flash© camera attached to a specific tree/shrub. Cameras were placed at each gridline once per season and twice per year (wet and dry seasons) and the same protocol was followed for 2014 and 2015. Stations were preferentially placed at jeep track intersections, wildlife trails, or in river beds. Before all cameras were placed in the field the time and date settings were checked and cameras were set to take photos at one minute intervals once motion sensors were triggered. A total of 32 camera stations were set out for the period of this study and data was analysed from 30 of these stations

For this particular section, all images acquired from camera traps were analysed in Timelapse Image Analyser 2.0 (Greenberg Consulting Inc. 2016) where the time, date, species, total number of individuals, gender and ages were recorded. In order to determine whether elephants influenced the presence of other species in the reserve, images recorded from camera grids were analysed in terms of all species that occur in MWR and not just elephants. Images recorded from camera traps set at water points, only included elephants so as to determine which water points were preferred and how family herds and bulls differed in their water point usage. The assumptions mentioned above apply to this section but for clarification, an observation at a water point was defined as the presence of elephants (bulls or herds) at a water point for a period of no shorter than 5 minutes and no longer than an hour. Once the time frame was over, unless proven otherwise, a new observation was started with a new elephant. All data from Timelapse Image Analyser 2.0 (Greenberg Consulting Inc. 2016) were exported into Microsoft Excel 2013, sorted and later analysed. Lastly, all mapping displaying data from camera grids as well as water points was conducted in QGIS 2.16.0 (Creative Commons Attribution-ShareAllike 3.0 Licence (CC BY-SA)).

Statistical Analysis

All statistical analyses were performed using Statistica, version 13 (©Statsoft Inc., 2016). To determine whether there was any significant statistical change in firstly, the size of the elephant population and secondly, the age structure of the population from 2006 to 2015, a regression analysis was used. To determine whether there was any significant difference between the presence of elephant in MWR in different seasons (wet or dry) and years (2014 and 2015) a Mann-Whitney U Test was used. In addition, a factor analysis, the varimax normalised rotation, and a cluster analysis was used to determine whether there was any correlation between the presence of elephants and other herbivore species. Lastly, in order to determine if waterhole usage by the elephant population (family herds and bulls) differed significantly on a seasonal basis a chi-squared test and an ANOVA with a bootstrap multiple comparisons analysis were used. Lastly, all mapping was completed using QGIS, version 2.16 (Creative Commons Attribution-ShareAlike 3.0 Licence) and shapefiles were provided by African Parks (Pty) Ltd.

Results

To determine current population size, age and sex structure

The 2015 aerial census counted a total of 389 individual elephants throughout MWR. Using mark-recapture methods the current study identified a total of 366 individuals of these individuals from January 2015 to April 2016 (Table 3.1.). Within the 366 individuals identified, 47 different family herds were identified as well as 91 solitary bulls (Appendix 2.3). The age structure of the population composed of 43 infants, 87 calves, 53 juveniles, 55 small adults, 98 medium sized adults and 30 large adults (Table 3.1.). The largest age class portion of the population was the medium adults (26.8%), followed by calves (23.8%) (Table 3.1., Figure 3.2.). Sex ratios for individuals under the age of 10 years was even at a ratio of 1:1, however, there were 84 individuals of unknown gender. The sex ratio for individuals between the ages of 10-60 years was relatively even at 1:1 (Table 3.1.; Figure 3.2.).

Table 3.1. Age and sex structure of the elephant population in MWR in 2015 and early 2016. The sex ratios and the proportion of each age class in the population are also shown. Sex for 84 calves and juveniles was not determined.

Age Class		Total	Males	Females	Unknown Sex	Sex Ratio	Age Class Proportion of Population (%)
Infant	(<1 year)	43	5	5	33		11,75
Calf	(1-4.9 years)	87	26	19	42	52:47 (1.1:1)	23,77
Juvenile	(5-9.9 years)	53	21	23	9		14,48
Small Adult	(10-19.9 years)	55	33	22			15,03
Medium Adult	(20-34.9 years)	98	48	50		91:92 (1:1)	26,78
Large Adult	(>35 years)	30	10	20			8,20
Total		366	143	139	84		100.00%

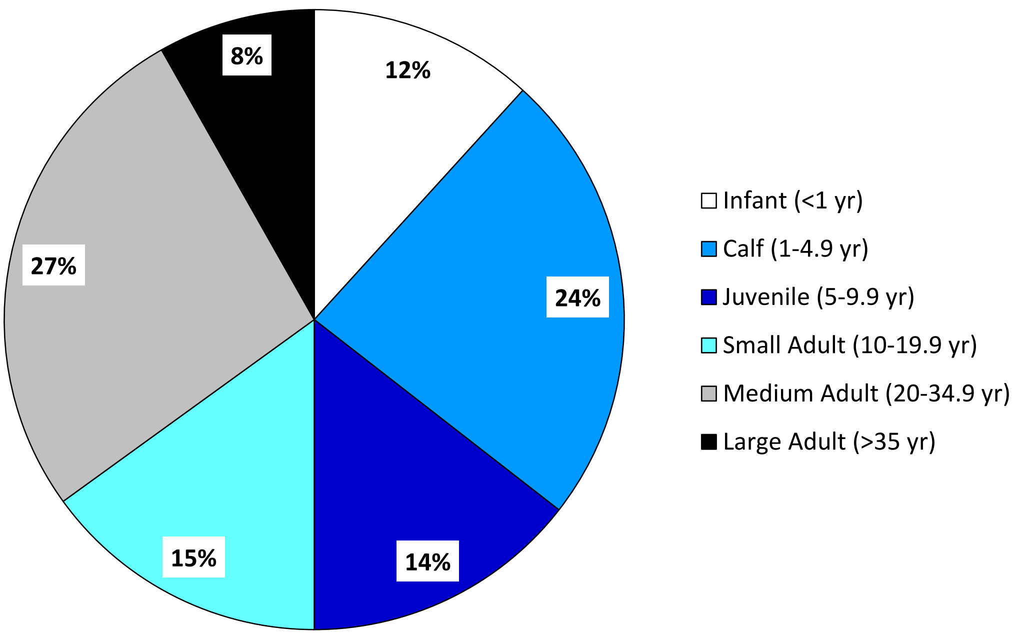


Figure 3.2. The proportional representation of each age class in the elephant population on MWR, Malawi, in the years 2015/2016.

To determine the demographic performance of the population since reintroduction

Since the reintroduction of elephant into MWR in 2006, 2008 and 2010 the population has increased significantly to an estimated total of 389 individuals (Figure 3.3.)(p=0.00; r^2=1). With minimal mortality of individuals, the six years from the conclusion of reintroductions in 2010 to the aerial count in 2015, saw an annual population growth rate of 13.8%. In terms of the change in population structure over time, there was a significant increase in the number of adult males (p=0.04; r^2=0.8) and adult females (p=0.01; r^2=0.9) from 2006 to 2015. However, due to the lack of data from the 2006 and 2008 reintroductions, statistical analysis on the younger age groups, namely juveniles and calves, as well as a more detailed analyses was not possible. This is as the current data set does not contain any data regarding gender and age classes for elephants' pre the 2010 reintroduction.

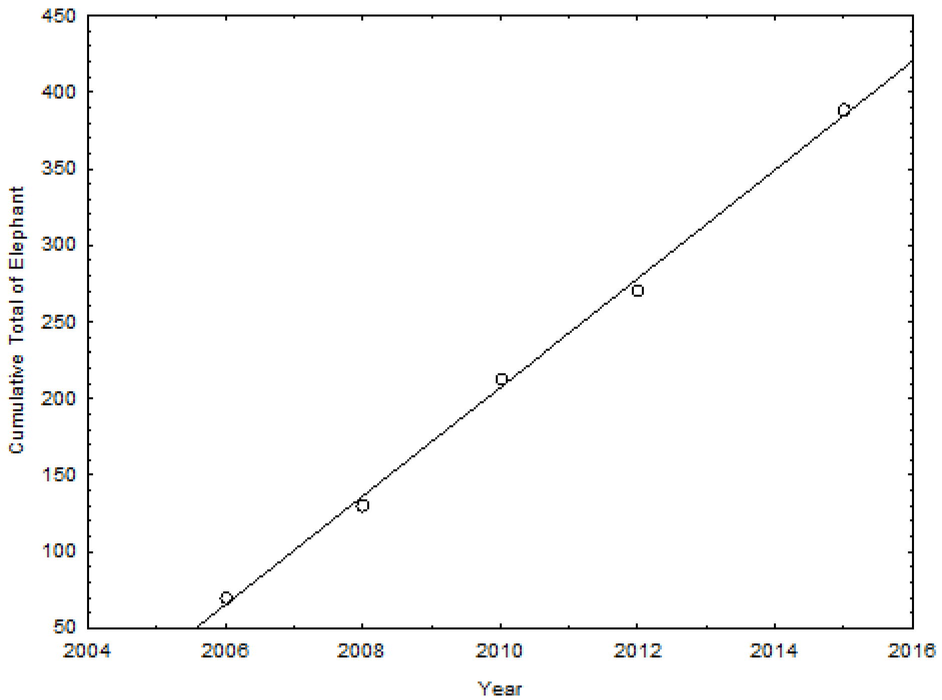


Figure 3.3. The cumulative total number of elephant in MWR since the start of the reintroduction process in 2006. (p=0.00007, r^2=0.9971)

To determine habitat use and movement

The movement patterns of the presence/absence of elephant on the reserve differed significantly in the wet and dry seasons (p=0.01) but there was no significant difference from year to year (p=0.5). In the wet seasons elephants appeared to expand their movement to the western side of the reserve that has few perennial water sources and is at a higher altitude (Figure 3.4.). In the dry seasons elephants appeared to remain close to perennial water sources such as the rivers, waterholes and springs on the eastern side of the reserve (Figure 3.4.). In both the dry and wet seasons it is clear that elephants prefer the north eastern area of the reserve that is close to the Shire and Mkulumadzi Rivers but a high number of individuals were also recorded in the south eastern parts of the reserve (Figure 3.4.). The map produced from the 2015 aerial survey, which was conducted in the dry season, demonstrated greater movement in the western part of the reserve and less movement in the south west, compared to the camera grids (Figure 3.5.). However, there was still a large number or elephants in the north eastern section of the reserve where the Shire and Mkulumadzi Rivers are located (Figure 3.5.).

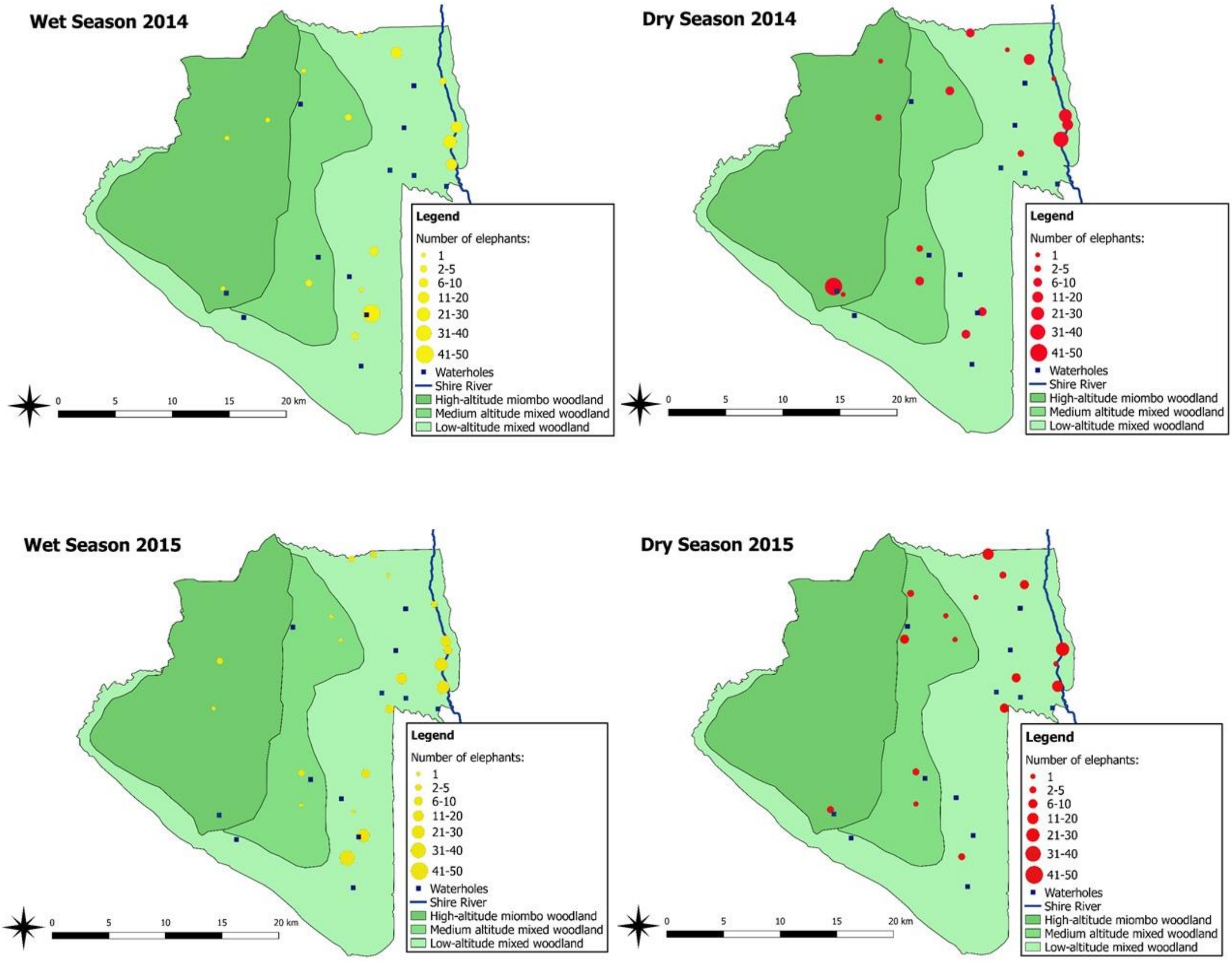


Figure 3.4. Maps representing the elephant presence across MWR in two different wet and dry seasons in relation to altitude and presence of perennial water sources. Number of individuals recorded at each site is correlated to the size of the circular marker.

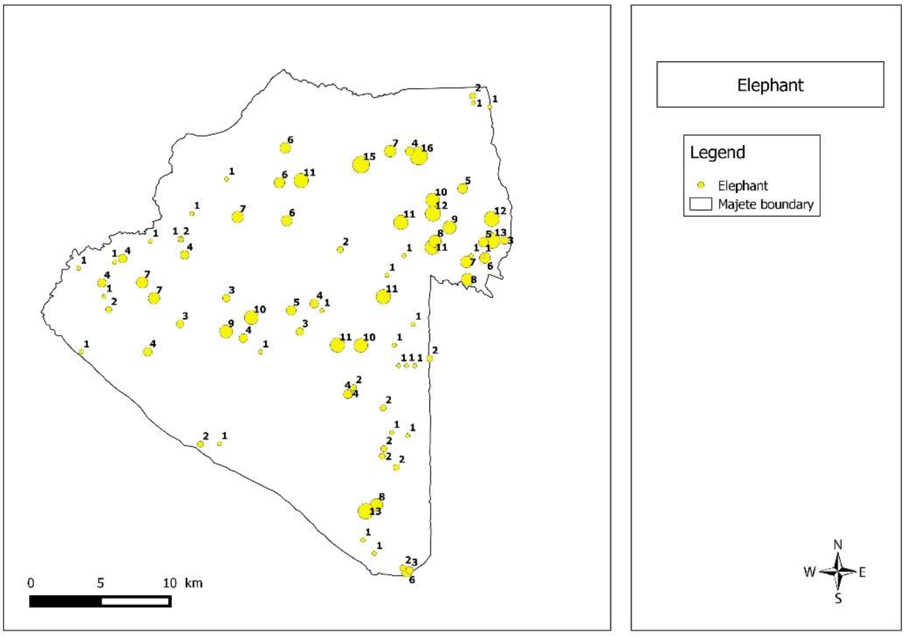


Figure 3.5. Map representing the elephant group number and position in MWR in the 2015 aerial survey. (per comms. African Parks (Pty) Ltd.)

To test whether the presence of elephant impacted other species around MWR, a factor analysis was used. This was done as a preliminary test to investigate whether the presence of elephant influenced the presence of other high density herbivore species on MWR such as waterbuck and buffalo. Elephant presence was found to be closely correlated to the presence of warthog, impala and waterbuck in both the wet and dry seasons (Figure 3.6.). Elephant presence was found to be weakly correlated to vervet monkeys, nyala and baboon in both the wet and dry seasons (Figure 3.6.).

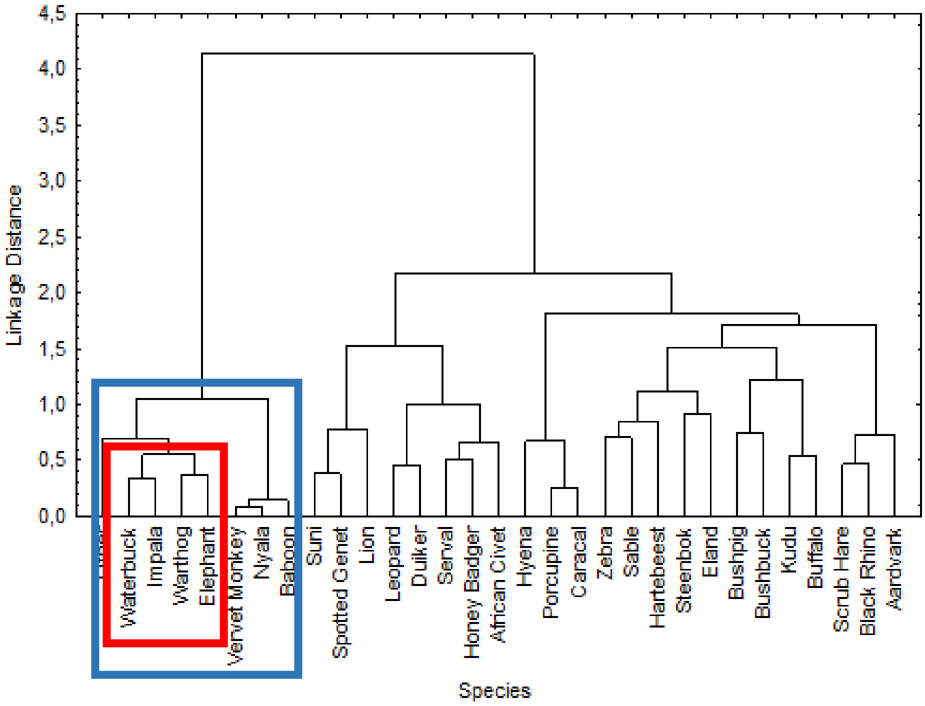
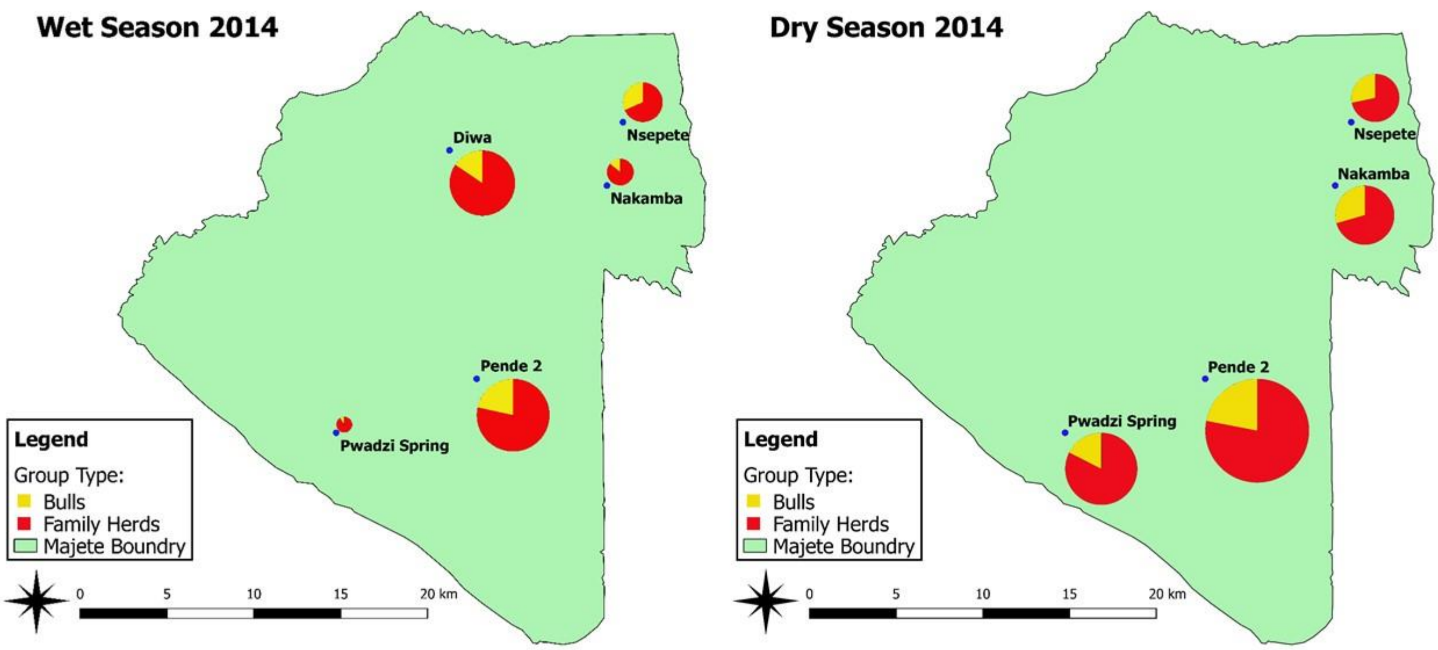


Figure 3.6. A joint tree cluster analysis representing the correlation between the presences of various species in MWR.

In general, there was a significant difference between elephant water point usage in the wet and dry seasons, as a greater number of observations were recorded in the dry when compared to the wet seasons (p=0.00; χ^2=216.61; df=5). More specifically the water points showing the highest number of observations in the wet season of 2014 were Diwa and Pende 2. In the dry season of 2014, Pende 2 and Pwadzi Spring had the highest number of observations. In the dry season of 2015 it was Pwadzi spring and Nsepete and lastly in the wet season of 2016 it was Pwadzi spring (Figure 3.7.). There was also a significant difference of water point usage between bulls and family herds in the different years and across seasons (p=0.00). In general, there were a higher number of observations of family herds at water points in both the dry and wet seasons compared to bulls. In the wet season of 2014, family herds dominated the usage of all the water points, although there appeared to be more bulls at Diwa and Pende 2 water points compared to the rest (Figure 3.7.). In the dry season of 2014, no data was available for Diwa (due to maintenance) but it appeared that family herds dominated the use of the water points and the highest number of observations were recorded at Pende 2 (Figure 3.7.). In the dry season of 2015 family herds again dominated water point usage and Pwadzi spring recorded the highest number of observations (Figure 3.7.). Lastly, the wet season of 2016 bulls appeared to dominate Diwa, Nsepete and Nakamba water points while the family herds appeared to dominate Pende 2 and Pwadzi spring and the highest number of observations were recorded at Pwadzi spring (Figure 3.7.).



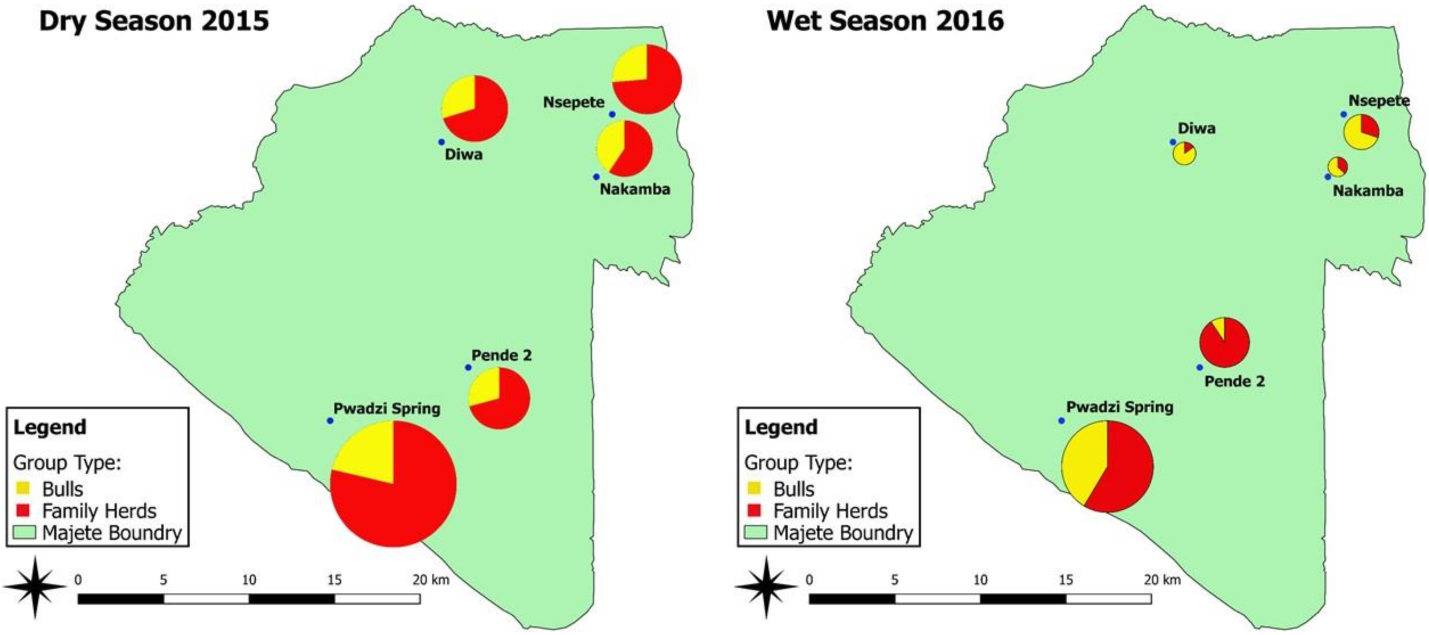


Figure 3.7. Maps representing elephants, more specifically bulls and family herds, water point usage in MWR in the wet and dry seasons of 2014, 2015 and 2016. The size of the pie chart is correlated to the number of observations at each water point.

Discussion

Population Status and Growth Rate

The most recent aerial count conducted at MWR counted a total of 389 individual elephants in 2015 and the current study was able to formally identify 366 of these individuals, using mark-recapture techniques, by April 2016. It has been established that aerial counts tend to under sample areas, more specifically woodland areas, and so it is proposed that the actual population size of elephant is larger than 389 and is more likely closer to 430 individuals (Caro 1999, Walsh *et al.* 2001, Whitehouse *et al.* 2001, Payne *et al.* 2003). In the absence of migration and heavy poaching, the Majete elephant population has grown at an estimated annual rate of 13.8% since the completion of reintroductions in 2010. The growth rate of the population will not have been uniform over time but given the current level of protection and the available range, it is predicted that the population will continue to increase.

Other African elephant populations, specifically those that are unfenced and therefore exposed to human-elephant conflict and poaching, such as the ANP and SNR populations, have been reported to have average population growth rates of only 2.2% and 0.17%, respectively (Moss 2001; Wittemyer *et al*. 2014). These low growth rates were, amongst other factors, attributed to the aging population in ANP and the migration in SNR (Moss 2001; Wittemyer *et al.* 2014). However, in fenced reserves with resource provision and minimal human-elephant conflict, including poaching, such as in AENP the population growth rate averaged 6.0% (Whitehouse & Hall Martin 2000). This suggests that increased protection and resource provision were the main contributors to the difference in population growth rates between ANP, SNR and AENP. However, MWR's population growth rate is far greater than these other populations indicating that resource provision and protection may not be the only factors contributing to the population growth rate in Majete.

Calef (1988) predicted that the maximum rate of increase for elephant populations is 7.0% per year. This maximum rate of increase is associated with optimal conditions, such as a small population that has been introduced into a new habitat that previously had no elephant, or a population that has been reduced to levels well below its carrying capacity (Calef 1988). A possible reason for the extremely high population growth rate on Majete is that the elephant population is experiencing optimal conditions required for maximum growth rate. When a population experiences these conditions, mortality is extremely low and fecundity approaches the physiological maximum, which suggests that the calving interval would be 22 months (one gestation length) after a birth if the first calf dies or 27 months after the birth of a surviving calf (Calef 1988; Moss 2001). This, however, cannot be sustained and the population will begin to stabilise with a stable age distribution of 48% of individuals older than 11 years, which is the average age of first reproduction, and 6.7% of infants (<1year) (Calef 1988). Elephant populations such as those in AENP have therefore already stabilised to a certain extent, hence their lower population growth rate. As the MWR population has an extremely high growth rate it can be argued that the population is operating under optimal conditions and has not yet stabilised.

This theory is further supported by the fact that the Majete population structure does not match the description of a population that has stabilised. The Majete population structure consists of 11.8% infants (<1 year) and 50% of individuals above the age of 11 years, which as mentioned is the average age of first reproduction. With such a high proportion of infants, a sex ratio of 1:1 in both adults and young and a minimal mortality rate, it is assumed that the population will continue to increase before eventually stabilising. According to Bothma & du Toit (2010) a rough estimate of the recommended ecological capacity of MWR, based on the average annual rainfall and the size of the reserve, is an estimated 304 individuals. Thus, the ecological capacity on MWR, specifically with regards to elephants, has already been surpassed and the population should begin to stabilise in the not too distant future due to increasing pressure on the vegetation. However, it must be acknowledged that instantaneous counts such as this one, (mark-recapture over a period of a year), could merely reflect the short term patterns of 'highs' and 'lows' and could potentially produce misleading estimates of the population's actual growth rate. In order to avoid this, population counts should be conducted every few years and not just rely on a single count.

Habitat Use and Movement

In general, the African elephant's dependence on surface water means that the availability and distribution of water sources strongly influences the species dispersal in a landscape (Chamaille-Jammes *et al.* 2008; Smit & Ferreira 2010). The camera grids that recorded species presence and absence around MWR suggested that the elephants preferred areas around water sources in both the dry and wet seasons. More specifically the highest number of individuals recorded in both seasons was in the Sanctuary, where the Shire and Mkulumadzi Rivers, one spring and four artificial waterholes were located. In the wet seasons a larger number of individuals were recorded in Pende, the south east region, compared to the dry season. However, the number of individuals recorded in Pwadzi, the south western region, and Namisempha, the north western region, increased slightly in the dry season. This is indicative of seasonal movement and in regions with a distinctly seasonal rainfall, such as MWR, regional elephant distribution during the dry season is dictated by surface water availability and location (Stokke & du Toit 2002; Shannon *et al.* 2005; Chamaille-Jammes *et al.* 2007; de Beer & van Aarde 2008, de Kneght *et al.* 2011). In the wet season elephants disperse widely across the landscape due to the higher availability of surface water through ephemeral pools and rivers (Stokke & du Toit 2002; Shannon *et al.* 2005; Chamaille-Jammes *et al.* 2007; de Beer & van Aarde 2008, de Kneght *et al.* 2011).

When comparing the camera grid maps to the aerial count map it is clear there was a lot of elephant movement that the camera grids did not record. This was probably due to the camera traps being restricted to the road network within the reserve, whereas the aerial count was able to record data throughout the reserve. The aerial count was conducted in the peak of the dry season in 2015, so it was anticipated that elephant movement would be restricted to perennial water sources mainly in the Sanctuary and Pende regions. Yet, the aerial count suggests that there was a lot more movement of elephants in the Diwa region than initially anticipated, an area that is water scarce. This suggests two things, firstly there may be additional water sources, in the form of springs, in the central and western regions. Secondly, both bulls and family herd's home ranges may be quite large and may span the majority of the reserve rather than just a few regions. This is supported by the fact that one of the family herds that was thought to reside in Pende was recorded at Diwa, the artificial waterhole that is located at the highest altitude in the Namisempha region, in the wet season (author, unpublished data). Additionally, another family herd was recorded in both the Sanctuary as well as Pende in the dry season (author, unpublished data). This indicates that there may be more movement occurring than initially anticipated. Additional studies using GPS collars would need to be conducted in order to determine the exact ranging behaviour of the elephant in MWR.

Elephants respond to their environment in a scale-dependent manner, at a coarse spatial scale forage characteristics drive habitat selection and at finer spatial scales surface water drives habitat selection (de Knegt *et al.* 2011). Habitat use generally increases with proximity to water sources and factors such as season and the nature of the surrounding habitat (ie: vegetation type, terrain or altitude) affect water point usage (Harris *et al.* 2008; Gaugris *et al.* 2009; Staub *et al.* 2013; Weinand 2013). The analyses indicated that waterhole usage in MWR changed seasonally, similar to the results obtained by Weinand (2013). This was confirmed as there was less usage of the selected water sources in the wet season when compared to the dry season. The waterholes that were used the most were Pende 2 and Pwadzi Spring. Weinand (2013) and other previous studies show that this is because both these water points are situated at lower altitudes, usually favoured by elephants, and both water points are surrounded by the preferred vegetation types of low altitude woodland and riparian vegetation (de Knegt *et al.* 2011; Staub *et al.* 2013). Staub *et al.* (2013) documented higher browsing levels in vegetation communities at lower altitudes in MWR and elephants primarily favoured riparian woodland, followed by *Acacia*-dominated woodland and lastly *Brachystegia*-dominated woodland. Naturally, the higher water point usage at Pende 2 and Pwadzi indicates that elephants prefer these two areas.

The water points in the Sanctuary, Nsepete and Nakamba, were amongst the least used perennial water points in MWR. This was unexpected as Weinand (2013) found that these water points were amongst the most used by elephants. A possible reason for the decrease in water point usage at the time of this study, is that the Sanctuary has the highest density of perennial water sources in the reserve and so elephant water point usage is spread out across the region and is not focused on these two artificial waterholes. This is supported by the likely fact that the piospheres in the Sanctuary have merged due to the closeness of perennial water points which are all within 5km of each other (Weinand 2013). Therefore, as elephants prefer to use habitat within 4km of water throughout the year (de Beer et al. 2006), distance does not limit elephant water point usage in the Sanctuary. In addition, the merging of the piospheres around water points in the Sanctuary suggests that elephant habitat use and water point use are both homogenous in the region.

In addition, in the study by Weinand (2013) there was a relatively high usage of Diwa waterhole compared to Nakamba and Nsepete waterholes. This result was unexpected as Diwa is at a higher altitude, is surrounded by undulating terrain and *Brachystegia*-dominated woodland, all of which elephants least prefer (Knegt *et al.* 2011; Staub *et al*. 2013). A possible reason for this result is that the elephant population in MWR has significantly increased since 2013 and so due to a higher density of elephant, home ranges and habitat use are now expanding into least preferred altitudes and vegetation types (Junker *et al.* 2008). This is supported by Chamaille-Jammes *et al.* (2007) who found that there was less of a difference in water point usage with elephants at a higher population density, compared to elephants at lower population densities. This is due to water points reaching their full capacity or becoming saturated with elephants at a higher density. This supports the aerial count and mark-recapture results, which indicate that the elephant population has increased dramatically to the point that they are now beginning to utilise less preferred regions of the reserve due to higher densities.

Lastly, there was an indication from the analyses that there was a significant difference between family herd and bull waterhole use in the wet and dry season. Family herds tended to dominate waterhole use in both seasons, apart from in the wet season in 2016 where bulls appeared to dominate waterhole usage in both the Sanctuary as well as at Diwa waterhole. Bulls are able to adapt their movement behaviour according to forage quality and abundance (Stokke & du Toit 2000; Woolley *et al*. 2009). Smaller bodied females, however, cannot exhibit the same flexibility as they have higher nutritional demands and the energetic constraints of group living with juveniles and calves (Stokke & du Toit 2000; Woolley *et al.* 2009). Additionally, in the dry season family units tend to remain close to perennial water sources, staying within 3.5km from water sources, compared to bulls who roam as far as 10km from perennial drinking water in the dry season (Stokke & du Toit 2002). In the wet season, due to ephemeral pools, all groups tend to average 5km from water points (Stokke & du Toit 2002). It is, therefore, possible in MWR that waterholes are dominated by family groups in the dry season due to their localised home ranges but bulls are able to roam widely and so spread their waterhole use throughout the reserve. The fact that bulls dominated the Sanctuary in the wet season of 2016 suggests that either family units were utilising other water sources in the Sanctuary or they expanded their home ranges into other areas of the reserve due to the abundance of water in the wet season.

Conclusion

In the absence of migration and heavy poaching the Majete elephant population has grown at an estimated annual rate of 13.8% since the completion of the reintroduction programme in 2010. The estimated size of the population for 2015/2016 is more than likely larger than 389 individuals. The population has an extremely high growth rate and it is postulated that it is operating under optimal conditions and has not yet begun to stabilise. This theory is supported by the population structure as it consists of 11.8% infants (<1 year) where a stable population would only consist of 6.7% infants (Calef 1988). With such a high proportion of infants, a sex ratio of 1:1 in both adults and young and a minimal mortality rate it is assumed the population will continue to increase but should stabilise in the near future.

In order to manage the current elephant population in MWR and to prevent any adverse effects on the environment, such as woody species loss, it is suggested that the population either stabilises or reduces its growth rate. In accordance with the current management strategy in MWR, the recommended management options are translocation and contraception (van Aarde & Jackson 2007). The current elephant population is already above the recommended ecological capacity, reducing the number to below the ecological capacity through translocation and thereafter implementing contraception on remaining herds will ultimately slow the growth rate (van Aarde & Jackson 2007). Long-term monitoring programmes of the elephants should be implemented in order to monitor the population's demographics and size. Recording cumulative data over time will provide important demographic information, for example, the average age females first give birth and the average calving interval of females, which is extremely useful in elephant management (Whitehouse and Hall-Martin 2000; Moss 2001). Furthermore, as recommended in Weinand (2013) long term monitoring programmes of elephants' impact on woody vegetation due to surface water availability need to be implemented especially in a fenced reserve such as MWR. The combination of population control measures (translocation and contraception), water point management and monitoring will provide the majority of information needed to develop a sufficient elephant management plan for MWR.

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Chapter 4

A preliminary investigation of the diet of African elephant (*Loxodonta africana*) in Majete Wildlife Reserve, Malawi, using stable isotope analysis

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Abstract

African elephants (*Loxodonta africana*) are classified as mixed feeders as they consume a combination of both C_3 browse and C_4 grass species. The aim of this study was to conduct a preliminary investigation to determine the seasonal dietary components of the African elephant in Majete Wildlife Reserve, Malawi, using stable isotope analysis of faecal samples. Stable isotope analysis of herbivore faecal matter is a method that allows one to determine the proportions of C_3 and C_4 resources in the diet of herbivore species and so provides a greater understanding of the feeding ecology in general. Elephants' diet displayed a clear seasonal difference in the proportion of C_3 browse consumed. In the dry seasons their diet consisted of 98% C_3 browse. The proportion of C_3 vegetation in the diet decreased to 59% in the early wet season and to 65% in the late wet season, indicating a greater proportion of C_4 vegetation being consumed in the wetter seasons. The results of this study will contribute towards a greater understanding of the ecological requirements of elephants in Majete Wildlife Reserve and will allow wildlife managers to make informed decisions with regards to population management strategies.

Keywords: African elephant, browser, carbon-13, grazer, stable isotope analysis

Introduction

The African elephant (*Loxodonta africana*) is known as a 'keystone' species as it plays a pivotal role in structuring both plant and animal communities in the habitats it occupies (Blanc *et al*. 2007). Elephants often dominate mammal biomass and the total mass of vegetation consumed by elephants on a daily basis, when compared to other herbivore species, is far greater due to their body size (White 1994). It is for this reason that elephants' are known agents of vegetation change in African woodlands, especially when high densities of the species build up in confined areas (Guy 1976; Cochrane 2003; Western & Maitumo 2004; Guldemond & van Aarde 2007). In Sengwa Wildlife Research Area, Zimbabwe, high elephant densities changed the structure and composition of miombo woodland, causing a 48% decrease of large trees and significantly increasing small trees and shrubs (Mapaure & Moe 2009). Elephants were responsible for local floristic changes as the dominant tree species, *Brachystegia boehmii,* was replaced by a less palatable species, namely *Pseudolachnostylis maprouneifolia* (Mapaure & Moe 2009). Therefore, due to their body size and the amount of vegetation consumed, elephants act as ecological engineers although this varies according to population densities and the ability of a population to migrate (Guldemond & van Aarde 2007; Loarie *et al.* 2009a).

In the past, elephant phylogenetic lineages have displayed both browsing and grazing members (Cerling *et al.* 1999). The elephant lineages, *Elephas* and *Loxodonta*, have been traced back as far as 5 million years to the late Miocene era of Africa where their initial appearance coincides with the worldwide expansion of C_4 biomass (Cerling *et al.* 1999). The ancestors of modern day elephants were almost entirely C_4 grazers until about 1 million years ago when they started to consume more C_3 browse species (Cerling *et al.* 1999). Modern *Elephas* and *Loxodonta* are almost exclusively browsers in all environments they occur in and so it is a possibility that they are in another evolutionary transition from being predominantly grazers to being predominantly browsers (van der Merwe *et al.* 1988; Cerling *et al.* 1999). Evidence of this is displayed in the fact that the majority of elephant populations have mixed C_3/C_4 diets whilst only a few select populations, such as in Addo Elephant National Park (hereafter, AENP), South Africa, and Tsavo (hereafter, TENP), Kenya, display near pure C_4 diets (van der Merwe *et al.* 1988; Cerling *et al.* 1999). Concurrently, extant elephant molar teeth have retained a high crowned form, which has long been the dental interpretation of a modification for abrasive grazing diet, yet in the present day the majority of elephant populations have large proportions of browse in their diet (Cerling *et al*. 1999; Cerling *et al*. 2004). Therefore, this further supports the hypothesis that modern day *L. africana* are transitioning to a C_3 browse based diet rather than maintaining a C_4 grazing diet.

Despite the change in the African elephants' diet, the fact that they consume a combination of both C_3 and C_4 plant species classifies them as mixed feeders (van der Merwe *et al.* 1988; Cerling *et al.* 1999; Cerling *et al.* 2004; Codron *et al.* 2006). Elephants are selective feeders and tend to prefer plant species such as, for example *Acacia, Colophospermum and Adansonia* (Cerling *et al.* 2004; Staub *et al.* 2013). The ratio of browse and grass in an elephants diet, as well as their preferred plant species, varies widely and therefore contention persists within African elephant literature regarding whether elephants are primarily browsers or grazers (Codron *et al.* 2006). For example, in the Bunyoro region in Uganda grazing was found to be a priority for elephants (Wing & Buss 1970). Whereas other observers have noted an important browsing component in elephants diet (Jackman & Bell 1884; Codron *et al.* 2006). Elephant diet preferences, therefore, depend on a number of factors including the region, water availability, rainfall, elevation, soil nutrient composition and vegetation cover (van der Merwe *et al.* 1988; Cerling *et al*. 2004; Codron *et al.* 2006; Loarie *et al.* 2009b).

Stable isotope ecology provides a means to quantify the consumption of browse and graze by various herbivore species (Cerling, *et al.* 1999; Codron *et al.* 2006). The basics of stable isotope ecology are the ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as these two elements both appear in a consumer's tissues and their values mimic the isotopic signatures of the food that was ingested (Codron *et al.* 2007). In subtropical savannas the bimodal distribution of $\delta^{13}C$ between plants photosynthetic pathways (C_3 and C_4) is recorded in the tissues of the consumer (Codron *et al.* 2007). Stable isotope ratios are distinct between plants; trees, shrubs and forbs tend to have C_3 photosynthetic pathways and so $\delta^{13}C$ values range between -22 and -35‰ and average around -27 ‰, whereas grasses tend to have C_4 photosynthetic pathways and $\delta^{13}C$ values that range between -10 and -15‰ (Smith & Epstein 1971; Cerling *et al.* 1999). Additionally, animal $\delta^{15}N$ values reflects the trophic position, it increases on different levels of the food chain and varies with the rainfall, ecophysiology, protein uptake and nutritional stress (Codron *et al.* 2007). Thus, stable isotope ecology provides a method of determining the quantity of carbon and nitrogen in the consumer's tissues, essentially allowing the proportion of graze and browse and the trophic levels to be determined (Cerling *et al*. 1999; Cerling *et al.* 2004; Codron *et al.* 2006; Codron *et al.* 2007).

When conducting stable isotope analysis, the different materials analysed allow the study of the diet of species at different time scales. Long lived tissues such as hair and teeth integrate an average over months or years and when sampled in series reveal dietary variations within the individual at this scale (Cerling *et al.* 1999; Cerling *et al.* 2004; Cerling *et al.* 2009). Animal faeces, on the other hand, is a useful indicator of dietary variation as it shows high resolution time scales, in order of several days rather than months or years (Codron *et al.* 2005; Codron *et al.* 2006; Codron *et al.* 2007; Codron *et al.* 2011). Due to this rapid turnover of data no mathematical correction is necessary as the differential growth rate and attenuation time is significantly less compared to the use of hair and teeth (Codron *et al.* 2007). Additionally, faeces are easy to sample in the field and sampling does not require interference through the manipulation or slaughter of animals (Codron *et al.* 2005; Codron *et al.* 2006; Codron *et al.* 2007). There are a number of studies that have shown the relationship and consistency between $\delta^{13}C$, less so $\delta^{15}N$ in C_3 and C_4 diets and faeces, and despite the fact that faeces represents the undigested portion of the diet, it is a relatively accurate reflection of the true diet of the individual (Codron *et al.* 2005; Codron *et al.* 2006; Codron *et al.* 2007).

Defining and understanding the extent of dietary flexibility of herbivores is important to the development and implementation of suitable management practises in conservation. This preliminary investigation aimed to determine the seasonal dietary components of the African elephants in Majete Wildlife Reserve, Malawi, using stable isotope analysis of faecal samples. The analyses were performed on faeces as it reflects the diet of the animal 2 to 3 days before deposition, allowing the investigation of seasonal change as the time of deposition will accurately reflect the time of year (Sponheimer *et al.* 2003). The fundamental hypothesis was that elephants would have a mixed diet of C_3 browse and C_4 graze and that the reflections of these components will vary between the dry season, which will contain more browse, and the wet season, which will contain more graze (Cerling *et al*. 2004; Codron *et al.* 2005; Codron *et al.* 2006; Codron *et al.* 2007; Cerling *et al*. 2009). The results and understanding gained will be considered when presenting conservation recommendations to reserve management.

Methods

Study Area

Majete Wildlife Reserve (MWR, hereafter) is located in the lower Shire valley region of southern Malawi (S15° 54'26.6"; E034°44'24.3"). It is a 700km^2 reserve with northern and eastern boundaries boarded by two perennial rivers, the Mkhulumadzi and the Shire. The altitudinal gradient varies, it is highest in the western region where steeply undulating hills are distorted by river valleys. The altitudinal gradient gradually decreases in the eastern region of the reserve where the terrain flattens towards the Shire River. Majete has two distinct seasons, the wet season that occurs between December and May and the dry season between June and November. The annual precipitation in the reserve is between 680-800mm in the eastern lowlands and 700-1000mm in the western highlands (Wienand 2013). Water availability is affected by season but there are approximately five perennial springs, along with ten artificial waterholes in the reserve (Weinand 2013).

The vegetation in the reserve is primarily woodland which varies according to altitude. Vegetation types include: high altitude miombo woodland, medium altitude mixed woodland, low altitude mixed woodland and savanna. High altitude miombo woodland occurs in the western hilly region, between 410 – 770m. Species that occur in this vegetation type include *Brachystegia boehmii*, *Julbernardia globiflora* and *Burkea africana* (Patel, H. Unpub). Medium altitude mixed woodland between 230 – 410m, is the ecotonal vegetation that occurs between the western hilly region and the eastern lowlands in the reserve. Vegetation species that occur in this ecotonal region include *Brachystegia boehmii, Pterocarpus rotundifolius* and *Combretum* species (Patel, H. Unpub). The low altitude mixed woodland in the eastern region occurs between 205 – 280m. Species that occur in this vegetation type include *Acacia* species and *Sterculia* species (Patel, H. Unpub). Lastly, savanna occurs in patches throughout MWR with a slightly higher concentration in the south east of the reserve, with *Combretum* and *Panicum* being the dominant species (Patel, H. Unpub)

MWR was gazetted in 1955 but by 2003 most of its large game had been decimated due to poaching and poor management. From 2003 - 2010, MWR underwent one of Africa's greatest reintroduction programmes, after a Public Private Partnership (PPP) agreement was made between African Parks, Majete (Pty) Ltd. and the Malawian government in early 2003. Wildlife reintroductions to MWR were undertaken in stages as the reserve was not yet fenced. The first stage involved fencing a smaller area of 140km^2 in the north-eastern region of the reserve in 2003, known as the Sanctuary, purely for reintroduction purposes. The second stage fenced the remaining boundary of the reserve which was completed in 2008, after which the initial sanctuary fence line was removed in November 2011 and wildlife was able to roam into the greater reserve. In total over 2550 individual animals of 14 different species were reintroduced to MWR. Species reintroduced into the reserve included elephant, black rhino, buffalo, sable hartebeest and a number of other antelope species.

Faecal and Vegetation Sampling and Analysis

To determine seasonal changes in the proportion of graze and browse for elephant in MWR, representative vegetation samples and elephant faecal matter samples were collected, identified and dried over a period of 14 months. Both the faeces and the vegetation samples were used for the stable isotopic analysis.

Elephant faecal samples were collected on a weekly basis throughout MWR from March 2015 to the end of February 2016, so as to compare the grass and browse proportions for both the wet and dry seasons. The seasons were defined as follows: late wet season (March – May 2015), early dry season (June – August 2015), late dry season (September – November 2015) and early wet season (December 2015 – February 2016). Only recently deposited, fresh or damp, faeces (not older than 12 hours) were collected to ensure that samples represented the appropriate season and were not contaminated by fungi, soil and insects (Wrench *et al.* 1996). Samples, the size of a small handful, were collected from the centre of two to three different faecal boluses of the same faecal pile and placed into brown envelopes. Each separate faecal pile encountered was taken to represent a different individual of the relevant species. All faecal samples were immediately left to dry in the sun until all moisture was evaporated and samples were thoroughly dry. Data such as the date, season, GPS location and species were recorded when samples were collected. A total of 67 faecal samples were collected, however due to mould only 40 samples were isotopically analysed.

To better interpret the carbon isotopic results from the faecal samples, local vegetation samples were also collected. Vegetation samples were taken from various tree, forb and grass species from within twelve circular transects (approximately 10m in diameter) established in each of the different habitats (woodland below 250m, woodland between 250 – 400m, woodland above 400m and savanna) throughout MWR (described in detail by Codron *et al.* 2005). Only a small sample, a few stems and leaves, of each plant species was collected and placed in brown paper envelopes for drying purposes. The date, species, GPS location and habitat type at the time of collection was recorded. A total of 140 plant samples were collected, of which 14 different tree species, 5 shrub species and 5 grass species were isotopically analysed. Both faecal and plant sampling was concentrated around the north-east (the Sanctuary) and the south-east region (Pende) of MWR. Additional data on $\delta^{13}C$ and $\delta^{15}N$ values of grasses and shrubs was acquired from Spies (2015).

All faecal and vegetation samples were oven dried at 60^{o}C for 24 hours and homogenized into a powder using a Beadbug Microtube Homogeniser 115V (USA), set at a speed of 330rmp for 3 minutes. Each sample was processed 3 times in the homogeniser in order to obtain a fine powder that was able to pass through a 1mm sieve. Aliquots of approximately 1.0 to 1.1 mg (faeces & plant material) were weighed into tin capsules (RJM Systems (Pty) Ltd., Product number D1006, Tin Capsules Pressed, Standard Weight 6x4mm) and placed in assay trays ready for analysis. Carbon isotope ratios and percent nitrogen were obtained by placing each weighed sample separately into a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria. A laboratory running standard (Merck Gel: $\delta^{13}C$ = -20.57‰, $\delta^{15}N$=6.8‰, C%=43.83, N%=14.64) and blank sample were run after every 12 unknown samples.

$^{13}C/^{12}C$ ratios are expressed in the standard delta (δ) notation in per thousand (‰) relative to Vienna Pee-Dee Belemnite (VPDB) standard and to air for the nitrogen isotopes values (Coplan 1996; Radloff *et al*. 2013). Results are expressed using the standard equation:

$$\delta X(‰) = [(R_{sample}-R_{standard})/R_{standard}-1]x1000$$

Where X = ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$ respectively. Analytical precision was <0.05‰ for $\delta^{13}C$ and <0.13‰ for $\delta^{15}N$.

Statistical Analysis

To determine whether there was a significant difference between the $\delta^{13}C$ values of C_3 and C_4 plants a two tailed t-test was used (Statistica 13). Additionally, to determine whether there was a significant difference between elephant faeces $\delta^{13}C$ values between seasons, a one-way analysis of variance (ANOVA) was used (Statistica 13). To determine the proportional contribution of C_3 plants (browsing) in each season the Bayesian stable-isotope mixing model SIAR in R 3.3.1 was used (Phillips 2001; Phillips & Gregg 2001; Phillips & Koch 2002; Parnell *et al.* 2010). The average $\delta^{13}C$ values for C_3 and C_4 plants was determined as -29.11‰ and -12.92‰ respectively and were used as endpoint values. Discrimination factors ($\delta^{13}C$) from plants to faeces of +1.1 ±0.3‰ for C_4 plants, and +0.7 ±0.3‰ for C_3 plants were entered into the system and the concentration was set to zero (Sponheimer *et al.* 2003; Codron *et al.* 2005; Radloff 2013). Median and 95% credibility intervals (Cr.I) were determined and all isotope values are presented as mean ±SD. However, when not working in R a diet-faeces fractionation of -0.9% was used (Sponheimer *et al.* 2003; Codron *et al.* 2005).

Results

The plants in MWR had $\delta^{13}C$ values entirely consistent with expectations for C_3 and C_4 vegetation. Uncorrected $\delta^{13}C$ and $\delta^{15}N$ values as well as the standard corrected $\delta^{13}C$ and $\delta^{15}N$ values for the C_3 and C_4 vegetation samples are presented in Table 4.1. There was a notable difference between the $\delta^{13}C$ values of C_3 compared to C_4 plants as the trees and forbs were significantly depleted in carbon compared to the grasses (Mann-Whitney U test; z-value=3.85, p=0.000120). The standard corrected $\delta^{13}C$ values for the 19 C_4 samples had a range from -11.47‰ to -14.44‰ and an average of -12.92‰ (±0.96). Whereas the standard corrected $\delta^{13}C$ values of the 34 C_3 samples had a range of -26.45 ‰ to -31.54‰ and an average of -29.11‰ (±1.26).

Additionally, the $\delta^{15}N$ values represent the crude protein content of each plant sample. For C_4 plants the $\delta^{15}N$ values ranged from -2.53% to 7.72% with an average of 0.91% (±2.76) and had a broader range and a greater average value than the nitrogen $\delta^{15}N$ values for the C_3 plants. These values ranged from -3.55% to 3.86% with an average of 0.03% (±1.88), however the difference between the $\delta^{15}N$ values for C_3 and C_4 plants was not statistically significant (Mann-Whitney U test; z-value=0.58, *p*=0.561276).

Table 4.4. $\delta^{13}C$ and $\delta^{15}N$ values (‰) of C_3 shrubs and trees and C_4 grass specimens used as a reference in the stable isotope analysis of the diet of elephant in MWR, Malawi. The standard corrected values were determined by the Isotope Laboratory, Mammal Research Institute, University of Pretoria.

Species	Type	C3/C4	δ15 N	δ15N (Std corrected)	δ13 C	δ13C (Std corrected)	C:N Ratio
Heteropogon contortus	Grass	C4	-1.55	-1.60	-14.73	-13.55	43.18
Heteropogon contortus	Grass	C4	-1.78	-1.83	-14.60	-13.44	47.78
Heteropogon contortus	Grass	C4	-1.26	-0.80	-12.17	-12.17	21.75
Heteropogon contortus	Grass	C4	0.86	1.30	-11.70	-11.72	25.31
Heteropogon contortus	Grass	C4	-0.85	-0.39	-11.56	-11.58	32.75
Erogrostis aspera	Grass	C4	-0.86	-0.90	-15.12	-13.93	45.04
Urochloa mosambiscensis	Grass	C4	1.15	1.10	-14.42	-13.23	39.85
Urochloa mosambiscensis	Grass	C4	0.82	1.27	-12.48	-12.47	19.77
Urochloa mosambiscensis	Grass	C4	0.73	1.17	-12.57	-12.56	16.25
Panicum maximum	Grass	C4	-0.83	-0.88	-14.79	-13.62	45.22
Cynodon dactylon	Grass	C4	3.16	3.58	-14.32	-14.27	18.33
Cynodon dactylon	Grass	C4	2.30	2.73	-13.85	-13.80	16.85
Cynodon dactylon	Grass	C4	2.49	2.92	-14.50	-14.44	24.78
Dactylotenium aegyptium	Grass	C4	1.66	2.10	-13.72	-13.68	24.24
Dactylotenium aegyptium	Grass	C4	7.34	7.72	-12.87	-12.85	17.31
Dactylotenium aegyptium	Grass	C4	5.37	5.77	-13.12	-13.09	26.53
Hyparrhenia rufa	Grass	C4	-1.97	-1.50	-11.60	-11.62	34.01
Hyparrhenia rufa	Grass	C4	-3.01	-2.53	-11.93	-11.94	40.68
Hyparrhenia rufa	Grass	C4	-2.40	-1.93	-11.45	-11.47	29.09
Neorautanenia mitis	Shrub	C3	-1.90	-1.95	-30.63	-29.47	14.35
Becium grandiflorum	Shrub	C3	0.24	0.19	-30.95	-29.79	22.08
Pilea tetraphylla	Shrub	C3	0.09	0.04	-32.70	-31.51	14.42
Asystasia gangetica	Shrub	C3	2.25	2.50	-30.07	-28.88	16.82
Grewica Bicolour	Shrub	C3	0.44	0.39	-30.71	-29.54	22.33
Brachystegia utilis	Tree	C3	-0.17	-0.22	-27.63	-26.45	35.00
Monotes africanus	Tree	C3	-0.37	-0.24	-30.79	-29.61	29.78
Diospyros kirkii	Tree	C3	-2.92	-2.96	-30.15	-28.97	36.49
Diospyros kirkii	Tree	C3	-2.92	-3.03	-30.16	-29.02	37.15
Julbernardia globiflora	Tree	C3	0.47	0.81	-28.76	-27.60	25.59
Julbernardia globiflora	Tree	C3	0.86	0.42	-28.61	-27.47	26.02
Pseudolachnostylis maprouneifolia	Tree	C3	-3.09	-3.13	-30.05	-28.90	30.89
Pseudolachnostylis maprouneifolia	Tree	C3	-0.37	-0.42	-29.17	-27.97	26.04
Acacia nilotica	Tree	C3	-1.27	-1.15	-31.63	-30.45	30.18
Combretum adenogonium	Tree	C3	-3.15	-3.55	-29.54	-28.36	35.18
Sterculia quinqueloba	Tree	C3	2.23	2.18	-30.92	-29.74	31.16
Terminalia Sericea	Tree	C3	-1.41	-1.46	-29.80	-28.63	38.38

Diplorhynchus condylocarpon	Tree	C3	-0.17	-0.22	-29.95	-28.78	26.64
Diplorhynchus condylocarpon	Tree	C3	-1.28	-1.33	-29.49	-28.34	29.38
Diplorhynchus condylocarpon	Tree	C3	0.61	1.06	-28.13	-27.72	21.84
Diplorhynchus condylocarpon	Tree	C3	2.37	2.80	-27.10	-26.72	16.76
Diplorhynchus condylocarpon	Tree	C3	1.24	1.68	-27.47	-27.08	19.45
Petrocarpus lucens	Tree	C3	-0.81	-0.86	-30.11	-28.97	18.01
Petrocarpus lucens	Tree	C3	-0.82	-0.69	-30.25	-29.07	18.42
Acacia nigrescens	Tree	C3	1.41	1.36	-30.06	-28.90	22.41
Acacia nigrescens	Tree	C3	3.26	3.68	-30.68	-30.20	11.85
Acacia nigrescens	Tree	C3	2.51	2.94	-30.00	-29.54	15.98
Acacia nigrescens	Tree	C3	3.44	3.86	-32.06	-31.54	18.06
Tamarindus indica	Tree	C3	-1.04	-1.24	-32.14	-30.65	22.38
Tamarindus indica	Tree	C3	-1.19	-1.08	-31.80	-30.98	20.99
Combretum Zeyheri	Tree	C3	0.23	0.35	-31.03	-29.85	23.16
Dalbergia melanoxylon	Tree	C3	-0.35	0.10	-29.19	-28.75	12.61
Dalbergia melanoxylon	Tree	C3	-0.64	-0.18	-30.35	-29.78	12.38
Dalbergia melanoxylon	Tree	C3	0.03	0.48	-31.00	-30.51	14.12

The uncorrected $\delta^{13}C$ and $\delta^{15}N$ values as well as the standard corrected $\delta^{13}C$ and $\delta^{15}N$ values for the elephant faecal samples collected in the early dry, early wet, late dry and late wet seasons are presented in Table 4.2. The $\delta^{13}C$ values for the faeces ranged from -18.29‰ to -30.49‰ over the entire sampling period. In the early dry season $\delta^{13}C$ values ranged from -27.30‰ to -30.49‰ with an average of -29.16‰ (±0.82). In the early wet season $\delta^{13}C$ values ranged from -18.29‰ to -29.12‰ with an average of -22.22‰ (±4.17). In the late dry season $\delta^{13}C$ values ranged from -28.04‰ to -29.26‰ with an average of -28.65‰ (±0.39). In the late wet season $\delta^{13}C$ values ranged from -19.48‰ to -26.27‰ with an average of -23.01‰ (±2.52).

A Kruskal-Wallis test revealed significant differences in faecal carbon ($\delta^{13}C$) between seasons; the early dry season and the early wet season (z-value=4.29, p=0.000105) and the early dry season and the late wet season (z-value=4.29, p=0.000107). There was also a significant difference in faecal carbon ($\delta^{13}C$) between the late dry season and the early wet season (z-value=3.05, p=0.013879) and the late dry season and the late wet season (z-value=2.98, p=0.017070). However, there was no significant difference in faecal carbon ($\delta^{13}C$) between the early and late dry seasons (z-value=1.27, p=1.00) and the early and late wet seasons (z-value=0.20, p=1.00). Additionally, the nitrogen $\delta^{15}N$ values for the elephant faeces ranged from -0.33 % to 1.88% over the entire sampling period with an average of 0.71% (±0.59).

Table 4.5. δ^{15}N and δ^{13}C values (‰) of faecal samples representing the diet of elephant in the early dry season 2015, late dry season 2015 an the late wet season 2015 and early wet season 2016 in MWR, Malawi. The standard corrected values were determined by laboratory technicians at the Stable Isotope Lab, Mammal Research Institute, University of Pretoria.

Species	Season	δ15 N	δ15N (Std corrected)	δ13 C	δ13C (Std corrected)	C:N Ratio
Elephant	Early Dry	1.51	1.62	-30.49	-29.31	43.90
Elephant	Early Dry	0.50	0.60	-29.88	-28.69	45.93
Elephant	Early Dry	0.56	0.67	-30.53	-29.34	45.28
Elephant	Early Dry	-0.02	0.10	-30.34	-29.15	51.27
Elephant	Early Dry	1.41	1.52	-30.97	-29.79	51.20
Elephant	Early Dry	-0.15	-0.03	-28.48	-27.30	48.72
Elephant	Early Dry	1.02	1.14	-31.67	-30.49	31.11
Elephant	Early Dry	-0.10	0.01	-29.64	-28.46	47.99
Elephant	Early Dry	0.41	0.52	-30.39	-29.20	56.99
Elephant	Early Dry	0.64	0.75	-30.93	-29.75	51.14
Elephant	Early Dry	0.75	0.86	-30.46	-29.28	52.03
Elephant	Early Wet	1.79	1.88	-22.64	-21.44	32.16
Elephant	Early Wet	0.85	0.94	-20.01	-18.82	42.81
Elephant	Early Wet	-0.12	-0.04	-30.32	-29.12	51.44
Elephant	Early Wet	0.27	0.35	-22.65	-21.45	42.25
Elephant	Early Wet	1.61	1.69	-19.79	-18.59	31.63
Elephant	Early Wet	-0.20	-0.12	-21.03	-19.83	32.25
Elephant	Early Wet	0.51	0.59	-19.49	-18.29	35.80
Elephant	Early Wet	0.51	0.59	-27.19	-26.00	28.71
Elephant	Early Wet	0.96	1.04	-29.94	-28.74	54.90
Elephant	Early Wet	1.42	1.50	-21.15	-19.96	34.65
Elephant	Late Dry	0.52	0.62	-30.14	-28.95	44.28
Elephant	Late Dry	0.92	1.01	-29.86	-28.67	40.22
Elephant	Late Dry	0.02	0.12	-29.66	-28.47	54.87
Elephant	Late Dry	-0.24	-0.14	-30.44	-29.26	46.93
Elephant	Late Dry	-0.43	-0.33	-30.45	-29.26	38.84
Elephant	Late Dry	-0.20	-0.10	-29.23	-28.04	43.62
Elephant	Late Dry	1.33	1.43	-29.89	-28.70	45.27
Elephant	Late Dry	0.70	0.79	-29.57	-28.38	46.32
Elephant	Late Dry	0.49	0.58	-29.61	-28.42	46.96
Elephant	Late Dry	0.28	0.38	-29.44	-28.26	53.26
Elephant	Late Dry	-0.31	-0.21	-30.00	-28.81	41.64
Elephant	Late Wet	1.00	1.06	-22.43	-21.23	29.00
Elephant	Late Wet	0.27	0.34	-22.66	-21.46	38.15
Elephant	Late Wet	1.41	1.48	-23.03	-21.83	30.87
Elephant	Late Wet	0.69	0.76	-22.67	-21.47	33.23
Elephant	Late Wet	1.48	1.55	-27.87	-26.67	27.23
Elephant	Late Wet	-0.05	0.02	-22.93	-21.73	44.06
Elephant	Late Wet	0.97	1.05	-27.11	-25.91	28.71
Elephant	Late Wet	1.03	1.10	-25.90	-24.70	32.13
Elephant	Late Wet	0.55	0.61	-27.42	-26.21	33.83
Elephant	Late Wet	0.56	0.63	-26.29	-25.09	32.59

Elephant	Late Wet	0.66	0.72	-20.68	-19.48	30.69
Elephant	Late Wet	1.41	1.47	-21.58	-20.37	35.50

The $\delta^{15}N$ and $\delta^{13}C$ values of C_3 and C_4 vegetation as well as the elephant faecal samples collected in the various seasons is displayed in Figure 4.1. There is a clear, almost predominant contribution of C_3 vegetation to the diet of elephant in the early dry and late dry season. Whereas, in the early and late wet seasons elephants displayed a dietary shift towards the C_4 vegetation, indicating a greater diversity of browse (C_3) and grass (C_4) in the diet compared to the early and late dry seasons. The contribution of C_3 browse to the diet of elephants ranged from 59% to 98% for the entire sampling period (Table 4.3.). More specifically, in the early dry and late dry season the proportion of C_3 in the diet of elephant averaged 98% (95% Cr.I.: 96-100%) and 98% (Cr.I.: 95-100%), indicating that the diet consisted almost exclusively of C3 browse vegetation. However, the proportion of C_3 vegetation in the diet decreased in the early wet season to an average of 59% (Cr.I.: 45-75%) and in the late wet season to 65% (Cr.I.: 56-74%), indicating a greater proportion of C_4 vegetation being consumed in the wet seasons.

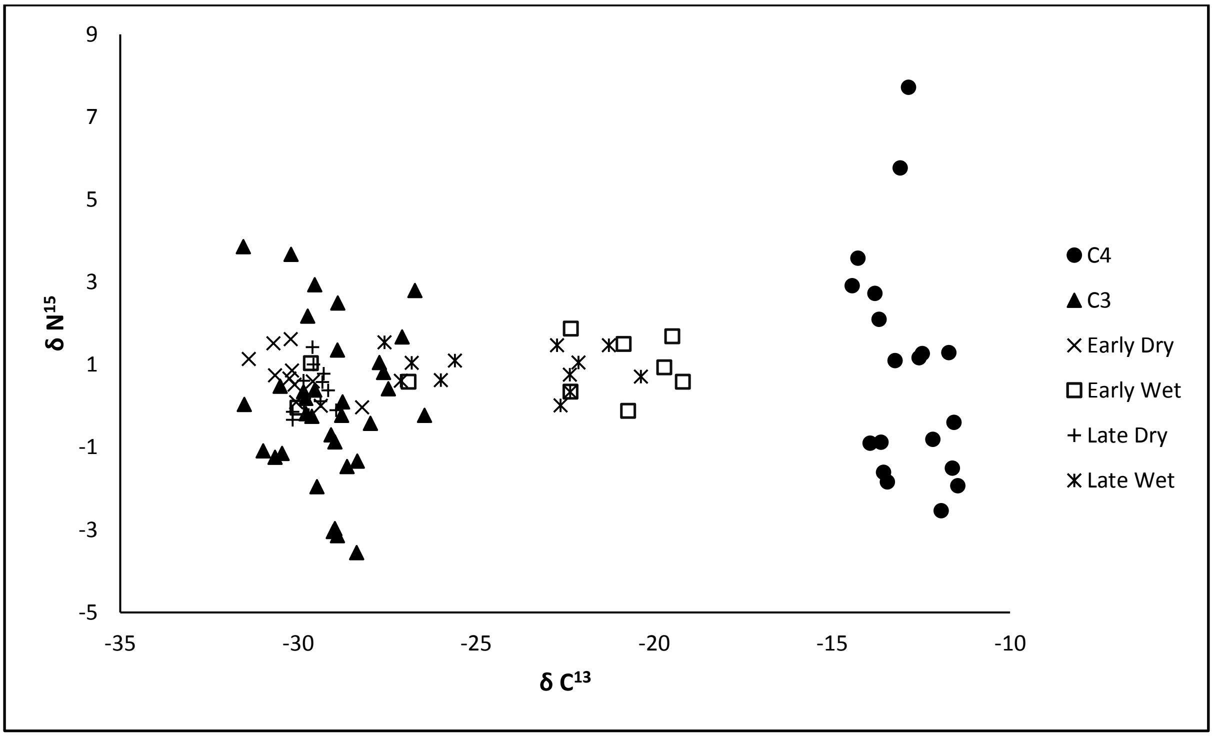

Figure 4.1. The isotopic values of C_4 and C_3 vegetation, along with the isotopic values of carbon and nitrogen in the diet of elephant (*Loxodonta africana*) in the early dry season 2015, late dry season 2015, late wet season 2015 and early wet season 2016 in MWR, Malawi.

Table 4.6. Percentage browse consumption of elephant in MWR, Malawi, as determined from stable carbon isotope analysis of faecal samples (n=number of samples). Percentage browse consumption was determined using a Bayesian stable-isotope mixing model using C_3 (-29.23‰) and C_4 (-13.12‰) plant end-members.

Season	*n*	Elephant δ13C (‰)	±SD	Elephant % browse (95% Cr.I)
Early Dry	11	-29.16	0.82	98 (96-100)
Early Wet	10	-22.22	4.17	59 (45-75)
Late Dry	11	-28.65	0.39	98 (95-100)
Late Wet	12	-23.01	2.52	65 (56-74)

Discussion

The main objective of this study was to investigate whether season had an effect on the diet of elephants in MWR, Malawi. In order to achieve this objective only plant $\delta^{13}C$ values were corrected with discrimination factors in the SIAR package (R 3.3.1) and analysed to determine the proportion of C_3 and C_4 biomass in the faecal samples. The $\delta^{15}N$ values were of little use as the current understanding of nitrogen isotopes is poor and the variation of nitrogen isotopic values in plant and animal faecal matter is more complex than that of the carbon isotopes due to environmental factors affecting nitrogen fixation and fractionation. Researchers have thus been cautioned when analysing and interpreting δ15N values (Sandberg *et al.* 2012; Dr Frans Radloff per. Comms).

According to a number of studies, the isotopic classification of elephant's diets is mixed feeding but depending on their location, certain populations may have near-pure grass- or browse-based diets (Wing & Buss 1970; Barnes 1983; Cerling *et al.* 1999; de Boer *et al.* 2000; Codron *et al.* 2005; Cerling *et al*. 2004; Codron *et al.* 2006; Codron *et al.* 2011). In this study, there was a significant change in elephant diet from the early and late dry seasons, where the majority (98%) of food consumed was C_3 browse, to the early and late wet seasons where the proportion of browse consumed decreased to 59% (Cr.I:45-75%) and 65% (Cr.I: 56-74%) respectively. This concurs with the prediction that the C_4 content of the elephant's diet would increase in the wet season due to fresh grass growth providing greater palatability, lower tannin concentrations and higher nutritional value compared to many C_3 browse species (Cooper & Owen-Smith 1985; Sukumar & Ramesh 1992; de Boer et al. 2000). Therefore, this finding is supported by numerous other studies that suggest elephants have a dietary shift from a nearly pure C_3 browse diet in the dry seasons to a greater proportion of C_4 plants being consumed in the wetter seasons (Barnes 1983; van der Merwe *et al.* 1988; Cerling *et al.* 1999; Codron *et al*. 2005; Cerling *et al.* 2004; Codron *et al.* 2006; Codron *et al.* 2011).

Additionally, the proportion of C_4 graze consumed in this study, 2% in the drier seasons, 41% in the early wet and 35% in the late wet, is comparable to other studies that have used similar methods to determine the seasonal proportion of C_3 and C_4 biomass in elephant diets. Codron *et al.* (2006) found that elephants in the northern Kruger National Park, South Africa, had a diet composed of 40% C_4 graze in the dry season and 50% graze in the wet season, whereas elephants in the southern areas of the park had a diet composed of 10% C_4 graze in the dry season and 50% graze in the wet season. Cerling *et al.* (2009) found that elephants in northern Kenya had a diet composed of 5-20% C_4 graze in the dry season and 40-60% C_4 graze in the wet season. Throughout isotopic dietary studies conducted on elephant, very few elephant populations have been recorded as essentially pure C_4 grazers in the wet season. This is supported by van der Merwe et al. (1988) who found that elephants from Namibia, South Africa, Botswana, Zambia and Malawi have an essentially pure C_3 diet with very little C_4 intake. The author did, however, find an exception in Kenya as the elephant's diet had a significantly large proportion of C_4 graze in the diet. The author credited this to the "elephant problem" where by a high number of elephants reduced the woodlands, that were gradually replaced by extensive grass cover and so elephants were largely unable to access C_3 browse (Napier Bax 1963, Cerling *et al*. 2004). Therefore, it can be suggested that the proportion of C_3 and C_4 biomass in elephant diets can vary according to location as well as seasonal rainfall. Although, in this study the elephants of MWR tended to consume far less C_4 graze in the drier seasons compared to the other studies, this could be attributed to the severity of the dry season in the Shire basin, where MWR is located, whereby the extreme high temperatures and lack of water diminish the available vegetation and in particular the grass species.

Apart from the data displaying a near pure C_3 browse diet in the dry season, the wet season samples displayed a wide range of $\delta^{13}C$ values in both the early and late wet seasons. The results suggest that individuals have both a mixed feeding diet and a pure C_3 browse diet in the wetter seasons. This was unexpected as it was thought that when grass is available in the wet seasons, the fact that it has a greater palatability, is higher in nutritional value and generally has lower tannin concentrations compared to many browse species, would make grass the preferred food source (Cooper & Owen-Smith 1985; de Boer *et al.* 2000; Codron *et al.* 2006). A possible reason for this result could be location, perhaps certain habitat types and certain areas of MWR contain less grass and preferred browse species in the wetter seasons and so could yield a near pure C_3 browse diet. However, the majority of the samples were collected in the Sanctuary (north-west of MWR), where water is plentiful in the form of four artificial waterholes and the Shire River and the habitat type varies between woodland below 250m, woodland between 250-400m and savanna. With so little variation in the location of where the faecal samples were collected it is unlikely that location played a significant role in deciding a near pure C_3 diet or a mixed feeding diet. However, the elephant home ranges may very well have played a significant role in the proportion of C_3/C_4 biomass in the diet. Therefore, the difference in diet in the wetter seasons could be attributed to two factors. Firstly, it would be beneficial to understand the home ranges of different individuals in the reserve to fully understand the isotopic results of the seasonal diet and secondly individual personal preference, perhaps some individuals prefer browse species even in the wetter seasons.

However, the fact that this study showed no significance in $\delta^{13}C$ values or change in the proportion of C_3 browse in samples within seasons (early and late) is interesting. Typically, because plant growth varies throughout the year according to the amount of rainfall, one may expect change in the proportion of C_3 browse and C_4 graze in the diets. In the dry season (early and late) the proportion of C_3 browse remains the same, 98%. This suggests that there was very little, if any, grass available throughout the dry season. In addition, van der Merwe *et al.* (1988) found that elephants in Kasungu National Park, Malawi, consumed between 30-45% C_4 graze in the early wet season, 60% C_4 graze in the late wet season, approximately 23% C_4 graze in the early dry season and 10% C_4 graze in the late dry season. This indicates that there should be a greater change in the proportion of C_4 graze within seasons, for example between early wet and late wet seasons. The lack of any significant change in the $\delta^{13}C$ values within seasons in this study could be due to the methodology. One way of possibly observing a greater variation within seasons would be to collect and analyse a larger number of samples. As elephants are diverse feeders it would have perhaps been more beneficial to analyse one hundred and twenty faecal samples per month as opposed to just ten per season.

For future studies on elephant diet and the diet of other herbivore species in MWR several important steps need to be taken to improve the current study and to provide a greater in-depth analysis on the seasonal change in diet. The steps are as follows:

1) The reserve should be divided into the four main habitat types: high altitude woodland, medium altitude woodland, low altitude woodland and savanna. These four habitat types should then be divided into sampling blocks according to the size of the habitat and waterhole location. Ideally there should be at least three sampling blocks in each habitat type. (J. Codron per comms.)
2) A thorough vegetation analysis, such as plant transects, should be conducted in each sampling block. A minimum of three different grass species and five different browse species should be collected, with three to five samples of each species, in both the wet and dry season. (Codron *et al.* 2006; J. Codron per comms.)
3) Sub-sampling of different plant parts will need to accompany the vegetation analysis. Browse species will need separate leaves, fruit, roots and bark sampled. Grass species will need seeds, leaves and roots sampled. The different plant species and their parts will need to be

isotopically analysed separately to get an idea of the isotopic variation in the plant species in MWR. (J. Codron per comms.)

4) In terms of elephant faecal sampling, ten faecal samples need to be collected per sampling block in each habitat type on a monthly basis. Essentially, a total of 120 samples should be collected monthly. All faecal samples should be analysed for stable carbon and nitrogen isotopes. (Codron *et al.* 2006; J. Codron per comms.)

5) Previous studies suggest that elephant, in particular, take between twelve and twenty two hours to fully digest their food, from consumption to defecation, and they are capable of moving large distances in a day (Laws & Parker 1968; Rees 1982; Clauss et al. 2007; Campos-Arceiz et al. 2008; Stokke & du Toit 2002). It would be difficult to justify that samples collected in a specific location and habitat type would be a fair representation of that site. This is supported by de Boer et al. (2000) who found that species composition was relatively unaffected by the habitat in which the faecal pile was found and so the long digestive process and the opportunistic feeding pattern of elephant masks the species composition of each habitat (Jarman 1971). One way to overcome this issue is to collect faecal samples of other sympatric herbivores in terms of pure browsers (kudu), pure grazers (zebra) and mixed feeders (impala) (Condron *et al.* 2006). These additional samples will represent the majority of plant species in the different habitat types more accurately than elephant faecal samples as species such as kudu, zebra and impala do not travel the great distances elephants do on a daily basis (Codron *et al*. 2006). This will provide an accurate representation of each habitat type as well as a robust isotope baseline for elephants in MWR from both the plant and sympatric herbivore perspective. Therefore, comparing the carbon values between elephant faecal samples to other herbivore species would provide an idea as to whether the elephant faecal samples represent a certain habitat type and allow for the calculations of the distance travelled and the time between consumption and defaecation (J. Condron per comms.).

6) Lastly, in addition to isotope analysis of species faecal matter mictohistological techniques should be used to determine the actual dietary composition of each elephant faecal sample (Stewart 1967). This method allows for the identification of the vegetative remains to a group or species level with the use of dietary reference slides of local vegetation samples. Using this method will give researchers an idea of what vegetation types are being targeted more than others at certain times of the year as well as eliminate the uncertainty that sample location provides. Further details of this method are referred to in Stewart (1967); Suter *et al.* (2004); de Jong *et al.* (1995); Blanco-Fontao *et al.* (2010) and Bergstrom (2013).

To date three other studies that have focused on the feeding habits of elephant in MWR. Staub *et al.* (2013) found that browsing of elephant on MWR increased with the proximity to water sources and that a strong preference was shown for riparian woodlands and *Acacia* dominated woodlands. Whereas *Brachystegia* dominated woodlands were relatively unaffected by elephant browsing (Jachmann & Bell, 1985; Staub *et al.* 2013). Wienand (2013) agreed with Staub *et al*. (2013) and further found that the use of water points by elephant was seasonal, in that visitation of water points in the wet season was minimal compared to the dry season when visitation rates increased. Furthermore, the water points with the highest elephant visitation rates in MWR were situated in low altitude woodland and the water points with the lowest visitation rates were those situated in the high altitude *Brachystegia* dominated woodlands (Weinand 2013). Komoto (2013) agreed with both the above studies and found a strong correlation between tree mortality and heavy elephant browsing in MWR. The study also proposed that the highest elephant impact on woody tree species was in the north-eastern part of the reserve, the Sanctuary, and the lowest impact was in the *Brachystegia* dominated woodland (Komoto 2013). Therefore, the water points in the Sanctuary of MWR are most used by elephants due to flat, low altitude terrain, favoured vegetation types are prevalent such as *Combretum* and *Acacia* species, there is a high availability of perennial water as both mentioned rivers are accessible.

The combination of the results of these three mentioned studies, as well as the results from this study suggest that the feeding habits of elephants in MWR were strongly seasonal. In the wet season, when water was plentiful and nutritious grass was available, the elephants were able to migrate to areas of the reserve largely inaccessible during other times of year. However, in dry season the low altitudinal areas that contain riparian and *Acacia* dominated woodland were under increasing pressure from elephants especially the areas closer to perennial water points. This is supported by this study as results indicated that the elephants almost exclusively feed on browse in the dry season in MWR. Therefore, as elephant numbers continue to increase in the reserve, the Sanctuary (the main tourist hub) which contains four artificial water points, a perennial spring, the Shire and Mkulumadzi Rivers, and is low in altitude and has the preferred vegetation types will be under increasing pressure to support a growing elephant population.

The increase in the human population in Southern Africa has resulted in the fragmentation and isolation of many of Africa's wilderness areas. In order to prevent human-wildlife conflict in the remaining wilderness areas an increasing number of reserves are being fenced to not only protect the local people but also the flora and fauna of the reserves. This ultimately results in an artificial ecosystem as many animal species are unable to migrate and so intensive management is required to preserve the biodiversity of the protected areas. The elephant population in MWR needs to be closely monitored to prevent overpopulation and to prevent the species out competing other herbivores and disrupting the balance of the ecosystem as a whole.

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Chapter Five

Research findings, conclusions and management recommendations for African Parks Majete management staff

Overview

It is anticipated that the high elephant population on Majete Wildlife Reserve (MWR, hereafter) post-reintroduction will begin impacting ecosystem processes, woody vegetation cover and other herbivore species as the pressure on resources such as water and acceptable forage increases. This study essentially investigated and provided baseline information on the size, structure and gender ratio of the elephant population, by means of individual identification techniques, since the reintroductions in 2006, 2008 and 2010. In addition, this study focused on seasonal movement and habitat use of the elephant by employing the use of camera traps positioned in grids and at selected water sources, as well as determining the approximate browse and grass contributions to their diet throughout the year. The findings of this research, along with the supporting information from the literature review, will contribute to the understanding of the baseline ecology of elephant in MWR. In addition, it will assist in the development of management strategies used to control elephant population numbers and mitigate vegetation degradation. In this report, the key study findings are summarised and the management implications of these findings are discussed in detail.

Research Findings

Chapter Three: The population structure and habitat use of African elephant

- The most recent aerial count (Nov 2015) conducted in MWR counted a total of 389 individual elephants and by March 2016, the current study was able to formally identify 366 of these individuals, using mark-recapture techniques. Aerial counts tend to under sample areas, more specifically woodland areas, so it is suggested that the actual population size of elephant is larger than 389.
- In the absence of immigration, emigration, human-elephant conflict and heavy poaching the Majete elephant population has grown at an estimated annual rate of 13.8% since the completion of reintroductions in 2010.
- The structure of the population was found to be as follows: 11.8% infants (<1 year), 23.8% calves (1-4.9 years), 14.5% juveniles (5-9.9 years), 15.0% small adult (10-19.9 years), 26.8%

medium adult (20-34.9 years) and 8.2% large adult (>35 years). The sex ratio of individuals below and above the age of 10 years was 1:1.

- Camera grid data analysis suggests that elephants prefer areas around water sources in both the wet and the dry seasons. The largest number of individuals recorded in both seasons was in the Sanctuary area and the number of individuals recorded in the Pwadzi and Namisempha regions increased slightly in the dry season.
- Water points were used more in the dry season compared to the wet season.
- Water points were not equally used in the dry or the wet seasons but least favourable water points, such as Diwa which is situated at a high altitude and is surround by a *Brachystegia*-dominated vegetation type, experienced an increase in usage since the study conducted by Weinand (2013).
- In general the water points with the highest usage were Pende 2 and Pwadzi (based in the low altitudinal region south-west in MWR), the Sanctuary water points had a much lower usage and this is possibly due to the over saturation of perennial water points in the region.
- Family herds dominated water point usage in both the wet and the dry season, except in the wet season 2016 where bulls utilised the Sanctuary water points more than family herds. The domination of water points by family herds is possibly due to the constraints of group living as it limits home ranges to perennial water points especially in the dry season, whereas solitary bulls are less water dependent and are able to migrate through large areas of MWR in both seasons.

Chapter Four: Stable isotope analysis of African elephant diet

- The stable isotope analysis of vegetation samples from MWR provided distinct isotopic values of carbon ($\delta^{13}C$) for seven grass (C_4) species and twenty browse (C_3) species. These values were used as reference points for the stable isotope analysis of elephant faeces.
- Elephants are mixed feeders that are able to adjust their diet depending on the season. It was determined that the elephants' diet had the highest C_3 vegetation content in the early and late dry seasons. However, in the early and late wet seasons elephant diet displayed a shift towards C_4 vegetation, signifying a greater diversity of browse (C_3) and grass (C_4) in the diet compared to the early and late dry seasons. Therefore, elephants consume a higher proportion of C_3 browse relative to C_4 grass in the dry seasons and shift their diets in the wetter seasons to incorporate more grass species.

Conclusions and Management Recommendations

African elephants form an important part of African ecosystems as they play a keystone role in the diversity of habitats they occupy, from deserts and savannas to rainforests (Styles & Skinner 2000). They have an effect on the canopy cover, the distribution of other species and the dispersal of seeds (Styles & Skinner 2000; Shoshani *et al.* 2004; Kerley & Landman 2006). However, preserving populations of elephants while maintaining biodiversity is a constant challenge for the management of protected areas and more often than not many of these areas are faced with the "elephant problem". The "elephant problem" is defined by high elephant numbers in conservation areas as they are perceived to alter the vegetation in the area (Caughley 1976; Barnes 1983; van Aarde & Jackson 2007). In the past, the changes in the abundance of elephants, or the alteration of vegetation was viewed as an undesirable disruption of environmental equilibrium conditions and an irreversible threat to biodiversity (Caughley 1976; Barnes 1983; Gillson & Lindsay 2003). However, this concept of the balance of nature is out dated as vegetation composition is now understood to change over time in response to a variety of variables, such as climatic variation, and so there has been a fundamental shift to the flux of nature (non-equilibrium) paradigm, where the ecological processes that promote biodiversity are essentially about change and not stable equilibria (Gillson & Lindsay 2003, Owen-Smith *et al.* 2006). Therefore, managing elephants at defined management levels is not sensible; numbers should fluctuate through time and space due to the availability of resources, density dependence and environmental forces (Gillson & Lindsay 2003; Skarpe *et al*. 2004; Owen-Smith *et al*. 2006).

Despite this shift to the flux of nature paradigm many protected areas are still faced with the problem of high elephant numbers. These high elephant numbers are induced by anthropogenic factors and include the supplementation of water, fencing and the reduction and fragmentation of landscapes that prevent natural migration patterns (van Aarde & Jackson 2007). Artificial water sources allow more extensive dry season ranging, creating the opportunity to overexploit vegetation areas that would have otherwise been inaccessible to elephant except in the wet season (Loarie *et al.* 2009; Owen-Smith *et al*. 2006; Kalwiji *et al*. 2010). Additionally, fences prevent seasonal migration of individuals in and out of an area and so cause elephants to 'bunch up' against them during the wet season as their home ranges increase, again locally increasing the pressure of elephants on their resources (Owen-Smith *et al*. 2006; Guldemond & van Aarde 2007; Loarie *et al.* 2009). Therefore, the combination of artificial waterholes and fencing creates elephant populations that are most likely to damage the vegetation in an area and the other species that depend on the vegetation, especially during unusually dry years, as elephants are unable to migrate to find food (Shrader et al. 2010).

Understanding the non-equilibrium paradigm is essential for the management of the elephant population in MWR. The ecological capacity for elephant in a given area is not a fixed figure, but one that varies from year to year and from season to season. Two of the major challenges that face the ecological capacity for elephant are the temporal and spatial scale of the reserve, such as available habitat and rainfall (van Aarde & Jackson 2007; Bothma & du Toit 2010). However, as a broad guideline the ecological capacity for MWR was calculated using two methods. The first is from Bothma & du Toit (2010) which is based on the following equation that was developed for areas where elephants occur naturally and takes into account the reserve size and annual rainfall.

$$\text{Log}_{10}\text{large herbivore biomass in kg per km}^2 = 1.685 \times \log_{10} \text{mean annual rainfall in mm} - 1.095$$

MWR is a 70 000 ha reserve with an annual precipitation of 680 – 800mm in the Eastern lowlands and 700 – 1000mm in the Western Highlands. Rainfall is incredibly important in setting the stocking density of an area and in order to be conservative in the calculation a value of 700mm of annual rainfall was used. Therefore, according to Bothma & du Toit (2010) the recommended ecological capacity of MWR is 304 individual elephants. It must be reiterated, however, that this value is a broad guideline and will vary according to the various habitat types, water supply and other herbivore species and their population sizes.

The second method used to calculate the ecological capacity for elephant on MWR is from van Oudtshoorn (2015) and focuses on the browsing rather than the grazing capacity of elephants. As the results from Chapter 4 indicate that elephants in MWR do not consume significant amounts of grass. The Browsing Units per Hectare (BU/ha) for MWR were calculated using data from Staub *et al.* (2013) for trees greater than 2.0 m in height, or a Diameter and Breast Height (DBH) greater than 10 cm, and the result was 1937.66 BU/ha. The browsing capacity for elephant for MWR was calculated by dividing the Browsing Units needed by elephant, 41500 BU/needed, by the Browsing Units available, 1937.66 BU/ha, and the result was 21.4 ha/elephant which is equivalent to 402 individual elephants in MWR. Although this value for the browsing capacity of elephants in MWR is suitable for 2013, when Staub *et al.* (2013) conducted their study, when compared to the current stocking rate of elephants in 2015, which is 22.1 ha/elephant, it is clear that elephants are approaching or have started to exceed the browsing capacity on the reserve. However, these values have only taken elephants into account and other browsers on the reserve, such as Kudu for example, need to be included in the calculations, no doubt changing the browsing capacity for MWR and decreasing the stocking rate of elephant. However, further research is needed regarding the other browsing species and the current state of the woody vegetation in MWR before final numbers for elephant can be provided. From personal observation while conducting field work in MWR, it is believed that the stocking rate of elephant should fluctuate between 250 to 300 individuals. Therefore, the observed increase in the elephant population as well as the increase in other herbivore populations as revealed from the 2015 aerial survey suggests that MWR is overstocked and so the woody vegetation is under increasing pressure and is potentially being degraded.

Evidence of this was first reported by both Staub *et al.* (2013) and Weinand (2013) as both studies focused on the interaction of elephant with the woody vegetation in MWR. Staub et al. (2013) found that browsing intensity increased with proximity to water and that browsing was most concentrated in riparian woodland and least concentrated in *Brachystegia*-dominated woodland. Weinand (2013) found similar results and found that the most utilised water points were in the Sanctuary, where elephant browsing around the water points was high. Weinand (2013) found that the there was a positive but weak spatial relationship between elephant browsing and distance to water in this region due to the abundance of perennial water sources. The results from the current study noted that since 2013 the elephant population has increased and the water point usage by elephants is becoming saturated as there has been an increase in usage of the least preferred sites since 2013. Thus, indicating that due to the pressures of an increasing population density, the elephants have begun to utilise their least preferred areas, namely regions at high altitude with less preferred vegetation such as *Brachystegia*-dominated woodland, and so have increased their habitat usage to areas that previously did not incur a high elephant presence.

Evaluation of management options

The non-equilibrium or flux of ecosystems is an integral part of ecosystem dynamics. External factors, such as fire, floods and droughts, are important in maintaining a diversity of plants and animals as well as generating space and a variety in ecosystems (Owen-Smith *et al.* 2006). This suggests that the disturbance caused by elephants could likewise be beneficial for ecosystem dynamics. However, it is not the local severity of elephant disturbance that is important but rather the spatial extent of it and so local overgrazing or over browsing by various large herbivore species is inconsequential or even beneficial if only a small portion of the land is affected (Gillson & Lindsay 2003, Owen-Smith *et al.* 2006). Concern arises when adverse effects occur and spread to cover large areas, decreasing the mosaic of the diversity of habitats (Whyte *et al*. 2003, Owen-Smith *et al.* 2006). The decrease in habitat heterogeneity is a reality for many fenced reserves with high elephant numbers and so management systems and plans are a necessity in order to preserve the remaining biodiversity in an area as well as maintain healthy populations of other herbivore species.

African Parks already have a number of effective management strategies in place in MWR and so only the relevant management suggestions for the elephant population will be discussed. It has been established that the current elephant population in MWR is too high and needs to be controlled before it has any adverse effects on the vegetation and other herbivore species. However, it must be emphasised that elephant management requires a combination of prudent deliverable strategies that includes invasive management techniques, directly affecting the elephant population such as translocation, and non-invasive management techniques, indirectly affecting the population such as water point management. It is a combination of these practises that will obtain the optimum management results and so both invasive and non-invasive management practises will be discussed for MWR.

Translocation

Translocation, an invasive management practise, reduces local elephant densities by removing elephants from high density to low density areas, establishing new populations or increasing existing populations in new conservation areas (Rogers & Sherwill 2008). The advantage of translocation is that it increases the range of elephants. The disadvantages are that it is a highly specialised and an extremely costly procedure that requires well-trained capture and transfer teams, as well as a variety of heavy duty equipment such as cranes and specialised transport (van Aarde & Jackson 2007; Rogers & Sherwill 2008). In addition, there are few conservation areas left in Southern Africa that can still accommodate extra elephants and even if individuals are translocated they still need to be managed, especially if the new area is fenced (van Aarde & Jackson 2007). From 1989 to 2001, a large scale translocation programme was completed in South Africa that translocated elephants from the Kruger National Park (hereafter, KNP) to 58 small fenced reserves. (Slotow *et al.* 2005). The average population growth rate in these small reserves averaged 8.3%, post translocation, indicating that the programme was largely successful (Slotow *et al.* 2005). This, however, increases the complexity of elephant management on these small reserves and many have either had to implement contraception programmes or continue with translocation in order to maintain population numbers at practical levels (Slotow *et al.* 2005).

Translocation is a primary management option for the elephant population in MWR. African Parks have planned to translocate 150 elephant from MWR to Nkhotakhota Wildlife Reserve, in central Malawi, in June/July 2017. Assuming that the elephant population consists of 389 individuals, according to the aerial survey, it will be decreased to 239 individuals post translocation, which is the recommended stocking rate for MWR. In order to promote the stabilisation of the population in terms of growth rate, it is recommended that the MWR population is maintained at 48% individuals above the age of 11 years and 6.8 % infants (<1year) (Calef 1988). Chapter 3, indicated that there are approximately 91 bulls (>11 years) and 38 elephant herds in MWR with an average herd size of 7 individuals, 2 adults (>11 years) and 5 young (<11 years). Using these averages, the suggested proportion of individuals that should be translocated is estimated to be 70 young (<11 years) and 80 adults (>11 years) which varies between 14 -17 herds and a minimum of 30 bulls. These numbers will vary when actual herd sizes are taken into account. However, it is noted that if the sex ratio of the MWR elephant population is skewed towards bulls the population growth rate will decline (Whyte *et al.* 1998), thus it is recommended that fewer adult bulls than adult cows are translocated.

Contraception

Contraception, an invasive management practise, manipulates the fertility in elephants using two main methods that have both been tested in Southern Africa, steroids and immunocontraception (Rogers & Sherwill 2008). Steroids have thus far been less successful than immunocontraception and so may be the less preferred method for MWR. Immunocontraception is a promising technique involving immunising cows with a foreign protein (porcine zona pellucida, pZP), and encouraging the production of antibodies that prevent fertilisation (Fayrer-Hosken *et al*. 2000; Rogers & Sherwill 2008). Field trials conducted in the Kruger National Park had success rates of 60% to 80% and have demonstrated that the method is effective in preventing pregnancies (Rogers & Sherwill 2008). The added advantage of pZP is that it is reversible, it has no adverse health effects, it is safe to use during pregnancy and has no behavioural side effects on elephant cows (Rogers & Sherwill 2008). Immunocontraception technology is continuously improving, the vaccine is delivered by darting and can be effective for a 12 month period but its long term effectiveness in controlling populations is still being evaluated (Fayrer-Hosken *et al*. 2000; Rogers & Sherwill 2008). There are many positives to elephant contraception including the possibility of lengthening inter-calving intervals and increasing the age of first calving (Pimm & van Aarde 2001). However, there are also limitations to contraception as it is incapable of reducing population sizes in the short term and to stabilise elephant numbers in large populations is very costly and time consuming (Whyte *et al.* 1998; Pimm & van Aarde 2001; van Aarde & Jackson 2007; Rogers & Sherwill 2008). To control the elephant population in the Kruger National Park by contraception would require the treatment of 2250 cows each year over an initial period of 11 years (Whyte *et al.* 1998). Therefore, contraception has both positive and negative attributes and on small fenced reserves may very well be the answer to increasing elephant populations as this management scheme would still be economically viable. However, on large reserves with large elephant populations, such as KNP, the cost of contraception may be too high as it an ongoing process that requires booster treatments (van Aarde *et al.* 1999; Fayrer-Hosken *et al.* 2000; Pimm & van Aarde 2001).

Once the translocation of 150 individuals in 2017 is complete, it is highly recommended that contraception is implemented in MWR. This is because the decrease in elephant density in MWR will encourage an increase in the population growth rate once again, and if contraception is not implemented, it will be necessary to translocate another large number of individuals in the years to come (van Aarde & Jackson 2007; Chamaille-Jammes *et al.* 2008). It is estimated that the remaining number of adult females left in MWR will range from 50 -65 and if an annual population growth of 0% is required, immunocontraception models have demonstrated that contraception of 75% of these breeding-age females with an annual mortality rate of 2-3% will be sufficient (Delsink & Kirkpatrick 2012). It must be stressed that results expected, such as zero population growth rate, from the use of contraception may only be visible about 11 years from the initiation of the programme. This is due to the steady recruitment of females, born before the use of contraception, into the breeding population (Whyte 1998). The fertility rates, intercalving rates and mortality rates will affect the outcome of contraception and as these are unknown for the MWR population it is emphasized that contraception results are site specific and cannot be generalised (Whyte *et al.* 1998; van Aarde & Jackson 2007; Delsink & Kirkpatrick 2012).

Botanical Reserves and Zoning

The establishment of botanical reserves, a non-invasive management technique, within fenced parks protects rare and endangered vegetation that is at high risk from elephant activities due to fencing (Rogers & Sherwill 2008). The KNP and the Addo Elephant National Park (hereafter, AENP) are both parks that have high elephant numbers that are having a detrimental effect on the biodiversity (Lombard *et al.* 2001; Whyte *et al.* 2003). Since the ban on culling in the KNP, management incorporated a new policy that divided the park into six management regions that included two botanical reserves where elephants were totally excluded, two high elephant impact zones and two low elephant impact zones where population numbers decrease at a rate of 7% per year (Whyte *et al.* 2003). AENP adopted a similar strategy with elephant exclusion zones to encourage botanical growth, these exclusion zones now contain plant species that are unable to grow elsewhere in the reserve due to high herbivory (Lombard *et al*. 2001). The limitations of this form of management are that it does not necessarily address the problem of high elephant numbers, the expense of installing and maintaining fences and it is mostly appropriate for small areas of highly threatened endemic vegetation (Rogers & Sherwill 2008). Botanical Reserves are a potential management solution for MWR in terms of vegetation preservation. However, there is a lack of information on the extent of vegetation degradation caused by elephant in MWR, as well as which plant species are being threatened. It is suggested that further research is conducted and thresholds of acceptable levels of elephant impacts on vegetation are determined before this management strategy is implemented.

Habitat Utilisation and Restriction: closing water points

The positioning of water points, a non-invasive management technique, manipulates local elephant densities in large, water limited reserves (Chamaille-Jammes *et al.* 2007). The removal of any artificial water sources located in areas away from rivers will effectively limit elephant foraging range in the dry season which has the potential to limit the impact on susceptible tree species that primarily grow at higher altitudes (Rogers & Sherwill 2008; Loarie *et al.* 2009). In addition, the overuse of areas close to water sources in the dry season, otherwise known as piosphere effects, will increase elephant's foraging range and the greater distances moved within the dry season will supposedly increase calf mortality and decreasing population growth rates (Duffy et al. 2002; Owen-Smith et al. 2006; Rogers & Sherwill 2008). Chapter 3 suggested that elephant habitat use in the Sanctuary has become homogenised due to the overabundance of perennial water sources in the region. This supports the findings of Weinand (2013) who found that elephant browsing levels did not decrease with increasing distance from water in both seasons. The permanent closure of one artificial water hole in the Sanctuary is recommended, perhaps Nakamba or Nsepete, in order to reduce water availability in the region (Weinand 2013). The limitation is that MWR relies heavily on tourist revenue and the artificial waterholes in the Sanctuary are key tourist attractions as they provide great wildlife viewing opportunities in the dry season. The tourist experience may be negatively affected by crowding of people at remaining waterholes and so MWR will need to balance the needs of less mobile herbivore species and tourism with the management of elephant habitat use in an area.

Habitat utilisation and restriction is achieved through the combination of artificial waterhole locations and the implementation of zoning in the reserve which will require certain regions to be sacrificed for elephant use. The Sanctuary could potentially be designated as a high elephant impact zone due to the overabundance of perennial water sources as well as tourism demands. The remaining regions in the reserve would then be designated as low elephant impact zones and would contain fewer water sources at a minimum distance of 10km apart to reduce elephant habitat use (Weinand 2013). The concept of habitat heterogeneity with regards to elephant herbivory across MWR should be incorporated in the elephant management plan, promoting mosaics of different elephant browsing levels in different habitat types across MWR (Weinand 2013). This could be achieved by the strategic positioning of waterholes and the use of fencing to exclude elephants from certain areas (Owen-Smith *et al.* 2006; Chamaille-Jammes *et al.* 2007; O'Connor *et al.* 2007; Weinand 2013). As mentioned above, in order to implement zoning as a management tool in MWR further research needs to be conducted and decisions need to be made in terms of which areas will be zoned as high, low or no elephant impact (Weinand 2013).

Conclusion

In conclusion, the ecological effects of elephant can vary considerably between populations and depends on a number of factors that include rainfall, vegetation type and landscape features

(Guldemond & van Aarde 2008). In the present day, management can control the ecological effects or the intensity at which elephants utilise the landscapes through the use of invasive management techniques, such as contraception, and non-invasive management techniques, such as water provision. Spatial variability is most desirable in fenced reserves and in the modern day paradigm flux of conservation management it is preferred that elephant densities reflect a range of local densities which can be used as an index of potential habitat use intensity (Ferreira *et al.* 2012). Elephant populations respond to the variation in spatial and temporal resources in the short term through migration or dispersal and in the long term through changes in their demography (Young *et al.* 2009). In MWR it is recommended that management use both translocation and contraception in order to achieve the best possible results in controlling the population numbers. In addition, management should also employ the combination of zoning and water availability in order to promote spatial and temporal variability in elephant habitat use In MWR. However, elephants are long-lived mammals that have the longest life-history strategy of all terrestrial animals. This results in slow spatial and demographic population responses to management induced population regulations and restoration of ecological limitations and so ecological responses may take time to manifest.

As a parting word it is important to note that if reserve management only focus on reducing elephant numbers in protected areas it will only address the symptoms of an ecological problem that was initiated by management in the first place (van Aarde *et al.* 2007). In the majority of reserves fencing and artificial water supply are the root of the 'elephant problem' as they prevent the seasonal migration of elephants which, in unfenced systems, allows for vegetation recovery (van Aarde & Jackson 2007; van Aarde *et al.* 2007; Ferreira *et al.* 2012). Moreover, the provision of water, a key limiting factor in natural systems, reduces the natural mortality of elephants and so numbers become unnaturally high (van Aarde & Jackson 2007; van Aarde et al. 2007). Instead, reserve management need to focus on the issues that induce the symptoms of high elephant numbers in reserves, specifically fencing and water management, and the restoration of seasonal movement patterns of elephant (van Aarde & Jackson 2007). Therefore, the management of elephant should not solely focus on numbers but rather incorporate and focus on the idea of temporal and spatial scales.

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Appendices

Appendix 1

The wildlife reintroduction history of Majete Wildlife Reserve

Wildlife was reintroduced into Majete Wildlife Reserve in stages, pre 2008 all introductions were made into the Sanctuary as it was the only region that had a complete fence. Total fencing was completed in 2008 and further wildlife reintroductions were made to the rest of the reserve. The Sanctuary fence was only removed in 2011.

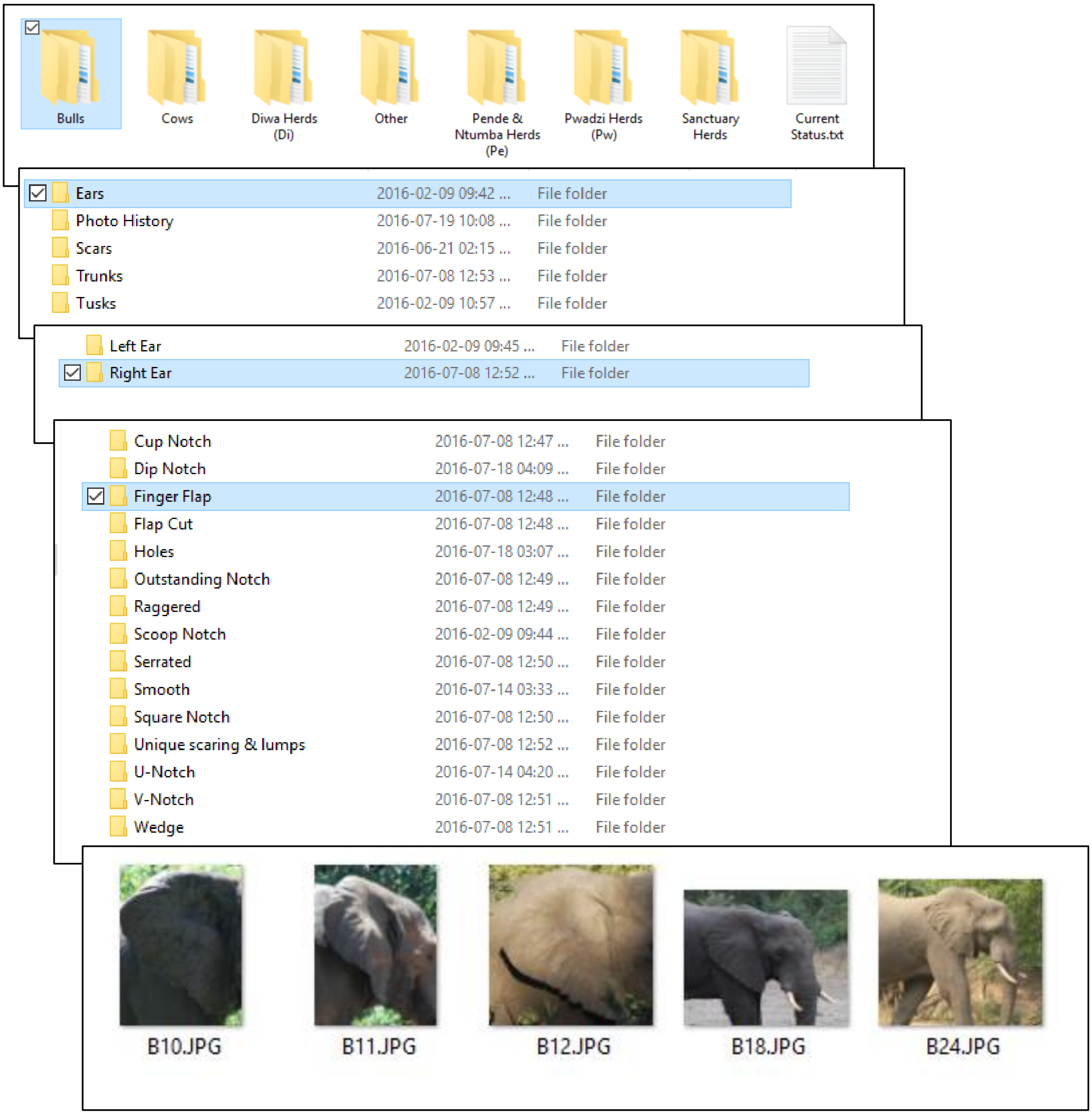
Table A.1. Details of wildlife reintroductions to various regions of Majete Wildlife Reserve between 2003 and 2010.

	Sanctuary							The rest of Majete			
Species	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2008**	**2009**	**2010**	**Total**
Elephant				70				60	83		**213**
Black Rhino	2				6						**8**
Buffalo	120	100						86			**306**
Sable	100							153		99	**352**
Hartebeest		4		10		15	30				**59**
Waterbuck	98							198		106	**402**
Zebra		37	50	9		38			40		**174**
Eland		20				32			25		**77**
Impala	216							210		311	**737**
Nyala	6	15						38			**59**
Warthog	60							98			**158**

Appendix 2

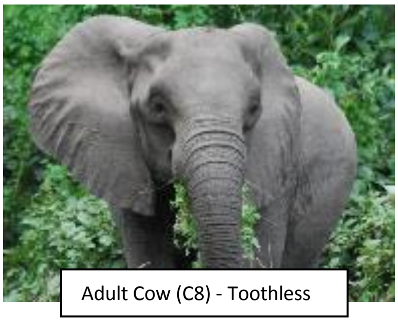
Appendix 2.1

An example of the Majete Elephant Database. The database was designed with a pyramid of folders, the first layer focuses on the gender of an individual or different regions herd frequent. The second layer focuses on the anatomy of individuals, specifically looking at notable characteristics of each one. The final layer lists the categories of characteristics, for example, the shapes of scars on the ears were listed in the figure below. By identifying notable characteristics of individuals met in the field one can later identify them in the database. The same applies to herds.



Appendix 2.2

An example of a well-known family herd in MWR. Each of the adult cows was given a unique code such as ‘C8’ which stands for ‘Cow 8’. When each herd was recorded in the database, the name given to the herd was composed of the adult females’ codes as well as the number of individuals in a herd. The finer data recorded for each herd specifically looked at all the individuals in a herd, aging them and sexing them.


Adult Cow (C8) - Toothless


Adult Cow (C9)


Adult Cow (C10)


Juvenile Female (C26)


Calf Male


Calf Male


Calf Female


Infant Male


Infant Female

Appendix 2.3

A.2. A Table representing the number of family herds and solitary bulls in MWR and their total number, sex and age structure in the years 2015 and 2016.

Number	Code (Code allocated to each individual eg: C1 = Cow One)	Group Type (Family Herd, Solitary Bull)	Total Number of Individuals	Number of Large Adult Females	Number of Medium Adult Females	Number of Small Adult Females	Number of Male Juveniles	Number of Female Juveniles	Number of Unknown Juveniles	Number of Male Calves	Number of Female Calves	Number of Unknown Calves	Number of Male Infants	Number of Female Infants	Number of Unknown Infants
1	C1_C2_C13	Family Herd	10	0	3	0	0	1	0	3	0	0	1	2	0
2	C3_C7_C14	Family Herd	7	0	1	1	0	1	0	1	2	0	1	0	0
5	C4_C5_C6_C15_ C17	Family Herd	15	1	2	2	0	2	0	3	1	2	1	0	1
6	C8_C9_C10_C26	Family Herd	10	0	2	2	1	0	0	1	2	0	1	1	0
7	C11_C12	Family Herd	7	0	1	1	0	0	0	1	2	0	0	0	2
8	C19	Family Herd	6	0	2	0	0	0	0	0	0	2	0	0	2
9	C20_C21_C22_C23	Family Herd	11	1	2	2	1	1	2	0	1	1	1	0	0
10	C24_C25_C29	Family Herd	8	3	0	0	1	1	0	2	0	0	0	0	1
13	C32_C33	Family Herd	7	1	1	0	0	1	1	0	0	1	0	0	2
14	C34_C35_C36	Family Herd	10	2	1	1	1	1	0	1	0	2	0	0	1
15	C37_C38_C39_C40	Family Herd	12	0	3	1	1	2	0	1	1	2	0	0	1
18	PwC1_PwC29	Family Herd	4	0	1	1	0	0	0	1	0	1	0	0	0
19	PwC2	Family Herd	5	1	0	0	0	1	0	1	1	0	0	0	1
20	PwC3	Family Herd	6	0	1	1	1	0	0	0	0	2	0	0	1
21	PwC5_PwC6_ PwC15	Family Herd	11	0	2	1	2	1	0	2	1	0	0	1	1
22	PwC7_PwC8	Family Herd	7	1	1	1	1	0	0	1	1	0	0	0	1

23	PwC9	Family Herd	4	0	1	0	1	0	0	1	0	0	0	0	1
24	PwC10	Family Herd	5	1	0	0	1	0	0	0	0	2	0	0	1
25	PwC11_PwC14	Family Herd	7	0	2	0	0	1	0	0	0	2	0	0	2
26	PwC12_PwC13	Family Herd	8	1	1	0	1	1	0	0	0	3	0	0	1
27	PwC16	Family Herd	4	0	1	0	0	0	0	1	0	1	0	0	1
28	PwC17	Family Herd	5	0	1	0	1	0	0	0	0	2	0	0	1
29	PwC18	Family Herd	5	0	1	0	1	1	0	0	0	1	0	0	1
30	PwC19_PwC22	Family Herd	6	0	1	1	1	0	0	0	1	1	0	0	1
31	PwC20	Family Herd	3	1	0	0	1	0	0	0	0	1	0	0	0
32	PwC23	Family Herd	4	0	1	0	0	1	0	1	0	0	0	1	0
33	PwC24	Family Herd	2	0	1	0	0	0	0	1	0	0	0	0	0
34	PwC25_PwC26_ PwC27	Family Herd	8	0	1	2	0	2	0	0	0	2	0	0	1
36	PeC1_PeC2	Family Herd	9	0	2	1	0	0	2	1	1	1	0	0	1
38	PeC5_PeC17	Family Herd	7	1	1	0	1	0	0	0	2	1	0	0	0
39	PeC6_PeC7_PeC8_ PeC14	Family Herd	11	1	2	1	0	1	1	2	1	0	0	0	2
40	PeC9_PeC16	Family Herd	6	0	2	0	0	1	0	0	0	2	0	0	1
41	PeC10_Pe C11_PeC12_PeC13_ PeC15	Family Herd	12	1	2	2	1	1	0	1	1	2	0	0	1
42	PeC19 _ PeC22_ PeC27	Family Herd	8	1	2	0	1	1	0	0	0	2	0	0	1
43	PeC20_PeC21	Family Herd	9	1	1	0	0	0	2	0	0	2	0	0	2
44	PeC23_PeC24	Family Herd	4	0	2	0	0	0	1	0	0	1	0	0	0
46	DiC2	Family Herd	8	2	1	0	1	0	0	0	1	2	0	0	1

47	DiC4_DiC5	Family Herd	5	0	1	1	1	1	0	0	0	1	0	0	0
48	B1	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
49	B2	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
50	B3	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
51	B4	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
52	B5	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
53	B6	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
54	B7	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
55	B8	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
56	B9	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
57	B10	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
58	B11	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
59	B12	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
60	B13	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
61	B14	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
62	B15	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
63	B16	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
64	B17	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
65	B18	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
66	B19	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
67	B20	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0

68	B21	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
69	B22	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
70	B23	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
71	B24	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
72	B25	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
73	B26	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
74	B26	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
75	B27	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
76	B28	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
77	B29	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
78	B30	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
79	B31	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
80	B32	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
81	B33	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
82	B34	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
83	B35	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
84	B36	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
85	B37	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
86	B38	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
87	B39	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
88	B40	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0

89	B41	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
90	B42	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
91	B43	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
92	B44	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
93	B45	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
94	B46	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
95	B47	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
96	B48	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
97	B49	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
98	B50	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
99	B51	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
100	B52	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
101	PwB1	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
102	PwB2	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
103	PwB3	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
104	PwB4	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
105	PwB5	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
106	PwB6	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
107	PwB7	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
108	PwB8	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
109	PwB9	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0

110	PwB10	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
111	PwB11	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
112	PwB12	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
113	PwB13	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
114	PwB14	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
115	PwB15	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
116	PwB16	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
117	PwB17	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
118	PwB18	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
119	PwB19	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
120	PwB20	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
121	PwB21	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
122	PeB1	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
123	PeB2	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
124	Pe B3	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
125	Pe B4	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
126	Pe B5	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
127	Pe B6	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
128	Pe B7	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
129	Pe B8	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
130	Pe B9	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0

131	Pe B10	Bull	1	1	0	0	0	0	0	0	0	0	0	0	0
132	Pe B11	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
133	Pe B13	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
134	Pe B14	Bull	1	0	0	1	0	0	0	0	0	0	0	0	0
135	Pe B15	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
136	Pe B16	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
137	Pe B17	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
138	Pe B18	Bull	1	0	1	0	0	0	0	0	0	0	0	0	0
Total			**366**	**30**	**98**	**55**	**21**	**23**	**9**	**26**	**19**	**42**	**5**	**5**	**33**