

The influence of immuno-contraception on the ecology
of African savanna elephants (*Loxodonta africana*) in a
small game reserve in the Eastern Cape, South Africa

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

Department of Zoology and Entomology

Natalie Fowler

January 2023

Supervisors – D. Parker and N. Mgqatsa

ABSTRACT

African savanna elephants (*Loxodonta africana*) can alter the vegetation structure on a landscape which has both positive and negative consequences for biodiversity. This ecological role can be dependent on the density of elephants in a given area and how the area is transformed. Elephants are currently listed as an endangered species on the International Union for Conservation of Nature (IUCN) global red list. Despite this endangered status, strong conservation efforts in southern Africa have increased elephant numbers in protected areas. In South Africa, many of these protected areas are small (<1000 km²) and fenced. Thus, without the freedom to roam over large areas, elephant impacts on vegetation and other ecosystem processes may be exacerbated. Increased growth rates and higher population densities, have prompted wildlife managers to explore several population-level management techniques to slow elephant growth rates in small, protected areas. One such technique is the use of immuno-contraception. My study focused on three datasets (Pre, During and Post porcine zona pellucida (PZP) treatments) of one elephant population over an 18-year period in a small game reserve in the Eastern Cape, South Africa. The first aim of my study was to compare the female demography and reproductive parameters of treated (with PZP) and non-treated females (no PZP). I predicted that the population growth would decrease as more elephant cows were contracepted as well as them having longer inter-calving intervals than non-treated cows. Further, I predicted that there would be a skewed sex ratio of male calves born to treated cows. Lastly, I predicted that fertility rates would be lower in treated cows than in non-treated cows. I calculated the annual population growth rates, inter-calving intervals, sex ratios, age at first calving, fecundity rates and fertility rates of all breeding cows. Population growth rates were similar

to other managed populations although, compared to a relatively untouched elephant population, annual growth rates in my study site were high. The inter-calving intervals and age at first birth were low compared to other African protected areas which were most likely influenced by the use of PZP, rainfall and a lack of density dependence. Treated cows did not have longer inter-calving intervals compared to non-treated cows nor was there a male biased sex ratio of the offspring of treated cows. The second aim was to assess the spatial ecology of this elephant population and how it may be influenced by immuno-contraception. I predicted that the use of PZP would increase the elephant herd's core range as there were fewer reproducing cows. I also predicted that PZP would alter the elephant's habitat use making them less selective in terms of the vegetation types they selected. I compared the home ranges of the elephant population among the three treatments (Pre PZP, During PZP and Post PZP treatment). Home ranges were larger when elephants were treated with PZP compared to the Pre and Post treatments. The herd utilized most of the reserve during the use of PZP whereas prior to contraception, their space use was mostly concentrated on the eastern side of the reserve. Additionally, the vegetation utilization was inconsistent across the differing timeframes, specifically between pre PZP and during PZP. Prior to the use of PZP, the elephant herd utilized the old lands and riverine thicket the most whereas during the use of PZP, the grasslands and karroid habitats were used the most. The most likely influence of the changes in home ranges and vegetation utilization were rainfall, the use of PZP and resource availability. My results suggest that the use of PZP is essential for controlling elephant population numbers. However, there may be some long-term effects (e.g., behavioural changes) of the use of PZP in elephant populations in small game reserves. Thus, I recommend continued monitoring of all aspects of elephant ecology on reserves where PZP is used as a contraceptive technique.

TABLE OF CONTENTS

ABSTRACT	2
TABLE OF CONTENTS	4
ACKNOWLEDGEMENTS.....	6
CHAPTER ONE	7
GENERAL INTRODUCTION.....	7
CHAPTER TWO	17
STUDY ANIMAL AND STUDY AREA.....	17
2.1 STUDY ANIMAL	17
2.1.1 Taxonomy	17
2.1.2 Description	18
2.1.3 Distribution and habitat	19
2.1.4 Behavioural ecology	19
2.1.5 Reproductive biology.....	21
2.1.6 Foraging ecology and diet	22
2.1.7 Conservation status.....	22
2.2 STUDY AREA	23
2.2.1 Location and history	23
2.2.2 Hydrology	26
2.2.3 Geology and topography.....	27
2.2.4 Vegetation	28
2.2.5 Elephant population	31
2.2.6 Monitoring and identification	32
2.2.7 Immuno-contraceptive plan.....	34
CHAPTER THREE.....	38
DEMOGRPAHY AND REPRODUCTION	38
3.1 INTRODUCTION	38
3.2 METHODS	40
3.3 RESULTS	44
3.4 DISCUSSION	54
3.5 CONCLUSIONS	66
CHAPTER FOUR	68
SPATIAL ECOLOGY.....	68
4.1. INTRODUCTION	68
4.2 METHODS	72

ACKNOWLEDGEMENTS

- I would like to thank my supervisors Prof. Dan Parker and Dr Nokubonga Mqatsa for their unwavering guidance, quick responses, and support through this journey.
- I give thanks to Amakhala Game Reserve for allowing me to use their historical data to analyse their elephant population. To Amakhala for employing me to work as their ecologist for the last seven years. It has been nothing but a spectacular journey.
- I would like to thank Mark Palmer for his knowledge and support to teach me the fundamentals of ecology on Amakhala and for being such an influential mentor and pushing me to strive for the best.
- I would like to thank Dr Mike Slattery, Dr Victoria Bennett, and the Institute for Environmental Studies at Texas Christian University for their support and guidance on this project.
- Lastly, to my family as they give never-ending, unquestionable support to my passionate goals.

CHAPTER ONE

GENERAL INTRODUCTION

African elephants (*Loxodonta africana*) can alter the biodiversity of a landscape in both positive and negative aspects. This ecological role can be dependent on the density of elephants in a given area and how the area is transformed (Forrer, 2017).

These mega-herbivores (weight exceeding 1,000 kg) can influence biodiversity in many positive ways, like creating pathways for other species ensuring full potential habitat use (Kerley et al., 1999). Elephants can also increase the quality of forage which is referred to as “gardening”. Gardening is where elephants reduce the height of trees and in turn provides more food and creates better quality regrowth for other browsers (Kerley et al., 2008).

Elephants play a vital role in the dispersal of seeds through being messy feeders and through endozoochory (ingesting the seeds and dispersing them through their dung) (Janzen & Martin, 1982). Elephants can also change entire vegetation types. For example, they can convert woodland to more open and grass-dominated habitat and contribute towards nutrient cycling (Kerley et al., 2008). Elephants are also able to uproot trees, thus allowing the release of locked up nutrients in the trunks of trees and from deep soil layers (Pastor et al., 2006).

However, elephants can also induce negative impacts on plant communities and, in turn, affect other animals by creating localised plant species extinction, referred to as extirpation (Kerley & Landman, 2006; Valeix et al., 2011). Elephants can uproot trees through toppling, and this can also cause the tree to completely die, resulting in a reduction in vegetation cover (Nasseri et al., 2010; Valeix et al., 2011). Elephants can also indirectly affect other

herbivores by influencing the potential browse availability by creating pathways that reduce the amount of vegetation coverage (Kerley et al., 2008). Due to the size of elephants, they must consume large amounts of biomass which can result in competition with other herbivores (Kohi, 2013). When elephants break trees, the tree can employ defensive strategies to deter future herbivore activities such as mopane trees (*Colophospermum mopane*) produce secondary components (condensed tannins) after severe defoliation which is known to discourage herbivores from future browsing (Kohi, 2013).

Elephants are currently listed as an endangered species on the International Union for Conservation of Nature (IUCN) global red list (Gobush et al., 2021). Despite this overall status, strong conservation efforts in southern Africa have increased elephant numbers in protected areas (Chase et al., 2016). In South Africa, many of these protected areas are small (<1000 km²) and fenced (Selier et al. 2016).

Thus, without the freedom to roam over large areas, elephant impacts on vegetation and other ecosystem processes may be exacerbated (Conybeare, 2004; Druce et al., 2011).

Fencing, increased protection and artificial water sources have all contributed to the rise in elephant population growth rates in small, protected areas (Forrer, 2017). These increased growth rates and higher population densities have prompted wildlife managers to explore several population-level management techniques to slow elephant growth rates in small, protected areas (Forrer, 2017).

In the 1960s through to the 1990s, elephant culling was advocated in different protected areas in southern Africa as a form of population control (van Aarde et al., 1999). During this time, culling was thought to be the most effective way for managing large elephant populations (Kerley & Shrader, 2007). However, the negative consequences of culling only

started to be observed thirty years later. These negative effects included abnormal behaviours like depression, unpredictable asocial behaviour, and higher levels of aggression (Kerley & Shrader, 2007). An alternative to culling is to translocate elephants to other areas, but this is a difficult task as the amount of land available for elephants continues to decrease in South Africa and translocations are extremely costly (Delsink et al., 2006).

The use of immuno-contraceptives for slowing elephant growth rates has increased over time and is playing a major part in elephant management throughout South Africa (Kerley et al., 2007). These contraceptives, known as anti-gonadotrophin releasing hormone (GnRH) and porcine zona pellucida (PZP) both act as a form of reproductive vaccine and are the two main immuno-contraceptives currently being used on elephants in South Africa (Kerley et al., 2006)

The GnRH vaccine is a prepared inoculant created to induce an immune response against the endogenous GnRH (Bertschinger & Lueders, 2018). This vaccine triggers antibody production by introducing a foreign protein to the animal's immune system. In response to exogenous GnRH, antibodies will neutralize the GnRH produced naturally in the body. Therefore, the testicles or ovaries will not be stimulated and become inactive (Lueders et al., 2019).

GnRH has been used mainly for elephant bulls to downregulate testosterone production for behavioural modification, but it has also been used in elephant cows to induce anoestrus (Bertschinger & Lueders, 2018). GnRH is not widely used for elephant cows due to the lack of oestrous cycling it causes. The GnRH vaccine also requires regular boosters (1st booster 4 weeks after primer injection, then every month for at least 3 months, then every 4 months,

after 1 year, every 6 months, then maybe spaced out to yearly injections) and it is not used as a reversible contraceptive (Lueders et al., 2019).

The alternative immuno-contraceptive, PZP, is more widely used in southern Africa in elephant cows (Fayrer-Hosken et al., 2000). The injection of the PZP antigen results in the production of specific antibodies being produced by the female elephant, which then either neutralise the antigen (typical for hormones) or block a reproductive process such as fertilisation (Bertschinger & Caldwell, 2016). The antibodies create a film around the egg to prevent the sperm from fertilising the egg (Figure 1.1a and 1.1b) (Bertschinger et al., 2018). To improve the immune response, the antigens are combined with an adjuvant or adjuvants (an ingredient to help strengthen the immune system response to the vaccine) (Miller et al., 2004). PZP is produced from pigs' ovaries obtained from pig abattoirs (approved by the Department of Agriculture, Forestry, Fisheries [DAFF] in South Africa). The final product consists of solubilised zona pellucida proteins with a given concentration (Dunbar et al., 1980).

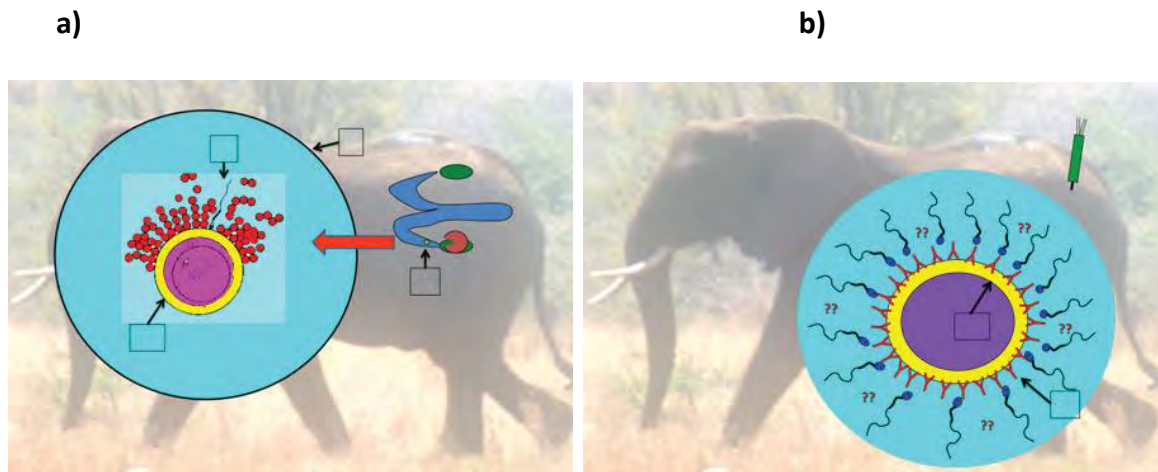


Figure 1.1a. Ovulated oocyte (oo) in the uterine lumen (ul). Sperm (sp) binding to a receptor site on the zona pellucida capsule (zpc). **1.1b.** Antibodies (ab) following vaccine delivery with a dart bind to the zona pellucida capsule (zpc) and prevent sperm from attaching to receptor sites inhibiting fertilisation and pregnancy (Bertschinger et al., 2018).

The practical benefit of administering PZP is its remote delivery, meaning the animal does not need to be immobilised thus, it is a less invasive approach compared with surgical sterilization (Lueders et al., 2019). A helicopter or vehicle is used to inject the elephant through a drop out dart and dart gun by a registered veterinarian. The dart will fall out on its own within a 48-hour period. Another benefit of the use of PZP is that it allows the cow to continue her oestrous cycle. The vaccine essentially creates a film around the egg, preventing fertilisation. This contraceptive is also known to be reversible, thus allowing cows to commence reproduction (Bertschinger et al., 2018). Lastly, this vaccine is safe when administered during pregnancy (Bertschinger et al., 2018) and is cost effective for smaller elephant populations (Whyte et al., 1998).

There are several impracticalities of the immuno-contraceptive, PZP, for free-ranging wildlife population control. Upon the initial dose of PZP, the elephant cow must receive a

booster six weeks post initial dose (Castiglione et al., 2012). The contraceptive also requires an annual booster after the initial dose which is not practical for large populations of elephants where individual identities are not necessarily known. Lastly, the vaccine needs to be stored frozen thus making it difficult to use in remote areas (Berchert & Fraker, 2015). Efficacy can also be compromised because of human and/or dart product error such as the veterinarian using the incorrect protocol in mixing the vaccine with the adjuvants, incorrect loading of the dart, a good shot placement of the dart, the persons confidence in identifying the sought-after elephant cow and/or the confidence in the dart itself by incorrect loading of the dart, manufacturing error or a needle blocked by a skin plug (van der Walt et al., 2022).

Immuno-contraception approaches in free-ranging wildlife began in 1987 with the earliest recorded attempt tested on wild horses (*Equus caballus*) with GnRH on Cumberland Island National Seashore, Georgia, USA (Goodloe et al., 1991). Zona pellucida vaccine was patented as a contraceptive in 1976 (Kirkpatrick et al., 1997) and was tested in 1987, concluding that PZP could successfully inhibit fertility in equids (Liu et al., 1989). PZP was then tested on a range of mammals like captive white-tailed deer (*Odocoileus virginianus*) (Turner et al., 1992; Turner et al., 1996; Miller et al., 2000), zoo animals such as, but not limited to Roosevelt elk (*Cervus elaphus roosevelti*), axis deer (*Cervus axis*) and African elephants (Kirkpatrick et al., 1996).

Kirkpatrick et al. (2011) identified four main challenges of wildlife contraception. One of the challenges was to identify successful contraception in captive animals, and this was established in trials using captive animals in 1987 (Kirkpatrick et al., 2011). The second challenge for wildlife contraception was documenting the safety of the immuno-contraceptives in terms of their potential to change the physiology of the treated animal,

whether the contraceptive was reversible, if the vaccine caused any adverse behavioural changes and lastly if there were any short or long term adverse physical effects from the use of the contraceptive. The main findings showed that PZP affected each species differently, suggesting that each species needs to be evaluated independently for any potential side effects of the contraceptives (Kirkpatrick et al., 2011). Wild mares treated long-term with PZP showed no signs of permanent or significant changes in ovaries and uteri (Fayrer-Hosken et al., 2000; Delsink et al., 2006). Contrary to the wild mares, non-human primates had temporal changes in ovarian function (Sacco et al., 1986) and baboons (*Papio hamadryas*) (Miller et al., 2001) and horses had decreased oestrogen production after being treated with PZP (Kirkpatrick et al., 1997). PZP-treated rabbits (*Oryctolagus cuniculus*) showed a depletion of primordial follicles (Wood et al., 1981). The reversibility of PZP also varied for each species tested. For example, PZP was reversible after at least five consecutive years of treatment in wild horses but was not reversible after seven consecutive years (Kirkpatrick & Turner, 2002) but for captive white-tailed deer reversibility occurred after 1-4 years of the use of PZP (Turner et al., 1996; Miller et al., 2000). The third challenge of wildlife contraception was developing practical and safe delivery of PZP to free-ranging wildlife. The first field trial was in 1988 on Assateague Island National Seashore- a barrier island off the coast of Maryland, USA in wild horses (Kirkpatrick et al., 1990). This trial proved remote delivery of PZP to wildlife was possible without handling the individual. PZP was first trialled on free-roaming elephants in 1996, in Kruger National Park (KNP), Limpopo, South Africa via a helicopter (Fayrer-Hosken et al., 2000). Despite successful efficacy in trials of PZP on elephants, multiple reviews suggested there was uncertainty in the long-term safety and reversibility, therefore, the widespread implementation of this immuno-contraceptive was not recommended (Perdok et al., 2007). The reasoning behind

the hesitance of not using PZP on elephants was due to elephants' extreme longevity and complex social structure and insufficient long-term studies (Hermes et al., 2004; Perdok et al., 2007). A comprehensive review of the efficacy of PZP in African elephant cows was completed in 2018 based on 22 years of research in KNP, Greater Makakali Game Reserve (GMGR), Limpopo, South Africa, and Thornybush Private Game Reserve (TPGR), Limpopo, South Africa. In 1995, the first trial was administered in elephants to provide proof of principle, which was successful (Fayrer-Hosken et al., 1999). The first field study on elephants was in KNP in 1996 (Fayrer-Hosken et al., 2000). The first trial in KNP was not as successful (efficacy was low compared to treatment in mares) (Kirkpatrick & Turner, 2008) as predicted but after modification of the protocols, the second trial was much more effective, showing 100% efficacy (Fayrer-Hosken et al., 2000). The next testing phase of testing PZP on elephants was in GMGR in 2000. All breeding elephant cows (>12 years) were identified and received the immuno-contraceptive via drop-out dart. In 2002, the cows receiving annual boosters showed 100% efficacy of PZP (Delsink et al., 2006, 2007; Delsink & Kirkpatrick, 2012). The following year, changes were made in the dosages of PZP as the dose of the vaccine does not increase in the relative weight of the vaccinated animal, therefore the doses could be lowered, thus making PZP more cost effective (Kirkpatrick et al., 1995; Millar et al., 1989). The annual population growth rates of elephants in GMGR went from 8.9% prior to contraception to 1-3% growth post contraception, suggesting that the use of PZP was effective in slowing elephant population growth (Bertschinger et al., 2017; Delsink et al., 2007). An additional six game reserves started the use of PZP between 2002 and 2005 and they all confirmed the safety in using PZP during all stages of pregnancy in elephants (Bertschinger et al., 2018). These reserves suggested that PZP is likely to be effective for about three years after it has been administered due to long gestation periods of elephants

and the only known side effect from the use of PZP was swelling at the injection site (Bertschinger et al., 2008). The main reoccurring topics in literature regarding the use of immuno-contraceptives in African elephants were the unknown effects of long-term use of PZP in relation to reversibility, the physiology of treated cows, change in space-use and behavioural effects. There have been multiple studies on short to medium term effects of PZP on reversibility, changes in physiology, space use and behaviours (Delsink & Kirkpatrick, 2012; Fayrer-Hosken et al., 2000; Ahlers et al., 2012; Delsink et al., 2006). Reversibility was demonstrated after two successive years of PZP treatment in some study sites (Delsink et al., 2013). GMGR also demonstrated the reversibility success after short term (5 years) use of PZP (Delsink et al., 2006). More recently, a study involving multiple reserves investigated the reversal potential for six cows that had been treated for three and four consecutive years. Two cows treated for four years conceived 25 and 35 months after their last treatment of PZP which suggested the interval of reversibility is variable between individual cows (Bertschinger et al., 2012). At TPGR they measured ovarian activity with behavioural observations of fourteen cows who had been treated with PZP for two consecutive years and showed oestrous cycling to be within normal ranges of averages documented in the literature (Ahlers et al., 2012). In other studies, 12-14 months long, ovarian function was tested on cows that were treated consecutively for two to three years (Ahlers et al., 2012) and four years (Benavides et al., 2012). All the cows showed evidence of luteal activity (Bertschinger et al., 2012). In GMGR, no significant changes of the use of PZP in the herd's ranging behaviour and the fission/fusion of the herd remained unchanged within the first four years of the study (2000 to 2004) (Delsink et al., 2013). There have been no other studies to date on the use of PZP and potential spatial changes.

All previous studies have demonstrated that there are no recorded short-term, negative effects of using the immuno-contraceptive, PZP on African elephants in regard to reversibility, physiological, spatial and behaviour. However, a limitation of these studies is the timeframe that was assessed for the use of PZP. The 2018 review from Bertschinger et al. (2018), highlighted the need to conduct more research of the longer term (>20 years) effects on reversibility, duration of treatment, social structure and individual behaviour of treated elephant cows. Another limitation of the studies was the failure to use “control” or baseline data of treated elephants. No studies have assessed elephant population responses to contraceptive use before, during and after treatment.

Tarlow and Blumstein (2007) expressed the importance of identifying and quantifying the direct and indirect effects of anthropogenic activities on animals for effective wildlife conservation. Therefore, my study assesses three datasets (Pre, During and Post PZP treatment) for one elephant population over an 18-year period in a small game reserve in the Eastern Cape of South Africa. The first aim of my study was to compare the female demography and reproductive parameters of this elephant population in relation to PZP use. The second aim was to assess the spatial ecology of this elephant population in relation to contraceptive treatment.

CHAPTER TWO

STUDY ANIMAL AND STUDY AREA

2.1 STUDY ANIMAL

2.1.1 Taxonomy

The African elephant is part of the Order Proboscidea, from proboscis (Greek), directing to the elephant's distinguished trunk (Shoshani & Shoshani, 2000). Elephants form the Elephantidae family which contains six genera in which two are still living: *Elephas* and *Loxodonta*. *Elephas maximus* is the Asian elephant and the *Loxodonta africana* is the African elephant. Fossil remains placed Asian elephants in Africa, therefore descendants of the first member of this genus migrated out of Africa. African elephants originated in East Africa and then spread throughout most of the African continent (Rholand et al., 2010).

African elephants are further divided into two species which are the African savanna or bush elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*) (Rholand et al., 2010). Historically, there was much debate about whether the savanna elephant and the forest elephant were, in fact, sub-species. In 2021, the IUCN recognized the two as separate species based on their morphological, ecological and behavioural differences (Groves & Grubb, 2000; Roca et al., 2001; Eggert et al., 2002; Debruyne, 2005). It is estimated that the savanna elephant and the forest elephant diverged 2-5 million years ago (Rholand et al., 2010).

2.1.2 Description

The African elephant (hereafter elephant) is the largest terrestrial animal and is considered to be a mega-herbivore (exceeding 1000 kg) (Owen-Smith, 1988; Gara, 2016). They are long-lived mammals, living up to sixty years old in the wild (Moss, 2001). Additionally, elephants are odd toed with their forefoot having five toes and the rear having three toes (Nowak, 1999). Sexual dimorphism is present amongst elephants (Hanks, 1972). Females reach a maximum body weight above three tons and males above six tons (Kerley & Landman, 2006). Female elephants average shoulder height is 2.6 meters and bulls can reach shoulder height of 3.2 meters (Hanks, 1972). The forehead shape of a female elephant is angled while a male's forehead is flat (Haynes, 1991). Elephants have an elongated trunk which is an extension of their nose and upper lip (Laurson & Bekoff, 1978). Trunks not only function for smelling but are also a prehensile organ capable of grasping objects (Haynes, 1991).

Elephants use their trunks for drinking water by inhaling it in the trunk then releasing in their mouth (Haynes, 1991). The trunk is a specialized foraging adaptation by allowing the elephant to achieve a high rate of food intake (Kerley & Landman, 2005). Trunks, in conjunction with their high shoulder height, allows elephants to feed up to eight meters above the ground (Croze, 1974). The ears of African elephants are large and cover the whole shoulder (Haynes, 1991). Large ears help thermoregulation by flapping of the ears which creates air currents to cool the blood in the blood vessels on the ears (Shoshani, 1978). In addition, elephants use their ears for communication and balance. Other features of elephants are their grey body, with thick skin that is covered in sparse bristle hairs (Haynes, 1991). Both sexes have tusks where bulls generally have larger, thicker tusks than females, used for fighting for dominance. Tusks have evolved from teeth as it is made up of dentine, a hard, dense, bony tissue. Tusks protrude from tusk cavities on either side of the mouth.

Tusks are used for foraging by stripping bark off trees and digging up roots of woody and succulent species (Barnes, 1982; Lessing, 2007). Elephants show favouritism in a tusk, identified as “right-tusked” or “left-tusked” and can often be recognized with more wear (Fowler, 1993). Elephants have highly specialized dentition by which elephants develop six set of molars in their lifetime. The first three set of molars grow and are lost by the age of ten years old. The fourth set of molars are lost on average between 22 and 23 years old and the fifth set of molars is lost when the elephant is between 45 and 48 years old. The last set of molars are worn by the age of 65. Elephants can only live as long as their teeth support them (Jachmann, 1988).

2.1.3 Distribution and habitat

Historically, elephants were distributed throughout Africa excluding the Sahara. By the Middle Ages, elephants were eliminated from North Africa and in the 1700 and 1800s they began to disappear from southern Africa (Blanc et al., 2007). Elephants are currently distributed in Sub-Saharan Africa including Angola, Uganda, Kenya, Botswana, Tanzania, Malawi, South Africa, Namibia, and Zimbabwe (Blanc et al., 2003). Elephants cover heterogeneous landscapes including grasslands, woodlands, wetlands, arid and semi-arid deserts, and subtropical and temperate forests (Gobush et al., 2021). Elephants require these large landscapes to accommodate their high food intake, water dependency and reproductive requirements (Gara, 2016).

2.1.4 Behavioural ecology

Elephants are active throughout the day in which on average sixteen hours account for feeding (Clegg & O’Connor, 2017). Elephants sleep for four to five hours a day but not

necessarily all in one period (Eltringham, 1982). They usually drink and bathe daily but can go several days without doing so. These animals are proficient swimmers and use water in various forms such as drinking, swimming, and bathing (Caloi & Palombo, 1992). Mud bathing is an essential way for elephants to regulate their body temperature and to form a protective layer on their skin from ultraviolet radiation (Wright & Luck, 1984).

Home ranges vary in size in small areas (<1000 km²) from 9 km² to 1000 km² (Douglas-Hamilton et al., 2005). The home ranges are influenced by resource availability such as food (quality and quantity) and water, for example, where food and water are plentiful, home ranges are generally smaller than where these resources are limiting (Tufto et al., 1996).

Elephant group home ranges can also overlap with one another (Shoshani, 1992). Elephants have a complex social structure and strong cognitive abilities (Fritz, 2017). Elephants live in a fission–fusion society, at the centre of which is the matriarch. Matriarchs are generally older females that guide their families to resources and co-ordinate group defence (Freeman et al., 2013). Douglas-Hamilton (1972) observed elephants for 4.5 years in Lake Manyara National Park (LMNP), Tanzania and termed “kinship group” as two or more family groups that have close ties. Females remain in the herd with their offspring while males leave their natal herd around twelve to fifteen years of age (Freeman et al., 2013). Bulls become independent and associate with other adult bulls (Hollister-Smith et al., 2007). Independent males will join breeding herds in search for mates, thus, creating mixed groups (Shannon et al., 2008). Elephants communicate through touch, vocalization, infrasonic and olfaction (Payne et al., 1986). Family members will communicate through touch and often with the trunk. Elephants have four distinct types of vocalizations: rumbling, trumpeting, squealing, and screaming (British and Irish Association of Zoos and Aquariums, 2022). Infrasonic communication can travel several kilometres. Temporal gland secretion (TGS) occurs in both

male and female elephants for differing reasons. Elephant bull TGS occurs usually during musth periods (Ganswindt et al., 2005) while cow TGS is associated with excitement and distress (Douglas-Hamilton et al., 2006). All these types of communication relay forms of distress, dominance, excitement, fear, mate-searching, and preservation of social bonds (Poole et al., 1988; Poole & Moss, 1989).

2.1.5 Reproductive biology

Elephant cows become sexually mature between eight and ten years old (Moss et al., 2011). Elephant bulls reach sexual maturity at a much older age (20 - 30 years old) than females because males require a longer period to acquire competitive abilities (Haynes, 1991). Cows are in oestrous for twelve to sixteen weeks at a time (Niemuller et al., 1993). Females experience a 620 to 680 day gestation period (Allen et al., 2003). The age of first calf is typically between eleven and thirteen years of age (Laws, 1969). The inter-calving interval ranges from four years to nine years dependent on nutrition and population density (Estes, 1992). Females can breed year-round, but research shows there is a strong positive correlation between conception and birth rates and seasonal precipitation (Laws, 1970; Smuts, 1975; Gough & Kerley, 2006; Wittemyer et al., 2007; Freeman et al., 2009; Foley & Faust, 2010). Females tend to halt breeding by the age of fifty (Lee et al., 2016). Elephant bulls also go through a reproductive cycle, known as musth, which is uncommon in mammals. Musth is a period strongly correlated with heightened testosterone levels (Ganswindt et al., 2005).

2.1.6 Foraging ecology and diet

Elephants are mixed feeders, utilizing a large range of plants (grass and browse) fruit, bulbs, roots, and bark (Kerley & Landman, 2006). In the Eastern Cape, South Africa elephants most preferred plants are sweet-thorn acacia (*Vachellia karroo*), spekboom (*Portulacaria afra*) and several *Aloe* species (Kerley & Landman, 2006). Being hindgut fermenters means that the digestive efficiency of elephants is low as less than half of the food is assimilated and the rest passes through as faeces (Shoshani, 1998). Elephants can ingest large amounts of fibre, unlike ruminants, and they have a low metabolic rate per unit of body mass which enables them to obtain adequate nutrition from plant material low in nutrient content (Kerley & Landman, 2006). Nevertheless, due to their large body size, elephants consume an estimated sixty kilograms of dry mass vegetation per day (Owen-Smith, 1988).

2.1.7 Conservation status

In 2020, the IUCN red list considered elephants as a vulnerable species (Gobush et al., 2021) due to the global population decreasing over 50% in three generations (Nuwer, 2021).

Elephants experienced a drastic decline in numbers from 2008 and heightened in 2011 due to ivory poaching (Gobush et al., 2021). In 2016, the global population was estimated at $415,428 \pm 20,111$ individuals. These individuals are distributed in areas of which 30% is protected land (Thouless et al., 2016). Current threats to the survival of elephants are human exploitation by poaching for ivory, pathogens like anthrax (Lindeque & Turnbull, 1994), tuberculosis (Kerr et al., 2019) and cyanobacteria in drinking water (National Parks Rescue, 2020). Habitat loss due to land conversion and human-elephant conflict results in smaller, fragmented elephant populations (Singh et al., 2002). Despite the global decline in elephants, there have been successful conservation efforts in southern Africa due to anti-

poaching measures on the ground and supportive legislation (Gobush et al., 2021). In South Africa, the change in land use from agriculture to ecotourism over time has also created small (<1000 km²), closed systems which have contributed to the success of increased elephant numbers. At these reserves, some elephant populations are believed to be overpopulated due to being female biased, low mortality rates and high population growth (Slotow et al., 2005).

2.2 STUDY AREA

2.2.1 Location and history

My study was conducted on Amakhala Game Reserve (hereafter Amakhala), in the Eastern Cape province of South Africa (Figure 2.2.1). It is situated about eighty kilometres, northeast of Gqeberha (formally known as Port Elizabeth). The reserves' primary goal is ecotourism and biodiversity conservation (Vos, 2022).



Figure 2.2.1 Location of Amakhala in the Eastern Cape, South Africa.

Prior to the existence of Amakhala, from the 1850's to 1998, the land was utilized for stock farming with beef (*Bos taurus*), sheep (*Ovis aries*) and Angora goats (*Capra aegagrus hircus*). There were also irrigated lands for dairy operations as well as cultivated land for citrus (*Citrus spp.*), pineapple (*Ananas comosus*), oats (*Avena sativa*), chicory (*Cichorium intybus*) and wheat (*Triticum aestivum*). Four families joined their land together in 1999 to establish Amakhala.

Amakhala consists of three sections, totalling 8,605 hectares (Figure 2.2.2). These sections are divided by a physical barrier, the national highway, N2 and fences. The main reserve consists of a total of 6,189 hectares which includes large herbivores such as buffalo (*Syncerus caffer*), zebra (*Equus quagga*), elephants, giraffes (*Giraffa camelopardalis*), white

rhinoceroses (*Ceratotherium simum*) and hippopotamus (*Hippopotamus amphibius*). The main reserve also contains cheetah (*Acinonyx jubatus*), lion (*Panthera leo*) and leopard (*Panthera pardus*). The main reserve has the R342 public road running through it from north to south.

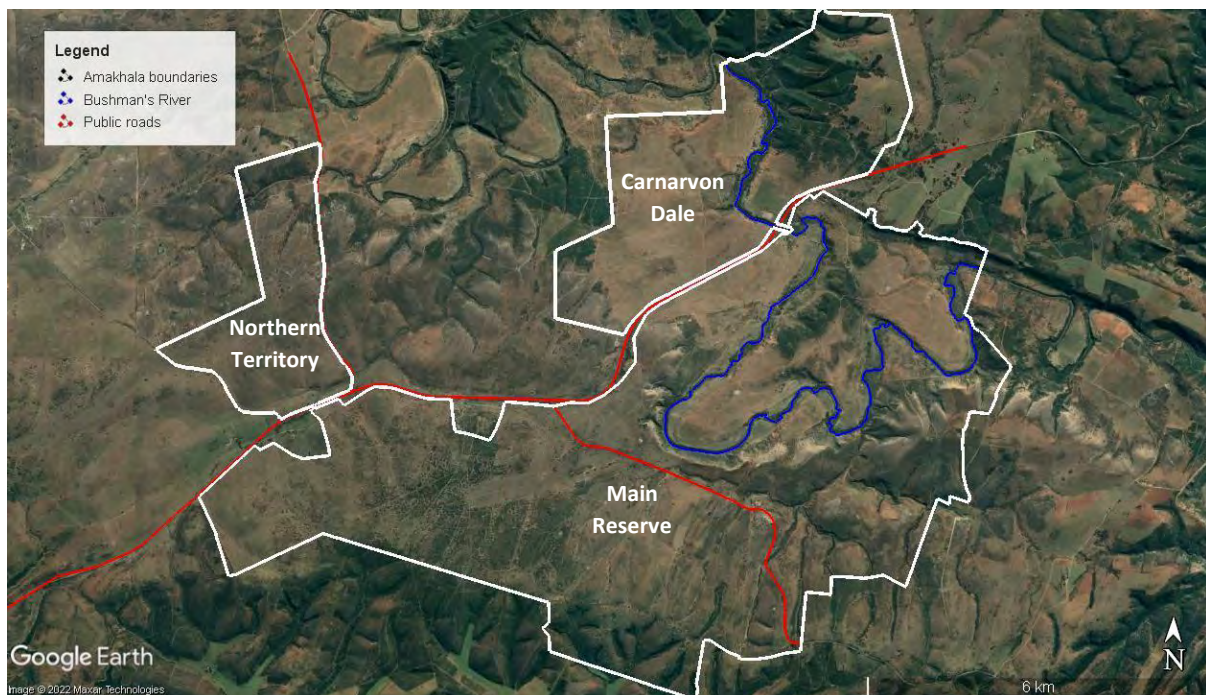


Figure 2.2.2 Map of the three sections of Amakhala; Main Reserve, Carnarvon Dale, and Northern Territory.

The Carnarvon Dale section incorporates 1,692 hectares and has plains game like giraffe, zebra, red hartebeest (*Alcelaphus buselaphus caama*), black wildebeest (*Connochaetes gnou*) and cheetah.

The Northern Territory is 724 hectares in size and is mainly a breeding area for herbivores like the endangered Cape Mountain zebra (*Equus zebra zebra*). My study focussed on the main reserve of Amakhala, where the elephant population resides.

2.2.2 Hydrology

Non-seasonal rainfall dominates the region, with peaks in February, March, October, and November (Vos, 2022). During my study (2003 – 2021), the mean annual rainfall was 509.27 mm. The highest annual rainfall recorded was 796.5 mm in 2011, while the lowest annual rainfall was 216.3.7 mm in 1972 (Figure 2.2.3).

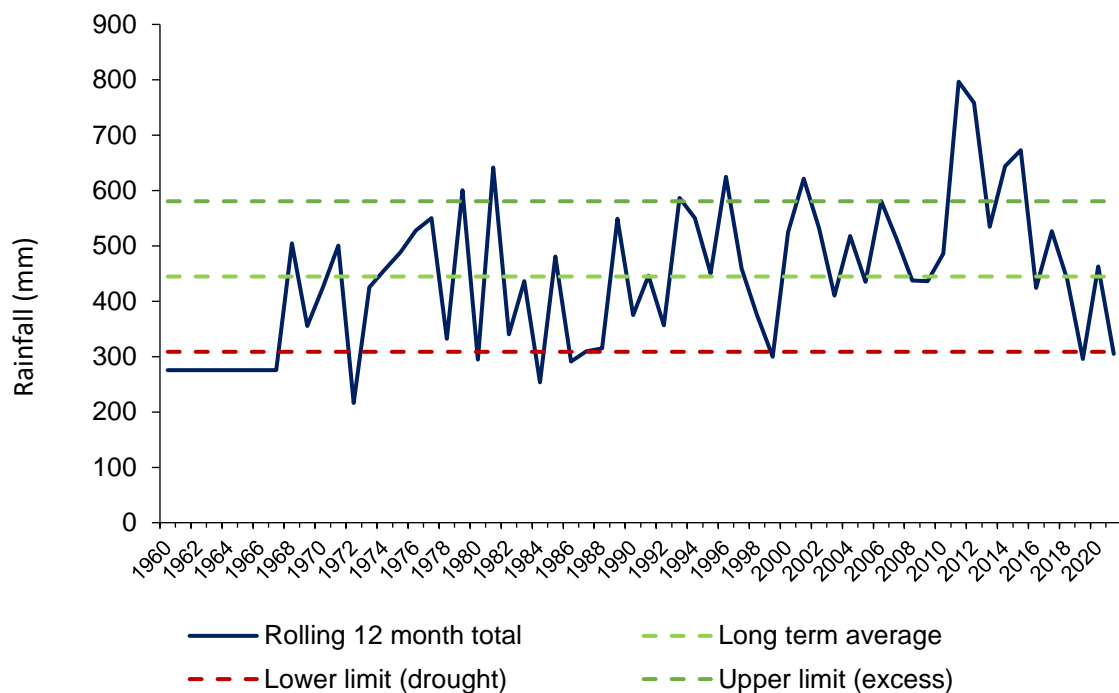


Figure 2.2.3. Rainfall recorded over a 60-year period on Amakhala Game Reserve including the longer-term average, lower limit, and upper limit ranges.

The main reserve on Amakhala has both natural and artificial water sources. The Bushman’s river runs into the main reserve in the north-eastern section and exits in the eastern part of the reserve. The stretch of the river in the main reserve is approximately 20 kilometres long.

From 2003 to 2017, the Bushman's river retained water. During the drought years from 2018 to 2021, the Bushman's river dwindled down to only small, shallow pools of water.

The artificial watering holes are pumped by solar panels from boreholes to disperse the herbivore populations across the main reserve. There are a total of six artificial pans, mostly on the southern and western sides of the reserve (Figure 2.2.4).

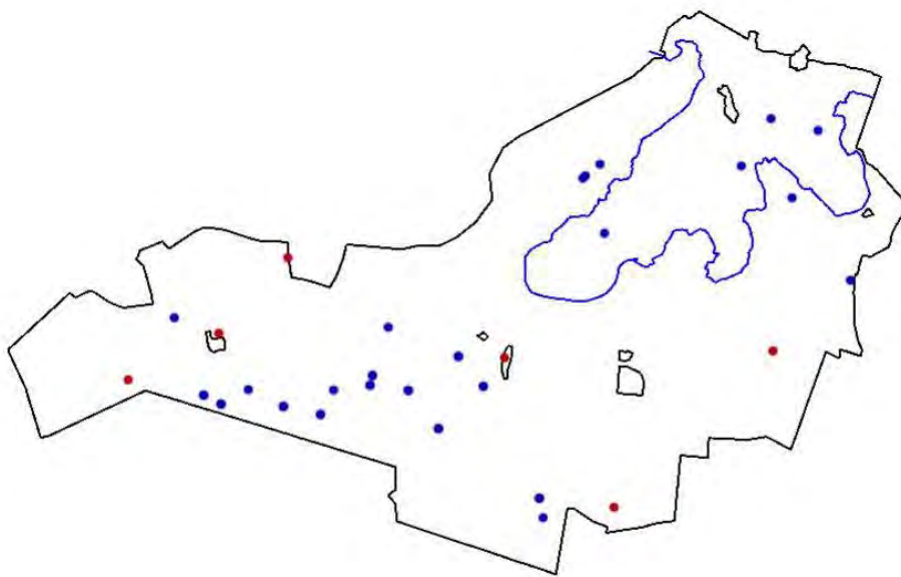


Figure 2.2.4. Natural (blue dots) and artificial (red dots) pans on the main reserve of Amakhala.

2.2.3 Geology and topography

The reserve includes gently rolling alluvial plains along the Bushman's river on the eastern side at approximately 170 m.a.s.l. with an elevated plateau to the southwest at approximately 350 m.a.s.l. (Vos, 2022). The deeply incised river basin has many drainage lines in steep valleys and is surrounded by folded and uplifted strata of the Cape and Karoo Supergroup (Vos, 2022). The savannas in the southwest show moderately undulating plains.

Valley thicket is found on open, moderately steep, valley slopes. Karoo Supergroup sedimentary rocks, namely, the Dwyka and Ecca Groups, form part of a belt overlying the Cape Supergroup rocks (Hoare et al., 2006). Erosion during the tertiary period and sea levels dropping created the large valleys that encompass the thicket vegetation (Vos, 2022). The valley thicket is predominantly found on the Witteberg and Dwyka Groups, Weltevrede and Witpoort Formations on clayey soils. The savannas predominantly occur on Witpoort, Weltevrede and Nanaga Formations. The soils derived from these varied rocks are variable from coarse-textured and shallow rocky soils which are nutrient poor (Cape Supergroup) on upper slopes to fertile, deep fine-textured soils in valley bottoms. The variable biomes and vegetation types on Amakhala reflect the diverse geology and soils present (Mucina & Rutherford, 2006).

2.2.4 Vegetation

The diversity of vegetation types reflects the diverse habitats, geology, soils, and micro-climates on Amakhala. The south-western areas which tend toward Sourveld, occur at higher altitudes, and have slightly higher rainfall. The Sweetveld is represented by the grasslands to the northeast occurring in the valley bottom along the Bushman's river at lower altitude with a slightly lower annual rainfall (Vos, 2022).

Amakhala falls within the broader Albany Thicket biome and is divided into two main vegetation types (Mucina & Rutherford, 2006), the Kowie Thicket and the Albany Coastal Belt. However, most of the vegetation on Amakhala has been shaped to a large extent by historical human influences. Therefore, Amakhala is divided into eight vegetation types

(Figure 2.2.5) in which some of these vegetation types resemble other biomes, but they are not strictly true representations of those biomes, e.g., Savanna (Table 2.2.1).

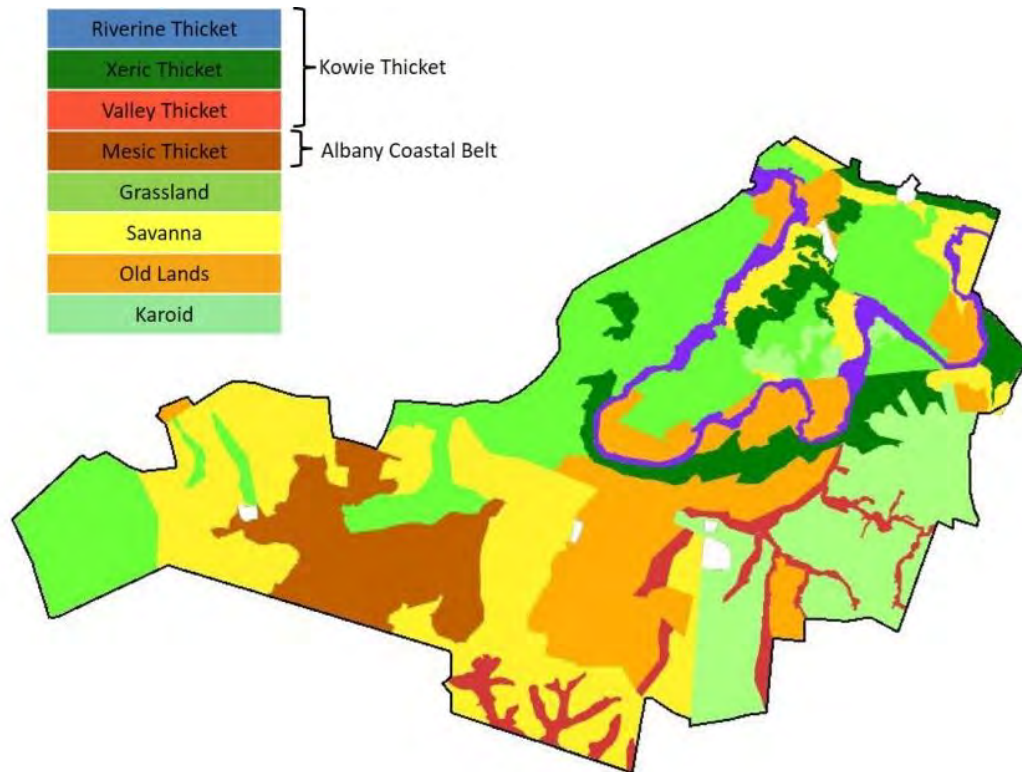


Figure 2.2.5. The eight vegetation types on Amakhala Game Reserve, Eastern Cape, South Africa.

Table 2.2.1. The eight vegetation types represented on Amakhala Game Reserve and their accompanying descriptions and indicator species.

Vegetation Types	Description	Indicator species
Riverine thicket	Encompasses the riparian margin of the Bushman's River.	<i>Combretum caffrum</i> , <i>Salix mucronata</i> , <i>Senegalia caffra</i> , <i>Vachellia karroo</i> , <i>Celtis africana</i> , <i>Searsia lancea</i> and <i>Plumbago auriculata</i> .

Valley thicket	Also referred to as Woody Subtropical Thicket and generally occurs on the south facing slopes where direct radiation from the sun is reduced. The absence of succulents differentiates it from the Xeric thicket.	<i>Euphorbia triangularis, Olea europaea africana, Ptaeroxylon obliquum, Mystroxylon aethiopicum, Scutia myrtina and Cussonia spicata</i>
Xeric thicket	The truest representation of the Albany Thicket biome. It generally occurs on slopes subject to direct radiation from the sun, and therefore dominants north facing slopes. The high percentage of succulents is a characteristic as a major diagnostic feature, in particular, <i>Portulacaria afra</i> , which acts as an indicator species, as well as the dominant species.	<i>Portulacaria afra, Crassula muscosa and C. perforate, Schotia afra, Carissa bispinosa, Pappia capensis, Euclea undulata, Sideroxylon inerme and Aloe spp.</i>
Mesic thicket	Part of Albany Coastal Belt with sandy substrates of the Nanaga Formation. It is colloquially referred to as the dune forest. It contains a grass layer that is lacking in other thicket vegetation types.	<i>Zanthoxylon capense, Pterocelastrus tricuspidatus, Canthium inerme, Gymnosporia nemorosa, Brachylaena discolor, Diospyros dichrophylla, Panicum coloratum, Digitaria eriantha, Eragrostis curvula and Tristachya leucothrix</i>
Grassland	Grasslands found of Amakhala have typically been cleared in the past for farming and now provide forage for grazing species. Contains less than 30% tree cover, lower lying grassland areas are typically on clay and alluvial sediments.	<i>Themeda triandra, Eragrostis curvula, Digitaria eriantha, Cynodon dactylon, Heteropogon contortus, Brachiaria serriata, Sporobolus africanus, Tristachya leucothrix, Searsia longispina and Vachellia karroo</i>
Savanna	Tree coverage ranging from 30% to 70%, the rest similar to grassland	<i>Vachellia karroo, Diospyros dichrophylla, Searsia pyroides, Searsia lucida, Olea europaea, Euclea undulata, Euclea natalensis, Scutia myrtina, Themeda triandra, Eragrostis curvula, Digitaria eriantha and Tristachya leucothrix</i>

Old lands	Land used for cultivating crops and are in various stages of rehabilitation. In early stages of succession, dominated by ephemeral weedy species	<i>Conyza scabrida, Galenia pubescens, Kali tragus, Cynodon dactylon</i>
Karroid	nutrient poor soils, dominant of unpalatable dwarf shrubs, succulents, usually absent of grasses	<i>Pteronia incana, Mesembryanthemaceae, Chrysocoma ciliata. Malephora crocea. Drosanthemum hispidum</i>

2.2.5 Elephant population

Amakhala introduced a total of ten elephants from Phinda Private Game Reserve (PPGR), KwaZulu-Natal, South Africa onto the main reserve in 2003. This initial introduction consisted of three adult females (≥ 9 years), four sub-adult males (5-15 years), two sub-adult females (5-8 years) and one juvenile female (0 to 5 years). Of these ten elephants, they were further broken down into three different family groups, the A family, B family and C family. During capture in PPGR, it was believed these were three unrelated groups of elephants thus resulting in three matriarchs on Amakhala in one herd as they rarely ever separated. One of the sub-adult females was never seen again on the reserve post-release and is believed that she was not part of the family unit that was translocated, became separated and died. In 2005, two adult elephant bulls were translocated from the nearby Addo Elephant National Park (AENP) to prevent young bulls displaying abnormal behaviour such as killing white rhino and abnormal physiology such as entering musth too early (Slotow et al., 2001; Slotow & van Dyk, 2001). These older bulls acted as mentors for the younger males and prevented delinquency behaviour from manifesting (Slotow et al., 2000). In 2007, one of the AENP bulls was electrocuted and died. The remaining AENP bull was translocated

to the Northern Territory in 2016 due to severe fighting-related injuries. There were no introductions or removals from the elephant population between 2017 and 2021.

2.2.6 Monitoring and identification

As part of the elephant management plan for the reserve, the elephants on Amakhala have been monitored from 2006 to present by use of GPS/VHS tracking collars (Razzaq, 2007). Weekly behavioural and feeding data collection also occurred sporadically throughout my study period. The monitoring of the elephant herd allowed for the development of identification kits for each individual. Each elephant has unique features for identification such as their ears with unique notches and cut-outs of their ears as well as the shape and size of their tusks (Figure 2.2.6). The identification kits allowed for records of births, deaths, injuries, and behaviours of the entire elephant population. Therefore, the monitors recorded which elephant gave birth to which calf and a family tree was generated (Appendix 1).

Name: CAULLY Sex: Male DOB: 01-01-1989 Age in 2019: 30 yrs

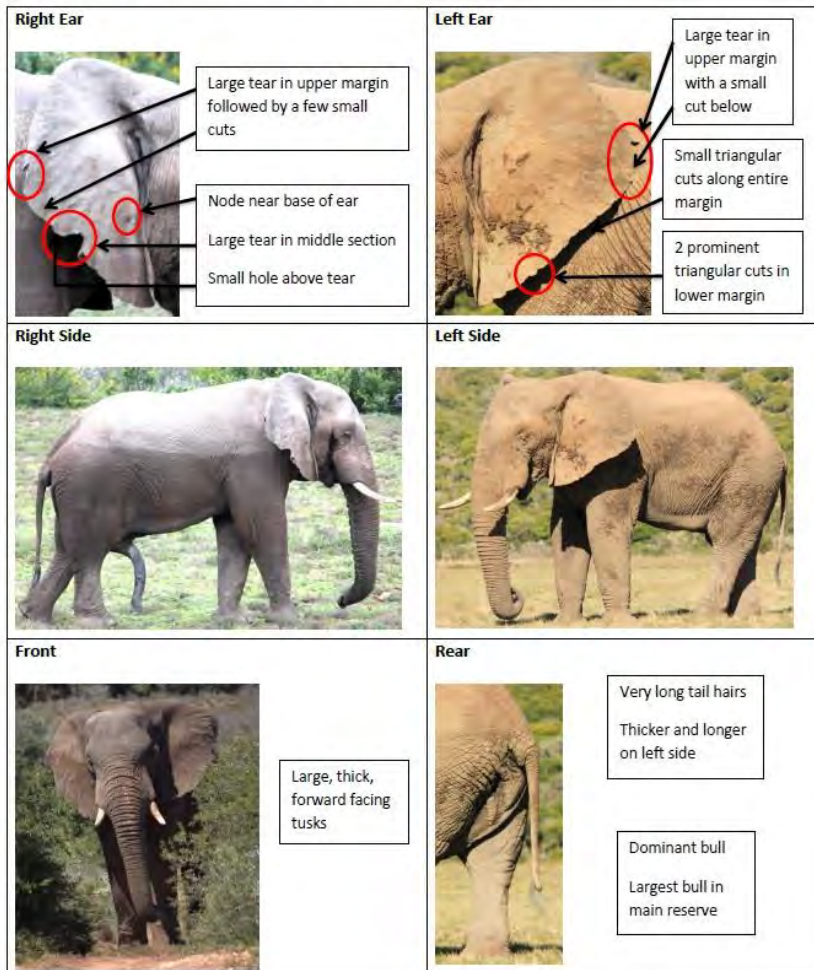


Figure 2.2.6. Elephant identification kit of Amakhala's elephant bull (Fowler, 2017).

Table 2.2.2 displays a breakdown of the number of elephants in each age and sex category of Amakhala's elephant population in 2021.

Table 2.2.2. Breakdown of the age and sex of Amakhala's elephant population in 2021.

Age/sex	Adult	Sub-adult	Juvenile
Female	10	1	1
Male	6	2	5

2.2.7 Immuno-contraceptive plan

The elephant population on Amakhala experienced high growth rates during 2004 through to 2009 (see chapter 3). Due to this rapid growth, the immuno-contraceptive program (ICP), using PZP, was implemented in 2008 to slow down the inter-calving period of the cows. The ICP was planned and discussed between experienced personnel such as experts in the field of implantation and research of PZP in wild elephants, wildlife veterinarians and ecologists of Amakhala. The ICP was not implemented to completely prevent cows from reproducing but to reduce population growth to stay under the calculated carrying capacity (Razzaq, 2007). The ICP allowed all young cows to give birth to their first calf, thereafter, join the ICP. The plan also put the cows on a rotational basis between the three family groups that comprised the breeding herd. The aim was to still allow the biological and social needs of the family groups to be met by having continuous calves present in the herd. Figure 2.2.7 is a population prediction model displaying the population size of the elephants on Amakhala if there was no contraception, three-year ICP and a six-year ICP in place (Razzaq, 2007). It became evident that if the reserve did not initiate this program, the elephant population would have reached the economic or optimal carrying capacity (includes a 25% buffer to accommodate factors such as variation in rainfall and wildlife is more selective in feeding than livestock).

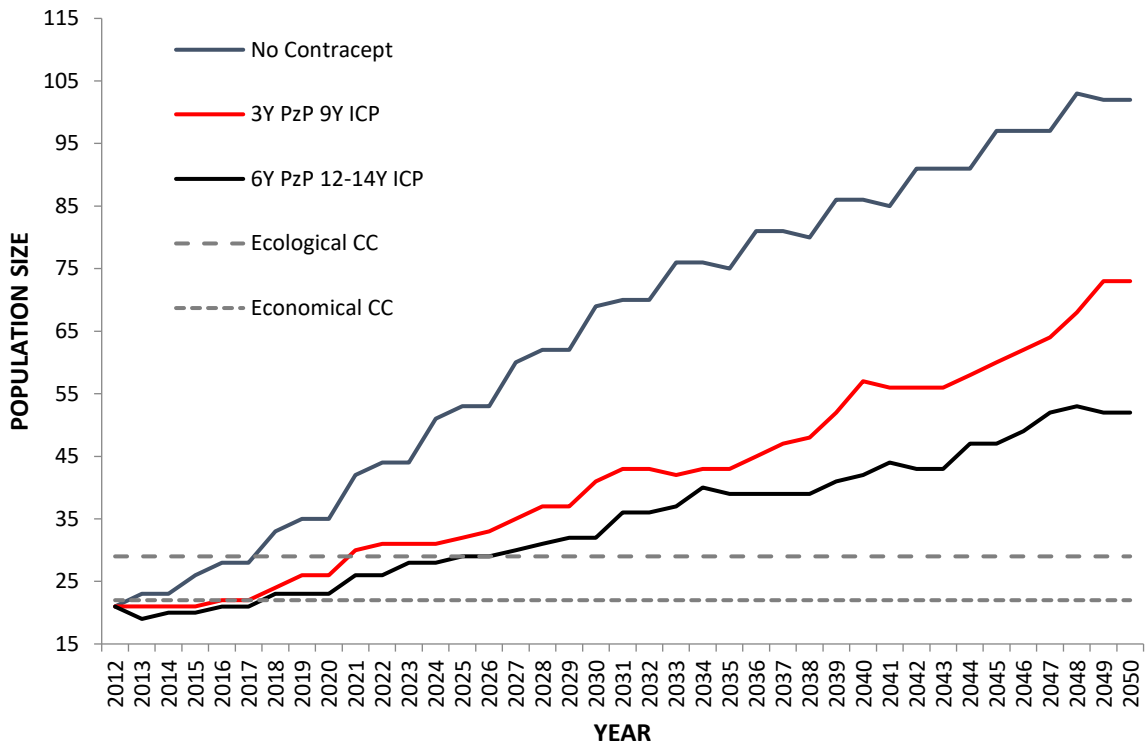


Figure 2.2.7. Population prediction model of Amakhala’s elephant population showing the no PZP population predictions, 3-year PZP program predictions, 6-year PZP program predictions with the ecological and economic carrying capacity for the elephant population on Amakhala.

Records were kept of each individual, sexually mature cow when they gave birth to their first calf, gave birth to a calf after the first, when they were administered PZP, taken off of PZP and conceived once the PZP program started (Table 2.2.3).

Table 2.2.3. Reproductive history of elephant breeding females on Amakhala Game Reserve

where C = contracepted, 1B = first birth, B = birth, cd = off of ICP

Individual	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Alatisha	C	B	C	cd	cd	cd								
Baluleka	C	B	C	C	C	C	C	C	cd	cd	cd	cd	cd	
Chupa	C	B	C	C	C	C	C	C	cd	cd	cd	cd	cd	
Ambalo		1B	C	B	C	cd	B	C	C	C	C	C	B	C
Chwayita				1B	C	C	C	C	C	C	cd	cd	cd	cd
Amanzi														1B
Ayanda									1B	C	B	C	C	C
Cebisa												1B	C	C
Chebe											1B			
Bongani												1B	C	C

Table 2.2.4 represents the Amakhala female elephants and their contraception history from 2008 to 2021. This information includes the year the individual was given the contraceptive as well as the dosage. The initial dose (400 ug) given to a cow who has just started the program. Post six weeks of the initial dose, another booster (200 ug) was given. The dose (200 ug) given subsequently after the initial two doses is the annual booster (Delsink et al., 2006).

Table 2.2.4. Breakdown of each breeding cow’s immuno-contraceptive history from 2008-2021, includes the ug dosage (400 ug initial dose, 200 ug follow up dose then after annual booster).

Year	Alatisha	Baluleka	Cupha	Ambalo	Chwayita	Ayanda	Bongani	Cebisa	Amanzi
2008	400	400	400						
	200	200	200						
2009				200					
	200	200	200						
				200					
2010	200	200	200	200					
2011		200	200	200					
2012		200	200	200	400				
					200				
					200				
2013		200	200		200				
2014		200	200						
					200				
2015		200	200	400	200				
2016				400	200				
2017				200	200	400			
						200			
2018				200		200			
2019				200			400		
						200	200		
								400	
								200	
2020						200	200		400
									200
				400					
				200					
2021				200		200	200	200	

CHAPTER THREE

DEMOGRPAHY AND REPRODUCTION

3.1 INTRODUCTION

Elephants are a long-lived species in which females are considered to have reproductive longevity as they can breed up to approximately 50 years of age (Hanks, 1972). As such, their population control is of great concern in many fenced conservation areas in Africa (Gough & Kerley, 2006). Elephants can also transform habitats due to their large body size and nutritional requirements (Gough & Kerley, 2006). Therefore, managing these large herbivores in confined systems can be challenging (van Wyk & Fairall, 1969). Studying the demographics and reproductive parameters of individually identified animals are essential for understanding the dynamics and relationships between social structure and demography of elephant populations (Foley & Faust, 2010). Parameters such as population growth can be influenced by inter-calving intervals, density, mortality, and environmental conditions (Foley & Faust, 2010). Further, the nutritional status of a cow can affect the sex ratios of her offspring by skewing towards one sex (Trivers & Willard, 1973). Populations under density limited resource availability may show skewed male ratios. In addition, males are more expensive than female calves in terms of parental investment and future breeding opportunities by which the male's early growth is related to later reproductive success (Clutton-Brock et al., 1982; Clutton-Brock et al., 1981; Lee & Moss, 1986; Wolff, 1988; Clark et al., 1990). Moreover, conception in elephants is strongly correlated with increased rainfall as the availability of high-quality forage results in increased body condition of a cow therefore can increase conception rates (Hanks, 1969). Nutrition also plays a role in affecting the age of reaching sexually maturity thereby affecting age at first calving (Sadlier,

1969). Elephant cows that have high quality forage can reach sexual maturity earlier than those that only have access to poor quality forage (Sadler, 1969). Laws (1969) indicated that recruitment and early mortality in elephants are influenced by favourable and unfavourable environmental conditions. These demographic and reproductive parameters are in some ways influenced by environmental conditions such as seasonality, forage quality, rainfall, resource availability, population densities, population histories and anthropogenic factors such as artificial water sources and population control (culling and contraceptives) (Foley & Faust, 2010; Delsink et al., 2013). Therefore, understanding the demographic and reproduction status, and response to different anthropogenic pressures and ecological conditions is invaluable for practical use in elephant management (Wittemyer et al., 2013). Elephants have been re-introduced in South Africa on reserves, mainly for tourism, approximately within the last thirty years, mostly originating from Kruger National Park, South Africa (Garai et al., 2004). In these relatively small, fenced reserves there is immense pressure to balance the use of elephants to promote conservation efforts and sustain an economical industry through tourism (Kepe, 2001). Due to these systems being enclosed, natural migration and natural mortalities are hindered resulting in natural population control being compromised (Woolley et al., 2008). These small reserves are now relying on translocations and the use of immuno-contraceptives to regulate their elephant population numbers (Garai et al., 2004). In response to the introduced immuno-contraceptive methods, there is a need for research to be carried out on how immuno-contraceptives, specifically PZP, affects the reproductive demography of elephant populations on these small reserves. For management to be able to provide strategies that are both in line with their management plans and have minimal disruption to these highly intelligent and social

elephant populations, a better understanding of the consequences of contraception are needed.

The purpose of this chapter was to examine the demographic and reproductive parameters of elephants on Amakhala and to answer the following research questions:

- What was the population growth rate of the elephant population on Amakhala between 2003 and 2021? I predicted that the population growth rate would decrease as more elephant cows were contracepted with PZP.
- What are the inter-calving intervals of the female elephants of treated and non-treated cows? I predicted that the inter-calving intervals of treated elephant cows would be longer than in non-treated cows.
- What are the sex ratios of the elephant offspring on Amakhala? I predicted that there would be a skewed sex ratio of male calves born to treated elephant cows.
- What is the mean age of first calving on Amakhala? I predicted that the mean age of first calving would be like other elephant populations in Africa.
- What are the fertility and fecundity rates of the elephant cows on Amakhala between 2003 and 2021? I predicted that the fertility and fecundity rates would be lower as more elephant cows were treated with PZP.

3.2 METHODS

The demography and reproductive data of the elephant population on Amakhala were collected through monitoring and record keeping from 2003 to 2021. The reproductive history of the elephant breeding cows on Amakhala from 2008 to 2021 are shown in Table 3.2.1. A detailed description of monitoring techniques is provided in Chapter two.

Table 3.2.1 Reproductive history of elephant breeding females on Amakhala Game Reserve

where C = contracepted, 1B = first birth, B = birth, cd = off of ICP

Individual	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Alatisha	C	B	C	cd	cd	cd								
Baluleka	C	B	C	C	C	C	C	C	cd	cd	cd	cd	cd	
Chupa	C	B	C	C	C	C	C	C	cd	cd	cd	cd	cd	
Ambalo		1B	C	B	C	cd	B	C	C	C	C	C	B	C
Chwayita				1B	C	C	C	C	C	C	cd	cd	cd	cd
Amanzi														1B
Ayanda									1B	C	B	C	C	C
Cebisa												1B	C	C
Chebe											1B			
Bongani												1B	C	C

Population growth rate

Population growth rates were determined by calculating the instantaneous annual growth rate, which included introductions, removals, and mortalities for a specified year (Kilpatrick et al., 2020). Population growth rate (r) for a population was calculated as:

$$r = (N_{tx} - N_{t\ x-1} + Rem_t - Introt) / N_{t\ x-1} * 100$$

N_{tx} is the population size in year x and $N_{t\ x-1}$ is the population size in the previous year.

Rem_t is the number of elephants removed in the year under review and $Introt$ is the number of elephants introduced in the year (Goodman, 2013).

Inter-calving Intervals

To calculate inter-calving intervals, only cows that had given birth to two or more calves during the study period were used (Hitchins & Anderson, 1983). There was a total of five cows used to analyse the inter-calving intervals. The intervals were calculated in months and years by determining the number of months and years between two successive births (Mostert et al., 2010). The five cows were separated into “treated” (n = 3) versus “non-treated” (n = 2) individuals. The non-treated cows had not been administered with the immuno-contraceptive, PZP and the treated cows had been given the contraceptive at least once.

To test for any statistical significance, I first tested for normality by using the F-test Two-Sample for Variances in Microsoft 365 Excel (Mahbobi & Tiemann, 2015). The normality of variances being assumed when $P > 0.05$. The F-test projected the variances are approximately equal to one another (P value = 0.37) therefore I used the T-test Two-Sample Assuming Equal Variance to assess any statistical significance in the inter-calving intervals of treated and non-treated elephant cows (Mack, 2020).

Sex ratio

The calf sex ratio was calculated as a ratio, of male to female. All the cows that gave birth to a calf (n = 10) were used to calculate the sex ratios. The elephants were further distinguished between “treated” (n = 2) and “non-treated” (n = 10) cows (use of immuno-contraceptive versus no use) to compare the two groups. All ten cows gave birth to their first calf prior to receiving PZP, therefore ten cows are represented in the non-treated females. Of the ten females, two cows gave birth after being treated with the contraceptive.

The potential statistical differences in sex ratios were tested by first using the F-test Two-Sample for Variances in Microsoft 365 Excel to test for normality of variances (Mahbobi & Tiemann, 2015). The F-test calculated the variances are approximately equal (P value = 0.33) due to the P-value being greater than 0.05 therefore, I used the T-test Two-Sample Assuming Equal Variance to assess any statistical significance in the percentage of male offspring between treated and non-treated cows (Mack, 2020).

Age at first calving

The elephant cows (n = 7) that had given birth to their first calf on Amakhala were used to determine the mean age at first calving. Conception dates were backdated from known births by 22 months due to the length of their gestation period (Lueders et al., 2012).

Fecundity and fertility

Fecundity is the number of calves surviving after the end of the year in proportion to the number of mature females (≥ 4.25 years old) at the start of the year (Nhleko, 2014). The youngest cow to have conceived was 4.25 years old, therefore the age of mature females will be represented at this age. The fecundity was calculated as:

$$\text{FECt} = \text{Surviving birthst} / \text{Ad Ft-1}$$

Where, surviving birthst is the number of surviving calves in the year under review and Ad Ft-1 is the number of adult females (≥ 4.25 years old) in the previous year (Goodman, 2013).

The fertility rate was derived from the number of calves born in a specific year with regards to the number of sexually mature females (≥ 4.25 years old) at the start of each year. The fertility rate (FERt) was calculated as follows:

$$\text{FERt} = \text{Birthst} / \text{Ad Ft-1}$$

Where, Birthst is the number of births in the year under review and Ad Ft-1 is the number of adult females (females ≥ 4.25 years old) in the previous year (Goodman, 2013).

3.3 RESULTS

Population growth rate

The mean annual growth rate of the elephant population on Amakhala was 6% per annum between 2003 and 2021. The highest annual growth rate for the elephant population on Amakhala was in 2009 at 27% (Figure 3.3.1). Years 2004 and 2007 also had over a 20% growth rate which accounted for the highest growth rates in the 18 years of the reserves historical records. There were no introductions or removals in those years. Despite the high growth rate of 23% in 2007, there was a death of one calf.

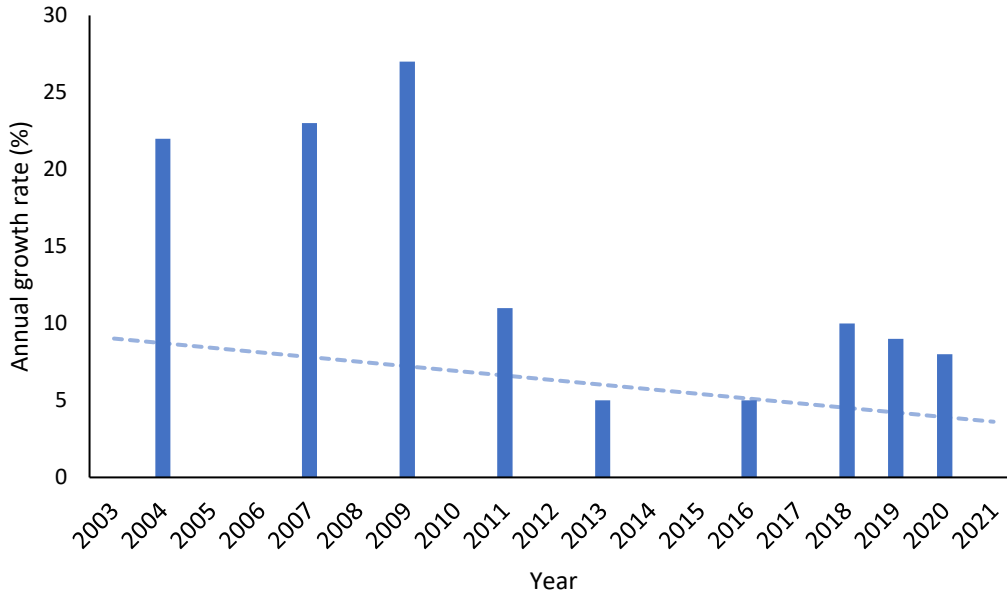


Figure 3.3.1. Elephant population annual growth rates for the years 2003-2021 on Amakhala Game Reserve, Eastern Cape, South Africa. The trendline suggests the annual population growth decreased over my study period.

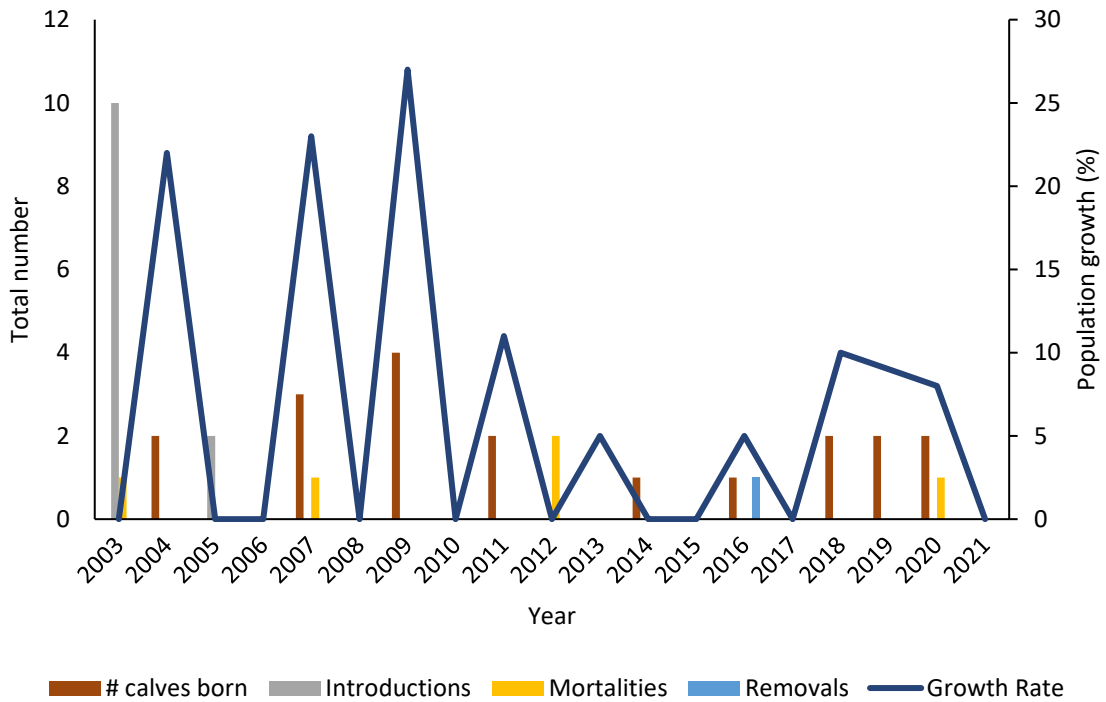


Figure 3.3.2. Elephant population growth rates during 2003-2021 on Amakhala Game Reserve, Eastern Cape, South Africa (horizontal line), including births of calves, introductions, mortalities and removals. There are years where no births occurred.

From 2010 to 2021, the annual growth rate decreased from over 20% to below 11% (Figure 3.3.2). There was a spike in births from 2018 to 2020 as four cows becoming sexually mature and had their first calf. PZP was used on nine of the ten breeding females once they had their first calf, staggered at different intervals. There was no growth in the population in 2021 as all the breeding females had given birth to their first calf, were on PZP and/or had been removed from the ICP.

Inter-calving intervals

Overall, the inter-calving mean amongst all the female elephants on Amakhala was 2.99 years. The average inter-calving intervals ranged from 2.25 years to 3.96 years.

With and without treatment

The average inter-calving interval of the treated elephant cows was 2.89 years (Table 3.3.1). Most of the treated cows had only given birth to one calf between the years of 2003 and 2021. One of the cows (Ayanda) inter-calving interval was 2.25 years. She was administered the contraceptive two months late as she conceived only 5.5 months after she gave birth to her first calf. Another cow (Ambalo) had an inter-calving average of 3.54 years although her shortest inter-calving interval was 2.16 years which was the shortest interval of all cows on Amakhala. Her calf who was born in 2011, died in 2012 therefore she did not receive her

annual PZP booster for the year 2013. The remaining four elephant cows had not yet conceived a second calf as they were put on the contraceptive program after their first calf was born at staggered intervals for three to five consecutive years.

Table 3.3.1 Breakdown of six treated elephant cows inter-calving average in months and years on Amakhala Game Reserve, Eastern Cape, South Africa. The table indicates the individual elephant, total calves born and the inter-calving average of the adult cows.

Elephant cow	Total calves born	Mean inter-calving interval (months/years)
Ambalo	4	42.5m/3.54y
Chwayita	1	n/a
Ayanda	2	27m/2.25y
Amanzi	1	n/a
Cebisa	1	n/a
Bongani	1	n/a
Total mean inter-calving interval		34.8m/2.89y

The three elephant cows that did not receive treatment between 2003 and 2007 had an inter-calving average of 3.1 years (Table 3.3.2). These three cows received the immuno-contraceptive in 2008, therefore, only the period between 2003 to 2009 of no treatment is represented (all three cows were already pregnant in 2008 when they received the first dose). The shortest inter-calving average of the non-treated females was 2.45 years (Table 3.3.2). The longest inter-calving average of the non-treated females was 3.96 years. The cow, Chebe had only given birth to one calf during the study period, therefore, was not included.

Table 3.3.2. Breakdown of four non-treated elephant cows inter-calving mean in months and years on Amakhala Game Reserve, Eastern Cape, South Africa. The table indicates the individual elephant, total calves born and the inter-calving average of the adult cows.

Individual	Total calves born	Mean inter-calving months/years
Alatisha	3	33m/2.75y
Baluleka	3	29.4m/2.45y
Cupha	2	47.5m/3.96y
Chebe	1	n/a
Total mean inter-calving average		37.2m/3.05y

The T-test Two-Sample Assuming Equal Variance indicated there was no evidence of a statistically significant difference in the mean inter-calving intervals between the treated and non-treated cows ($t = -0.21$; $df = 3$; $P\text{-value} = 0.85$) (Figure 3.3.3).

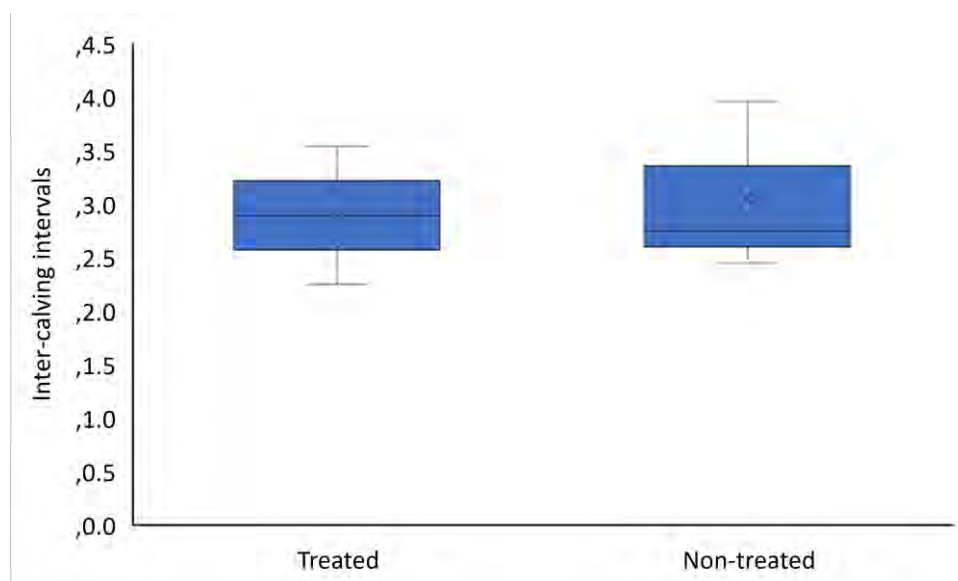


Figure 3.3.3. Boxplot representing the inter-calving intervals of the treated and non-treated elephant cows.

Sex ratios

A total of nineteen calves were born on Amakhala between 2003 and 2021. Of the nineteen calves born, eleven were male calves (58%), seven were females (37%) and the sex of one calf was unknown as it died only after it was a few days old (5%) (Figure 3.3.4).

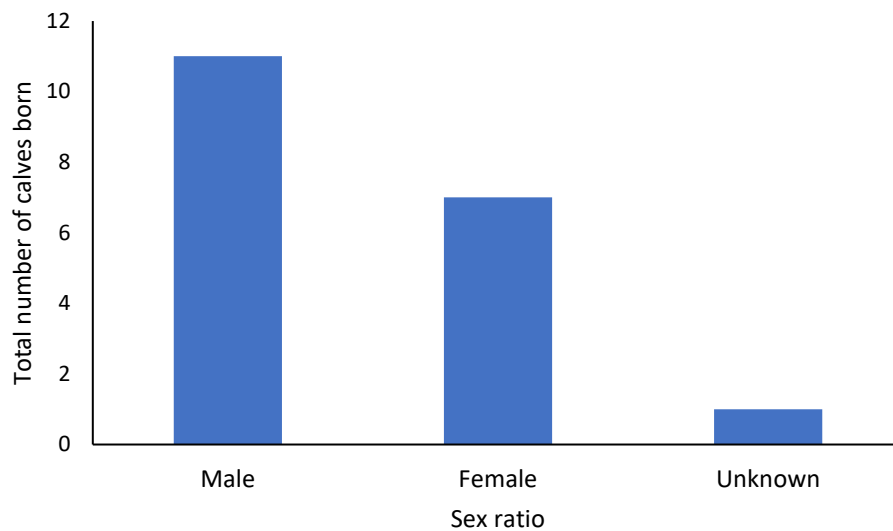


Figure 3.3.4. Sex ratio of 19 calves born on Amakhala Game Reserve from 2003-2021.

The sex ratio was skewed towards males amongst the whole breeding herd as seen in Figure 3.3.5. Two of the ten cows had more male calves than females. Two cows had a 50:50 sex ratio and one cow gave birth to only females. The remaining five cows only produced one calf from 2003-2021 and all were males.

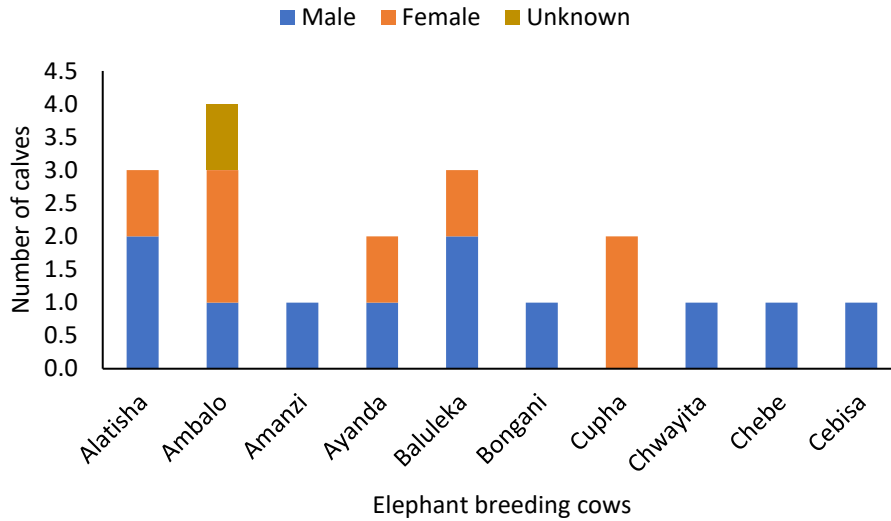


Figure 3.3.5. Sex ratio of each individual cows' calves born on Amakhala Game Reserve from 2003-2021.

With and without treatment

One of the cows gave birth to three calves after she was treated with PZP. There was an even sex ratio of one male, one female and one unsexed calf as seen in Figure 3.3.6. The second treated cow gave birth to a male calf.

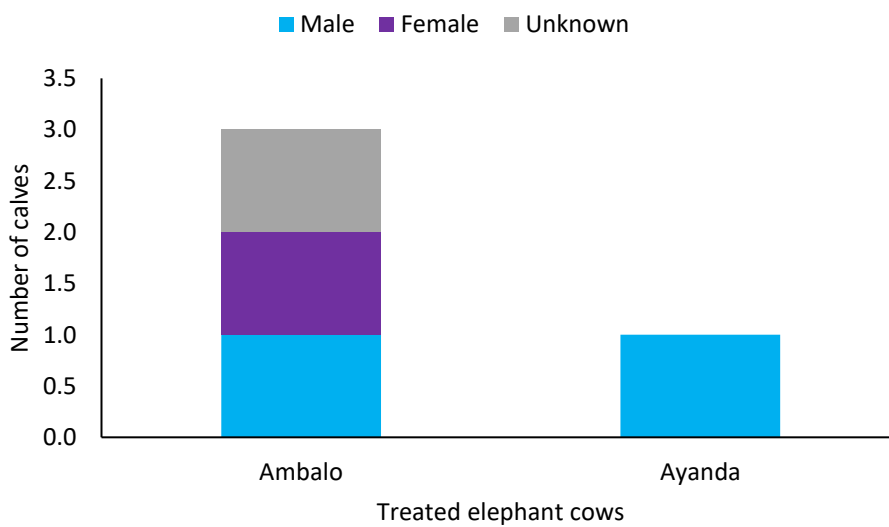


Figure 3.3.6. Sex ratio of each individual elephant cows' calves that was given the immuno-contraceptive after they each had their first calf on Amakhala Game Reserve.

Of the non-treated cows, there were nine males born and six females born. The sex ratio was skewed to males 1.5:1 (Figure 3.3.7). Five cows gave birth to only one calf and were all males. One cow gave birth to only female calves. Two cows gave birth to two males and one female.

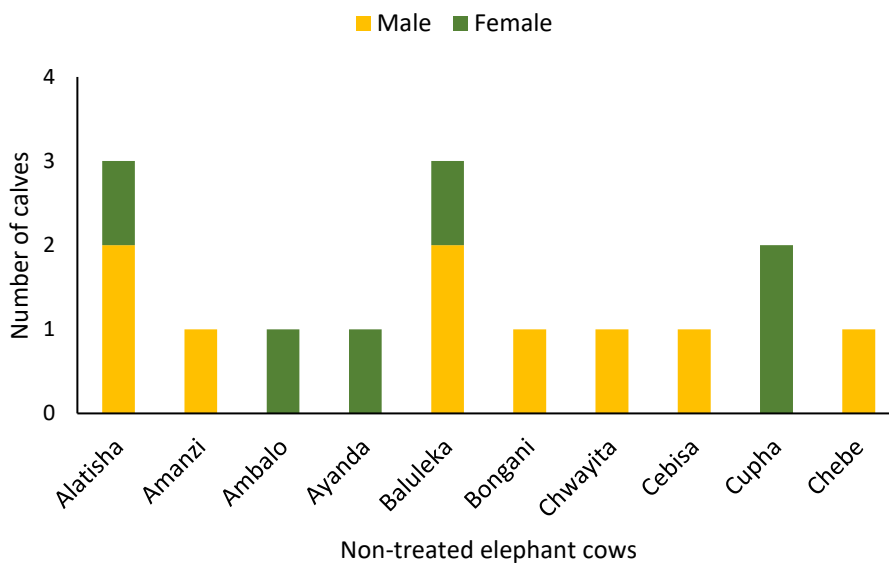


Figure 3.3.7. Sex ratio of each individual elephant cows' calves that was not given the immuno-contraceptive.

There was no evidence of a statistically significant difference shown in the T-test Two-Sample Assuming Equal Variance in the percent of male offspring between the treated and non-treated cows ($t = 0.09$; $df = 10$; $P\text{-value} = 0.93$) (Figure 3.3.8).

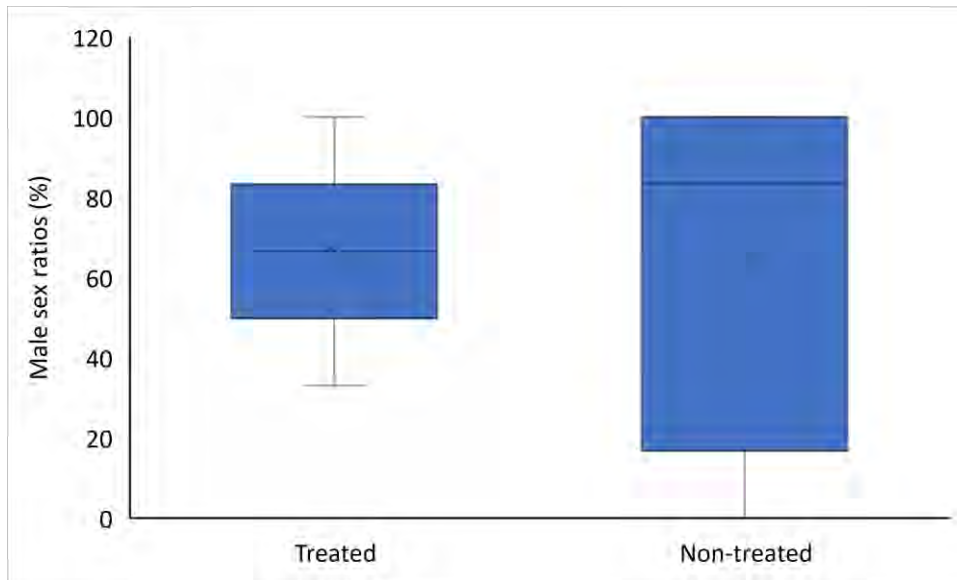


Figure 3.3.8. Boxplot displaying the percentage of male offspring of treated and non-treated elephant cows.

Age at first calving

The mean age at first calving among the seven cows on Amakhala was 10 years old. Three cows (Cupha, Baluleka and Alatisha) were excluded from the average as they did not have their first calf on Amakhala. The age of first calf ranges from seven years old to thirteen years old (Table 3.3.3). One of the cows (Ayanda) was seven years old when she gave birth to her first calf. She was the youngest female to conceive out of the seven cows. The oldest cow (Amanzi) conceived at eleven years old.

Table 3.3.3. The age at first calving and age of conception of the elephant cows on Amakhala Game Reserve, Eastern Cape, South Africa.

Elephant cow	Age at first calf	Year conceived	Age conceived in years
Ambalo	11	Sept 2007	8.75
Chwayita	9	Dec 2009	7.90
Ayanda	7	Oct 2014	4.25
Amanzi	13	Aug 2018	11
Chebe	11	Jan 2016	8.75
Cebisa	9	Aug 2017	7.70
Bongani	10	Nov 2018	9.25
Mean	10		8.23

Fecundity and fertility rates

The mean fecundity rate for the breeding females over the study period was 0.14. The highest fecundity rate was 0.80 in 2009. The lowest fecundity and fertility rate was zero, covering a total of ten years between 2003 and 2021.

The mean fertility rate of Amakhala’s elephant breeding cows was 0.16. Between 2003 to 2009, the four breeding females all conceived within the same year of each other, therefore, all gave birth to calves in the same years to follow. The reproductive similarity in the cows helps to explain why there were no calves born in 2003, 2005, 2006 and 2008 due to the 22-month long gestation period. The year 2009 had the highest fecundity and fertility rates at 0.80. Three of the four adult cows gave birth that year, in addition, the contraceptive program had not been implemented (Table 3.3.4).

Table 3.3.4. Fecundity and fertility rates each year from 2003 to 2021 using the youngest age of conception (4.25 yo). It considers the number of breeding cows, total calves born, survival of calves, and mortality of calves.

Year	# Adult cows	Total calves born	# calves survived	# calves died	Fecundity rate	Fertility rate
2003	4				0	0
2004	4	2	2	2	0.50	0.50
2005	4				0	0
2006	5				0	0
2007	5	3	3		0.60	0.60
2008	5				0	0
2009	5	4	4		0.80	0.80
2010	5				0	0
2011	7	2	1	1	0.14	0.40
2012	7				0	0
2013	10				0	0
2014	10	1	1		0.10	0.10
2015	10				0	0
2016	10	1	1		0.10	0.10
2017	10				0	0
2018	11	2	2		0.18	0.20
2019	11	2	2		0.18	0.18
2020	11	2	1	1	0.09	0.18
2021	11				0	0
Mean					0.14	0.16

3.4 DISCUSSION

Population growth rate

The average population growth rate of the elephant population on Amakhala between 2003 and 2021 was 6%. During these eighteen years, the population experienced annual growth rates ranging from 0% to 27% growth. Newly established large herbivores in previously

unoccupied environments generally result in a rapid growth rate following their introduction (Rachlow & Berger, 1998). My results mirrored this suggestion in that the highest rates were in the first seven years of the population being introduced onto Amakhala (2003 to 2009). Compared to other reserves and parks in South Africa, Amakhala mean annual growth rate is the second lowest (Table 3.4.1). In South Africa, Addo Elephant National Park (AENP) had the lowest growth rate at 5.8% (Gough & Kerley, 2006). Pilanesberg National Park (PNP) had the highest at 10.6% (Mackey et al., 2006). It is important to consider that the elephants in South African reserves are affected by range compression and population management. In Amboseli National Park (ANP) in Kenya, the elephant population has been relatively untouched by human interference, therefore, represents a more true and natural annual growth rate at 2.2% (Moss, 1988).

Table 3.4.1. Annual population growth rates among elephants in reserves and parks in South Africa and Kenya.

Reserve/Park	Average growth per annum
Amboseli National Park, Kenya (Moss, 2001)	2.20%
Addo Elephant National Park (Gough & Kerley, 2006)	5.80%
Hluhluwe-iMfolozi Park (Kuiper et al., 2018)	7.11%
Phinda Private Game Reserve (Mackey et al., 2006)	8.20%
Pilanesberg National Park (Mackey et al., 2006)	10.60%
Estimated max (Calef, 1988)	7%

The high annual growth between 2003 and 2009 could also be due to no cows on the immuno-contraceptive. The three cows that had already given birth to their first calf received their first dose of PZP in 2008 despite there being an all-time exponential growth

the following year in 2009. The population experienced growth at the onset of the program as PZP does not affect in progress pregnancies. Population growth continued until all the pregnant females calved then the vaccine could take effect (Delsink et al., 2013). The growth rates began to decrease two years (2010) post administering the vaccine, PZP, therefore, presenting 100% efficacy. The growth represented in 2011 was from a cow giving birth to her first calf, therefore not on the contraceptive program. During the years between 2012 and 2017, the population growth rates were low. This was, in part, due to the majority of cows on PZP for consecutive years and no first-time mothers giving birth to a calf. One cow's young calf drowned in 2012 thus she was taken off the ICP to calve again. She then conceived and gave birth to a calf in 2014.

High growth rates of elephant populations have been seen where ecotourism defines the objectives of a specific area (Delsink et al., 2013). Increased road infrastructure and artificial waterholes are implemented for enhanced tourist viewing in enclosed systems. The increased roads and water sources allow for elephants to have smaller home ranges and to breed more rapidly amongst favouring conditions (Delsink et al., 2013). In AENP, the access to artificial water sources and the consistent body condition of the elephants may have contributed to the high population growth observed at that site (Freeman et al., 2013). Amakhala is a reserve solely reliant on ecotourism. There are eight artificial watering holes spread across the 60 km² fenced area. The largest distance between two of these water sources is 3.54 km long. Therefore, Amakhala's high population growth rates could have been affected by an abundance of artificial water sources.

During 2003-2009, the rainfall on Amakhala remained mostly above the long-term average of 445 mm per year. During this time, it was representative of optimal veld conditions, thus,

most likely enhancing the body conditions of the elephant population resulting in high growth rates (Foley & Faust, 2010). At the onset of the rainy season, when food quality increases, it triggers an increase in progesterin hormone levels in elephant cows, therefore, the onset of reproductive activity (Wittemyer, et al., 2007).

The rainfall was well above the long-term average between 2011 and 2015. There were high growth rates in 2017 and 2018 which could have been due to the high rainfall during the gestation periods for the elephant cows near the latter end of the above average rainfall in 2015. The high mean population growth of Amakhala's elephant herd was most probably influenced by favourable conditions such as high-quality forage from above average rainfall and excess water availability from artificial sources (Foley & Faust, 2010).

The trend indicates the annual growth rates of Amakhala's elephant population decreased over time. As predicted, the decrease during the study period was reflective of the onset of the ICP.

Inter-calving intervals

The mean inter-calving interval is considered to be the most important parameter weighing on growth rates of elephant populations (Hanks & McIntosh, 1973). The average of Amakhala's inter-calving period was 2.99 years. The inter-calving period ranged from 2.16 years to 5.21 years. Amakhala's mean inter-calving interval was lower than twelve populations represented across the African continent. Amakhala's interval was significantly lower than Tsavo National Park, Kenya (TsNP) at 6.8 years and Murchison's Falls National Park, Uganda (MFNP) at 8.6 years, which all were historically stocked at high densities. Amakhala's mean interval (2.99 years) was closest to AENP (3.3 years), which is approximately forty kilometres away, therefore has the most similar rainfall and vegetation (Wittemyer et al., 2013). KNP had a 3.8 year mean inter-calving interval that had elephants

culled in the population. Additionally, Tarangire National Park, Tanzania (TNP) at 3.3 years was recovering from illegal hunting (Moss, 2001, Wittemyer et al., 2013). Amakhala's elephant population was not density dependent (average 0.3 elephants/km²) during the study period like TsNP nor was it culled or illegally hunted like KNP and TNP (Amakhala Game Reserve, unpublished records). Amakhala's elephants could be correlated with the above-mentioned reserves in terms of disruption by anthropogenic factors, specifically with the use of PZP as the vaccine alters the reproduction of cows.

Rainfall has been shown to have a positive relationship with lower inter-calving intervals in elephant populations (Wittemyer et al., 2013). On Amakhala, the rainfall did not fall under the long-term average until towards the end of the study period in 2019 where it fell below the lower limit due to drought conditions. There were no calves born in 2021 but this was most likely not due to the drought conditions as most of the cows were either contracepted or had been recently taken off the ICP, thus may be pregnant but not yet 22 months for a cow to have given birth.

The mean inter-calving interval of the two treated cows was 2.89 years. The treated cow interval was slightly lower than the non-treated inter-calving interval (3.05 years). One of the cows' (Ambalo) mean inter-calving interval was 3.54 years, although her shortest interval was 2.16 years, the shortest amongst all Amakhala females. The short inter-calving intervals of the treated cows could have been influenced by the above average rainfall which has been shown to be correlated with lower inter-calving intervals (Wittemyer et al., 2013).

The inter-calving intervals of the non-treated cows from 2003-2009 averaged 3.05 years. Amakhala's interval is below the 5% mean of other elephant populations throughout Africa (Wittemyer et al., 2013). Specifically, the non-treated cows' intervals are below averages of

AENP (3.3 years), ANP (4.5 years) and KNP (3.8 years) although the longest inter-calving average of the non-treated females was 3.96 years which aligned with averages in AENP, ANP and KNP (Wittemyer et al., 2013).

The minimum interval between calving and the next conception is approximately one year (Laws et al, 1975). The minimum interval of one year between calving was not the case for all three non-treated Amakhala elephant cows. Their conception post-birth ranged from 0.42 years to 3.33 years. Four of the six calving interval conception rates were below one year. The small inter-calving rates on Amakhala could be correlated with the use of artificial watering holes (Delsink et al., 2013) as well as above average rainfall during those years resulting in good body condition (Gough & Kerley, 2006). Lastly, low elephant population density on Amakhala throughout the study period could have been correlated with the short inter-calving intervals. Gaillard et al. (2000) and Eberhardt (2002) found that as population densities increase, juvenile mortality rates increase, the age of first reproduction increases as well as a decrease in adult female reproductive rates in which is likely a result of changes in food resources.

There is a slight tendency for interbirth intervals to be longer among mothers with a previous male calf (Lee & Moss, 1986). The longer interbirth intervals could only be determined for one of the cows (Alatisha) as she had given birth to two males and one female. The interval between her male and female calf was 3.25 years and the interval between her female and male calf was 2.25 years.

Overall, Amakhala's mean inter-calving intervals were lower than that of multiple elephant populations across Africa. The short intervals were most likely due to favouring conditions such as above average rainfall influencing the increase in nutritious food supply, low population densities and high-density water sources. Further, the treated cows had slightly

shorter inter-calving intervals than the non-treated cows thus rejecting my prediction that treated cows would have longer inter-calving intervals.

Sex ratio

Kruuk et al. (1999) suggests that more females will be born under high density dependence conditions and lowered resource availability (e.g., drought). With more resources available, cows produce male calves. In ungulate studies, there is potentially a link between resource availability and the tendency for females in good condition to produce male-biased sex ratios (Trivers & Willard, 1973). In eight other ungulate studies, females in good condition produced a significantly higher proportion of male offspring than females in poorer condition in the same population (Kruuk et al, 1999). On Amakhala, overall, there were slightly more male calves (n = 11) born than females (n = 7) but there were no significant differences in sexes born between treated and non-treated cows. Therefore, it is suggested that PZP did not affect the sexes of offspring and my prediction of a skewed male sex ratio of treated females was rejected.

The overall higher number of males born in the herd could be due to the population being at a low density (under carrying capacity) from 2003 to 2019. The rainfall was above the long-term average for most of the years between 2003-2019, although the rainfall dropped below the long-term average in 2019 through 2021. High rainfall could help explain why there were more male calves born throughout the population as the cows had enough nutrition available to them therefore overall, in better body condition. The higher male sex ratio during years 2020 and 2021 on Amakhala contradicts the theory above by Kruuk et al. (1999) which states that at higher densities, female calves will be born. The elephant densities on Amakhala in 2020 and 2021 were slightly above the recommended density

(0.41 elephants per km²) at 0.43 elephants per km² but is unlikely correlated. Early investment by mothers should be directed towards males when parental investment has a greater effect on male reproductive success and early growth is related to later reproductive success (Clutton-Brock et al., 1982). Elephant cows with a surviving male tended to have a longer inter-calving interval than did cows with a surviving female (Lee & Moss, 1986) as male calves tend to suckle for longer periods of time and need more milk due to their size difference (sexual dimorphism) (Lee & Moss, 1986). The longer inter-calving period was only true for one of the cows (Alatisha) who had an inter-calving period of 3.25 years after a male calf was born and only 2.25 years after a female calf.

One cow (Ambalo) was relieved from the PZP program (was not given PZP) twice during the study period. She gave birth to one female and one male after the contraception. According to the Trivers-Willard model (1973) of sex allocation in offspring of dimorphic species, the body condition of cows who did not reproduce will likely be higher than females with calves due to less stress of reproduction. It is possible that there will be a male bias in the offspring of previously contracepted females (Kerley & Shrader, 2007). However, there is not enough data from Amakhala to support this theory.

Age at first calving

The average age at first calving across twelve elephant populations within the African continent is 13.4 years old (Wittemyer et al., 2013). Amakhala's age at first calving mean was 10 years old. This age is substantially lower than most population averages therefore my predictions were false. It has been shown that there is an association with reproductive onset and rainfall and density (Laws et al., 1975). During 2003-2018, Amakhala experienced rainfall that was in line with the long-term average or above the average at the upper limit.

The density of the elephant population ranges from 0.17 to 0.37 elephants per km² and a mean of 0.31 elephants per km² from 2003 to 2018. A carrying capacity assessment for the elephant population was performed in 2003 and the recommended stocking density was 0.41 elephants per km² (Knight, 2003). With respect to similar vegetation and climate, in AENP the estimated carrying capacity of elephant densities were 0.4 elephants per km² (Penzhorn et al., 1974) and 0.25-0.54 elephants per km² (Boshoff et al., 2002). Van Jaarsfeld et al. (1999) found no evidence of effects of density dependence in elephant populations with a mean density of 0.33 elephants per km². However, van Aarde et al. (1999) found evidence of density dependence in KNP at a density of 0.37 elephants per km². Therefore, the above average veld conditions along with low elephant densities per km² could have contributed to the young primiparous age of the majority of Amakhala's cows. The exceptional early-age reproduction observed in North Luangwa National Park (NLNP) females is most likely a function of low population density and high mortality (Owens & Owens, 2009). In other mammalian populations, particularly ungulates experiencing high rates of mortality and low densities, individuals become sexually mature at younger ages and frequently exhibit increased fecundity (Clutton-Brock et al., 1982). Amakhala did not have high mortality rates through the eighteen-year study period. The average density of the elephant population at 0.33 elephants per km² was below the recommended capacity of 0.41 elephants per km² (Knight, 2003).

One of the cows (Ayanda) who conceived at the age of 4.25 years was the youngest to give birth at seven years old. The youngest recorded age of a female reaching parturition was eight years old in ANP (Moss, 2001). In Tanzania, the youngest known primiparous age was eight years (Moss, 2001; Foley, 2002). Ayanda could have conceived at such a young age because of available nutrition. Sadleir (1969) has reviewed the effects of nutrition on the

attainment of puberty in wild mammals. The level of nutrition plays a prominent part in determining the age of puberty in the few groups of mammals (Hanks, 1972). Ayanda was born in 2009 and gave birth in 2016 to her first calf. From 2006 to 2015 the rainfall was above the long-term average, thus, suggesting optimal veld conditions and high nutritional value of the forage. Elephant family groups rely on interactions between females and calves to help stabilize those relationships within these groups therefore contraception essentially removes calves from these family groups therefore decreases the cohesion of the unit (Kerley & Shrader, 2007). Between 2012 and 2015 only one calf was born on Amakhala due to the use of PZP. Potentially, Ayanda gave birth at such a young age to compensate for the other breeding females who were not reproducing as there was only one calf under the age of five years in the family group at the time Ayanda gave birth in 2016. Due to the strong social bonds and the importance of the presence of calves in family groups (Kerley & Shrader, 2007), I suggest the cow, Ayanda may have altered her physiologically state to produce calves as there were no calves present in the herd at the time.

Fecundity and fertility

Inter-calving intervals and gestation determine the number of females that give birth each year (Owen-Smith, 1988). Thus, the reproductive success of Amakhala's elephant cows was dependent on inter-calving intervals and the 22-month gestation. The fecundity rate was 0.09 average for Samburu National reserve (Wittemyer et al., 2013). The average fecundity rate on Amakhala was 0.14 which translates into 14% of the breeding females calved and the calves survived to the next year. The above average fecundity rates on Amakhala were most likely attributed to the favouring forage conditions in which contributes to the proximate control by conditions affecting oestrus and mating (Owens-Smith, 1988).

The mean fertility rate on Amakhala was 0.16. On average, 16% of the sexually mature females gave birth in each year. Under favourable conditions such as high rainfall, the inter-calving interval is low which causes the fertility rates to increase (Hrabar & du Toit, 2005; Fike, 2011). The high rainfall and short inter-calving intervals on Amakhala most likely influenced the high fertility rates in the first half of my study period. The fertility rates decreased from 0.50 in 2004 to 0.18 in 2020 in which was in line with my prediction that as more females were contracepted, the fertility rates would decrease.

One of the cows (Alatisha), was introduced in 2003 and was administered PZP in 2008 for three consecutive years. She produced a calf in 2009 and was not given PZP again after three consecutive years during the study period. Estimates of the time for a cow to conceive after being released from contraception is approximately equal to the number of years an elephant cow has been subjected to the vaccination (Bertschinger et al., 2008). It was predicted that Alatisha would conceive in 2014 and give birth in 2016. By 2021, at the age of 40, she still had not given birth to a calf. The cause of this could be several factors such as the PZP could have made her infertile (Paterson et al., 1998, 1999), it was a matriarch decision for her not to reproduce (Kachel et al., 2011) and/or an age factor (Laws, 1969, 1970).

In Miller et al. (2000), horses that were vaccinated with the immuno-contraceptive for longer periods of time resulted in the delay of recovery of fertility for up to four years. This immunization contraceptive ultimately results in a decline in the ovulation rate (Kirkpatrick et al., 1997). In some rodent and primate species, the ZP vaccine has been associated with ovarian damage which is likely to result in permanent infertility (Paterson et al., 1998, 1999). There is uncertainty of the long-term safety and reversibility after the use of PZP in elephants (Paterson et al., 1999, Muller et al., 1997). Therefore, the cow, Alatisha could

have suffered from effects of PZP by delaying her fecundity and fertility recovery or damage to her ovaries thus resulting in infertility. I recommend further research into this area to determine whether PZP can influence elephant fertility.

Usually the largest, oldest female in the family group is the matriarch (Douglas-Hamilton, 1972). Alatisha was twenty-two years old at the start of the study in 2003. She was the third eldest female and considered to be one of the matriarchs. Gradual, age-related decreases in physiological functions occur in most individuals, typically coinciding with somatic and reproductive senescence (Kachel et al., 2011). Declines in fertility with age are common in most mammal life histories (Bellino et al., 2003; Emery Thompson et al., 2007). Freeman et al. (2013) distinguished the number of years since a non-pregnant female gave birth to her last calf (post-partum duration) was longer for older females with a higher social status, as well as during the dry season. These results indicate that social standing and age of elephants are related to reproductive function, and that older females exhibit reductions in ovarian capacity. In ANP, the average age of fertility decline was 49 years old in elephant cows (Lee et al., 2016). Given that at the age of forty, Alatisha, had not given birth to another calf after stopping the treatment of PZP for eleven years despite being on the program for only three consecutive years, her age and status in the herd could have influenced these conditions. In contrast, elephant cows in KNP within the age bracket 51 to 60 years old, 88% of those females were pregnant and/or lactating suggesting fewer senescent cows in KNP compared to other elephant populations (Smuts, 1975). McAuliffe and Whitehead (2005) defined senescence as an adaptive trade-off between continued reproduction and assisting kin. Behavioural mechanisms may also promote older females reaching reproductive senescence (Laws, 1969, 1970). The highly involved relationship a matriarch elephant has with the family group along with cooperative behaviours like allo-

mothering among related females (Douglas-Hamilton, 1972; Wittemyer et al., 2005) suggests that early reproductive senescence may be selected for elephants (Freeman et al., 2013). The early reproductive senescence could promote an older cow, like a matriarch to cease reproduction and assist with her kin's offspring. This trade-off would in turn increase the kin's reproductive rates and cease reproduction of the old cows (Johnstone & Cant, 2010).

While the social decision for the matriarch, Alatisa to not breed could have affected her fecundity, the immuno-contraceptive could have also interfered with Alatisa's fecundity. Crucially, there are indications that long non-reproductive periods may accelerate the onset of reproductive senescence in female elephants (Hermes et al., 2004). Fertility senescence in elephant cows ranges within specific elephant populations, thus is difficult to propose certain factors influencing Alatisa's suggested infertility.

3.5 CONCLUSIONS

The elephant breeding herd on Amakhala demonstrated varying differences in demographic and reproductive parameters compared to other elephant populations in Africa. The high growth rates of Amakhala's elephants were most likely due to overall, good rainfall, below average inter-calving intervals, and reproduction of the first calf at a young age during the study period. My prediction that the elephant population growth rates would decrease as more elephant cows were contracepted was supported. Foley and Faust (2010) recognized that climate variability had a strong impact on elephant reproductive biology. Overall, the favourable conditions and lack of density dependence on Amakhala during most of the study period in terms of good rainfall and resource availability (water and forage) were most

likely the key factors for such high reproduction success in the elephant breeding herd (Foley & Faust, 2010.) The rainfall during the study period was regularly above the long-term average thus resulting in good quality of forage therefore the increase in body condition of the elephant cows. The increase in body condition could have influenced the inter-calving intervals, skewed sex ratios and age at first calving of the elephant breeding cows on Amakhala. PZP could have indirectly contributed to the young age of first calving as well as the low inter-calving intervals of the elephant cows by the cows compensating for the treated females as treated cows had shorter inter-calving intervals than non-treated cows. Additionally, the immuno-contraceptive could have affected the fertility of Amakhala's older cows in conjunction with social decisions made from the matriarch to not breed. PZP is clearly effective at slowing the population growth rate of Amakhala's elephant population. There are indications from the data presented in my study that PZP had an influence on some reproductive parameters but more data on this specific herd over time will need to be assessed.

CHAPTER FOUR

SPATIAL ECOLOGY

4.1. INTRODUCTION

African elephants are large, mixed feeders that require extensive home range areas for survival. Essential resources within elephant home ranges include food, water, resting sites, access to mates and caring for their young (Burt, 1943; Delany, 1982). A standard home range may be spread across multiple environments and heterogeneous landscapes (Grainger et al., 2005; Nkosi et al., 2019) in which the home range is quantified from its space use by analysing the spread of areas used (Worton, 1989). Heterogeneous landscapes contain homogeneously vegetated areas in which they each vary in composition and spatial grouping (Turner et al., 2001). These homogenous vegetation patches are dependent on soil structure, climate, topography, and geology (Boshoff & Kerley, 2001).

Core range size is defined by the areas concentrated within home ranges used by the animal (Samuel et al., 1985). In Maputo Elephant Reserve (MER), defined core ranges suggested that habitat use was not random, and elephants may follow a central place foraging strategy (Lewison & Carter, 2004). Elephant home ranges in fenced areas range from 10 km² to 80 km² and from 90 km² to 800 km² in open areas (Douglas-Hamilton et al., 2005). In LMNP, the home range for elephants was 33 km² (Douglas-Hamilton, 1972) and in KNP the home range was 436 km² (Hall-Martin, 1984).

Resource availability (forage and water), seasonality and reproductive success can all influence an elephant's home range size (Shannon et al., 2006). Elephants seek out relatively high nutritional forage in different vegetation types (Shannon et al., 2006).

Nutritional requirements of elephants are expected to determine the home range size (Schoener, 1981). Female elephants are more selective in their foraging habits (Shannon et al., 2008) causing them to choose areas with high plant species diversity (Illius & Gordon, 1987). The large size of elephants determines their feeding habits involving uprooting trees, breaking branches and being messy feeders (Bakker et al., 2016). Elephant's home range size is generally larger at low densities due to their large body and size feeding requirements (Owen-Smith, 1988). Elephants are water dependent animals, therefore, their home range is influenced by water resource availability. In vast, semi-arid areas, with limited water, elephants' home ranges are much larger (Lindeque & Lindeque, 1991) than in areas where artificial water sources are provided. Artificial water sources, like in KNP, are more likely to provide small and stable elephant home ranges (Whyte, 2001). Furthermore, in Etosha National Park (ENP) and Khaudum National Park (KhNP), Namibia, elephant home range sizes decreased with expanded watering hole densities during both the dry and wet seasons (Grainger et al., 2005). These studies suggest that water is a powerful determinate of the space use of elephants and may potentially play a larger role in the size of elephant home ranges than landscape heterogeneity (Grainger et al., 2005). De Beer and van Aarde (2008) hypothesized in Ngamiland District 11 (NG11), Botswana, with the only permanent water source, the Okavango River, that the vegetative heterogeneity would play a larger role in determining the home range size than in areas where management provided water. However, this did not hold for NG11 and it has been suggested that even in unmanaged situations, the need for water may still be important in determining home range sizes (van Aarde et al., 2006; de Beer & van Aarde, 2008). Studies have been done in semi-arid environments that describe elephants as riparian species in which factors like availability of palatable vegetation and water affect space use (Viljoen, 1989; Ottichilo, 1986;

Sommerlatte, 1976). In Pongola Game Reserve (PGR), KwaZulu-Natal, relatively small home ranges were observed and were most likely due to the widespread permanent supply of drinking water and the abundance of relatively high nutritional forage in small patches of different homogeneous vegetation (Shannon et al., 2008).

Seasonality can also influence the spatio-temporal distribution of key resources which can then directly impact elephant's space use. During the wet season, crude protein content in grasses increases, thus improving the quality of nutrition in grasses (Clegg & O' Connor, 2017). Elephants are more selective in their forage during the wet season when the availability of water is less restrictive on their movements (de Beer et al., 2006; Ntumi et al., 2005; Osborn, 2004; Western & Lindsay, 1984). The dry season impacts the elephants' key resources by reduced nutritious vegetation and a decrease in natural water sources. In theory, elephants are under induced nutritional constraints in the dry season, therefore, the need to expand their home range to meet their food requirements is expected. Conflicting observations suggest that elephants are more likely to concentrate their feeding in areas close to water during the dry season, therefore, intake lower quality of food rather than expanding their home range to meet their food requirements (Owen-Smith, 1988; Chamaille'-Jammes et al., 2007; de Beer et al., 2006; Gaylard et al., 2003; Leggett, 2006; Osborn & Parker, 2003; Redfern et al., 2003; Smit et al., 2007). Vegetation and water availability determine dietary composition thus rainfall and seasonality determine elephants' diets (Laws, 1970; Barnes, 1982; Birkett & Stevens-Wood, 2005; Loarie et al., 2009).

Elephant family group home ranges are also influenced by reproduction success and survival of young. These family groups deploy strategies to increase the survival of their young.

Elephant cows are more likely to avoid areas with predators such as lion (*Panthera leo*) as

the lions pose an elevated predation risk for elephant calves (Stokke & du Toit, 2002). This spatial avoidance is thought to be an anti-predator behaviour to protect the elephant calves (Power & Compion, 2009). Family groups are also more likely to seek thicket habitats due to their offspring being sensitive to extreme heat (Mumby et al., 2013).

Mlambo et al. (2021) emphasized the urgent need to understand the elephant's home range and space use under human-induced pressures. Home and core ranges are affected by natural occurrences like resource availability and seasonality, but unnatural variables also affect elephant space use such as anthropogenic influences like habitat degradation (Goldenberg et al., 2018) and potentially population control measures. Due to the success of establishing and conserving elephant populations in small, fenced areas in South Africa, overpopulation has occurred thus resulting in the use of contraceptives to slow population growth (Chapter 3; Forrer, 2017). It is therefore important to establish if these contraceptives influence home ranges and vegetation use of these elephant populations for reserve management to make evident based decisions for maintaining biodiversity and ecosystem function in these enclosed systems (Chamaille-Jammes et al., 2007; Loarie et al., 2009; Gillson & Lindsay, 2003).

The aim of this chapter was to estimate home ranges and core ranges for the elephant breeding herd on Amakhala before, during and after the contraception of the matriarch. Specifically, I wished to test whether PZP altered the space use of the matriarch and, by extension, the breeding herd. I made use of three timeframes for this part of my study. The first timeframe (2006 to 2008) was prior to the matriarch, Alatisha, receiving the immuno-contraceptive, PZP (hereafter referred to Pre). In 2008, she received an initial dose of PZP but was already pregnant and gave birth in the following year in 2009 therefore the vaccine

did not yet take effect. The second timeframe was between 2009 and 2013 when the cow was on the contraceptive, including the period in which is the expected time it takes to completely be released of PZP (hereafter referred to During) (Bertschinger et al., 2008). She was on PZP for three consecutive years thus taking three years for the PZP to wear off. Lastly, the third timeframe (2014 to 2021), was when the cow was suspected to be completely off contraceptives and able to conceive (hereafter referred to Post).

For this chapter, I asked the following research questions.

Research questions:

- Do immuno-contraceptives alter the space use of elephant breeding herds?
Specifically, is there spatial avoidance of core home range use before, during or after vaccine administration? I predicted that the use of immuno-contraceptives would increase the elephant herds' core range as there are fewer reproducing cows, thus less nutritional constraints from no calves.
- Do immuno-contraceptives change the habitat selection of cows as they may be less likely to be selective due to less stress of caring for a calf? I predicted that the immuno-contraceptive, PZP would alter the elephant's habitat use by being less selective on vegetation types.

4.2 METHODS

To determine if immuno-contraceptives influence the spatial use of the elephant breeding herd, historical, satellite Global Positioning System (GPS) collar data were used. One elephant cow, Alatisha (a matriarch), was fitted with a GPS and Very High Frequency (VHF)

collar for fifteen consecutive years (2006-2021) as part of the routine reserve management, and approved elephant management plan of Amakhala (Razzaq, 2007). The GPS settings were not cohesive over the fifteen years as some years collected one GPS fix per day while other years collected four fixes per day. Therefore, only one GPS fix per day was used for all years. This approach also allowed me to account for any autocorrelation of GPS fixes in my analyses (Boyce et al., 2010). There was a total of 4,122 fixes during the fifteen-year study period ranging from 238 to 1,799 fixes with a mean of 257 fixes per year. The data were considered representative of the entire herd due to their complex social structure (Fritz, 2017). Female African elephants are closely bonded to their relatives and generally remain in natal groups for life thus being kin-based groups (Moss, 1988). As Alatisha is one of the matriarchs, her dominance influences the herds' movements and behaviour (Wittemyer & Getz, 2007). The GPS data from the elephant cow were imported into Excel Microsoft 365. Errors or duplicates were first checked in Excel then the spreadsheet was further formatted into associated years of 'Pre' 'During' and 'Post' into three separate datasets. Each dataset was imported into QGIS version 3.16.4-Hannover as a Comma Separated Values (CSV) file.

Home range

Elephant home ranges based on minimum convex polygons have been shown to be dependent on the number of points (Whyte, 2001), therefore, the kernel density analysis was used to calculate the home range and core range (Hooge & Eichenlaub, 1997) of the elephant breeding herd on Amakhala. The kernel density produces an area with very little bias, gives surface estimates with low errors (Seaman & Powell, 1996) and can identify multiple core areas. The kernel density was used for each category (Pre, During and Post) of GPS fixes. For each category, the standard distance and mean were calculated using the

spatial point pattern analysis in QGIS to calculate the optimum radius. The optimum radius (*hopt*) is defined by (Medrano et al., 2021):

$$hopt=[2/3n]^{1/4}\sigma$$

where: n= sample size

σ = standard distance

Once the optimum radius was calculated, the kernel density home range and core range were created. I used a 95% kernel density test which determined the home range of the elephant herd. Furthermore, I ran a 50% kernel density test to determine the core range of the herd (Worton, 1989).

To determine if there was any statistical difference in the mean home range between the categories (Pre, During and Post), the categories were further divided into four seasons (winter, spring, summer, autumn). Winter was associated with the months June to August, spring months were from September to November, summer months were from December to February and lastly, autumn was from March to May. The seasons were not divided into simply wet or dry seasons due to non-seasonal, sporadic rainfall that occurs on Amakhala (Vos, 2022). To test for any statistical differences in my dataset, I first tested for normality and homogeneity of variances by using the Shapiro-Wilk normality test in R-Studio version 2022.07. Build 576. The normality and homogeneity of variances being assumed when $P > 0.05$ (Shapiro & Wilk, 1968). The Shapiro test projected the means were not normal as the P-value was less than 0.05 therefore, I used Friedman test to assess any statistical significance in the mean home range across the three categories (Liu & Xu, 2022).

Vegetation utilization

There are eight vegetation types on Amakhala (Chapter 2). During 2006 to 2013, the reserve consisted of 53.2 km². At the end of 2013, an addition of land was added to Amakhala on the southern side, introducing more of the valley thicket, savanna, and old land vegetation types, resulting in a total of 59 km². In 2016, additional land was included on the south-eastern side of the reserve which consisted of karroid thicket type with a total of 60.1 km². Therefore, the categories are broken down into four separate datasets to represent the different sizes of the reserve over time. The vegetation map was exported from GoogleEarth Pro as Keyhole Markup Language (KML) files then imported into QGIS as polygons. Each category (Pre, During, Post 1 and Post 2) GPS fixes were separately overlaid with the vegetation map in QGIS. The count points in polygon tool was used to determine how many GPS fixes per category landed in each vegetation type. Then the proportion of fixes per unit area (vegetation type) was calculated by using the total fixes per vegetation type and dividing it into the area size of the given homogeneous area. Post 1 and Post 2 were averaged together for results for the Post category. A Chi-square test of independence was used to determine if the vegetation types were randomly selected or preferred. This statistical analysis was done in R-Studio.

4.3 RESULTS

Home Range

The home range and core range size varied for each category as seen in Table 4.3.1. The Pre home range covered 61.2% of the total reserve size. The Pre core range represented 6.7% of the reserve. The During home range consisted of 99.1% and the core range 51.4% of the

total area. Lastly, the Post home range accounted for 98.1% and core range 59.3% of the total reserve. Table 4.3.2 represents the years affiliated with the three categories (Pre, During and Post PZP).

Table 4.3.1. Home ranges and core ranges in each category (Pre, During and Post) for the elephant breeding herd on Amakhala.

Category	Home range (km ²)	Core range (km ²)
Pre	32.6	3.6
During	52.7	27.3
Post	59.0	35.6

Table 4.3.2. The years associated with the Pre, During and Post PZP on Amakhala.

Category	Years
Pre PZP	2006-2008
During PZP	2009-2013
Post PZP	2014-2021

The smallest home range of the elephant breeding herd was prior to the use of contraceptives (Pre) at 32.6 km². The Pre home range extended west of the R342 public road but was far less frequented than the river basin on the eastern side of the reserve. The herd's core range in the Pre category was 3.6 km² and was solely in the river basin of Amakhala (Figure 4.3.1).

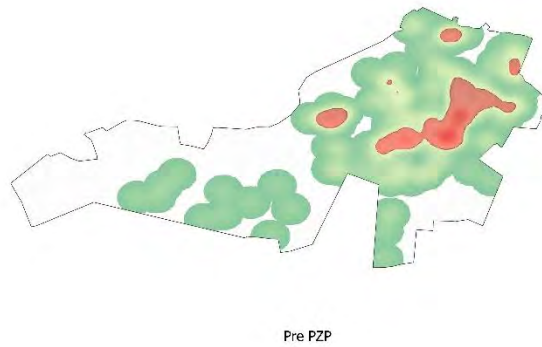


Figure 4.3.1. Pre PZP home range (green) and core range (red) of Amakhala's elephant breeding herd with associated GPS fixes.

The second largest home range size occurred when the cow was on PZP (During) at 52.7 km² (Figure 4.3.2). The herd utilized the western side of the reserve during the use of PZP far more than Pre PZP. The During core range remained heavily in the river basin, similar to Pre PZP although the south-eastern section of the reserve was frequented more in the During category.



Figure 4.3.2. During PZP home range (green) and core range (red) of Amakhala's elephant breeding herd with associated GPS fixes.

The largest home range occurred in Post PZP was 59 km². The Post category core range was more consolidated on the eastern and southeastern half of the reserve than that of Pre and During. The herd utilized the southern side of the reserve far more Post PZP than the other two categories (Figure 4.3.3).

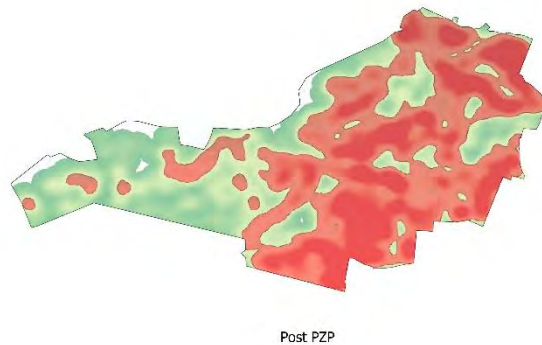


Figure 4.3.3. Post PZP home range (green) and core range (red) of Amakhala's elephant breeding herd with associated GPS fixes.

The overlap of the core ranges for all three categories was on the eastern side of the reserve where the river basin occurred. The overlap in core ranges between the three categories was a total of 3.6 km² which accounted for 10.1% of the largest core range (Post). The During and Post categories had more similarities in the home ranges than that of Pre, spreading across most of the reserve.

The mean proportion of the home range in the Pre category was 0.58. (Figure 4.3.4). The mean proportion in the During category and the Post category were both 0.96. The Friedman test showed that the mean home range across the three categories differed significantly (F-value = 5.4; df = 3; P-value = 0.0026).

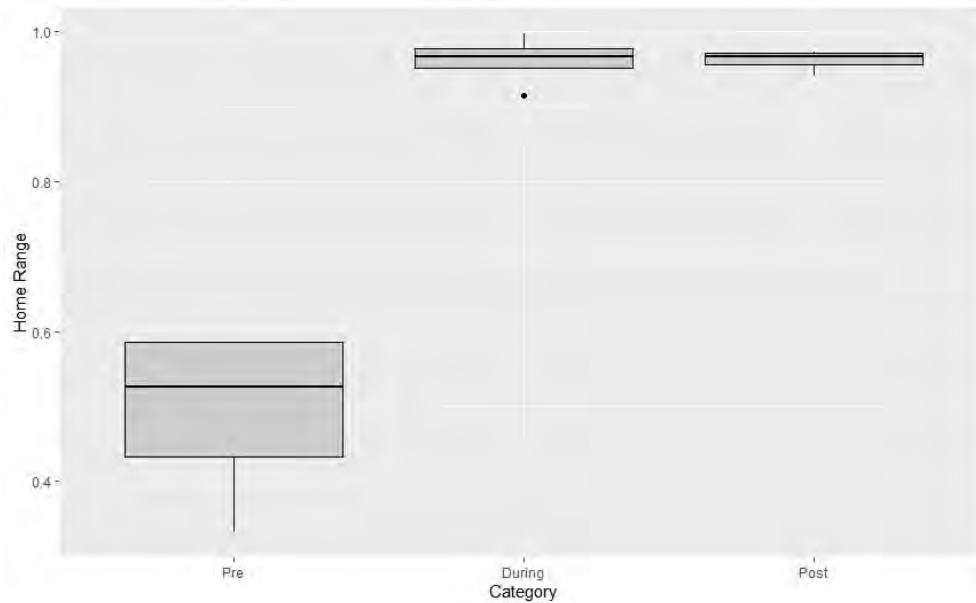


Figure 4.3.4. Boxplot representing the mean home range proportions within the three categories Pre, During and Post the contraception of the matriarch.

Vegetation utilization

The elephant breeding herd utilized all eight of the vegetation types on Amakhala during the study period. Some vegetation types were more frequented than others. The most utilized vegetation type of all categories was grassland. Overall, the two most under-utilized vegetation types were the mesic and valley thickets. The elephant herd made use of the savanna vegetation relatively the same in all four categories between 13 and 18 percent of the total fixes. The four categories with linked years are seen in Table 4.3.3.

Table 4.3.3. The years that were associated with PZP categories on Amakhala.

Category	Years
Pre PZP	2006-2008
During PZP	2009-2013
Post 1 PZP	2014-2016
Post 2 PZP	2017-2021

Prior to the use of contraceptives (Pre), the herd frequented the old lands 22% of the time as seen in Table 4.3.4. The riverine thicket was the second most utilized habitat despite the thicket representing the second smallest area amongst all eight vegetation types at 4%. The least utilized areas pre PZP was the valley and mesic thicket. The valley thicket encompasses 2% of the entire reserve and the mesic, 10%. The herd never used the grasslands on the far western side of the reserve prior to the use of contraceptives (Figure 4.3.5).

Table 4.3.4. Percentages of each vegetation type and GPS fixes within each vegetation type pre PZP

Vegetation types	area(%)	total fixes (%)
Old lands	14	22
Riverine thicket	4	21
Xeric thicket	8	17
Grassland	28	15
Savanna	21	13
Karroid	13	6
Valley thicket	2	4
Mesic thicket	10	3

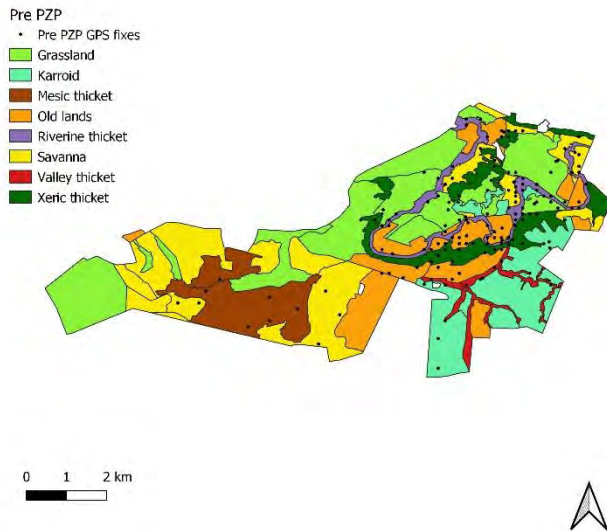


Figure 4.3.5. Pre PZP vegetation use with GPS fixes of Amakhala’s elephant breeding herd from 2006 to 2008.

During PZP, the elephant herd utilized the grasslands and karroid the most at 17% (Table 4.3.5). The grasslands on the far western side of the reserve were utilized during the use of PZP (Figure 4.3.6). The xeric and valley thicket were the least selected habitat (7%) when the cow was on the contraceptive.

Table 4.3.5. Percentages of each vegetation type and GPS fixes within each vegetation type during PZP.

Vegetation types	area (%)	total fixes (%)
Grassland	28	17
Karroid	13	17
Savanna	21	16
Old lands	14	15
Riverine thicket	4	12
Mesic thicket	10	8
Xeric thicket	8	7
Valley thicket	2	7

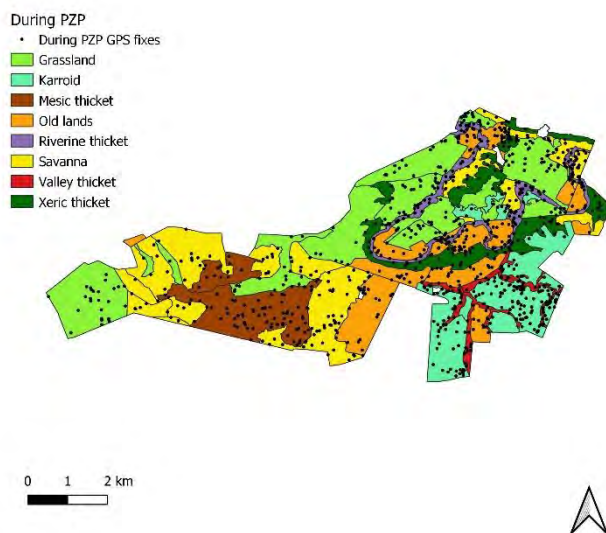


Figure 4.3.6. During PZP vegetation use with GPS fixes of Amakhala’s elephant breeding herd from 2009 to 2013.

The grasslands represented the largest vegetation type during Post 1 PZP and was the most utilized area by the elephant herd (Table 4.3.6 and Figure 4.3.7). The total percent of GPS

fixes in the riverine thicket during 2014 to 2016 was second highest at 16% despite representing the smallest vegetation type on Amakhala. The karroid habitat was the most under-utilized vegetation type at 2% in Post 1.

Table 4.3.6. Percentages of each vegetation type and GPS fixes within each vegetation type Post 1 PZP (2014 to 2016).

Vegetation types	area (%)	total fixes (%)
Grassland	28	29
Riverine Thicket	4	16
Xeric Thicket	8	15
Savanna	27	13
Valley Thicket	5	12
Old Lands	17	9
Mesic Thicket	10	4
Karroid	13	2

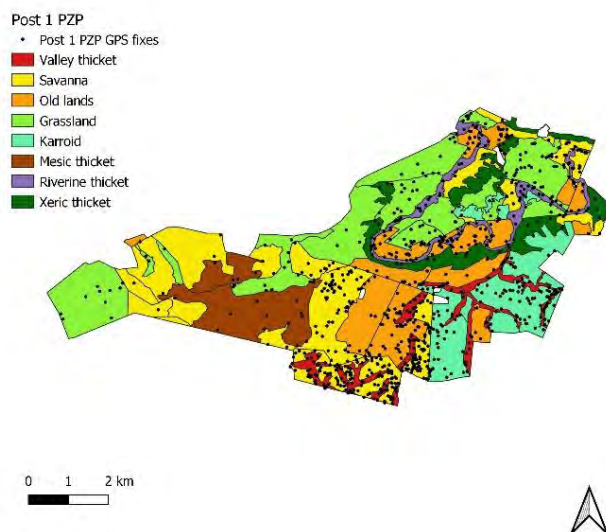


Figure 4.3.7. Post 1 PZP vegetation use with GPS fixes of Amakhala’s elephant breeding herd from 2014 to 2016.

The savannas were utilized the most during Post 2 PZP, similar to the percentage of fixes of the other three categories. The second most utilized area was the old lands at 15%. The xeric thicket and mesic thicket were the least selected habitats during 2017 to 2021 seen in Table 4.3.7 and Figure 4.3.8.

Table 4.3.7. Percentages of each vegetation type and GPS fixes within each vegetation type Post 2 PZP (2017 to 2021).

Vegetation types	area (%)	total fixes (%)
Savanna	27	18
Old Lands	17	15
Grassland	28	14
Karroid	15	14
Riverine Thicket	4	14
Valley Thicket	5	11
Xeric Thicket	8	10
Mesic Thicket	10	5

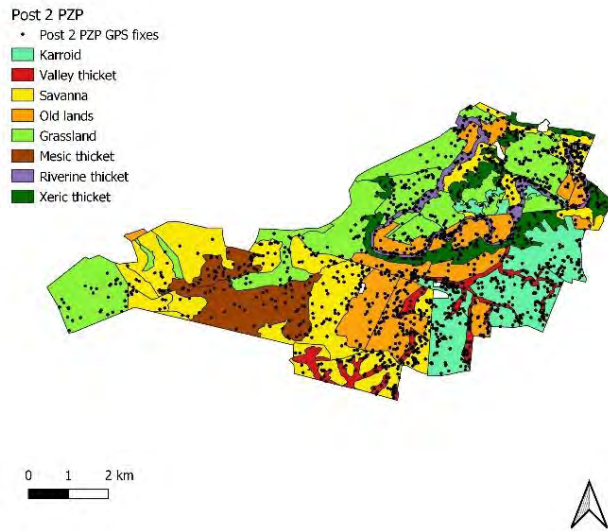


Figure 4.3.8. Post 2 PZP vegetation use with GPS fixes of Amakhala’s elephant breeding herd from 2017 to 2021.

Despite the visual changes in habitat use over time, there was no significant difference in the herd’s utilization of vegetation types between the three categories ($\chi^2 = 0.199$; $df = 14$; P value = 1).

4.4 DISCUSSION

Home range

The proportion of the mean home ranges for the elephant herd for all categories was not consistent on Amakhala. The home range was smallest during the Pre PZP covering 61.2% of the reserve. The largest proportion of the home range was in the During category, with the elephant herd utilizing 99.1% of the reserve. Post PZP was slightly less than the During category, covering 98.1% of the reserve size from 2014 to 2021. There was overlap in the

elephant's core range of the three categories although it covered approximately 3.6 km² of the reserve which was about 6% of the entirety of the area. Despite some overlap between the different category core ranges, there was a drastic change in space use from Pre PZP to During and Post, whereas During and Post core ranges were more similar.

The elephants core range during Pre PZP was small at 3.6 km². There were several factors that could have influenced this small core range. The core range is located in the river basin where the Bushman's river enters in the northeast and leaves Amakhala on the eastern side. The Bushman's river was full of water during the Pre category period from 2006 to 2008. Elephants are considered a riparian species where elephant key resources are available such as nutritious forage and water (Viljoen, 1989; Ottichilo, 1986; Sommerlatte, 1976). The river most likely enabled the elephants to have access to water for drinking, bathing, mud baths, and swimming along with high quality forage like sweet-thorn acacia (*Vachellia karroo*). Therefore, there would be no need to move far as the key resources were all within the river basin. Another factor that could have influenced the size of the elephant's core range was the rainfall during 2006 to 2008. Rainfall during these specified years was above the long-term average of 444 mm. The range of the annual rainfall was between 445 mm and 581 mm during 2006 to 2008. The above average rainfall most likely influenced the quality of vegetation on the reserve as well as kept natural water sources full like the Bushman's river. Lastly, the small core range could be correlated with calves' present in the herd therefore restricted the movements of the family group. Kerley and Shrader (2007) noted that established family groups with calves present remain relatively close to water due to the limitations of how long calves can survive without drinking. Amakhala's family group had five calves under the age of five years old present during 2006 to 2008.

During PZP, the elephant herd had the largest home range proportionate to the size of the reserve during the time period of 52.7 km² which encompassed 99.1% of the total reserve. When the cow, Alatisa, was on contraceptives, the herds' core range was 27.3 km² which was 51.4% of the whole area. Although the home range in the During category was largest, the core range was the second smallest within the three categories. The areas frequented in the During core range remained in the river basin but was also inclusive of the southern and western side of the reserve. Contraception could change space use and feeding patterns of non-reproducing females as they will have lower nutritional and energetic requirements as they are not producing young (Kerley & Shrader, 2007). During contraception, the home range of the elephant herd changed drastically by expanding from the prior use of contraceptives as the matriarch had already received PZP for two consecutive years. The change in space use and feeding patterns due to PZP could have influenced the change in home ranges between Pre and During.

From 2009 to 2013 the annual rainfall ranged from 445 mm to 796.5 mm which fell above the long-term average (444 mm) as well as above the excess limit (581 mm). The rainfall in the During category was significantly higher than in the Pre category. The excess rain could have affected the elephants to utilize more space in 2009 to 2013. The natural pans on Amakhala are spread throughout the reserve and are at a high density. The quality of vegetation would have been above average due to the influx of rain. Due to these factors, the elephants would have been able to access both quality and quantity of forage without limiting their range. There were eight calves under the age of five years during the years 2009 and 2013. Due to the high number of calves present and the large home range, this contradicts the assumption from Kerley and Shrader (2007) that contracepted cows are likely to move further from water due to no calves present. However, due to the excess of

rain and abundance of natural water sources around the whole reserve, the family groups would not have had to travel far for drinking water.

The home range of the elephant herd Post PZP was 59 km², equal to 98.1% of the total reserve area. The core range was 35.6 km² which represented 59.3% of the reserve. At the end of 2013, the reserve expanded with land by 5.8 km². This additional land consisted of deep valley thicket, savanna, and old lands on the southern side of the reserve. Towards the end of 2016, additional land was added in the form of karroid thicket. This change accounted for an increase of 1.1 km² on the south-eastern side of the reserve. The expansion of land in late 2013 and 2016 consisted of valley thicket in which the elephants' core range expanded as well. The newly added karroid and valley thicket vegetation could have affected the space use of the elephant herd in various ways. Although the karroid habitat contains little nutritious forage for elephants, it does provide succulents in which elephants prefer, thus a possible explanation to indicate why there was an increase of karroid vegetation seen in Post 1 PZP. Moreover, there was an influx of calves born to first time mothers from 2016 to 2021. The herd could have utilized the newly added valleys to protect the calves in the wooded habitats. Family groups are likely to seek wooded habitats as calves are sensitive to extreme heat (Mumby et al., 2013).

Another factor that could have influenced the large core range of elephants from 2014 to 2021 was the lion population that was introduced on the main reserve at the end of 2013. The lions' core range was in the river basin. This situation could have elicited an anti-predator response from the elephants towards the lions to spatially avoid this predator (Power & Compion, 2009). Elephant cows are more likely to avoid areas with predators

because they pose a predation risk on elephant calves (Stokke & du Toit, 2002), therefore the elephant herd expanded their space use outside of the lions' core range.

Furthermore, the amount of rainfall that fell between 2014 and 2021 varied considerably. From 2014 to 2016, the annual rainfall was mostly above the excess limit between 581 mm and 672.7 mm. At the end of 2016 to 2021 the rain decreased significantly compared to 2014 to 2016. The rainfall ranged from 309 mm to 526.2 mm. Throughout this period, the rain was below the long-term average and even on a couple of occasions was below the lower limit which is drought conditions. There was only one month in 2017 and 2020 where the rainfall was above the long-term average. Changes in rainfall result in the uneven distribution of resources (water and food) and could result in changes of home ranges (Hebbelmann, 2013). Therefore, lack of rain could have influenced the elephant's home range size during the Post category. The natural water sources like the Bushman's river started to dry up in 2018 and the riverbed was only left with small, fragmented pools of low-quality water. Artificial water sources increased in numbers in the western and southern sections of the reserve due to the lack of natural pans holding water. The use of artificial water sources for the elephant herd could have increased their space use. The onset of the drought would have decreased the quality of forage as well as lack of new growth, therefore the elephants would have to forage on more, low quality vegetation and in turn must cover larger areas to provide enough sustenance for their large daily intake.

Overall, there was a clear distinction between the space utilization of the elephant herd between the three categories. As predicted, the most probable causes of the major change in space use from Pre PZP to During PZP based on the data presented in my study was the

use of PZP as the only changes between the two time periods was the introduction of PZP and an increase in rainfall during the use of PZP.

Vegetation utilization

Overall, the most utilized vegetation type on Amakhala between the four categories (Pre, During, Post 1 and Post 2) were the grasslands. The grasslands cover the largest section of the vegetation types on the main reserve at 28%. All four categories utilized the savanna habitat, the most consistently utilized habitat throughout the study period. The most under-utilized vegetation type was the mesic thicket.

The subtropical thicket represents 25% of the Eastern Cape (Kerley et al., 1995). The subtropical thicket lies within Amakhala, further divided into various thicket vegetation types (xeric, mesic, valley and riverine) in which elephants historically frequented these areas (Kerley et al., 1995). Contradictory to elephants historically favouring thicket habitats in the Eastern Cape, as predicted, Amakhala's elephants utilized the mesic thicket and the valley thicket the least amongst the four categories. Instead, the elephant herd frequented the grasslands the most out of all vegetation types.

Throughout most of the study period, the rainfall was above the long-term average of 444 mm. In TNP, when there were good years of rainfall, the elephants fed year-round on perennial grasses rather than switching to browse when the predicted dry season would commence (Foley & Faust, 2010). Amakhala's elephant could have chosen grasslands over thickets like the TNP elephants due to the good rainfall years. The savanna habitat on Amakhala contains a diversity of woody species and grass species which elephants prefer as they are mixed feeders (Kerley & Landman, 2006), thus resulting in the most consistent

usage of this habitat throughout all categories. The savanna homogeneous area on Amakhala contains sweet-thorn acacia which is favoured by elephants (Paley & Kerley, 1998). The savanna vegetation also includes species such as common currant rhus (*Searsia pyroides*), wild olive trees (*Olea europaea*), cat-thorn (*Scutia myrtina*) as well as dominant grasses which are red grass (*Themeda triandra*), weeping love grass (*Eragrostis curvula*) and common finger grass (*Digitaria eriantha*) (Fowler, 2020).

During the Pre PZP period, the most frequented vegetation type by the elephant herd was the old lands at 22%. The most common grass species in old lands was couch grass (*Cynodon dactylon*) (Fowler, 2020). Paley and Kerley (1998) observed in AENP, couch grass was the dominant grass species in the diet of elephants. Steekvy (*Ruschia intricata*) commonly occurs on old lands on Amakhala (Fowler, 2020). Steekvy is a succulent which stores water in their leaves with fleshy skin. Elephants feed on succulents as it is soft and full of water (Roux, 2006). The abundance of couch grass and steekvy in the old lands could explain why the elephants utilized predominantly old lands for foraging. The second most utilized habitat was the riverine thicket. Family groups of elephants often choose areas with high plant species diversity (Illius & Gordon, 1987) due to their more selective feeding habits (Shannon et al., 2008). This is likely true for Amakhala's elephant herd prior to the use of contraceptives as the riverine thicket has a diverse range of plant species. The riverine thicket contains ample material on which to browse (Tello, 1973; de Boer et al., 2000; DCB, 2000). Species such as South African bush willow (*Combretum caffrum*), Cape silver willow (*Salix mucronata*) and sweet-thorn acacia, occur in the riverine thicket and are consumed by elephants (Vos, 2022). The third most frequented vegetation type by the elephant herd was the xeric thicket prior to the use of contraceptives which only occurs in the river basin. Elephants feed on succulents such as spekboom (*Portulacaria afra*) and aloes (*aloe* spp.) in

which these species are indicators for the xeric thicket. All the three most utilized vegetation types are in proximity of each other in the river basin. The herd most likely favoured this area to accompany their mixed feeding habits of grazing opportunities in the old lands and browsing opportunities in the riverine and xeric thicket along with the ample supply of water from the Bushman's river.

The least utilized homogeneous area on Amakhala Pre PZP was the mesic thicket at 3%. This thicket contains diverse woody species of forage for elephants. Despite this, the locality of this vegetation type could have influenced the minimal usage by the elephant herd. The mesic thicket is on the southwestern side of the reserve where, at the time there was only small natural pans available and mostly grasslands and savanna. Due to the above average rainfall from 2009 to 2013, the Bushman's river was full of water and the quality of vegetation was high in the river basin. These favourable conditions aligned with a study performed in PGR where it was suggested that the permanent widespread of drinking water and abundance of high nutritional forage of different vegetation types most likely accounted for the relatively small range (Shannon et al., 2006).

During the use of contraceptives, the elephant's vegetation utilization changed from the Pre PZP vegetation utilization. During PZP, the elephants used most of the vegetation types extending to the western side of the reserve whereas pre PZP the elephants were focused mostly on the south-eastern side of the reserve. Contraception could change space use and feeding patterns of non-reproducing females as they will have lower nutritional and energetic requirements as they are not producing young (Kerley & Shrader, 2007). The use of contraceptives could have affected the feeding patterns of Amakhala's elephant herd as the herd used more vegetation types spreading across the reserve rather than confining themselves to solely the river basin like prior to the use of PZP.

The most frequented habitats during the use of PZP were the grasslands and karroid at 17%. The majority of grasslands utilized were in the river basin although the elephant herd ventured to the far western side of the reserve where grasslands was also used. The karroid habitat most used was on the south-eastern side of the reserve. The forage selection in karroid habitats is of limited quality for elephants' nutritional requirements as it contains perennial dwarf shrubs (some succulent) and perennial geophytes and shrubs (du Toit et al., 2015). The karroid habitat on Amakhala contains dwarf shrubs like blue bush (*Pteronia incana*), bergankerkaroo (*Helichrysum dregeanum*), bitterbush (*Chrysocoma ciliate*) as well as couch grass. Despite the low-quality forage, the karroid habitat was one of the habitats most frequented. The high utilization of the karroid vegetation could be due to the valley thicket near the karroid habitat in which the valley thicket contains ample, high-quality forage for elephants while the elephants fed off the couch grass and succulents in the karroid habitat. Further, the rainfall was above the excess limit for the years in conjunction with the use of contraceptives. Loarie et al. (2009) found that elephants selected more variable landscapes in wet seasons. Similarly, Amakhala's elephants utilized multiple vegetation types, spread across the reserve during the use of PZP, which coincided with high rainfall. The valley and xeric thicket were the least utilized vegetation types during the use of contraceptives. The valley thicket represented 2% of the reserve between 2009 to 2013. Despite the valley thicket containing preferred vegetation of elephants, this vegetation type was small in relation to the rest of the vegetation types on Amakhala. Again, the elephant herd may have been less selective while on contraceptives due to a lower requirement of nutrition as they are not producing calves (Kerley & Shrader, 2007).

The elephant's vegetation use shifted in Post 1 PZP compared to During PZP. The grasslands remained the most utilized vegetation type in Post 1, like During PZP. However, the

grasslands Post 1 use of PZP were utilized mostly in the river basin whereas During PZP the grassland utilization extended the far western side of the reserve. The second most frequented vegetation type Post 1 PZP was the riverine thicket which was more similar to the use prior to PZP. Post 1 PZP also resembled the Pre PZP utilization of the xeric thicket. The similarities between Pre PZP and Post 1 PZP could be attributed to the elephant cow's ability to reproduce again, therefore the necessity to increase a more selected, nutritious diet to optimize production of calves. The valley thicket utilization increased in Post 1 PZP and was most likely due to the addition of land which provided ample browse resources for the elephants such as *Mystroxydon aethiopicum*, *Scutia myrtina* and *Cussonia spicata*. The utilization of new land by Amakhala's elephants' conflicts with findings from Druce et al. (2008) where the elephants in Phinda Private Game Reserve (PPGR), KwaZulu-Natal, appeared to act cautiously in exploring new additional land by adapting their ranging and foraging behaviour to avoid unexplored areas. Further, the high rainfall could have contributed to the distribution of habitat use. Overall, the rainfall was above the average and during some months above the excess limit during the Post 1 period.

During 2017 to 2021 (Post 2), the amount of rain that fell on Amakhala, decreased drastically compared to the Pre, During and Post 1 categories, the rainfall was thus below the lower limit, resulting in drought conditions. Artificial water sources increased on the southern and western side of the reserve, away from the river basin due to the drought conditions. The Bushman's river dwindled to only small, fragmented pools of poor-quality water. The vegetation types most frequented in Post 2 were the savanna and old lands. Both locations of the two most frequented vegetation types were near artificial water sources nearby lodges. The most frequented parts of the savanna habitat were on the eastern side of the reserve where the elephants had access to a lodge swimming pool

pumped with fresh water. Additionally, the central part of the reserve consisted of savanna and old lands where another lodge provided a permanent water source. The old lands alongside this central water source comprised of an abundance of sweet-thorn acacia which elephants' favour. During the dry season, elephants tend to concentrate their foraging in areas close to water (Chamaille-Jammes et al., 2007; de Beer et al., 2006). The elephant herd of Amakhala most likely utilized savanna and old lands the most in Post 2 PZP because of the proximity to permanent water sources. The third most utilized habitats Post 2 PZP were the grasslands, karroid and riverine thickets at 14%. The elephants used the grasslands in the river basin more so than the other grassland areas on the reserve. Despite less water sources in the river basin due to the drought, the riverine thicket remained. The riverine thicket was still utilized during the drought period, most likely due to continuing to provide green browse unlike in the grasslands (Ntumi et al., 2005). The grasslands in the river basin were in close vicinity of the riverine thicket which could suggest why both habitats were utilized frequently. The xeric and mesic thickets were the most under-utilized habitats in Post 2 PZP. The under-utilization of the two thickets was most like the use of contraceptives period where the xeric and mesic thickets were also the least used habitats. The elephant herd could have chosen the key resource water similar to ENP and KhNP in which water was a strong determinant of space use, suggesting water may take precedence over vegetation (de Beer & van Aarde, 2008; Grainger et al., 2005).

4.5 CONCLUSIONS

The core ranges of each category of the elephant herd changed especially from the prior use of contraceptives to the use of contraceptives as the Pre PZP core range was much smaller, encompassing mostly the river basin whereas During and Post PZP were larger. The rainfall

was similar during Pre, During and Post 1 PZP. Due to the three oldest cows, including Alatisha ceasing to reproduce after the use of PZP during the study period, it could suggest their space use and feeding patterns changed as they no longer required high nutrition forage (Kerley & Shrader, 2007).

There were variations in the elephant's vegetation use between the four categories which influenced the home range sizes of the herd. The rainfall was above average from 2006 to 2016 which provided natural water sources like the Bushman's river and good quality forage. The below average rainfall from 2017 to 2021 resulted in limited resources like natural pans and forage availability could have influenced the shift in vegetation use. The river basin which included periods of full water and ample forage availability most of the study period most likely influenced the high proportion of time spent in the area as all key resources were met (water, browse and graze). When the Bushman's river dried up, the elephants sought out fresh water sources on the south and central side of the reserve through artificial sources. The use of PZP drastically changed the vegetation utilization from Pre PZP (the baseline data) to During PZP then reverted in Post 1 PZP to similarities of Pre PZP. Post 2 PZP vegetation utilization was a combination of Pre, During and Post 1 use.

The non-random use of space and differential habitat selection is a longstanding basic tenet of ecology (Rosenzweig, 1981). Few mammals use the space within their home ranges randomly most likely resulting from the non-random distribution of resources (Harris et al., 1990). Due to elephants' foraging behaviour, smaller protected areas are at a higher risk of negative impacts on vegetation and the landscape, than larger protected areas (Lombard et al., 2001; Duffy et al., 2002). The risk of higher negative impacts on small, protected areas is due to the lack of space for elephants to disperse seasonally, as well as restricted available

space in which sensitive plant species can find refuge (Lombard et al., 2001; Duffy et al., 2002). Furthermore, it is difficult to compare home range sizes within different conservation areas in southern Africa due to the vast influences determining an elephant's home range (seasonality, resource availability, size of conservation area). Therefore, having baseline data on each specific conservation area and comparing over time and observing trends will help with site specific management decisions. Factors such as rainfall, seasonality, and resource availability change between years and this makes it difficult to compare home ranges over time because of the strong influence these factors might have over elephants' movements. Therefore, my study indicated the importance of acquiring baseline data to compare with during and post data to determine changes and trends over time.

CHAPTER FIVE

SUMMARY AND MANAGEMENT RECOMMENDATIONS

5.1 Introduction

Strong conservation efforts in southern Africa have increased elephant numbers in protected areas (Forrer, 2017). In South Africa, many of these protected areas are small (<1000 km²) and fenced. Fencing, increased protection, together with artificial water sources have all contributed to a rise in elephant population growth rates in these protected areas (Forrer, 2017). The increased growth rates of elephant populations and higher population densities on small, protected areas have prompted wildlife managers to explore several population-level management techniques to slow elephant growth rates (Forrer, 2017), and the most practical technique thus far is the use of the immuno-contraceptive, PZP.

The use of PZP on elephants has been studied in the short-term, indicating the negative effects of this immuno-contraceptive on the reversibility, physiological, spatial, and behaviour of elephants (Delsink & Kirkpatrick, 2012; Fayrer-Hosken et al., 2000; Ahlers et al., 2012; Delsink et al., 2006). Nonetheless, the limitations of these studies were the relatively short timeframes that was evaluated as well as the studies not using baseline data to compare before the use of PZP and after the use of PZP to note any changes and/or effects. Therefore, my study was focused on a small reserve in the Eastern Cape, South Africa to first identify the demography and reproductive parameters of the elephant population and comparing treated (with PZP) and non-treated cows (no PZP). Secondly, I wanted to use three different categories (Pre, During and Post PZP) to compare the home range size and

vegetation utilization in each of these categories of the elephant herd to identify if there were any changes of space use.

5.2 Demography and reproduction

In my study, I wanted to investigate various demographic and reproductive parameters of an elephant population in a small, fenced protected area by comparing the parameters within treated and non-treated cows, and other protected areas in Africa. The parameters consisted of population growth rates, inter-calving intervals, sex ratios, age of first calving, fertility and fecundity rates. There are many factors that affect these parameters such as density, social status, seasonality, rainfall, age and anthropogenic factors (artificial water sources, contraceptives). Overall, my results showed that Amakhala's elephant breeding herd had lower than average reproductive parameters as a result of the application of PZP

The average annual population growth of elephants on Amakhala decreased as more elephant cows were contracepted with PZP. The decrease in annual population growth rates were similar to other managed elephant populations in Africa. Although, when compared to a more natural elephant population (Amboseli National Park, Kenya) that has been relatively untouched from anthropogenic factors (Moss, 1988), the population growth of elephants at Amakhala was much higher. The high growth rates could have been influenced by the above average rainfall, an increase in artificial water sources thus resulting in better body conditions of breeding elephant cows.

I predicted that the mean inter-calving intervals of treated cows would be longer than in non-treated cows. However, in comparison, the mean inter-calving intervals on treated and non-treated cows were similar at 2.9 and 3.1 years, respectively. Amakhala's elephant mean

inter-calving interval was the second lowest within 12 populations across the African continent. In some individual cows, the inter-calving rate (2.16 and 2.25 years) was significantly lower than any documented research. The low inter-birth period for Amakhala's elephants could have been correlated with the increased rainfall resulting in higher forage availability thus improving the cow's body conditions. The sex ratios of the elephant cow's offspring were slightly in favour of males which was most likely attributed to the low density of elephants during the study period and above average rainfall. My results did not indicate PZP had an effect on the sex ratios of the offspring. The average age of first calving of the female elephants on Amakhala were relatively like other populations within southern Africa. The youngest cow to give birth on Amakhala was at the age of seven in which was the youngest compared to the existing literature. The good veld conditions due to high annual rainfall and low density most likely contributed to the young age of first calving. Additionally, PZP could have influenced the young age at first calving. Fertility rates decreased as the use of contraceptives took effect in the elephant herd in my study site. PZP could have influenced an older cow to not conceive again after being removed from the ICP as it could have made her sterile.

The findings of my study suggest that the above average rainfall, the availability of water sources and lack of density dependence had the most influence on the below average reproductive parameters of the elephant population on Amakhala. However, the use of PZP could have also affected the low parameters in Amakhala's elephant population. More long-term data are needed to establish the effects of PZP on demographic and reproductive parameters in elephant cows.

5.3 Spatial ecology

Home ranges and vegetation utilization on Amakhala varied considerably between the prior use of contraceptives, during and after the use of PZP of the elephant herd. Many factors could have influenced these changes in home ranges over time. Prior to the use of PZP, the core range was much smaller than in During and Post categories and was only in the river basin. It is most likely that the herd resided in the river basin the most as all the key resources such as water, graze and browse were present in this area due to above average rainfall during those specific years.

During PZP, the elephant herds' home range expanded, covering over 99% of the reserve. The expansion of the home range could have been influenced by PZP whereas contracepted females require lower nutrition and energetic requirements than pregnant and lactating cows, therefore can utilize larger areas (Kerley & Shrader, 2007). Other factors impacting the change in space use from Pre PZP to During PZP could have been the high rainfall resulting in good forage conditions throughout the reserve as well as the high number of natural pans spread across the reserve.

The Post PZP home range of the elephant herd was the largest out of the three categories. There were two occasions where land was added to Amakhala, therefore, could have influenced the herd to utilize the untouched vegetation. Lions were introduced during this period and could have caused an anti-predator response by the elephant herd to protect their calves by changing their space use (Power & Compion, 2009). Lastly, the rainfall had dropped below the long-term average in the latter half of Post PZP. The low rainfall resulted in less nutritious vegetation and reliance on artificial water as the natural river and pans had

mostly dried up, thus, requiring the herd to utilize larger areas of the reserve to maintain their essential survival requirements.

The most used vegetation type of Amakhala during my study period was the grasslands and the most consistently used habitat was the savannas. Prior to the use of contraceptives, the old lands were the most utilized vegetation type, following the riverine thicket and xeric thicket. The thickets use in the river basin contained high quality food and were in close proximity to the Bushman's river as key resources were provided. During the use of PZP, the vegetation utilization changed from Pre PZP as the herd utilized the western and southern side of the reserve. The herd frequented the karroid and grasslands. The karroid habitat was most likely utilized as it neighboured the valley thicket which had preferred forage of elephants.

Post 1 PZP vegetation use changed from During PZP as the grasslands were only used in the river basin compared to During where the herd used the far western section of the grasslands. Post 1 PZP resembled the Pre PZP category the most as the river basin, specifically the riverine thicket was utilized. Post 2 PZP was like During PZP where the southern side of the reserve was used. The southern section incorporated the savanna and old lands which are near artificial water sources. These water sources were predominantly used by the elephants as the rain fell below the long-term average resulting in drought conditions (natural water sources diminished, poor veld conditions).

Overall, my study indicates above average rainfall was the most significant factor in influencing the demography and reproductive parameters as well as the spatial distribution of Amakhala's elephant herd. The rainfall would have presented high forage opportunities throughout the reserve thus resulting in good body conditions of the breeding females. The

use of PZP was another factor that could have impacted certain reproductive parameters of elephant cows as well as the space use of the elephant herd.

5.4 Recommendations

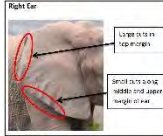





Overpopulation of elephants in a small, enclosed system without natural occurrences can lead to the detriment of the ecosystem within these areas (Conybeare, 2004; Druce et al., 2011). Therefore, the long-term management of elephants using the immuno-contraceptive, PZP to control population numbers in small reserves is most likely the most effective, practical way of controlling elephant population growth rates in small game reserves. It is practical in terms of delivery in small population, relatively cost effective and has proven to be effective at altering populations in multiple studies, including my study (Fayrer-Hosken et al., 2000).

My study illustrates the complexities of elephant population dynamics over time and across differing ecological conditions as elephants are highly intelligent with complex social structures. The need for elephants to reproduce is essential as the presence of calves helps to stabilize relationships in family groups as well as provides young females vital knowledge and practice of allo-mothering through caring for other elephant calves prior to them reproducing (Kerley & Shrader, 2007). Therefore, it is essential for calves to be present in breeding herds, thus using PZP in an effective way each cow is staggered at different intervals in order for some reproduction rather than have all breeding cows contracepted.

Amakhala's elephant population displayed changes in their reproductive parameters as well as their space use in the presence of PZP. My study's limitation was the amount of time represented during the study period post the use of PZP. Therefore, the continued monitoring of Amakhala's elephant population through reproductive records and spatial

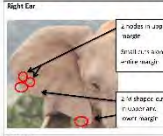




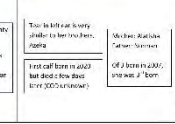
distribution is critical to determine if there are long-term effects of the use of PZP. Furthermore, my study did not represent any behavioural observations nor vegetation changes. Behavioural observations and monitoring of the vegetation would be beneficial to target changes in the social structure of the herd and to assess vegetation declines over time. It is advised for Amakhala's elephant population to stay below the recommended carrying capacity to avoid density dependence and to continue to be adaptive in the ICP of the breeding cows based off the invaluable data collection and the results of my study.

Name: ALATISHA F3 Sex: Female DOB: 1981 Age in 2021: 40 yo

Right Ear 	Left Ear 
Right Side 	Left Side 
Front 	Rear 







Offspring:
 1st born in 2001
 2nd born in 2002
 3rd born in 2003
 4th born in 2004
 5th born in 2005
 6th born in 2006
 7th born in 2007
 8th born in 2008
 9th born in 2009

Name: AMANZI Sex: Female DOB: 26 07 2007 Age in 2021: 14 yo

Right Ear 	Left Ear 
Right Side 	Left Side 
Front 	Rear 

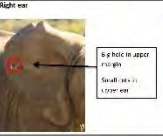
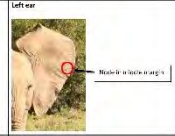




This is the first of every animal to be born here, right?
 1st call born in 2007 but died a few days later (2008 or 2009)
 2nd born in 2008, she was 2nd born
 3rd born in 2009, she was 3rd born

Name: ANANSI Sex: Male DOB: 16 10 2009 Age in 2021: 12 yo

Right Ear 	Left Ear 
Right Side 	Left Side 
Front 	Rear 

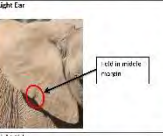





Thick straight tusk
 Call in hole a little bigger than right
 Mother: Abulaba
 Father: Nkwana
 Off born in 2009, he was the 2nd born

Name: Anathi Sex: Female DOB: 06 08 2016 Age in 2021: 5 yo

Right ear 	Left ear 
Right side 	Left side 
Front 	Rear 







no tusk
 Mother: Abulaba

Name: AYABONGA Sex: Female DOB: 29 11 2014 Age in 2021: 7 yo

Right Ear 	Left Ear 
Right side 	Left side 
Front 	Rear 


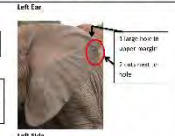



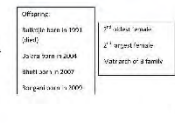
no tusk
 Mother: Abulaba

Name: BALARA Sex: Male DOB: 01 08 2004 Age in 2021: 17 yo

Right Ear 	Left Ear 
Right side 	Left side 
Front 	Rear 







Call tusk is very short and is the right tusk a little shorter than the left
 Mother: Abulaba
 Father: Nkwana
 Born in 4 months younger than Abulaba

Name: BALULEKA Sex: Female DOB: 01 01 1978 Age in 2021: 43 yo

Right Ear 	Left Ear 
Right side 	Left side 
Front 	Rear 

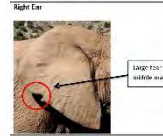





no tusk
 Offspring:
 1st born in 1999 (male)
 2nd born in 2004
 3rd born in 2007
 4th born in 2009

Name: BHUTI Sex: Male DOB: 18 03 2007 Age in 2021: 14 yo

Right Ear 	Left Ear 
Right Side 	Left Side 
Front 	Rear 







no tusk
 Mother: Abulaba
 Father: Nkwana
 Off born in 2007, she was 1st born

Name: BONGANI Sex: Female DOB: 06 07 2009 Age in 2021: 12 yo

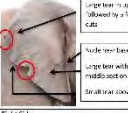





Right Ear 	Left Ear 
Right Side 	Left Side 
Front 	Rear 

no tusk
 Mother: Abulaba
 Father: Nkwana
 Off born in 2009, she was the 1st born
 Had 1st call in 2011 (age 2 years)







Name: BULANI Sex: Male DOB: 21.01.2019 Age in 2021: 2 yo

Right ear  Small fold in upper margin Fold in middle margin	Left ear  Small cub along outer margin below
Right side 	Left side 
Front  Crown: flat, right side Right side: shoulder slightly lower than left	Front  Mother: Isogen (born in 2016)







Name: CAULY Sex: Male DOB: 01.01.1989 Age in 2021: 32 yo

Right Ear  Larger fold in upper margin followed by a few small cubs Small fold in middle margin	Left Ear  Large fold in upper margin with a small cub below Small fold in middle margin A few small cubs along outer margin
Right Side 	Left Side 
Front  LARGE: 3 ribs, rounded back Big of neck, ears slightly below with a bit to be in straight	Front  Tusks: well rounded




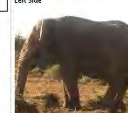


Name: CEBISA Sex: Female DOB: 11.12.2009 Age in 2021: 11 yo

Right Ear  Small triangular cub through out ear	Left Ear  3 hooks upper margin of ear Small triangular cub in middle margin
Right Side 	Left Side 
Front  Short in ear Left side longer and more downwards than right tank	Front  Mother: Paji a Father: Nyanani Offspring born in 2020, CEBISA had 4 born Offspring: Eruwani (in 2019)





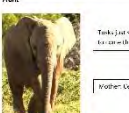

Name: CHEBE Sex: Female DOB: 20.04.2007 Age in 2021: 14 yo

Right Ear  Four distinct ear cubs along upper margin of ear	Left Ear  Cub specific at upper margin 3 small triangular cub in middle margin M-shaped in bottom margin
Right Side  Small cub: very close belly	Left Side 
Front  Short, wide, outboard trunk base Mother: Isogen (born in 2003, CEBISA 2 nd born)	Front  Offspring: Cerele (2018)







Name: CHULUMACHA Sex: Male DOB: 03.01.1997 Age in 2021: 24 yo

Right Ear  2 cubs side by side along middle margin	Left Ear  Small triangular cub in upper margin of ear Small triangle in middle margin
Right Side  Large nodes on top right shoulder	Left Side 
Front  Rocks in 1 tank in 2017 Small right side in 2018 fighting with Isogen. Parents on the right side	Front  Tusks gap between tips on left side of trunk, similar to his mother, CEBISA (1 tank)







Name: CHUMANI Sex: Male DOB: 15.06.2019 Age in 2021: 2 yo

Right Ear  Small cub along middle ear	Left Ear  Small cub along middle ear
Right Side 	Left Side 
Front  Tusks just starting to come through	Front  Mother: Isogen






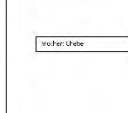
Name: CHWAYITA Sex: Female DOB: 01.02.2002 Age in 2021: 19 yo

Right Ear  2 cubs in middle margin 3 small cubs in lower margin 3 small cubs in lower margin with 2 small holes below Many small cub along middle of outer margin	Left Ear  Many small cub along middle of outer margin
Right Side 	Left Side 
Front  Very straight, looks flat with a slight bump on left side	Front  Mother: Isogen (born in 2002)

Name: CULA Sex: Male DOB: 23.10.2011 Age in 2021: 10 yo

Right Ear  Small triangular cub in middle margin Small fold above cub	Left Ear  Ear in upper margin A few small triangular cub in middle margin
Right Side 	Left Side 
Front  Thin, upright trunk. Left tank is slightly longer than right tank	Front  Mother: Chwayita (born in 2002)

Name: Cuma Sex: Male DOB: 24.03.2018 Age in 2021: 2 yo

Right ear  Small cub along middle ear	Left ear  Small cub along middle ear
Right side 	Left side 
Front  Outward facing ears	Front  Mother: Uebe

APPENDIX 2. Immuno-contraceptive trials and errors and efficacy of PZP on Amakhala's breeding females

Appendix 2.1. Trails and errors of PZP history on Amakhala.

Ambalo's calf drowned in 2012 therefore was taken off the program to allow her to calve again. She then calved at the end of 2014. She was placed back onto the program for five consecutive years. It was predicted that she would conceive in 2025 and give birth in 2027. She gave birth to her fourth calf in January 2020. It was suspected that in 2017, her annual PZP booster did not work. The vaccine batch given to this cow could have expired as the vaccine has to stay frozen prior to usage thus working in remote locations could have compromised the vaccine (Berchert & Fraker, 2015). There are limitations on the physical aspect of using dart guns and darts when administering PZP, such as the weight of the drop-out dart, a good shot placement, the reliability and accuracy of the brand of the dart and the chance of dart malfunction (van der Walt et al., 2022). Factors resulting in dart malfunction include incorrect loading of the dart, manufacturing error or a needle blocked by a skin plug (van der Walt et al., 2022).

Appendix 2.2. Overall efficacy of PZP in Amakhala's breeding cows.

In Amakhala's elephant cows, 78% of the total breeding cows had 100% PZP efficacy. The remaining 22% of the cows was represented by two individuals. Ambalo received the vaccine five months post birth in 2009 in which she had conceived almost four months post birth. It is highly likely she received PZP after she had already conceived. In 2020, the PZP efficacy for Ambalo was 0%. This could have been due to the batch of the vaccine that was no longer viable (not stored frozen properly) (Berchert & Fraker, 2015). If that was the case, then it would be expected that other cows who received the same batch would conceive but these cows did not conceive. Those cows still have not conceived by the end of the

study period. The dart containing the vaccine could have misfired, resulting in the full dose not being released and/or the dart was plugged (van der Walt et al., 2022). It is suspected in 2017, the vaccine did not work as her 2018 vaccine was administered one month post conception then given the 22-month gestation period, and she gave birth in January 2020. The second cow to have had an unexpected birth during the study period was Ayanda. This cow conceived 5.5 months after her first birth but only receiving the vaccine six months post birth. The most likely cause of this cow giving birth was human error and missing the critical time period on when to administer PZP. This was a learning curve for Amakhala as most literature averages interval-calving intervals around 4.5 years. In Ayanda’s case, her inter-calving interval was 2.25 years.

APPENDIX 3. Elephant population demographic and reproductive parameters from national parks and game reserves across the African continent.

National Parks and Game Reserves	Youngest Conception Age	Average primiparous age (years)	Mean calving interval (years)	Annual mortality	Density ele/km²	Yearly rain (mm)	Citation
Addo N.P. South Africa	9	12.5	3.3	1.40%	24.9	392	Gough & Kerley, 2006
Amakhala G.R. South Africa	4.3	10	2.99	1.70%	0.3	444	This study
Amboseli N.P. Kenya	7.1	13.7	4.5	4.15%	<2.6	350	Lee & Moss 2011; Moss, 2001

Etosha N.P. Namibia		11.1	3.8	5%	<2.6	250	Lindeque , 1988
Kruger N.P. South Africa	8	13	3.8	3.20%	<2.6	450- 700	Whyte et al., 1998; Freeman et al., 2009
Lake Manyara N.P. Tanzania	8	13	4.6	3.50%	16.1	650	Douglas- Hamilton , 1972
Luangwa N.P. Zambia	12	16	3.4		7.8-15.5	800	Hanks, 1972
Mkomazi N.P. Tanzania		12.2	4.2	5%	6.5	400	Laws et al., 1975
Murchison Falls N.P. Uganda	7	11	8.6		4.4	1085	Buss & Smith, 1966
Murchison North Uganda		16.3	9.1	5.16-6.6%	7.8-10.4	1085	Laws et al., 1975
Murchison South Uganda		17.8	5.6		15.5- 18.1	1085	Laws et al., 1975
Samburu N.R. Kenya	6.7	11.5	4	4.70%	<2.6	350	Wittemy er et al., 2013
Tarangire N.P. Tanzania	6.9	11.2	3.3	1.90%	<2.6	656	Foley & Faust, 2010
Tsavo N.P. Kenya		14.5	6.8	3.8-5%	7.8	200- 700	Laws et al., 1975
Captive	12	16.3					Dale, 2010

REFERENCES

- Adams, J., Garcia, A., & Foote, C.S. (1978). Some chemical constituents of the secretion from the temporal gland of the African elephant (*Loxodonta africana*). *Journal of Chemical Ecology* 4, 17–25. <https://doi.org/10.1007/BF00988256>.
- Ahlers, M., Ganswindt, B., Münschera, S., & Bertschinger, H.J. (2012). Faecal 20-oxo-pregnane concentrations in free ranging African elephants (*Loxodonta africana*) treated with porcine zona pellucida vaccine. *Theriogenology*, 78, 77–85.
- Allen, W.R., Mathias, S., Wooding, F.B.P., & van Aarde, R.J. (2003). Placentation in the African elephant (*Loxodonta africana*). II. Morphological changes in the uterus and placenta throughout gestation. *Placenta*, 24, 598–617. doi:10.1016/S0143-4004(03)00102-4.
- Amakhala Game Reserve's records, unpublished.
- Bakker, E.S., Gill, J.L., Johnson, N. & Svenning, J.C. (2015). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Biological Sciences*, 113 (4), 847-855. <https://doi.org/10.1073/pnas.1502545112>.
- Barnes, R.F.W. (1982). Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology*, 20, 123–136.
- Bechert, U., & Fraker, M.A. (2015). Immune response of African elephants to a single dose of SpayVac, a pZP contraceptive vaccine, over a seven year period. *Pachyderm*, 57.
- Bellino, F.L., & Wise, P.M. (2003). Nonhuman primate models of menopause workshop, *Biology of Reproduction*, 68 (1), 10-18. <https://doi.org/10.1095/biolreprod.102.005215>.
- Benavides Valades, G., Ganswindt, A., Annandale, H., Schulman, M.L., & Bertschinger, H.J. (2012). Non-invasive assessment of the reproductive cycle in free-ranging female African

elephants (*Loxodonta africana*) treated with a gonadotropin-releasing hormone (GnRH) vaccine for inducing anoestrus. *Reproductive Biology and Endocrinology*, 10, 63.
<https://doi.org/10.1186/1477-7827-10-63>.

Bertschinger, H.J., & Caldwell, P. (2016). Fertility suppression of some wildlife species in southern Africa – A review'. *Reproduction in Domestic Animals*, 51 (Suppl 1), 18–24.
<https://doi.org/10.1111/rda.12783>.

Bertschinger, H.J., & Lueders, I. (2018). Use of anti-gonadotropin-releasing hormone vaccines in African elephants (*Loxodonta africana*): A review. *Bothalia*, 48. 10.4102/abc.v48i2.2320.

Bertschinger, H.J., Delsink, A., Kirkpatrick, J., van Altena, J., Ahlers, M., Dickerson, T. Powrie, D., & Burger, A. (2012). Porcine Zona Pellucida immunocontraception of African elephants (*Loxodonta africana*): Beyond the experimental stage', in J. Cain, III & J. Marshal (eds.), *IVth International Wildlife Management Congress – Cooperative Wildlife Management Across Borders: Learning in the Face of Change*, The Wildlife Society, Durban, 95–102.

Bertschinger, H.J., Delsink, A., Schulman, M., & Kirkpatrick, J. (2017). Development and current status of African elephant (*Loxodonta africana*) immunocontraception using the porcine zona pellucida (PZP) vaccine in South Africa. *The 8th International Conference on Wildlife Fertility Control, Kellogg Conference Hotel, Gallaudet University, Washington, DC*, 14.

Bertschinger, H.J., Delsink, A., van Altena, J.J., & Kirkpatrick, J. (2018). Porcine zona pellucida vaccine immunocontraception of African elephant (*Loxodonta africana*) cows: A review of 22 years of research. *Bothalia*, 48. 10.4102/abc.v48i2.2324.

Bertschinger, H.J., Delsink, A., van Altena, J.J., Kirkpatrick, J., Killian, H., Ganswindt, A., Slotow, R., & Castley, G. (2008). Reproductive control of elephants. In: Scholes RJ, Mennell KG, eds.

Elephant Management: A Scientific Assessment for South African, Johannesburg:

Witwatersrand University Press. 257–328.

Birkett, A., & Stevens-Wood, B. (2005). Effect on low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *African Journal of Ecology*, 43 (2), 123-130.

<https://doi.org/10.1111/j.1365-2028.2005.00555.x>.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I., & Hart, J.A.

(2007). African elephant status report 2007: An update from the African elephant.

Blanc, J.J., Thouless, C.R., Hart, J.A., Dublin, H.T., Douglas-Hamilton, I., Craig, G.C., & Barnes, R.F.W.

(2003). African elephant status report 2002: An update from the African elephant database.

Occasional paper of the IUCN Species Survival Commission No. 29. Gland and Cambridge:

IUCN. ISBN 9782831707075.

Boshoff, A.F., & Kerley, L.J. (2001). Potential distributions of the medium- to large-sized mammals in

the Cape Floristic Region, based on historical accounts and habitat requirements. *African*

Zoology, 36 (2). <https://doi.org/10.1080/15627020.2001.11657142>.

Boshoff, A.F., Kerley, G.I.H., Cowling, R.M., & Wilson, S.L. (2002). The potential distributions, and

estimated spatial requirements and population sizes, of the medium to large sized mammals

in the planning domain of the Greater Addo Elephant National Park project. *Koedoe*, 45, 85–

116.

Boyce, M.S., Pitt, J., Northrup, J.M., Morehouse, A.T., Knopff, K.H., Cristescu, B., & Stenhouse, G.B.

(2010). Temporal autocorrelation functions for movement rates from global positioning

system radiotelemetry data. *Philosophical transactions of the Royal Society of London. Series*

B, Biological sciences, 365 (1550), 2213–2219. <https://doi.org/10.1098/rstb.2010.0080>.

- British and Irish Association of Zoos and Aquariums. (2022). Research reveals the four sounds of Asian elephants. *British and Irish Association of Zoos and Aquariums*, <https://biaza.org.uk/news/detail/research-reveals-the-four-sounds-of-asian-elephants>. Accessed 22 October 2022.
- Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals, *Journal of Mammalogy*, 24 (3), 346–352. <https://doi.org/10.2307/1374834>.
- Buss, I.O., & Smith, N.S. (1966). Observations on reproduction and breeding behavior of the African elephant. *The Journal of Wildlife Management*, 30 (2), 375-388.
- Calef, G.W. (1988). Maximum rate of increase in the African elephant. *African Journal of Ecology*, 26, 323–327.
- Caloi, L., & Palombo, M. (1992). Dwarf elephants of the past, *In: J. Shoshani, ed., Elephants; Majestic Creatures of the Wild*. Emmaus, PN: Rodale Press.
- Castiglione, F., Mantile, F., de Berardinis, P., & Prisco, A. (2012). How the interval between prime and boost injection affects the immune response in a computational model of the immune system. *Computational and Mathematical Methods in Medicine*, 2012, Article ID 842329, 1–9.
- Chamaille´-Jammes, S., Valeix, M., & Fritz, H. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, 44, 625–633.
- Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J., Djene, S.W., Elkan, P.W., & Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354.

- Clark, M.M., Bone, S., & Galef Jr, B.G. (1990). Evidence of sex biased postnatal maternal investment by Mongolian gerbils. *Animal Behaviour*, 39, 735–744.
- Clegg, B.W., & O'Connor, T.G. (2017). Determinants of seasonal changes in availability of food patches for elephants (*Loxodonta africana*) in a semi-arid African savanna. *PeerJ*, 5, e3453.
- Clutton-Brock, T.H., Albon, S.D., & Guinness, F.E. (1981). Parental investment in male and female offspring in polygynous mammals. *Nature*, 289, 487–489.
- Clutton-Brock, T.H., Guinness, F.E., & Albon, S.D. (1982). Red deer: behavior and ecology of two sexes. *University of Chicago press*.
- Conybeare, A.M. (2004). Elephant impacts on vegetation and other biodiversity in broadleaved woodlands of south-central Africa. *Biodiversity of the Four Corners Area: Technical reviews volume two* (chapters 5–15), Occasional Publications in Biodiversity No. 15, eds J.R. Timberlake and S.L. Childes, 1–35. Biodiversity Foundation for Africa, Bulawayo, and Zambezi Society, Harare.
- Croze, H. (1974). The Seronera bull problem: The elephants. *East African Wildlife Journal*, 12, 1–27.
- Dale, R.H. (2010). Birth statistics for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in human care: history and implications for elephant welfare. *Zoo Biology*, 29 (2), 87-103.
- Database. *Occasional Paper Series of the IUCN Species Survival Commission*, No. 33. IUCN/Species Survival Commission African Elephant Specialist Group, Gland, Switzerland.
- De Beer, Y., & van Aarde, R.J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments*, 72 (11), 2017-2025, ISSN 0140-1963.

- De Beer, Y., Killian, W., Versfeld, W., & van Aarde, R.J., (2006). Elephants and low rainfall alter woody vegetation in Etosha National park, Namibia. *Journal of Arid Environments*, 64, 412–421.
- De Boer, W.F., Ntumi, C.P., Correia, A.U., & Mafuca, J.M. (2000). Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*, 38, 188–201.
- Debruyne, R. (2005). A case study of apparent conflict between molecular phylogenies: the interrelationships of African elephants. *Cladistics*, 21 (1), 31-50.
- Delany, M.J. (1982). The mammals. *Mammal Ecology*, 1, 1-5.
- Delsink, A., Kirkpatrick, J., van Altena, J.J., Bertschinger, H.J., Ferreira, S., & Slotow, R. (2013). Lack of spatial and behavioural responses to immunocontraception application in African elephants (*Loxodonta Africana*). *Journal of Zoo and Wildlife Medicine: official publication of the American Association of Zoo Veterinarians*. 44. S52-74. 10.1638/1042-7260-44.4S.S52.
- Delsink, A., Kirkpatrick, J.F. (Compilers) (2012). *Free-ranging African elephant immunocontraception: A new paradigm for elephant management research*. Trident Press, Cape Town, 6-16.
- Delsink, A., van Altena, J.J., Grobler, D., Bertschinger, H.J., Kirkpatrick, J.F., & Slotow, R. (2006). Regulation of a small, discrete African elephant population through immunocontraception in the Makalali Conservancy, Limpopo, South Africa. *South African Journal of Science*, 403–405.
- Delsink, A., van Altena, J.J., Grobler, D., Bertschinger, H.J., Kirkpatrick, J.F., & Slotow, R. (2007). Implementing immunocontraception in free-ranging African elephants at Makalali Conservancy. *Journal of South African Veterinary Association*, 78, 25–30.

- Department of Biological Sciences, (2000). Vegetation map of Maputo Elephant Reserve. Eduardo Mondlane University, Mozambique.
- Douglas-Hamilton, I. (1972). On the ecology and behaviour of the African elephant: the elephants of Lake Manyara. PhD. Thesis, University of Oxford, England.
- Douglas-Hamilton, I., Krink, T., & Vollrath, F. (2005). Movement and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, 92, 158-163.
- Druce, H.C., Mackey, R.L., Slotow, R. (2011). How immunocontraception can contribute to elephant management in small, enclosed reserves: Munyawana population as a case study. *PLoS ONE* 6(12): e27952. doi: 10.1371/journal.pone.0027952.
- Druce, H.C., Pretorius, K., & Slotow, R. (2008). The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, 141 (12), 3127-3138.
- Du Toit, J., O'Connor, T., & van den Berg, L. (2015). Photographic evidence of fire-induced shifts from dwarf-shrub- to grass-dominated vegetation in Nama-Karoo. *South African Journal of Botany*, 101. 10.1016/j.sajb.2015.06.002.
- Duffy, K.J., van Os, R., Vos, S., van Aarde, J. Elish, G., & Stretch, A-M.B. (2002). Estimating impact of reintroduced elephant on trees in a small reserve. *South African Journal of Wildlife Research*, 32 (1), 23-29.
- Dunbar, B.S., Wardrip, N.J., & Hedrick, J.L. (1980). Isolation, physicochemical properties, and macromolecular composition of zona pellucida from porcine oocytes. *Biochemistry*, 19 (2), 356-365. doi: 10.1021/bi00543a017.

- Eberhardt, L.L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology*, 83 (10), 2841-2854. [https://doi.org/10.1890/0012-9658\(2002\)083\[2841:APFPAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2).
- Eggert, L.S., Rasner, C.A., & Woodruff D.S. (2002). The evolution and phylogeography of the African elephant inferred from mitochondrial DNA sequence and nuclear microsatellite markers. *Proceedings of the Royal Society London*, 269, 1993–2006. <http://doi.org/10.1098/rspb.2002.2070>.
- Eltringham, S.K. (1982). *Elephants*. Dorset: Blanford Press.
- Emery Thompson, M., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y., & Wrangham, R.W. (2007). Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology: CB*, 17 (24), 2150–2156. <https://doi.org/10.1016/j.cub.2007.11.033>.
- Estes, R.D. (1992). The behaviour guide to African mammals, including hoofed mammals, carnivores and primates. University of California Press, Ltd, London. 606.
- Fayrer-Hosken, R.A., Bertschinger, H.J., Kirkpatrick, J.F., Grobler, D., Lambreski, N., Honneyman, G. & Ulrich, T. (1999). Contraceptive potential of the porcine zona pellucida vaccine in the African elephant (*Loxodonta africana*). *Theriogenology*, 52, 835– 846. [https://doi.org/10.1016/S0093-691X\(99\)00176-4](https://doi.org/10.1016/S0093-691X(99)00176-4).
- Fayrer-Hosken, R.A., Grobler, D., van Altena, J.J., Kirkpatrick, J.F., & Bertschinger, H.J. (2000). Immunocontraception of free-roaming African elephants. *Nature*, 407, 149.

- Fike, B.R. (2011). The demography and population dynamics of a re-introduced black rhinoceros' population on the Great Fish River reserve, Eastern Cape province. MSc thesis, Rhodes University, South Africa.
- Foley, C.A.H. (2002). The effects of poaching on elephant social systems. PhD thesis, Princeton University, Princeton, USA.
- Foley, C.A.H., & Faust, L.J. (2010). Rapid population growth in an elephant (*Loxodonta Africana*) population recovering from poaching in Tarangire National Park, Tanzania. *Oryx*, 44, 205–212.
- Forrer, F.A. (2017). The population status, habitat use and seasonal diet of African elephant (*Loxodonta Africana*) in Majete Wildlife Reserve, Malawi. MSc Thesis, Department Conservation Ecology and Entomology, Stellenbosch University.
- Fowler, M.E. (1993). Zoo & Wild Animal Medicine. *Current Therapy* (3rd ed.). Philadelphia: W.B. Saunders.
- Fowler, N.F. (2017). Elephant identification kit of Amakhala Game Reserves elephant population. Unpublished.
- Fowler, N.F. (2020). 2020 Veld condition assessment of Amakhala Game Reserve. Unpublished.
- Freeman, E.W., Meyer, J.M., Putman, S.B., Schulte, B.A., & Brown, J.L. (2013). Ovarian cycle activity varies with respect to age and social status in free-ranging elephants in Addo Elephant National Park, South Africa. *Conservation Physiology*, 1 (1). doi: 10.1093/conphys/cot025. PMID: 27293609; PMCID: PMC4806622.

- Freeman, E.W., Whyte, I., & Brown, J.L. (2009). Reproductive evaluation of elephants culled in Kruger National Park, South Africa between 1975 and 1995. *African Journal of Ecology*, 47 (2), 192-201.
- Fritz, H. (2017). Long-term field studies of elephants: understanding the ecology and conservation of a long-lived ecosystem engineer. *Journal of Mammalogy*, 98, 603-611.
<https://doi.org/10.1093/jmammal/gyx023>.
- Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31, 367–393.
- Ganswindt, A., Rasmussen, H.B., Heistermann, M., & Hodges, J.K. (2005). The sexually active states of free-ranging male African elephants (*Loxodonta africana*): defining musth and non-musth using endocrinology, physical signals and behaviour. *Hormones and Behaviour*, 47, 83–91.
- Gara, T.W., Wang, T., Skidmore, A.K., Zengeya, F.M., Ngene, S.M., Murwira, A., & Ndaimani, H. (2016). Understanding the effect of landscape fragmentation and vegetation productivity on elephant habitat utilization in Amboseli ecosystem, Kenya. *African Journal of Ecology*, 55 (3), 259-269. <https://doi.org/10.1111/aje.12346>.
- Garai, M.E., Slotow, R., Reilly, B., & Carr, R.D. (2004). History and success of elephant re-introductions to small, fenced reserves in South Africa. *Pachyderm*, 37, 28–36.
- Gaylard, A., Owen-Smith, N., & Redfern, J. (2003). Surface water availability: implications for heterogeneity and ecosystem processes. In: du Toit, J.T., Biggs, H., Rodgers, K. (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington, DC, USA, 171–188.

- Gillson, L., & Lindsay, K. (2003). Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environmental Science*, 6, 411-419.
- Gobush, K.S., Edwards, C.T.T., Balfour, D., Wittemeyer, G., Maisels, F., & Taylor, R.D. (2021). [amended version of 2021 assessment]. *Loxodonta Africana*. *IUCN Red List of Threatened Species*, 2021: e.T181008073A204401095. doi: 10.2305/IUCN.UK.2021-2.RLTS.T18100808073A204401095.en.
- Goldenberg, S.Z., Douglas-Hamilton, I., & Wittemyer, G. (2018). Inter-generational change in African elephant range use is associated with poaching risk, primary productivity and adult mortality. *Proceedings of the Royal Society*. 285.
- Goodloe, R. B., Vakren, R.J., Othran, E.G., Bratton, S.P., & Trembicki, K.A. (1991). Genetic variation and its management applications in eastern U.S. feral horses. *Journal of Wildlife Management*, 55, 412-421.
- Goodman, P. (2013). Ezemvelo KZN Wildlife Monitoring Plan: Black rhinoceros (*Diceros bicornis minor*). Ezemvelo KZN Wildlife report.
- Gough, K., & Kerley, G. (2006). Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: Is there evidence of density dependent regulation? *Oryx*, 40. 441. 10.1017/S0030605306001189.
- Grainger, M., van Aarde, R., & Whyte, I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology*, 43, 369-375. 10.1111/j.1365-2028.2005.00592.x.
- Groves, C.P., & Grubb, P. (2000). Do *Loxodonta cyclotis* and *L. africana* interbreed? *Elephant*, 2 (4), 4.

- Hall-Martin, A.J. (1984). Symposium on the Kalahari ecosystem summary and conclusions. *Koedoe*, 327-333.
- Hanks, J. (1969). Seasonal breeding of the African elephant in Zambia. *African Journal of Ecology*, 7, 167.
- Hanks, J. (1972). Growth of the African elephant (*Loxodonta africana*). *East African Wildlife Journal*, 10 (4), 251-272. doi: 10.1111/j.1365-2028.1972.tb00870.x .
- Hanks, J., & McIntosh, J.E.A. (1973). Population dynamics of the African elephant (*Loxodonta africana*). *Journal of Zoology*, 1469-7998.
- Harris, S., Cresswell, W., Forde, P.G., Trewhella, W.J., Woolard, T., & Wray, S. (1990). Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20, 97–123.
- Haynes, G. (1991). Mammoths, mastodons and elephants: biology, behavior and the fossil record. Cambridge University Press, Cambridge. 413. ISBN:0-521-38435-4.
- Hebbelmann, L. (2013). Changes in adult female white rhino seasonal home ranges in relation to variation in food quality and availability. MSc Thesis, University of KwaZulu Natal, Durban.
- Hermes, R., Hildebrandt, T.B., & Göritz, F. (2004). Reproductive problems directly attributable to long-term captivity asymmetric reproductive aging. *Animal Reproduction Science*, 82–83:49–60.
- Hitchins, P.M., & Anderson, J.L. (1983). Reproduction, population characteristics and management of the black rhinoceros (*Diceros bicomis minor*) in the Hluhluwe/Corridor/Umfolozu Game Reserve Complex. *South African Journal of Wildlife Research*, 13 (3), 78–85.

- Hoare, D.B., Mucina, L., Rutherford, M.C., Vlok, J.H., Euston-Brown, D.I., Palmer, A.R., & Ward, R.A. (2006). Albany thicket biome. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia*, 19, 541-567.
- Hollister-Smith, J.A., Poole, J.H., Archie, E.A., Vance, E.A., Georgiadis, N.J., Moss, C.J., & Alberts, S.C. (2007). Age, musth, paternity success in wild male African elephants, *Loxodonta africana*. *Animal Behaviour*, 74, 287–296.
- Hooge, P.N., & Eichenlaub, B. (1997). Animal movement extension to Arcview. Ver. 1.1 Alaska Biological Science Center, U.S Geological Survey, Anchorage, U.S.A.
- Hrabar, H., & du Toit, J. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*. 8, 259 - 267.
10.1017/S1367943005002234.
- Illius, A.W., & Gordon, I.J. (1987). The allometry of food intake in grazing ruminants. *Journal of Animal Ecology*, 56, 989-999.
- Jachmann, H. (1988). Estimating age in African elephants: a revision of Law's molar evaluation technique. *African Journal of Ecology*, 22 (1), 51-56. doi: 10.1111/j.1365-2028.1988.tb01127.
- Janzen, D.H., & Martin, P.S. (1982). Neotropical anachronisms: The fruits the gomphotheres ate. *Science*, 215, 19–27.
- Johnston, R.A., & Cant, M. (2010). The evolution of menopause in cetaceans and humans: the role of demography. *Proceedings of the Royal Society*, 277, 3765-3771.
doi/10.1098/rspb.2010.0988.

- Kachel, A.F., Premo, L.S., & Hublin, J.J. (2011). Grandmothering and natural selection. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1704), 384-391.
- Kepe, T. (2001). Tourism, protected areas and development in South Africa: views of visitors to Mkambati Nature Reserve. *South African Journal of Wildlife*, 31 (3&4), 155-159.
- Kerley G.I.H. & Landman M. (2006). The impacts of elephants on biodiversity in the Eastern Cape subtropical Thickets. *South African Journal Science*, 102, 395–402.
- Kerley, G.I.H., & Landman, M. (2005). Gardeners of the Gods: the role of elephants in the Eastern Cape Subtropical Thickets. In *A compilation of contributions by the Scientific Community for SANParks, 2005. Elephant Effects on Biodiversity: an assessment of current knowledge and understanding as a basis for elephant management in SANParks*, ed. C.C. Grant, 173–190. Scientific Report 3/2005, South African National Parks, Skukuza.
- Kerley, G.I.H., & Shrader, A.M. (2007). Elephant contraception: Silver bullet or a potentially bitter pill? *South African Journal of Science*, 103 (5-6), 181-182.
http://www.scielo.org.za/scielo.php?script=sci_arttext&pid=S0038-23532007000300005&lng=en&tlng=en.
- Kerley, G.I.H., Knight, M.H., & de Kock, M. (1995). Desertification of subtropical thicket in the Eastern Cape, South Africa: Are there alternatives? *Environment Monitoring Assessment*, 37 (1-3), 211-30. doi: 10.1007/BF00546890. PMID: 24197850.
- Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W.F., Gaylard, A., Lindsay, W., & Slotow, R. (2008). Effects of elephants on ecosystems and biodiversity. *Journal of Elephant Management; A Scientific Assessment for South Africa*, doi: 10.18772/22008034792.

- Kerley, G.I.H., Mason, M.C., Weatherby, A., & Branch, W.R. (1999). The role of tortoises in the Thicket biome, South Africa: important meso-herbivores in a mega-herbivore dominated ecosystem? *Proc. 1997–1998 Symposia*, Desert Tortoise Council, 34–40.
- Kerr, T.J., de Waal, C.R., Buss, P.E., Hofmeyr, J., Lyaschenko, K.P., & Miller, M.A. (2019). Seroprevalence of *Mycobacterium tuberculosis* complex in free-ranging African elephants (*Loxodonta africana*) in Kruger National Park, South Africa. *Journal of Wildlife Diseases*, 55 (4), 923-927. <https://doi.org/10.7589/2018-12-292>.
- Kilpatrick, A.M., Hoyt, J.R., King, A.R., Kaarakka, H.M., Redell, J.A., White, J.P., & Langwig, K.E. (2020). Impact of censusing and research on wildlife populations. *Conservation Science and Practice*, 2:e264. <https://doi.org/10.1111/csp2.264>.
- Kirkpatrick, & J.F., Turner, A. (2002). Reversibility of action and safety during pregnancy of immunizing against porcine zona pellucida in wild mares (*Equus caballus*). *Reproductive Supplement*, 60, 117–124.
- Kirkpatrick, J.F., Lyda, R.O., & Frank, K.M. (2011). Contraceptive vaccines for wildlife: A review, *American Journal of Reproductive Immunology*, 66, 40–50. <https://doi.org/10.1111/j.1600-0897.2011.01003.x>.
- Kirkpatrick, J.F., & Turner, A. (2008). Achieving population goals in a long-lived wildlife species (*Equus caballus*) with contraception. *Wildlife Research*, 35, 513–519. <https://doi.org/10.1071/WR07106>.
- Kirkpatrick, J.F., Calle, P.P., Kalk, P., Liu, I.K.M., Bernoco, M., & Turner, J.W. (1996). Immunocontraception of captive exotic species. II. Formosa deer (*Cervus taiouanus*), axis deer (*Cervus axis*), Himalayan tahr (*Hemitragus jemlahicus*), Roosevelt elk (*Cervus elaphus*

roosevelti), muntjac deer (*Muntiacus reevesi*) and sambar deer (*Cervus unicolor*). *Journal of Zoo Wildlife Medicine*, 27, 482–495.

Kirkpatrick, J.F., Liu, I.K.M., & Turner, J.W. Jr. (1990). Remotely delivered immunocontraception in feral horses. *Wildlife Society Bulletin*, 18, 326–330.

Kirkpatrick, J.F., Turner, J.W. Jr., Liu, I.K.M., Fayrer-Hosken, R., Rutberg, A.T. (1997). Case studies in wildlife immunocontraception: wild and feral equids and white-tailed deer. *Reproduction, Fertility and Development*, 9, 105–110.

Kirkpatrick, J.F., Zimmermann, W., Kolter, L., Liu, I.K.M., & Turner, J.W. (1995). Immunocontraception of captive exotic species. I. Przewalski's horse (*Equus przewalskii*) and banteng (*Bos javanicus*). *Zoo Biology*, 14, 403–413.

Knight, M. (2003). An assessment of Amakhala Game Reserve for the introduction of elephants. Unpublished.

Kohi, E.M. (2013). The bulldozer herbivore: How animals benefit from elephant modifying an African savanna. PhD thesis, Wageningen University, Netherlands.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999). Population density affects sex ratio variation in red deer. *Nature*, 399, 459–461.

Kuiper, T., Druce, D., & Druce, H. (2018). Demography and social dynamics of an African elephant population 35 years after reintroduction as juveniles. *Journal of Applied Ecology*, 55. 10.1111/1365-2664.13199.

Laurson, B., & Bekoff, M. (1978). *Loxodonta africana*. *Mammalian Species*, (92), 1–8. doi: 10.2307/3503889.

Laws, R.M. (1969). Two Tsavo research projects. *Journal of Reproduction and Fertility*, 6, 495–531.

- Laws, R.M. (1970). Elephants as agents of habitat and landscape change in East Africa. *Oikos*, 21, 1–15.
- Laws, R.M., Parker, I.S.C., & Johnstone, R.C.B. (1975). Elephants and their habitats: The ecology of elephant in north Bunyoro, Uganda. *Oxford*, U.K.: Calrendon Press.
- Lee, P., & Moss, C. (1986). Early maternal investment in male and female African elephant calves. *Behavioural Ecology and Sociobiology*, 18, 353-361. 10.1007/BF00299666.
- Lee, P.C., Fishlock, V., Webber, C.E., & Moss, C.J. (2016). The reproductive advantages of a long life: longevity and senescence in wild female African elephants. *Behavioural Ecology and Sociobiology*, 70, 337-345.
- Leggett, K., (2006). Effects of artificial water points on the movement and behaviour of desert-dwelling elephants in north-western Namibia. *Pachyderm*, 40, 40–51.
- Lessing, J. (2007). Elephant feeding behaviour and forage offtake implications in the Addo Elephant National Park. MSc thesis, Nelson Mandela Metropolitan University, South Africa.
- Lewis, R.L., & Carter, J. (2004). Exploring behaviour of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus. *Ecology Modelling*, 171, 127–138.
- Lindeque, M. (1991). Age structure of the elephant population in the Etosha National Park, Namibia. *Madoqua*, 1991 (1).
- Lindeque, M., & Lindeque, P.M. (1991). Satellite tracking of elephants in northwestern Namibia. *African Journal of Ecology*, 29, 196–206.
- Lindeque, P.M., & Turnbull, P.C. (1994). Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. *The Onderstepoort Journal of Veterinary Research*, 61 (1), 71-83.

- Liu, I.K.M., Feldman, M., & Bernoco, M. (1989). Contraception in mares heteroimmunized with pig zonae pellucidae. *Journal of Reproductive Fertility*, 85, 19-29.
- Liu, J., & Xu, Y. (2022). T-Friedman Test: A New Statistical Test for Multiple Comparison with an Adjustable Conservativeness Measure. *International Journal of Computer Intelligent Systems*, 15, 29. <https://doi.org/10.1007/s44196-022-00083-8>.
- Loarie, S.R., van Aarde, R.J. & Pimm, S.L. (2009) Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, 142 (12), 3086-3098.
- Lombard, A.T., Johnson, C.F., Cowling, R.M., & Pressey, R.I. (2001). Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*, 102, 191–203.
- Lueders, I., Niemuller, C., Rich, P., Gray, C., Hermes, R., Goeritz, F., & Hildebrandt, T.B. (2012). Gestating for 22 months: luteal development and pregnancy maintenance in elephants. *Proceedings of the Royal Society of London, B. Biological Sciences*, 279, 3687–3696.
- Lueders, I., Oerke, A.K., Knauf-Witzens, T., Young, D., & Bertschinger, H.J. (2019). Use of gonadotrophin releasing hormone (GnRH) vaccines for behavioural and reproductive control in managed Asian elephant *Elephas maximus* and African elephant *Loxodonta africana*) populations. *International Zoo Yearbook*, 53. 10.1111/izy.12220.
- Mack, J. (2020). T Test: Analyzing, Applying, and Interpreting. Northcentral University, U.S.A.
- Mackey, R.L., Page, B.R., Duffy, K.J., & Slotow, R. (2006). Modelling elephant population growth in small, fenced, South African reserves. *Environmental Science*. Volume and page numbers?

- Mahbobi, M., & Tiemann, T.K. (2015). Stat analysis. *Introductory business statistics with interactive spreadsheets*, (1). <https://opentextbc.ca/introductorybusinessstatistics/chapter/f-test-and-one-way-anova-2/>.
- McAuliffe, K., & Whitehead, H. (2005). Eusociality, menopause and information in matrilineal whales. *Trends in Ecology and Evolution*, 20 (12), 650. doi: <https://doi.org/10.1016/j.tree.2005.09.003>.
- Medrano, J., Kheddar, & A., Lesne, A. (2021). Radius selection using kernel density estimation for the computation of nonlinear measures. *French National Centre for Scientific Research, Sofiane Ramdani Université de Montpellier, Chaos (Woodbury, N.Y.)* 31(8):083131
DOI:10.1063/5.0055797.
- Millar, S.E., Chamow, S.M., Baur, A.W., Oliver, C., Robey, F., & Dean, J. (1989). Vaccination with a synthetic zona pellucida peptide produces long-term contraception in female mice. *Science*, 246, 935–938. <https://doi.org/10.1126/science.2479101>.
- Miller, L.A., Crance, K., Gaddis, S., & Killian, G.J. (2001). Porcine zona pellucida immunocontraception: long-term health effects on white-tailed deer. *Journal of Wildlife Management*, 65, 942–945.
- Miller, L.A., Johns, B.E., & Killian, G.J. (2000). Long-term effects of PZP immunization on reproduction in white-tailed deer. *Vaccine*, 18, 568–574.
- Miller, L.A., Rhyan, J., & Killian, G. (2004). GonaCon™— a versatile GnRH contraceptive for a large variety of pest animal problems. *Proceedings of Vertebrates. Pest Conference*. 21, 269-273.

- Mlambo, L., Shekede, M.D., Adam, A., Odindi, J., & Murwira, A. (2021). Home range and space use by African elephants (*Loxodonta africana*) in Hwange National Park, Zimbabwe. *African Journal of Ecology*, 842-853. doi: org/10.1111/aje.12890.
- Moss, C.J. (1988). Elephant Memories: Thirteen years in the life of an elephant family. *William Morrow and Co*, New York.
- Moss, C.J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology*, 255, 145–156.
- Moss, C.J., Croze, H., & Lee, P.C. (2011). The Amboseli elephants: A long-term perspective on a long-lived mammal. *University of Chicago Press*, doi:10.7208/chicago/9780226542263.001.0001.
- Mostert, B., van Der Westhuizen, R., & Theron, H. (2010). Calving interval genetic parameters and trends for dairy breeds in South Africa. *South African Journal of Animal Science*, 40 (2), 156-162.
- Mucina, L., & Rutherford, M.C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.
- Muller, L.I., Warren, R.J., & Evans, D.L. (1997). Theory and practice of immunocontraception in wild mammals. *Wildlife Society Bulletin*, 25, 504–514.
- Mumby, H.S., Courtiol, A., Mar, K.U., & Lummaa, V. (2013). Birth seasonality and calf mortality in a large population of Asian elephants. *Ecology and Evolution*, 3 (11), 3794-3803.
<https://doi.org/10.1002/ece3.746>.
- Nasseri, N.A., McBrayer, L.D., & Schulte, B.A. (2010). The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. *African Journal of Ecology*, 133-140. <https://doi.org/10.1111/j.1365-2028.2010.01238.x>.

- National Parks Rescue (2020). Mysterious mass elephant die-off in Botswana was caused by cyanobacteria poisoning. *Nature*, Sciencealert.com. Retrieved 24 September 2022.
- Nhleko, Z.N. (2014). The demography, spatial ecology and reproductive success of the black rhinoceros, *Diceros bicornis*, in Hluhluwe-iMfolozi Park, Kwazulu-Natal, South Africa. PhD Thesis, Rhodes University, South Africa.
- Niemuller, C. A., Shaw, H. J., & Hodges, J. K. (1993). Non-invasive monitoring of ovarian function in Asian elephants (*Elephas maximus*) by measurement of urinary 5 α -pregnanetriol. *Journal of Reproductive Fertility*, 99, 617–625. doi:10.1530/jrf.0.0990617.
- Nkosi, S.E., Adam, E., Barrett, A.S., & Brown, L.R. (2019). A synopsis of field and remote sensing-based methods for studying African elephant (*Loxodonta africana*) impact on woody vegetation in Africa. *Applied Ecology and Environmental Research*, 17 (2), 4045-4066.
- Nowak, R.M. (1999). *Walker's mammals of the world* (6th ed.). Baltimore, Maryland: Johns Hopkins University Press.
- Ntumi, C.P., van Aarde, R.J., Fairall, N., & de Boer, W.F., (2005). Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. *South African Journal of Wildlife Research*, 35, 139–146.
- Nuwer, R. (2021). Both African elephant species are now endangered, one critically. *National Geographic*. <https://www.nationalgeographic.co.uk/environment-and-conservation/2021/03/both-african-elephant-species-are-now-endangered-one-critically>.
- Osborn, F.V. (2004). Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe. *African Journal of Ecology*, 42, 322–327.

- Osborn, F.V., & Parker, G.E., (2003). Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology*, 41, 68–74.
- Ottichilo, W.K. (1986). Population estimates and distribution patterns of elephants in the Tsavo ecosystem, Kenya in 1980. *African Journal of Ecology*, 24, 53–57.
- Owens, M.J., Owens, D. (2009). Early age reproduction in female savanna elephants (*Loxodonta africana*) after severe poaching. *African Journal of Ecology*, 47 (2), 214-222.
- Owen-Smith, N. (1988). Megaherbivores: The influence of very large body size on ecology. *Cambridge University Press*, Cambridge.
- Paley, R.G.T., & Kerley, G.I.H. (1998). The winter diet of elephant in Eastern Cape Subtropical Thicket, Addo Elephant National Park. *Koedoe*, 41 (1), 37-45. Pretoria. ISSN 0075-6458.
- Pastor, J., Cohen, Y., & Hobbs, N. (2006). The roles of large herbivores in ecosystem nutrient cycles. In K. Danell, R. Bergström, P. Duncan, & J. Pastor (Eds.), *Large herbivore ecology, ecosystem dynamics and conservation* (Conservation Biology, pp. 289-325), Cambridge: Cambridge University Press. doi:10.1017/CBO9780511617461.012.
- Paterson, M., Wilson, M.R., Jennings Z.A., Van Duin, M., & Aitken, R.J. (1999). Design and evaluation of a ZP3 peptide vaccine in a homologous primate model. *Molecular Human Reproduction*, 5 (4), 342–352.
- Paterson, M., Wilson, M.R., Van Duin, M., & Aitken, R.J. (1998). Evaluation of the contraceptive potential of recombinant human ZP3 and human ZP3 peptides in a primate model: their safety and efficacy. *American Journal of Reproductive Immunology*, 40 (3), 198-209.

- Payne, K.B., Langbauer, W.R., & Thomas, E.M. (1986). Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, 18 (4), 297-301. doi: 10.1007/BF00300007. S2CID 1480496.
- Penzhorn, B.L., Robbertse, P.J., & Olivier, M.C. (1974). The influence of the African elephant on the vegetation of the Addo Elephant National Park. *Koedoe*, 17, 137–158.
- Perdok, A., de Boer, W., & Stout, T. (2007). Prospects for managing African elephant population growth by immunocontraception: a review. *Pachyderm*, 42, 95–105. Retrieved from <https://pachydermjournal.org/index.php/pachyderm/article/view/115>.
- Poole, J.H., & Moss, C.J. (1989). Elephant mate searching: group dynamics and vocal and olfactory communication. *The biology of large mammals in their environment*, 111–125 (J. A. Jewel and G. M. O. Maloyi, eds.). Clarendon Press, Oxford, United Kingdom.
- Poole, J.H., Payne, K., Langbauer, W.R., & Moss, C.J. (1988). The social contexts of some very low-frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, 22, 385–392.
- Power, J., & Compion, R.X.S. (2009). Lion predation on elephants in the Savuti, Chobe National Park, Botswana, *African Zoology*, 44 (1), 3644, doi: 10.1080/15627020.2009.11407437.
- Rachlow, J.L., & Berger, J. (1998). Reproduction and population density trade-offs for the conservation of rhinos in situ. *Animal Conservation*, 1 (2), 101-106.
- Razzaq, S. (2007). Amakhala's elephant immuno-contraceptive plan. Unpublished.
- Redfern, J.V., Grant, R., Biggs, H., & Getz, W.M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84, 2092–2107.
- Rholand, N., Reich, D., Mallick, S., Meyer, M., Green, R.E., Georgiadis, N.J., Roca, A.L., & Hofreiter, M. (2010). Genomic DNA sequences from mastodon and woolly mammoth reveal deep

speciation of forest and savanna elephants. *Public Library of Science (PLOS) Biology*, 8 (12), e31000564.

Roca, A.L., Geogiadis, N., Pecon-Slattery, J., & O'Brien, S.J. (2001). Genetic evidence for two species of elephant in Africa. *Science*, 293, 1473-1477.

Rosenzweig, L.M. (1981). A theory of habitat selection. *Ecology*, 62, 327–335.

Roux, C. (2006). Feeding ecology, space use and habitat selection of elephants in two enclosed game reserves in the Eastern Cape province, South Africa. MSc thesis, Rhodes University, South Africa.

Sacco, A.G., Subramanian, M.G., Yurewicz, E.C., DeMayo, F.J., & Dukelow, W.R. (1986). Heteroimmunization of squirrel monkeys (*Saimiri sciureus*) with a purified porcine zonae antigen (PPZA): immune response and biological activity of antiserum. *Fertility and Sterility*, 39, 350–358.

Sadleir, R.M.F.S. (1969). The ecology of reproduction in wild and domestic animals. Methuen, London.

Samuel, M.D., Pierce, D.J., & Garton, E.O. (1985). Identifying Areas of Concentrated Use within the Home Range. *Journal of Animal Ecology*, 54 (3), 711–719. <https://doi.org/10.2307/4373>.

Schoener, T.W. (1981). An empirically based estimate of home range. *Theoretical Population Biology*. 20 (3), 281-325.

Seaman, D.E., & Powell, R.A. (1996). An evaluation of the accuracy of the kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085.

Selier, Slotow, R., & Di Minin, E. (2015). Elephant distribution in a transfrontier landscape: trade-offs between resource availability and human disturbance. *Biotropica*, 47 (3), 389-397.

- Shannon, G., Page, B., Slotow, R., & Duffy, K. (2006). African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, 41 (1), 37-44.
- Shannon, G., Page, B.R., Mackey, R.L., Duffy, K.J., & Slotow, R. (2008). Activity budgets and sexual segregation in African elephants (*Loxodonta africana*). *Journal of Mammalogy*, 89, 467–476.
<https://doi.org/10.1644/07-MAMM-A-132R.1>.
- Shapiro S.S., & Wilk M.B. (1968). Approximations for the null distribution of the W statistic. *Technometrics*, 10, 861-866.
- Shoshani, J, & Shoshani, S. (2000). What is an elephant? *Elephants*, New York: Checkmark Books; 18-35.
- Shoshani, J. (1978). General information on elephants with emphasis on tusks. *Elephant*. 1 (2), 20-31. doi: 10.22237/elephant/1491234053.
- Shoshani, J. (1992). *Elephants: Majestic Creatures of the Wild*. London: Simon and Schuster, 22–23.
- Shoshani, J. (1998). Understanding proboscidean evolution: a formidable task. *Trends in Ecology and Evolution*. 13 (12), 480–87. doi:10.1016/S0169-5347(98)01491-8. PMID 21238404.
- Singh, A.K., Singh, R.R., & Chowdhury, S. (2002). Human-elephant conflicts in changed landscapes of south West Bengal, India. *Indian forester*, 128 (10), 1119-1132.
- Slotow R., van Dyk, G., Poole, J., Page, B., & Klocke, A. (2000). Older bull elephants control young males. *Nature*, 408, 425–426.
- Slotow, R., & van Dyk G. (2001). Role of delinquent young ‘orphan’ male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. *Koedoe*, 44, 85–94.

- Slotow, R., Balfour, D., & Howison, O. (2001). Killing of black and white rhinoceros by African elephant in Hluhluwe–Umfolozi Park, South Africa. *Pachyderm*, 31, 14–20.
- Slotow, R., Garai, M., Reilly, B., Page, B., & Carr, R.D. (2005). Population dynamics of elephants re-introduced to small, fenced reserves in South Africa. *African Journal of Wildlife Research*, 35, 23-32.
- Smit, I.P.J., Grant, C.C., & Devereux, B.J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136, 85–99.
- Smuts, G.I. (1975). Reproduction and population characteristics of elephants in the Kruger National Park. *South African Journal of Wildlife Research - 24-month delayed open access*, 5, 1-10.
- Sommerlatte, M.W.C. (1976). A survey of elephant populations in north-eastern Botswana. Report to the Botswana Department, National Parks, and Tourism, Gaborone, Botswana.
- Stokke, S., & du Toit, J.T. (2002). Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, 40, 360–371.
- Tarlow, E.M., & Blumstein, D.T. (2007). Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*, 102, 429–451.
- Tello, J.L.P.L. (1973). Reconhecimento Ecológico da Reserva dos Elefantes do Maputo. *Veterinária dem Moçambique*, 6, 133–186.
- Thouless, C.R., Dublin, H.T., Blanc, J.J., Skinner, D.P., Daniel, T.E., Taylor, R.D., Maisels, F., Frederick, H.L., & Bouche, P. (2016). African elephant status report 2016: an update from the African Elephant Database (PDF). *Occasional Paper of the IUCN Species Survival Commission*, No. 60. Gland: IUCN SSC African Specialist Group. ISBN 978-8317-1813-2.

- Trivers, R.L., & Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179, 90–92.
- Tufto, J., Anderson, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: The Roe Deer. *Journal of Animal Ecology*, 65 (6), 715-724.
- Turner, J.W., Kirkpatrick, J.F., & Liu, I.K.M. (1996). Effectiveness, reversibility and serum antibody titres associated with immunocontraception in captive white-tailed deer. *Journal of Wildlife Management*, 31, 514–522.
- Turner, J.W., Liu, I.K.M., & Kirkpatrick, J.F. (1992). Remotely-delivered immunocontraception of captive white-tailed deer. *Journal of Wildlife Management*, 56, 154–157.
- Turner, M.G., Gardner, R.H., & O'Neill, R.V. (2001). Landscape ecology in theory and practice: pattern and process. *Springer Science & Business Media Inc.*, USA.
- Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., & Cumming, D. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, 144. 10.1016/j.biocon.2010.10.029.
- Van Aarde, R., Whyte, I., & Pimm, S. (1999). Culling and the dynamics of the Kruger National Park African elephant population. *Animal Conservation*, 2, 287–294.
- Van Aarde, R.J., Jackson, T.P., & Ferreira, S.M. (2006). Conservation science and elephant management in southern Africa. *South African Journal of Science*, 102, 385–388.
- Van der Walt, M.S., Daffue, W., Goedhals, J., van der Merwe, S., & Deacon, F. (2022). A preliminary study on the siphon mechanism in Giraffe (*Giraffa camelopardalis*). *Animals*, 12 (23), 3348. MDPI AG. Retrieved from <http://dx.doi.org/10.3390/ani12233348>.

- Van Jaarsveld, A.S., Nicholls, A.O., & Knight, M.H. (1999). Modelling and assessment of South African elephant *Loxodonta africana* population persistence. *Environmental Modelling and Assessment*, 4, 155–163.
- Van Wyk, P., & Fairall, N. (1969). The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*, 9, 57–95.
- Viljoen, P.J. (1989). Habitat selection and preferred food plants of a desert dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology*, 27, 227–240.
- Vos, W. (2022). The carrying capacity of Amakhala Private Game Reserve in the Eastern Cape province of South Africa. Unpublished.
- Western, D., & Lindsay, W.K. (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, 22, 229–244.
- Whyte, I., van Aarde, R., & Pimm, S.L. (1998). Managing the elephants of Kruger National Park. *Animal Conservation*, 1, 77–83.
- Whyte, I.J. (2001). Conservation management of the Kruger National Park elephant population. D.Sc. University of Pretoria, Pretoria.
- Wittemyer, G., & Getz, W.M. (2007). Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour*, 73 (4), 671–681. <https://doi.org/10.1016/j.anbehav.2006.10.008>.
- Wittemyer, G., Daballen, D., Douglas-Hamilton, I. (2013). Comparative demography of an at risk African elephant population. *PLoS ONE* 8(1): e53726. doi: 10.1371/journal.pone.0053726 68.

- Wittemyer, G., Douglas-Hamilton, I., & Getz, W.M. (2005). The socio-ecology of elephants: analysis of the processes creating multi-tiered social structures. *Animal Behaviour*, 69, 1357–1371.
- Wittemyer, G., Granswindt, A., & Hodges, K. (2007). The impact of ecological variability on the reproductive endocrinology of wild female African elephants. *Hormones and Behaviour*, 51, 346-354.
- Wolff, J.O. (1988). Maternal investment and sex ratio adjustment in American bison calves. *Behavioral Ecology and Sociobiology*, 23, 127–133.
- Wood, D.M., Liu, C., & Dunbar, B.S. (1981). Effect of alloimmunization and heteroimmunization with zona pellucida on fertility in rabbits. *Biology of Reproduction*, 25, 439–450.
- Woolley, L.A., Mackey, R.L., Page, B.R., & Slotow, R. (2008). Modelling the effect of age-specific mortality on elephant *Loxodonta africana* populations: can natural mortality provide regulation? *Oryx*, 42, 49–57.
- Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.
- Wright, P.G., & Luck, C.P. (1984). Do elephants need to sweat? *South African Journal of Zoology*, 19, 270–274.