Spatial and feeding ecology of elephants (*Loxodonta africana*) on Sanbona Wildlife Reserve, Little Karoo, South Africa

By

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Declaration

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Abstract

African elephants (*Loxodonta africana*) are megaherbivore mixed feeders. They are an important keystone species, influencing a variety of factors within an ecosystem. Historically elephants migrated throughout large parts of South Africa, including the valleys of the Little Karoo. However, these seasonal migration routes have long since disappeared and most of these large herbivores now only occur in South Africa within fenced reserves. This containment of populations can have a negative impact on landscapes as areas are utilised across seasons, thus not allowing vegetation a recovery period. In a sensitive semi-arid environment such as the Little Karoo, this has been a concern with the reintroduction of such large herbivores, as their spatial use and feeding ecology are largely unknown in this area. Sanbona Wildlife Reserve is a 57 600-ha reserve in the Little Karoo which has reintroduced various animals since its creation in 2002. Since the introduction of elephants in 2003 and 2009 the population has increased to 17 individuals between two herds.

Habitat heterogeneity, local rainfall, and spatio-temporal distribution of food and water are some of the key elements determining the size and structure of elephants' home ranges. GPS satellite collars were used to determine the areas utilised by both elephant herds on the reserve. An individual from each elephant herd was fitted with a GPS satellite collar which recorded their hourly movements over an 18-month period. The data collected were utilised to determine home ranges and core zones using the Kernel Density Estimate and Grid Square Methods. Weather patterns were also recorded throughout the study period through the use of weather stations and observations. This information was used to determine the influence of weather on seasonal spatial usage as well as the impact of water points on their movement on the reserve. Results indicated the importance of river lines within both elephant herds' core zones, however mountain slopes and open valleys were also utilised within their home ranges. The Northern herd's home range spanned over 25% of the available area (60.4 km^2) whereas the Southern herd had a home range of 73.9 km^2, 31% of the available area. Furthermore, results show that rainfall, temperature, seasonal vegetation growth and water availability influence seasonal spatial usage.

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The preferred space utilised correlates with the elephants' diet preferences. Previous studies of elephant diet in semi-arid to arid environments recorded the utilisation of a combination of graze (C_4), woody browse (C_3) and succulent browse (CAM), with season and habitat determining the percentage present in the diet. A combination of scan sampling and isotopic analysis of faeces samples was used to better understand the diet of elephants on Sanbona Wildlife Reserve. Results from the scan sampling show that a variety of plant species (at least 94) were recorded to constitute the elephants' diet. Through the combination of both methods over a 16-month period seasonal differences in diet and between herds was recorded. The Northern herd's diet consisted of 62% browse species, 28% graze and 10% succulents, compared to 79% browse, 2% graze and 19% succulent species in the Southern herd's diet.

The results of this study will help Sanbona Wildlife Reserve to better understand the ecological requirements of elephants within this area, as well as their impact on sensitive, slow growing plant species on the reserve. This information will allow wildlife management to make informed decisions with regards to population management strategies.

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Opsomming

Afrika-olifante (*Loxodonta africana)* is mega-herbivore, gemengde vreters. Hulle is ‘n belangrike hoeksteen-spesie wat ‘n verskeidenheid faktore binne ‘n ekosisteem beïnvloed. Geskiedkundig het olifante deur groot dele van Suid-Afrika, insluitende die valleie van die Klein Karoo, gemigreer. Daardie seisoenale migrasieroetes het egter lank reeds verdwyn en die meeste van hierdie groot herbivore kom nou slegs binne omheinde reservate in Suid-Afrika voor. Hierdie inperking van bevolkings kan ‘n negatiewe impak op landskappe meebring, aangesien gebiede oor seisoene heen benut word en die plantegroei dus nie ‘n hersteltydperk gegun word nie. In ‘n sensitiewe halfdorre omgewing soos die Klein Karoo was dit ‘n rede tot kommer met die hervestiging van sulke groot herbivore, aangesien hulle gebiedsbenutting en voedingsekologie grootliks onbekend is in hierdie gebied. Sanbona Wildreservaat is ‘n 57 600-ha reservaat in die Klein Karoo wat sedert sy oprigting in 2002 verskeie diere hervestig het. Sedert die vestiging van olifante in 2003 en 2009 het die bevolking aangewas tot 17 individue tussen twee kuddes.

Habitat-heterogeniteit, plaaslike reënval en tydruimtelike verspreiding van kos en water is party van die sleutel-elemente wat die omvang en struktuur van olifante se tuisgebiede bepaal. GPS-satellietkrae is gebruik om vas te stel watter gebiede deur albei olifantkuddes in die reservaat benut word. ‘n Individu uit elke olifantkudde is met ‘n GPS-satellietkraag toegerus, wat hul bewegings uurliks oor ‘n tydperk van 18 maande opgeneem het. Die data wat versamel is, is gebruik om met behulp van die Kerndigtheidsberaming- en Vierkantrooster-metodes tuisgebiede en kernsones te bepaal. Weerpatrone is ook deurgaans tydens die studie aangeteken met behulp van weerstasies en deur waarnemings. Hierdie inligting is gebruik om die invloed van weer op seisoenale gebiedsbenutting te bepaal, sowel as die impak van waterpunte op hul beweging binne die reservaat. Resultate het op die belangrikheid van rivierlyne binne albei olifantkuddes se kernsones gedui, alhoewel berghange en oop valleie ook binne hul tuisgebiede benut is. Die Noordelike kudde se tuisgebied het meer as 25% van hul beskikbare area (60.4 km^2) beslaan, waarteenoor die Suidelike kudde ‘n tuisgebied van 73.9 km^2 gehad het, 31% van die beskikbare area. Verdermeer toon resultate dat reënval, temperatuur, seisoenale plantegroei en beskikbaarheid van water seisoenale gebiedsbenutting beïnvloed.

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Die gebiede wat by voorkeur benut is, stem ooreen met die olifante se dieetvoorkeure. In vorige studies van olifante se dieet in halfdorre tot dorre omgewings is aangeteken dat ‘n kombinasie van gras (C4), houtagtige takvoer (C3) en vetplant-beweiding (CAM) benut word, waar seisoen en habitat bepaal watter persentasie in die dieet teenwoordig is. ‘n Kombinasie van visuele observasie steekproefneming en isotopiese ontleding van ontlastingsmonsters is gebruik om die dieet van olifante in die Sanbona Wildreservaat beter te begryp. Die resultate van die visuele observasie steekproefneming toon aan dat die olifante se dieet uit ‘n verskeidenheid van plantspesies bestaan (ten minste 94 is aangeteken). Met behulp van die kombinasie van albei metodes oor ‘n tydperk van 16 maande is seisoenale verskille in dieet en tussen kuddes aangeteken. Die Noordelike kudde se dieet het bestaan uit 62% takvoer-spesies, 28% grasspesies en 10% vetplante, vergeleke met 79% takvoer-, 2% gras- en 19% vetplantspesies in die Suidelike kudde se dieet.

Die resultate van hierdie studie sal die Sanbona Wildreservaat help om die ekologiese vereistes van olifante binne hierdie gebied beter te verstaan, sowel as hul impak op sensitiewe, stadig groeiende plantspesies in die reservaat. Hierdie inligting sal die wildbestuurspan in staat stel om ingeligte besluite omtrent bevolkingsbestuur strategieë te neem.

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I am forever grateful for the guidance from God and thankful that I am able to work amongst the miracles that He has created in nature. I praise Him for keeping me safe throughout my time on foot in the wilderness and opening my eyes to all the beauty around me.

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Dedication

I would like to dedicate this thesis to three very special people, my two Grandmothers and my Grandfather. Ouma Mari and Ouma Rita were two strong, wise women that were instrumental in helping to mould me into the person I am today. I carry you with me every day that I am out amongst the beauty of nature and wish you could be here to read this work. And to my Oupa Doug, for teaching me that life is an adventure that we must grab and share with as many people as possible, for it is only through sharing love and happiness with others that we truly find it in ourselves.

I dedicate this to the elephants of my life.

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List of Acronyms and Abbreviations

AWP	Artificial Water Point
CAM	Crassulatic Acid Metabolism
GIS	Geographic Information System
GPS	Global Positioning System
KDE	Kernel Density Estimate
SWR	Sanbona Wildlife Reserve

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Chapter 1: General Introduction

"An understanding of the natural world and what's in it is a source of not only a great curiosity but great fulfilment." David Attenborough

1.1. Background

Elephants are megaherbivore mixed feeders, feeding on both woody and herbaceous plants. They require large amounts of water and food, consuming an estimate of up to five percent of their body weight per day (Sinclair *et al*. 2006; Stephenson, 2007). Elephants need to consume a variety of plant species to ensure that they absorb the necessary range of nutrients due to their lack of a rumen (Olivier, 1978). Due to their digestive system they are often seen as 'wasteful' feeders, but are in fact an important keystone species (Landman *et al*., 2007). The balance between being a keystone species and having a negative impact on vegetation is a delicate balance that must be maintained (McShea *et al*. 1997; O'Connor *et al*. 2007).

The diet of elephants can consist of a combination of grass, bark, leaves, roots, fruits and herbs, with season and habitat determining the percentage present in the diet (Bax and Sheldrick, 1963; White *et al*. 1993). Studies on elephant diet in semi-arid to arid environments have recorded utilisation of browse, graze and succulents in varying percentages dependent on the availability (Guy, 1976; Viljoen, 1989; de Beer *et al*. 2006; Allen, 2009).

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Past studies have shown that during wet seasons elephants consume a larger intake of grass, supplemented by smaller amounts of leafy browse, whereas in the drier months the intake of woody vegetation increases as leafy browse and grass productivity decreases (Olivier, 1978; Barnes, 1982). Similarly, Owen-Smith and Chafota (2012) found that elephants in the Chobe area of Botswana shifted their diet from a high percentage of leaves, shoots and grass in the wet season, to larger percentages of twigs, bark and roots during the hotter, drier seasons. However, other studies in the Maputo Elephant Reserve in Mozambique, the Chebera Churchura National Park and the Babile Elephant Sanctuary in Ethiopia found that browse was more important than graze in the elephants' diets during both the wet and dry seasons (De Boer *et al*. 2000; Admasu, 2006; Biru and Bekele, 2012). The largest impact on woody vegetation occurs when elephants debark and break branches, and uproot plants. This has been recorded in the drier seasons when the impact on trees and shrubs is higher, increasing during droughts (Barnes, 1982). Tree debarking has been seen to occur just prior to flowering, fruiting, or new leaves being produced (Bax and Sheldrick, 1963; Guy 1976; Barnes, 1982). During this time more nutrients and water are transported between the roots and growing tips (Barnes, 1982). Debarking, therefore, varies between plant species and habitat, dependent on growth pattern and rainfall season.

Habitat can influence an elephant's diet. Elephant diets in savanna habitats have been recorded to contain close to 70% grass during the wet season, compared to forest elephants in tropical regions where the diet may consist of close to 90% of browse species (230 plant species of total species) (White *et al.*, 1993; Poole, 1996). In Namibia, Rodwell *et al*. (1995) determined that elephants make inter-annual repeated use of certain areas. Young *et* al. (2009) found that across six different savanna habitats that they studied that during the wet-season, elephants were less dependent on permanent water distribution, thus being able to range further and forage from over a larger area within larger home ranges than during dry-seasons. During dry-seasons it has been noted that the elephants' home ranges were smaller and more restricted to permanent water sources (Chamaille-James *et al*., 2007; Smit *et al*., 2007; Young *et al*., 2009). Vegetation and water availability therefore determine dietary composition; thus, rainfall and seasonality determine elephants' diets (Laws, 1970; Barnes, 1982; Birkett and Stevens-Wood, 2005; Loarie *et al*. 2009).

There are various factors that influence plant communities, such as water availability, nutrients, fire and herbivores (Ben-Shahar, 1993; Barnes, 2001; Scogings *et al*. 2012). Thus, in unfavourable

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times, such as during a drought, the impact on plant growth and recruitment can be detrimental when the increased pressure of herbivores is added (Lamprey *et al.*1967; Laws 1970; Western & van Praet 1973; Scogings *et al*. 2012). If seasonal ranges overlap, due to for example, range restrictions caused by fences allowing elephant herds to utilise the same areas across seasons, the impact on those areas could be accentuated (Höft & Höft, 1995). In a semi-arid environment such as the Little Karoo this has been a concern with the reintroduction of herbivores, such as white rhinoceros (*Ceratotherium simum*), elephants, giraffe (*Giraffa camelopardalis giraffa*) and hippopotamus (*Hippopotamus amphibius*), in particular as their spatial use and feeding ecology are largely unknown in this area (Vorster *et al*. 2017).

Various methods have been utilised to determine diet composition including: transects, backtracking, direct animal observations, fixed point photography with respect to vegetation structure change and isotopic analysis of plants, dentine, ivory, and bone (Guy, 1976; Viljoen, 1989; de Beer *et al*. 2006; Minnie, 2006; Allen, 2009).

Elephant movement and spatial usage have been studied across Africa to understand and assess the habitats and corridors needed to protect them (Douglas-Hamilton *et al*. 1971, 2005; Leggett, 2006; Young *et al*. 2009; Areendran *et al*. 2011). Habitat heterogeneity, seasonal rainfall, and spatio-temporal distribution of food and water are some of the key elements determining the size and structure of home ranges of elephants (Leggett, 2006; Lindeque and Lindeque, 1991; von Gerhardt-Weber, 2011). Fennessy (2006) noted that arid-adapted mammal species have larger home ranges than the same mammal species in higher rainfall areas, as is the situation with giraffe (*Camelopardalis angolensis*) in northern Namibia. Viljoen (1988 and 1989) found that elephants in the northern Namib Desert travelled large distances between preferred forage and water, with their core zones along river courses. These herds' home ranges then expand during the wet season to include preferred foraging areas around flood plains (Viljoen, 1989).

Before Western human settlement, elephants migrated over long distances and occurred in various habitats. This migration would allow for vegetation to recover between seasons (Babaasa, 2000). However, without the ability to migrate due to fences, and with the increased compression of elephants into smaller protected areas, habitat destruction and loss of biodiversity in reserves could likely occur as pressure on the local resources is increased within the confined space (van Aarde

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et al. 2006; Loarie *et al*. 2009). Historically, herds would have migrated through semi-arid areas such as the Succulent Karoo, and Fynbos biomes, occurring in a non-permanent capacity as rainfall and thus water availability varied (Ebedas *et al.*, 1995; Boshoff and Kerley, 2001). Some of the highest levels of endemism and plant diversity in Africa occur within the Succulent Karoo and Fynbos biomes, hence the concern with the reintroduction of large herbivores (Van Wyck and Smith, 2001).

Two hundred years after most of the naturally occurring herbivores and predators were eradicated from the Little Karoo, some of the species were reintroduced onto Sanbona Wildlife Reserve (Skead, 1980; Skinner and Chimimba, 2005). Sanbona Wildlife Reserve (hereafter referred to as SWR) is a 57 600-hectare reserve situated in the Little Karoo which lies between 33°15’ and 34°00' South, and 20°30' and 23°40’ East (Figure 1.1).

Figure 1.1. The location of Sanbona Wildlife Reserve (green polygon) in the Little Karoo, South Africa (Vorster, 2017).

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The reserve is comprised of a number of farms, originally used for cattle, sheep, goats, wheat and lucerne farming, that were accumulated by 2002, and have been allowed to return to a natural, pre-settler state (Vorster *et al*. 2017). Crops such as lucerne and wheat were removed from the floodplains, and alien vegetation clearing took place and is still ongoing on the reserve. An indigenous nursery was created on site to provide plants for rehabilitation projects, in particular the rehabilitation of the areas where the lodges were built. The reserve is surrounded by agricultural land in the form of small private nature reserves and lifestyle farms (Vorster *et al*., 2017). The reserve contains approximately 600 plant species within Renosterveld, Central Mountain Fynbos, Succulent Karoo, Thickets, and Riverine and floodplain vegetation types and supports two of the 34 internationally recognised biodiversity hotspots within the Fynbos and Succulent Karoo biomes (Vlok *et al*., 2005; Vorster *et al*., 2017). A large majority of the vegetation growing across the reserve is deemed unpalatable to livestock, however the riverine and floodplain areas are abundant with species such as *Vachellia karroo*, *Searsia* species., *Lycium* species, and *Atriplex* species.

In 2002, Sanbona was fenced according to the Nature Conservation Ordinance 1974, (Ord 19 of 1974) Section 35(4) b, to accommodate large and potentially dangerous game species. Several public roads and access roads to neighbouring farms run though Sanbona. The reserve was fenced along certain roads, and this created five management units (Figure 1.2). The primary reserve, Sanbona South, where the main tourism areas and predator reintroductions were planned, consisted of 38 100 ha. Sanbona North was 10 000 ha. Sanbona North and South were separated by a dividing game fence, along the Divisional Road 1381. In 2008, once this road was gazetted as a public servitude road, the fencing along these roads was moved to follow the natural boundary of the Warmwaterberg mountain range instead. This divided Sanbona North and Sanbona South more equally, allowing for changes in mammal management and tourism approaches (Figure 1.3).

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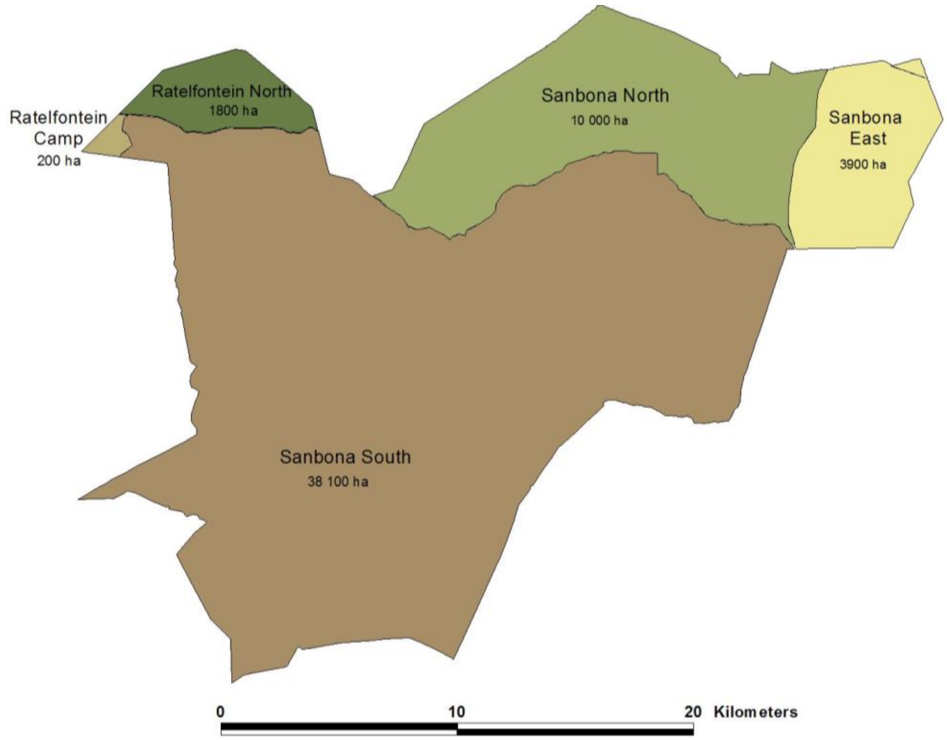

Figure 1.2. Environmental Management Units of Sanbona Wildlife Reserve from 2002 – 2008 (Vorster et al. 2017).

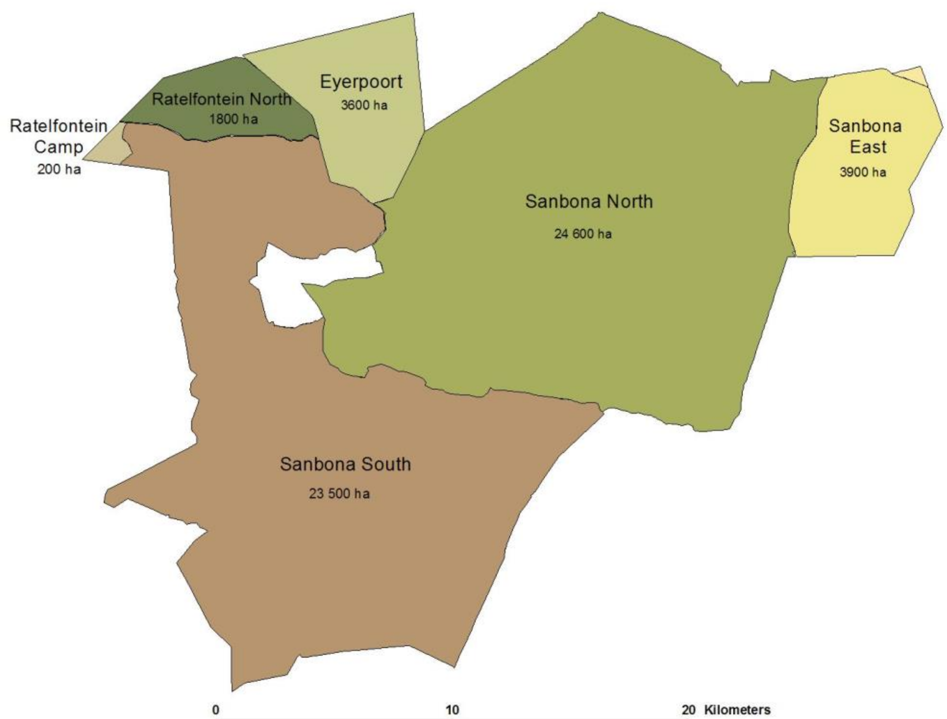

Figure 1.3. Current Environmental Management Units of Sanbona Wildlife Reserve (Vorster *et al*. 2017).

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Sanbona North (24 600 ha) lies north of the Warmwaterberg mountain range and receives an average of 195 mm of rain per annum due to the rain shadow effect of the mountain. This part of the reserve, which is currently the main game viewing area, is dominated by Succulent Karoo, as well as riverine areas with some Central Mountain Fynbos and Thickets (Vorster *et al.* 2017). Sanbona South (23 500 ha) is more mountainous and contains a large portion of land which is difficult to access, the Wilderness area, and receives an average of 315 mm of rain a year and consists of Renosterveld, Central Mountain Fynbos, and Thickets (Vorster *et al.* 2017). Lowland hills and ridgelines with shale-derived soils covered in small shrubs, leaf succulents and taller succulent shrubs occur in Sanbona North and South and are referred to as Randteveld by Vlok *et al*. (2005). In 2017 SWR acquired additional land. The additional management areas that make up the remaining hectares, Sanbona East (3 900 ha), Ratelfontein North (1 800 ha) and Eyerpoort (3 600 ha) are separated from Sanbona North and South by fences and were not included in the study (Figure 1.3). Surface water on the reserve is restricted to the Bellair Dam (which at full capacity can hold 4.2 billion cubic meters of water), seasonal natural springs and ephemeral rivers

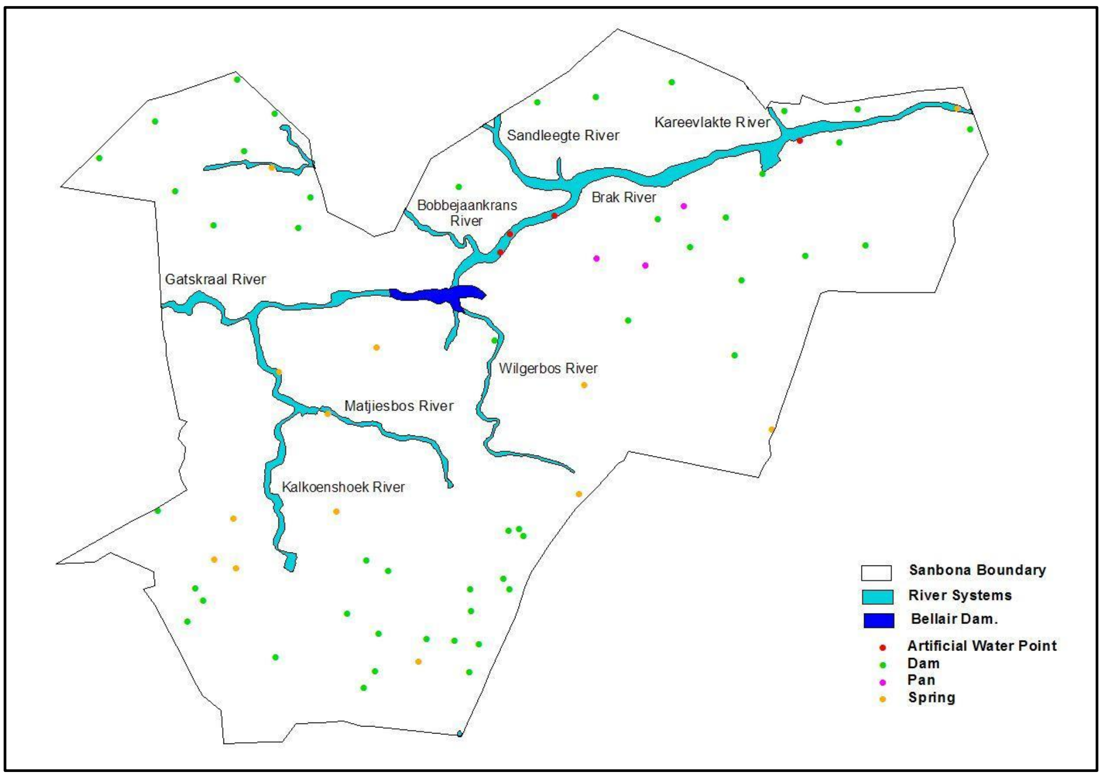

Figure 1.4. Sanbona Wildlife Reserve river systems, pans, springs and dams (Vorster et al. 2017).

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dependent upon annual rainfall as well as artificial water points (Figure 1.4) (Vorster *et al.* 2017). The Bellair dam (rebuilt in 2006 after flood damage) is situated in Sanbona North and is supplied by the Kalkoenshoek, Gatskraal and Wilgerbos rivers (Figure 1.4). The dam was recorded at 90% capacity at the start of the study in December 2015 and decreased to 37% capacity by the end of the study in May 2017.

SWR is home to a variety of small and large fauna, such as white rhinoceros, elephants, giraffe and hippopotamus and was the first reserve to reintroduce many of the larger herbivores and predators into the Little Karoo. Historic distribution of the mammals reintroduced was taken into consideration, as was the suitability and range of available habitat due to the change in available vegetation since their original distribution (Vorster *et al*., 2017). In 2003, five elephants, consisting of one bull and two cows with their calves, were introduced onto SWR South from Shamwari Game Reserve in the Eastern Cape. Although the population gradually increased to nine, natural loses occurred during 2008 which reduced the population to six (Vorster *et al*., 2017). Due to the loss of the adult bull and a cow, a second herd of five elephants was introduced onto SWR from Bushman Sands in the Eastern Cape in 2009. This herd consisted of a large bull, two adult cows and two calves, which increased the herd to eleven individuals. By 2010, the population had increased to thirteen. In 2013, the herd was split into two. One herd of four was taken to Sanbona South, forming the Southern herd, while the remaining nine formed the Northern herd.

Two initial elephant studies were conducted by Mader (2005) and Erasmus (2008), to identify the possible impact of elephants on the larger herbaceous plant species and to determine which areas they utilised. However, at the time these prior studies were carried out only one small elephant herd of seven individuals was present in the reserve. Mader's study looked at the possible impact of the original five introduced elephants on trees a year after their introduction. The "wondering quarter" sampling method was utilised to sample over 1 000 trees, looking at size and degree of utilisation, and then comparing results to the baseline survey that was conducted three months post elephant re-introduction (Mader, 2005). The study by Erasmus (2008) to monitor elephant feeding behaviour on SWR, was limited to only one summer season from November 2006 to February 2007. Since then the space available to elephants on the reserve has changed (increased), as has the composition of the herd. For the duration of the current study, (December 2015 to May 2017),

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the total population consisted of five individuals in Sanbona South and twelve in Sanbona North. The Sanbona Wildlife Management team thus felt that it was necessary to re-examine the spatial usage and diet of the elephants on the reserve due to various historical changes, such as available space and changes in population sizes. Since it is known that elephants alter their feeding habits seasonally (Kos *et al*., 2012; Clegg and O'Connor, 2017) it was decided to monitor both herds two days a month over a 16-month period, from December 2015 to April 2017, in order to gather seasonal data, which included the start of a drought cycle.

This study, using the combination of Global Positioning System (GPS) satellite tracking and scan sampling and isotopic faecal analysis, was the first of its kind in the Little Karoo and has provided a better understanding of the spatial use and diet of the elephant populations on SWR. The Little Karoo is well known for its endemic plant species (Vlok & Schutte-Vlok, 2015). Many conservationists and botanists were therefore wary of the re-introduction of large herbivores into the confined area of SWR, particularly concerned with the potential damaging impacts they may have on vegetation if not able to migrate. Over utilisation of slow growing succulents, shrubs and trees could cause a shift in vegetation towards more unpalatable plants, and ultimately lead to a decline in species diversity (Todd & Hoffman, 1999; Anderson & Hoffman, 2007; Hanke *et al*., 2014; Vorster, 2017). Although studies on elephant diet have been conducted in other succulent areas, such as the Addo Elephant National Park, Asante Sana game reserve, as well as the baseline studies conducted by Mader (2005) and Erasmus (2008) it remains unknown what role the succulents play in the elephants' diet in the Little Karoo (Stuart-Hill, 1992; Minnie, 2006; Landman *et al*., 2007). Through this study we will be able to better understand plant utilisation and therefore the possible impacts of the elephants on Little Karoo vegetation, such as that found on SWR.

1.2. Statement

This study presents findings of spatial usage and dietary ecology of elephants on SWR in the Little Karoo, South Africa, 14 years post original introduction. Since the introduction of elephants onto SWR and the two initial elephant studies mentioned above, the elephant population has increased in size and the areas available to the elephants have changed. For this reason, a new study was necessary to determine spatial use and diet of the two elephant herds on SWR. A study of spatial

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usage was conducted over an 18-month period from December 2015 to May 2017, to determine the area of the reserve utilised seasonally by each elephant herd. Diet for each herd was determined over 16-month period utilising two methods, namely scan sampling and isotopic faecal analysis. The combined findings of these studies were used to make management recommendations by looking at possible high impact areas and impacts on plant species.

1.3. Research Goal and Objectives

1.3.1 Goal

To determine which areas elephants occupy within a small, fenced reserve in the Little Karoo, as well as their diet. This in turn will be used to provide Sanbona Wildlife Reserve with guidelines for elephant management based on scientifically and ecologically sound research.

1.3.2. Objectives

i. To identify and describe which areas the elephant herds are utilising and whether season influences elephant spatial usage in both Sanbona South and Sanbona North.
ii. To determine the elephants' diet and whether there is a difference between the diet of the Southern and Northern herds, and whether this is influenced by season.
iii. To determine what percentage of the diet is made up of browse versus graze and the importance of succulents in their diet as it is a semi-arid, succulent area.
iv. To provide management recommendations for the elephants on SWR.
v. To discuss the possible influence of artificial watering holes on elephants' spatial use.

1.4. Research Questions

1.4.1 Spatial use

i. Which habitats are the Northern elephant herd utilising?
ii. Which habitats are the Southern elephant herd utilising?

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iii. Does spatial use vary between seasons?
iv. Do weather patterns influence elephant spatial usage?

1.4.2. Dietary analysis

i. What is the elephants' diet on SWR?
ii. Does diet differ between the two herds?
iii. Is there a seasonal difference in the elephants' diet?

1.5. Expected Outcomes

1.5.1. Spatial use

It is expected that home ranges and core zones will differ between the Northern and Southern elephant herds. It is further expected that there will a difference in spatial use among seasons and that a variety of terrain and vegetation types will be utilised.

1.5.2. Dietary analysis

It is expected that browse (C_3) will make up the largest proportion of the diet of both herds and that seasonal vegetation utilisation will differ within each herd. It is also predicted that diet between the Northern and Southern herds will differ as a result of the different habitats available to each herd.

1.6. Thesis outline

This thesis comprises four chapters. Chapters Two and Three have been written as standalone manuscripts to facilitate publication in peer-reviewed journals. For this reason, there may be some repetition within the thesis.

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Chapter Two describes the elephants' spatial usage on SWR and looks at possible factors influencing habitat use such as water point placement.

Chapter Three describes the elephants' diet, determining whether the Northern and Southern herds utilise different plant species and which species are most preferred. This chapter also looks at whether the different seasons influence diet.

Chapter Four is a summary of the main research findings and provides management recommendations for Sanbona Wildlife Reserve.

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Chapter 2: The spatial usage of elephants on Sanbona Wildlife Reserve, Little Karoo

"It's not difficult to stay inspired when one is dealing with elephants. They are infinitely inspirational—long-lived, intelligent, intensely social, charismatic, empathetic, amusing, endearing and more. Anyone could be inspired by elephants without ever seeing them in the wild."
Cynthia Moss

2.1. Abstract

African elephants (*Loxodonta africana*) and other large herbivores historically roamed through large parts of South Africa, including the valleys of the Little Karoo. The seasonal migration routes have long since disappeared and most of these large herbivores now only occur within fenced reserves. With the reintroduction of elephants into Sanbona Wildlife Reserve in the Little Karoo in 2003 and 2009, it is important to understand elephant spatial usage within this semi-arid area. The use of GPS satellite collars has made it possible to determine the areas utilised by both

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elephant herds on the reserve. One individual in each of the two elephant herds was collared in November 2015, and data was collected over an 18-month period allowing for the calculation of home ranges and core zones. Similar to what was found in various other semi-arid reserves, the results indicated the importance of river lines within the core zones, however mountain slopes and open valleys were also utilised. Weather patterns were also recorded, allowing for seasonal movement patterns to be determined, and the influence of the drought to be assessed. The strongest driver for movement patterns in both herds seemed to be food rather than water. The results allow for the identification of areas of possible impact and help to determine population limitations on Sanbona Wildlife Reserve.

2.2. Introduction

As a large herbivore keystone species, elephants play an important role in the ecosystems they live in (Owen-Smith, 1988). Many of the habitats in which elephants are being studied have seen elephant migrations, and the adaptations and impacts on vegetation and habitats for many generations (Laws, 1970; Owen-Smith, 1989; Cumming *et al*., 1997; Chafota, 1998). However, in the Little Karoo these data have been absent since the extirpation of elephants from this area. There is very little information about elephants in this area, except for references to elephant hunts, rock art and buried elephant ivory found close to Oudtshoorn (Skead, 1980; Boshoff *et al*. 2002; Carruthers *et al*. 2008; Cordova and Avery, 2017). With the re-introduction of elephants into this semi-arid, fenced area in 2003 and 2009, it is vital to understand their spatial usage in order to determine the areas of preference within the confines of the small reserve and hence possible areas that may be impacted. Determining home ranges would also indicate the populations limitations within the available space (Plotz *et al*. 2016).

Elephant movements and spatial use have been studied throughout Africa and are found to be complex and non-random (Cushman *et al*. 2010; Douglas-Hamilton *et al*. 2005; Leggett, 2006; de Beer and van Aarde, 2008; Loarie *et al*. 2009b; Young *et al*. 2009a, b). Forage availability and quality, water, suitable vegetation cover and topographical characteristics are some of the key driving factors that influence elephant spatial use (Owen-Smith, 1988; Sukumar, 2003).

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Understanding the spatial usage of large herbivores, such as elephants, enables us to better assess the quality of habitat and corridors needed to protect them, as well as to conserve the habitats in which they occur (Areendran *et al*. 2011). In the northern Namib Desert, elephants utilised the river courses as their core zones and expanded their home ranges to incorporate the preferred flood plains during the wet season (Viljoen, 1989). Viljoen (1989) also recorded that elephants avoided certain areas such as the mountains and rocky plains, whereas all other habitats were used on a short-term, opportunistic basis. In both of Viljoen's studies (1988 and 1989) he found that elephants in the northern Namib Desert travelled long distances between preferred food and water. The author thus concluded that the availability and quality of vegetation was a major factor in the desert-dwelling elephant's spatial usage (Viljoen, 1989). Through spatial analysis, Young *et al*. (2009a), and Areendran *et al*. (2011) found that vegetation, for both food and shade, and water availability were two important factors determining elephant home ranges.

A variety of methods have been utilised to study spatial use of elephants throughout Africa and India, including walking and driving transects, aerial surveys, camera trapping, radio tracking (VHF) and Global Positioning System (GPS) satellite tracking techniques (Leuthold and Sale, 1973; White and Garrott, 1990; Areendran *et al.*, 2011; Trimble, *et al*. 2011). Harris *et al*. (1990) conducted a study looking at various home-range studies using radio (VHF) tracking data in order to determine how best to improve the method. Douglas-Hamilton (1998) studied elephant spatial usage using satellite GPS tracking in Kenya, as did Lindeque and Lindeque (1991) in Namibia and South Africa, and Harris *et al*. (2008) in Mozambique, to mention but a few. With the use of GPS tracking it is now possible to better understand large animal movement patterns (Douglas-Hamilton *et al*., 2005). Areendran *et al.* (2011) found that through the integration of GPS technologies and Geographic Information System (GIS) they could successfully assess the suitability of areas for wide ranging mammals such as Asian elephants. With the advancements in GPS tracking the influence that terrain has on elephant home ranges can be assessed. Wall *et al*. (2006) found that through overlaying GPS data onto digital elevation and surface gradient models they were able to determine that elephants in northern Kenya avoided steep slopes. It was concluded that this avoidance of mountain slopes was due to "energy barriers" for the elephants (Wall *et al.*, 2006). This means that if elephants avoid slopes of certain steepness the space available to them on mountainous reserves would be decreased. In the Caprivi it was noted that

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the elephants often selected their core zones at higher elevations, utilising the woody vegetation growing on many of the dune ridges of the eastern Caprivi Strip (von Gerhardt-Weber, 2011). Throughout these studies it was found that home ranges differ in size depending on habitat. In Tanzania, home ranges of less than 60 km^2 were recorded (Douglas-Hamilton, 1971) compared to the deserts of Namibia where home ranges of up to 9 000 km^2 were found due to increased aridity and therefore forage and water availability (Lindeque and Lindeque, 1991). Similarly, Leuthold and Sale (1973) found that elephant herds in Tsavo West and Tsavo East had different sized home ranges due to differences in environmental factors such as rainfall. Furthermore, they found a direct positive correlation between the movement of elephants and rainfall patterns (Leuthold and Sale, 1973). Seasonal changes, such as rainfall, have also long been associated with elephant habitat use (Laws, 1970; Leuthold and Sale, 1973, Bohrer *et al*., 2014). However, Shannon *et al*. (2010) found that elephants expand their annual ranges during years of above average rainfall and that annual rainfall has a larger influence on range size than season within five protected areas in South Africa, ranging from 50 km^2 to 900 km^2 (Pongola Game Reserve, Phinda Private Game Reserve, Tembe Elephant Park, Pilanesberg National Park and Hluhluwe imfolozi Park). In Kenya, Bohrer *et al.* (2014) found that elephants responded quickly to changes in water availability and vegetation change due to rainfall events. Elephants migrated from lower savanna and shrubland areas in the wet season when water and grazing were available, to higher elevations in the forests on the Marsabit Mountain during the dry season (Bohrer *et al.*, 2014). Similarly, elephants in north western Namibia responded to distant rainfall by moving before precipitation occurred within their area (Lindeque and Lindeque, 1991).

In arid environments, such as Namibia, it was found that elephants have the ability to be highly mobile and opportunistic in order to utilise the limited food and water available (Lindeque and Lindeque, 1991), with Viljoen (1989) recording elephants moving up to 70 km between forage and water over a 96-hour period. During the dry seasons within sensitive arid to semi-arid environments there is the possibility of a higher impact on vegetation due to the limiting factor of forage for herbivores (von Gerhardt-Weber, 2011). For this reason, von Gerhardt-Weber (2011) found that the areas of high conservation importance are the dry season core areas.

With the scant records available for large herbivore ecology in general in the Little Karoo, as well as non-existent historic natural plant growth and vegetation records, for comparative purposes, it

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is important to understand the spatial usage of elephants within this semi-arid to arid environment. The pressure on vegetation as a result of contained populations of elephants is more severe in arid areas. This is because these areas are less resilient than mesic systems and this can additionally be amplified in times of drought (Wiseman *et al*. 2004). For this reason, small to medium fenced reserves have to intensely manage their elephant populations to restore their natural spatial and temporal variability (van Aarde *et* al. 2006; Smit and Ferreira, 2010). Such management options include the management of artificial water sources (Chamaillé-Jammes *et al*. 2007), and the potential increase in available land (Van Aarde & Jackson, 2007).

Controlling artificial water sources as a tool to manipulate landscape use by large herbivores has produced mixed results (Laws *et al.* 1975; Chamaillé-Jammes *et al*. 2007; Loarie *et al*. 2009a). Smit and Ferreira (2010) found that there were higher densities of elephants closer to major rivers in the Kruger National Park (KNP) than to small streams and areas away from water sources. This was linked to forage availability, especially during dry periods. Loarie *et al.* (2009a) found that increased man-made water holes allowed for the expansion of elephants' dry season range as the available water allows herds to utilise previously inaccessible areas. This can lead to elephants utilising an area throughout the year, not allowing for periods of rest due to seasonal migration and this in turn has a negative impact on arid areas (Loarie *et al*., 2009a). These areas of impact are further concentrated around fixed water points creating possible piospheres, the size of which increases during dry seasons (Lange, 1969; Chamaillé-Jammes *et al*., 2009; Landman *et al*., 2012). An example of this was found in the forests of North Bunyoro, Uganda. Here Laws *et al*. (1975) found that elephants did not disperse through the forest as they naturally would with changing seasons due to permanent artificial watering points (hereafter referred to as AWPs). A similar effect was found in Majete Wildlife Reserve, Malawi, also a small fenced reserve, where AWPs less than 5 km from one another in preferred vegetation types, attracted such high traffic from large herbivores during the dry season so as to cause piospheres to merge (Wienand, 2013).

AWPs were increased throughout the KNP between the 1960's and 1990's, bringing 82.5% of the area of KNP within 5 km of water (Pienaar, 1998), and having a negative effect on sensitive fauna and flora species. (Owen-Smith 1996). Owen-Smith (1996) suggested that a 2:1 ratio of wet season to dry season concentration zones should be maintained, in which wet season concentration zones are areas more than 5 km from permanent water, and dry season concentration zones less

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than 5 km. Chamaillé-Jammes *et al*. (2007) found that the distribution of surface water was a driver of elephant distribution in Hwange National Park, Zimbabwe. Surface water manipulation could thus be used to maintain landscape heterogeneity as areas are used at different concentrations at varying distances from water, and therefore water can be used to influence elephant spatial and vegetation usage in large fenced reserves (Chamaillé-Jammes *et al*. 2007; Smit *et al*. 2007).

Fence lines around reserves hamper elephant movement and can increase pressure on vegetation due to a reduction in seasonal range shifts, thereby increased foraging pressure in a confined space (Duffy *et al*., 2002; van Aarde *et al*., 2006; van Aarde & Jackson, 2007; Loarie *et al*., 2009a). By increasing land availability of animals, especially over a heterogenous landscape with seasonal variation, one can increase seasonal migration (Owen-Smith, 2004). This increase in seasonal migration or movement allows for rest periods during which time vegetation can recover (Gaylard *et al*., 2003).

However, the question remains: what is enough land to sustain a small elephant population in the Little Karoo and how does this vary in different habitats, for example, the succulent karoo and fynbos? Through spatial analysis we can: i) identify areas to better understand the impact elephants have on more sensitive environments such as the succulent karoo, ii) determine which areas are most important for their continued persistence within a confined space in the Little Karoo, and iii) more effectively implement management strategies to conserve both elephants and the habitats they utilise.

2.3. Materials and Methods

2.3.1 Study area

Sanbona Wildlife Reserve (SWR) is approximately 57 600-hectares in size and is situated in the Little Karoo, a semi-arid area consisting of valleys and mountain ranges, with the Langeberg and Outeniqua Mountain ranges to the south and the Swartberg Mountain range to the north (Nell, 2003). SWR is located at 33°43’24’’ south and 20°36’55’’ east and is split in half by the Warmwaterberg Mountain range. The Warmwaterberg range forms part of the Table Mountain

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Group and primarily consists of sandstone and quartzite, whilst the lower lying hills and valleys are part of the Bokkeveld Group, consisting predominantly of sandstones and mud-rock (Almond, 2009). The eastern mountain ranges on SWR form part of the Witteberg Group (Vorster *et al.*, 2017). The Witteberg and Bokkeveld Group bedrock allows for more nutrient rich soils to form than the acidic soils derived from the Table Mountain Group (Almond, 2009). The elevation in the study area ranges from 430 m above mean sea level (a.m.s.l.) in the Brak River to 1 344 m a.m.s.l. on top of the Warmwaterberg range (Vorster *et al.*, 2017).

There are two in-situ weather stations located on SWR, one in the Sanbona South section and one in Sanbona North. Annual temperatures range from -2°C to 41.8°C. December, January and February (summer) are the region's hottest months with a mean maximum ambient temperature of 30.6 °C, and June, July and August (winter) are the coldest months with a mean minimum temperature of 4.9 °C (Vorster *et al*., 2017). During the colder winter months clear skies can result in frost covering the ground in the early morning. Autumn (March, April and May) brings cooler weather with warm to mild days and cooler evenings (8.9 °C to 28.9 °C). Similarly, September, October and November (spring) are marked with cool to mild day temperatures and cooler evenings (7.9 °C to 27.2 °C).

The area falls within both a winter and summer rainfall region, with typically frontal (cyclonic) rainfall in winter between June and August, and summer rainfall in the form of convectional thunderstorms occurring in November, January, February and March (Vorster *et al*., 2017). Occasional droughts are common in the area, although extended droughts are rare (Desmet and Cowling, 1999).

The Warmwaterberg creates a rain shadow effect on the northern part of the reserve, which receives an average of 195 mm of rain per annum, compared to the southern part with an average of 315 mm per annum. This variation in rainfall creates a vegetation difference between the two areas, with the north being dominated by Succulent Karoo, Central Mountain Fynbos, Thickets and riverine areas, and the south consisting of Renosterveld, Central Mountain Fynbos, and Thickets. The amount of rain and the season within which it falls, fluctuates yearly with the area experiencing wet and drought cycles. The previous drought cycle occurred between early 2008 and March 2011. Between 2011 and 2015 the reserve received an annual average rainfall of 224

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mm (in the north) to 336 mm (in the south). In 2016, the first year of the following drought cycle, only 109 mm was recorded in the North and 160.9 mm in the South. In 2017 rainfall decreased even further in Sanbona North to 98 mm but increased slightly to 177.2 mm in Sanbona South.

Surface water on the reserve is restricted to a number of small AWPs, the Bellair dam, and seasonal natural springs and rivers, which are dependent on annual rainfall (Figure 1.4). The main river

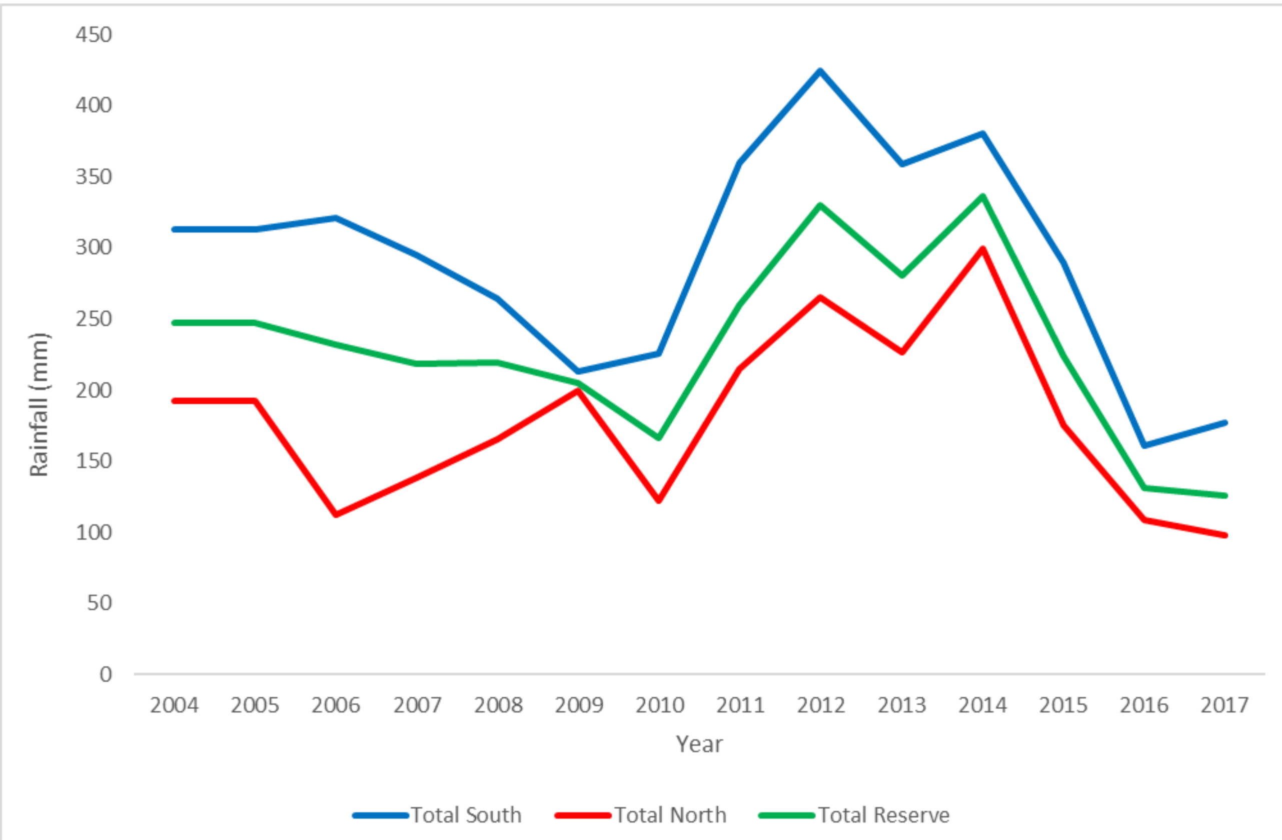

Figure 2.1. Average yearly rainfall (mm) for Sanbona North (red) and Sanbona South (blue), as well as the average across the reserve (green) from 2006 – 2017.

courses in Sanbona South are Matjiesbos, Kalkoenshoek and Gatskraal. The Brak, Sandleegte, Wilgerbos, Bobbejaankrans and Karee Vlakte are the dominant river courses and drainage lines in Sanbona North (Figure 1.4).

The low rainfall and varied geology of the area results in a high species richness of plants with 600 species occurring on SWR within 12 habitat types, namely: Apronveld, Arid Mosaic Renosterveld,

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Arid Mosaic Succulent Karoo, Gannaveld, Grassy, Mesic Renosterveld, Mosaic Asbosveld, Mosaic Grassy Fynbos, Quartz Apronveld, Quartz Gannaveld, Randteveld and River line and floodplains (Vlok and Schutte-Vlok, 2015).

The internal fencing of the reserve was erected to divide the north and the south along the Warmwaterberg range, allowing for specific mammal management and tourism approaches (Vorster *et al.*, 2017). Sanbona North comprises 24 600 ha and Sanbona South 23 500 ha. The two herds of elephants on SWR are therefore separated from one another and function independently. The Southern herd consists of five individuals and the Northern herd of twelve.

2.3.2. Satellite tracking

In November 2015, with permission, support and permits granted from CapeNature, the matriarch in the Northern herd and the large bull in the Southern herd were darted and immobilised from a helicopter by Sanbona Wildlife Reserve staff in strict accordance with ethical standards. Both elephants were fitted with GPS tracking collars with built-in Very High Frequency (VHF) transmitters manufactured by African Wildlife Tracking. The collars work with Inmarsat satellites on a mobile two-way communication platform utilising a two-way data satellite communication complete with GPS systems. The sampling rate was programmable and set to 1-hourly intervals from November 2015. The data from December 2015 to May 2017 were utilised for this study. Data base files were created by downloading the data points from the collar via the command unit to a laptop computer (DELL Inspiron 15, 3000 Series) twice a month. These data were analysed using ArcMap 10.5 to determine habitat utilization patterns. As the Southern herd only consisted of five individuals at the time of the study, the large bull remained with the herd, thus the GPS data collected from his collar reflected that of the breeding herd. It was decided to dart the bull and not the matriarch in the Southern herd as she already had a functioning VHF collar fitted in 2011 when the Southern herd was relocated from Sanbona North, albeit with an unknown remaining battery life.

2.3.3. Home ranges and core zones

The GPS data points and the resultant GIS map were used to plot the collared elephants' movements. Important spatial variables such as distances travelled between consecutive fixes,

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seasons and time of day (i.e. day or night) were calculated by analysing fixed data points. All of the hourly GPS data points for each herd recorded were utilised over the 18-month period to ensure a more accurate estimation of area utilised (Walter *et al*., 2015). Home ranges and core zones were calculated using i) the kernel density estimation method (KDE) in which each point has a density value which is calculated from the starting distance (Longley *et al*., 2005; Gibin *et al*., 2007) and ii) the grid square method, in which a grid is created over the area and the number of times an animal enters each cell is counted (Douglas-Hamilton *et al*. 2005) for comparative purposes. The KDE method estimates the probability or kernel density over each location point and removes outlying location points (Harris *et al*., 1990; Rodgers *et al*., 2005). The KDE method was chosen over the Grid Square method for the final home range and core zone calculation as its probability of spatial usage is more realistic (Leggett, 2005; Gibin *et al*., 2007). Although the Grid Square Method is useful at identifying utilisation hotspots within a given area it is not as accurate as KDE to estimating the boundary of home ranges (Stark *et al*., 2017). The KDE method was used in Erasmus' (2008) elephant study on Sanbona, thus by using KDE method the results can be compared to the previous study's. The probabilities 50% and 95%, were used to further identify the core areas (50%) and home ranges (95%) that the elephant herds were utilising (Silverman, 1986; White & Garrott 1990, Roux, 2006). These were then clipped to reserve boundaries (the available area for the elephants) and the sizes re-calculated. KDEs were determined for all four seasons during 2016, as well as for the summer (December to February) and autumns (March to May) of 2017 for both herds. The total spatial data for each herd was then overlaid onto DEM maps depicting the slopes and contours of the reserve to determine how the terrain influences spatial usage of elephants within SWR.

2.3.4. Land use types and habitat selection

The areas on SWR which the elephant herds were observed to utilise the most were determined utilising GPS coordinates as well as recordings from scan sampling. Areas of high animal usage on SWR were determined by Vorster (2017) through the compilation of animal census records (Figure 2.2). These records were compiled utilising data collected during annual aerial counts by helicopter from 2014 to 2016. (Vorster *et al*. 2017; Vorster 2017). Animals included in these census records were the larger herbivores such as elephants, white rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga)*, and various antelope

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species. The vegetation types dominating home ranges and core zones were described (Vorster *et al.* 2017).

KDEs were overlaid onto a vegetation map of the area (Vlok and Schutte-Vlok, 2015) to determine which of the thirteen habitat types were most utilised in each season, as well as throughout the study period. This was calculated by determining the number of points totalling each KDE within the Vegetation polygon using ArcMap 10.5.

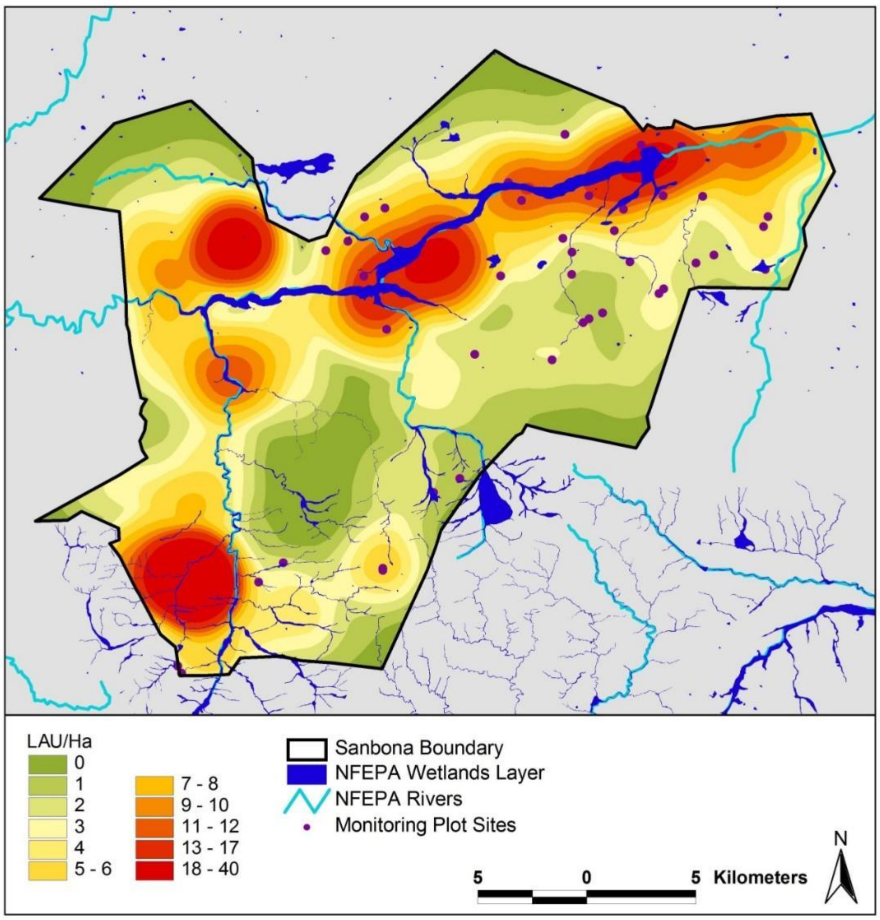

Figure 2.2. Map of animal census records of Sanbona for the period 2014-2016 showing the combined density of animals, indicating areas of potential higher impact. (Vorster, 2017).

All watering holes were mapped to determine the distance between available water and thus the distance elephants would have to travel between foraging and water. Each water point was given a buffer zone of 1 and 2 km to determine the percentage of the available area within 1 km and 2

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km from a watering hole as was done by Pienaar (1998) in the Kruger National Park. These areas were identified to determine which points play an important role within their home ranges and core zones.

2.3.5. Statistics

All statistical analyses were performed using Statistica, version 13 (©Statsoft Inc., 2016). To determine whether there was any significant statistical change in the size of the Southern and Northern herds' home ranges a two-sample t-test between percentages was conducted. To determine whether there was any significant difference between the spatial usage of each elephant herd in SWR in different seasons an ANOVA test was done. To determine whether there was a significant difference between habitats used by elephants in each herd as well as seasonal habitat-use in each elephant herd, a two-sample t-test between percentages was conducted. Lastly, in order to determine if waterhole usage by the elephant populations differed significantly on a seasonal basis a chi-squared test and an ANOVA test were performed.

2.4. Results

2.4.1. Satellite tracking

Hourly downloads were recorded from December 2015 to June 2017 for each herd. A total of 15 135 GPS locations were recorded for the Northern herd, and 14 341 GPS locations for the Southern herd. The difference in the total number of satellite data points was due to satellite transmission problems. Both these sample sizes are large enough to give an accurate estimation (Seaman & Powell, 1996).

2.4.2. Home Ranges and Core Zones

The Northern elephant herd's home range spreads over just less than a quarter of Sanbona North, 60.4 km^2, 25% of available space (Figure 2.3). The core zone of the Northern herd (4 km^2, 7% of home range) encompasses lower lying areas such as drainages, floodplains and valleys, however a few mountain slopes and hills are utilised (Figure 2.4). It incorporates the Brak river line and associated floodplains, and the area around Bellair dam (in particular the flood plains on the western side of the dam). These areas are the same areas utilised by higher Large Animal

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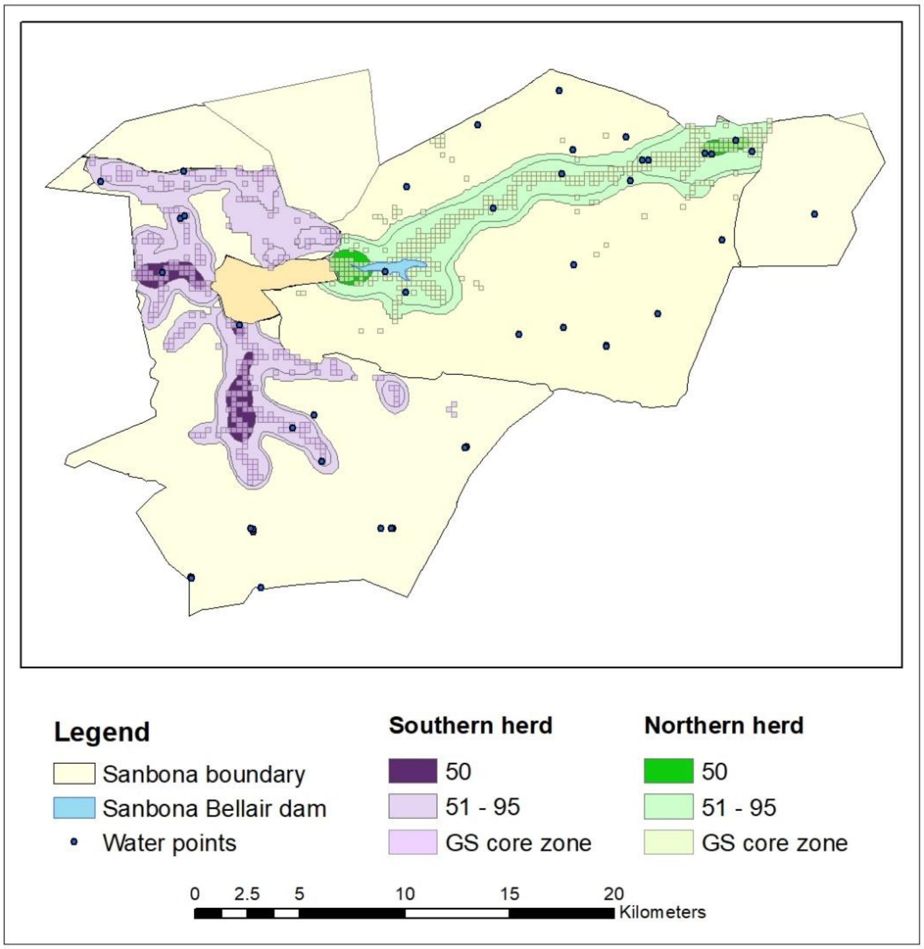

Figure 2.3. Kernel Density Estimate Home ranges (95%) and Core zones (50%) of Northern elephant herd (green) and Southern elephant herd (purple), as well as the core zone determined by the Grid Square method (GS) as a comparison (shown by the blocks).

Units (LAU) per hectare (Figure 2.2). Other major drainage lines and select valleys and gorges were also used regularly, however they were not included within the Kernel Density home range calculation but were included when utilising the Grid Square Method. The Northern herd's total home range stretches over seven of the eight vegetation habitats described in the area available to them, namely Apronveld, Arid Mosaic Renosterveld, Arid Mosaic Succulent Karoo, Gannaveld, Grassy, Quartz Gannaveld, Randteveld and River and Floodplain. The Southern elephant herd's home range encompassed 73.9 km^2, 31% of the total available area, comprised mostly of the major drainage lines within the available space and the northern reaches of Sanbona South. Their core zones (7.3 km^2, 10% of home range) were concentrated within the three major

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drainage lines, the Kalkoenshoek, Gatskraal and Matjiesbos, certain tributaries of these drainage lines, and the northern section of the available area (further known as Ratelfontein South) (Figure 1.3 and Figure 2.4). The Southern herd utilised eight of the nine vegetation habitat types within Sanbona South as described by Vlok and Schutte-Vlok (2015). These were namely Arid Mesic Renosterveld, Arid Mosaic Succulent Karoo, Gannaveld, Mosaic Asbosveld, Mosaic Grassy Fynbos, Quartz Gannaveld, Randteveld and River and Floodplain.

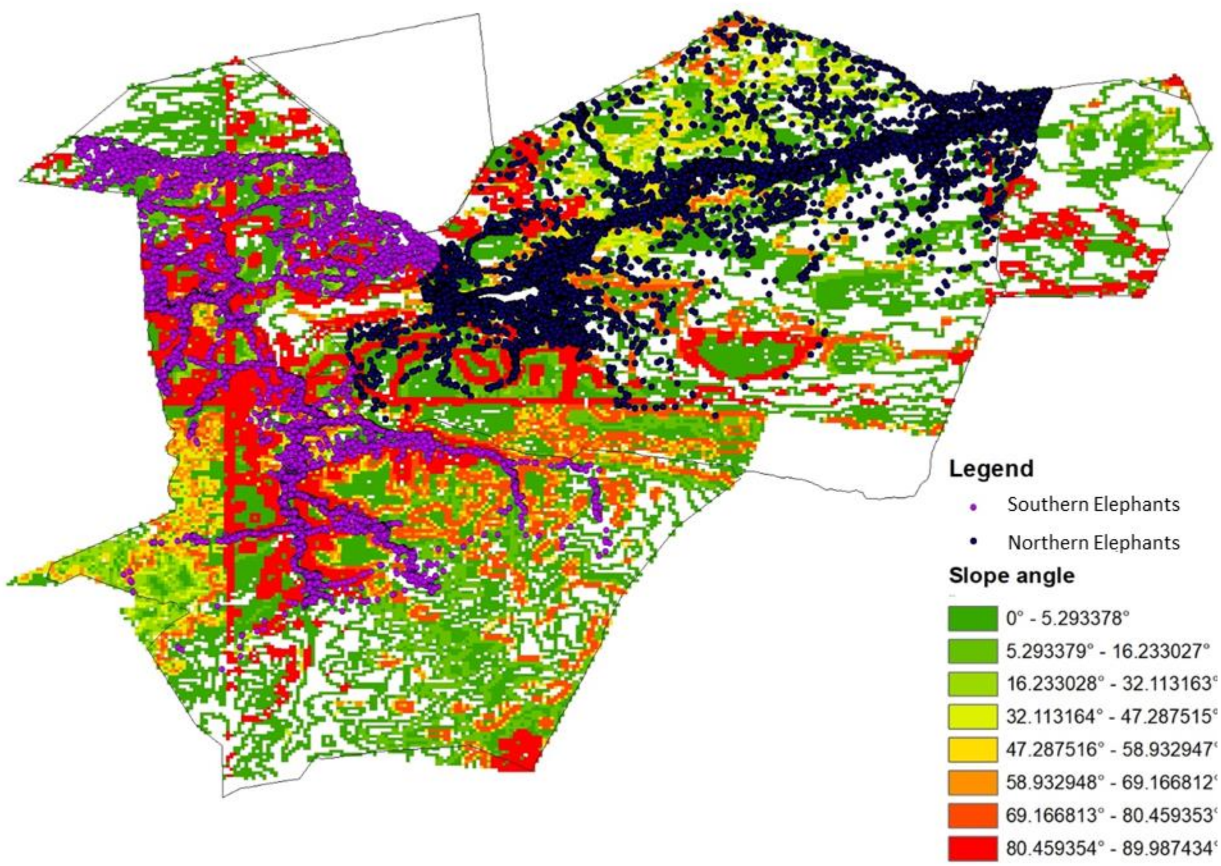

Figure 2.4. Total GPS data collected for the Northern (dark blue) and Southern herds (purple) over a 16 month time frame overlaid onto a DEM Hillslope map showing the angles of the slope through the depiction of a colour scale

A significant difference in habitat use between the Northern and Southern herd was found throughout the study period ($p < 0.001$).

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2.4.2 Seasonal Spatial usage

As SWR does not have a distinct wet or dry season, with rainfall months varying yearly, seasons were divided into summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Slight variations in spatial usage were seen between seasons (Table 2.1). Due to the fact that there are only two herds on the

Table 2.1. Percent of time the Northern and Southern elephant herds spent in each of the vegatation habitats described by Vlok and Schutte-Vlok for SWR in each season calculated by looking at GPS points logged for each herd during each season for the study period overlayed onto the Vlok *et al*. (2005) vegetation map

Northern herd							
HABITAT	Summer 2016	Summer 2017	Autumn 2016	Autumn 2017	Winter 2016	Spring	Average
Apronveld	9%	8%	10%	10%	13%	11%	10%
Arid Mos Renosterveld	0%	1%	1%	0%	0%	2%	1%
Arid Mos Succulent Karoo	4%	14%	8%	4%	6%	19%	9%
Gannaveld	17%	14%	9%	32%	10%	7%	15%
Grassy	0%	0%	1%	0%	0%	1%	0%
Mesic Proteoid	0%	0%	0%	0%	0%	0%	0%
Mesic Renosterveld	0%	0%	0%	0%	0%	0%	0%
Mos Asbosveld	0%	0%	0%	0%	0%	0%	0%
Mos Grassy Fynbos	0%	0%	0%	0%	0%	0%	0%
Quartz Apronveld	0%	0%	0%	0%	0%	0%	0%
Quartz Gannaveld	2%	2%	6%	1%	12%	4%	4%
Randteveld	15%	13%	21%	7%	21%	21%	16%
River	54%	48%	45%	46%	38%	36%	44%
Southern herd							
HABITAT	Summer 2016	Summer 2017	Autumn 2016	Autumn 2017	Winter 2016	Spring	Average
Apronveld	0%	0%	0%	0%	0%	0%	0%
Arid Mos Renosterveld	7%	11%	9%	12%	20%	20%	13%
Arid Mos Succulent Karoo	17%	12%	19%	14%	12%	10%	14%
Gannaveld	5%	16%	7%	5%	2%	8%	7%
Grassy	0%	0%	0%	0%	0%	0%	0%
Mesic Proteoid	0%	0%	0%	0%	0%	0%	0%
Mesic Renosterveld	0%	0%	0%	0%	0%	0%	0%
Mos Asbosveld	0%	0%	0%	0%	0%	0%	0%
Mos Grassy Fynbos	0%	0%	0%	0%	0%	2%	0%
Quartz Apronveld	0%	0%	0%	0%	0%	0%	0%
Quartz Gannaveld	3%	0%	5%	7%	9%	7%	5%
Randteveld	8%	0%	16%	20%	14%	12%	12%
River	61%	60%	43%	43%	43%	41%	49%

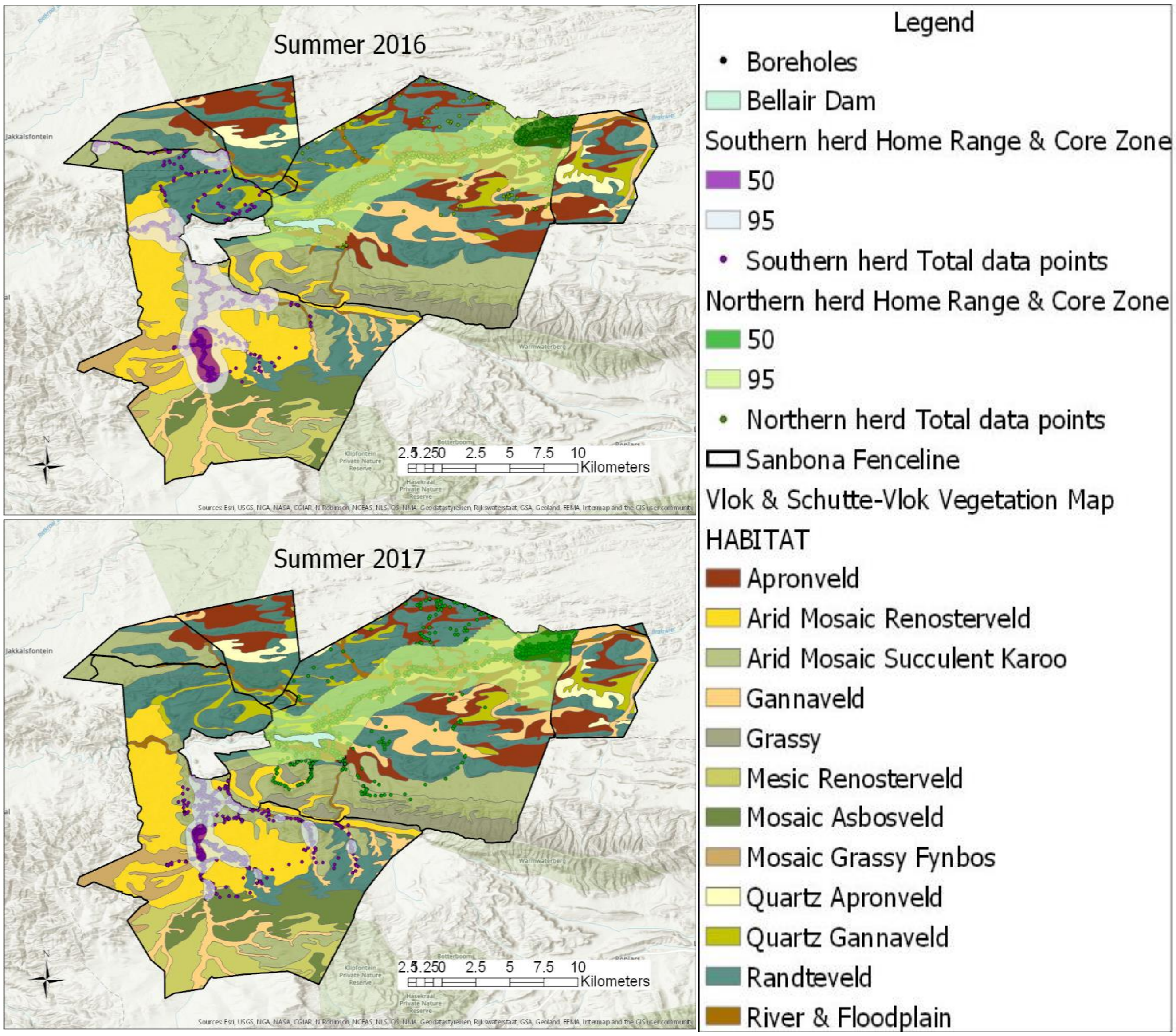

Figure 2.5. Home ranges (95% KDE) and Core zones (50% KDE) of the Northern elephant herd (green) and Southern elephant herd (purple) during the Summer of 2016 and 2017 and the total data points recorded for each herd during this time, overlaid onto Vlok *et al*. (2005) vegetation map for the area.

reserve the sample size over the 18-month period was not large enough to determine statistical significance between seasons. However, statistically significant differences were found amongst certain seasonal habitat usage within each herd during the study period (Table 2.2).

During the hottest time of the year, December to February (summer), both herds were observed utilising the more densely vegetated drainage lines ($p < 0.001$ for both summer 2016 and 2017, for both herds when comparing all habitat types to Rivers and Floodplains) (Table 2.1), spending a greater amount of time closer to preferred water sources. It was observed that the Northern herd spent more time on the western side of Bellair dam, as well as in the eastern part of the Brak river line, where *Vachellia karroo* and *Searsia* species are more prevalent. Both areas are close to water

Table 2.2. t – and p values depicting vegetation habitats utilised by each elephant herd between seasons for the duration of the study.

Northern Herd								
Seasons	**Autumn 2016: Autumn 2017**	**Summer 2016: Summer 2017**	**Spring 2016: Autumn 2016**	**Spring 2016: Summer 2016**	**Spring 2016: Winter 2016**	**Summer 2016: Autumn 2016**	**Summer 2016: Winter 2016**	**Winter 2016: Autumn 2016**
Degrees of Freedom	4316	4259	4366	4347	4377	4371	4382	4401
Habitat types								
Apronveld	t<0.001, p=1.000	t=1.169, p=0.243	t=1.078, p=0.281	t=2.198, p=0.028	t=2.036, p=0.042	t=1.128, p=0.256	t=4.23, p<0.001	t=3.119, p=0.002
Arid Mosaic Renosterveld	t<0.001, p=1.000	t=4.677, p<0.001	t=2.721, p=0.007	t=6.677, p<0.001	t=6.677, p<0.001	t=4.678, p<0.001	t=1.00, p<0.001	t=4.71, p<0.001
Arid Mosaic Succulent Karoo	t=5.518, p<0.001	t=11.465, p<0.001	t=10.647, p<0.001	t=4.442, p<0.001	t=13.029, p<0.001	t=5.565, p<0.001	t=3.036, p=0.003	t=2.601, p=0.009
Gannaveld	t=18.783, p<0.001	t=2.703, p=0.007	t=2.435, p=0.015	t=10.145, p<0.001	t=3.557, p=0.001	t=7.87, p<0.001	t=6.786, p<0.001	t=1.131, p=0.258
Grassy	t=4.618, p<0.001	t<0.001, p=1.000	t<0.001, p<0.001	t=4.678, p<0.001	t=4.71, p<0.001	t=4.678, p<0.001	t<0.001, p=1.000	t=4.71, p<0.001
Quartz Gannaveld	t=8.885, p<0.001	t<0.001, p=1.000	t=3.031, p=0.003	t=3.867, p<0.001	t=9.739, p<0.001	t=6.742, p<0.001	t=12.946, p<0.001	t=6.953, p<0.001
Randteveld	t=13.207, p<0.001	t=1.88, p=0.061	t<0.001, p<0.001	t=5.15, p<0.001	t<0.001, p=1.000	t=5.162, p<0.001	t=5.168, p<0.001	t<0.001, p=1.000
River and Floodplain	t=0.66, p=0.510	t=3.917, p<0.001	t=6.058, p<0.001	t=11.93, p<0.001	t=1.371, p=0.171	t=5.952, p<0.001	t=10.629, p<0.001	t=4.714, p<0.001
Southern Herd								
Seasons	**Autumn 2016: Autumn 2017**	**Summer 2016: Summer 2017**	**Spring 2016: Autumn 2016**	**Spring 2016: Summer 2016**	**Spring 2016: Winter 2016**	**Summer 2016: Autumn 2016**	**Summer 2016: Winter 2016**	**Winter 2016: Autumn 2016**
Degrees of Freedom	4307	4234	4351	4331	4359	4358	4366	4386
Habitat types								
Arid Mosaic Renosterveld	t=3.215, p=0.001	t=4.558, p<0.001	t=10.316, p<0.001	t=12.525, p<0.001	t<0.001, p=1.000	t=2.433, p=0.015	t=12.555, p<0.001	t=10.344, p<0.001
Arid Mosaic Succulent Karoo	t=4.416, p<0.001	t=4.612, p<0.001	t=8.425, p<0.001	t=6.741, p<0.001	t=2.11, p=0.035	t=1.719, p=0.086	t<0.001, p=1.000	t=6.407, p<0.001
Gannaveld	t=2.76, p=0.006	t=11.741, p<0.001	t=1.253, p=0.211	t=4.006, p<0.001	t=9.111, p<0.001	t=2.779, p=0.006	t=16.202, p<0.001	t=7.992, p<0.001
Mos Grassy Fynbos	t<0.001, p=1.000	t<0.001, p=1.000	t=6.652, p<0.001	t=6.621, p<0.001	t=6.663, p<0.001	t<0.001, p=1.000	t<0.001, p=1.000	t<0.001, p=1.000
Quartz Gannaveld	t=2.767, p=0.006	t=7.934, p<0.001	t=2.779, p=0.006	t=6.042, p<0.001	t=2.433, p=0.015	t=3.368, p=0.001	t=8.336, p<0.001	t=5.191, p<0.001
Randteveld	t=3.419, p=0.001	t=13.128, p<0.001	t=3.801, p<0.001	t=4.389, p<0.001	t=1.963, p=0.050	t=8.122, p<0.001	t=6.332, p<0.001	t=1.855, p=0.064
River and Floodplain	t<0.001, p=1.000	t=0.666, p=0.506	t=1.337, p=0.182	t=13.168, p<0.001	t=1.338, p=0.181	t=11.894, p<0.001	t=11.905, p<0.001	t<0.001, p=1.000

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and have canopy cover providing shade. GPS locations also indicated that the Northern herd utilised valleys and open plains adjacent to the Brak river line, utilising Randteveld ($p < 0.001$ when compared to all other seasons), Apronveld ($p < 0.03$ between summer and spring, and winter, but $p = 0.26$ between summer and autumn) and Gannaveld ($p < 0.001$) habitat types on the far eastern side of their habitat during the early hours of the morning and at night (Figure 2.5, Table 2.1 and Table 2.2). The Southern herd spent the majority of the summer months in the Kalkoenshoek river line, utilising adjacent drainages and valleys such as the Matjiesbos and Gatskraal river lines ($p < 0.001$) and open plains further to the north in the Arid Mosaic Renosterveld, Randteveld, Arid Mosaic Succulent Karoo and Quartz Ganna vegetation habitats (Table 2.2, Figure 2.5).

When comparing the two summer seasons of the Northern herd visually, there was an increase in the use of valleys and open areas away from the Brak river line and Bellair dam during the summer of 2017 compared to the summer of 2016 ($t < 0.001$, $p = 0.001$) (Table 2.2, Figure 2.6). The Northern herd utilised the same percentage of Sanbona North during both summers (31% of area available), however concentrating in different parts of the reserve (Figure 2.6). It was observed that the Southern herd's spatial usage was distinctly different in the summer of 2016, 39 km^2, 17% of available area, when compared to that of 2017, 18 km^2, 8% of available area ($p = 0.004$) (Figure 2.6).

As the weather cooled from March to May (Autumn) the herds utilised more areas across their home ranges, with the Northern herd concentrating more in the western part of their home range in 2016 (73.6 km^2) compared to 2017 when they utilised the Eastern range of the Brak river line more (37.9 km^2) (Figure 2.6). The Southern herd utilised a similar percentage of their available area in the Autumns of 2016 and 2017 (29% and 30%), with less GPS locations recorded in the recorded in the Arid Mosaic Renosterveld ($p = 0.015$) and Randteveld ($p < 0.001$) (Figure 2.6).

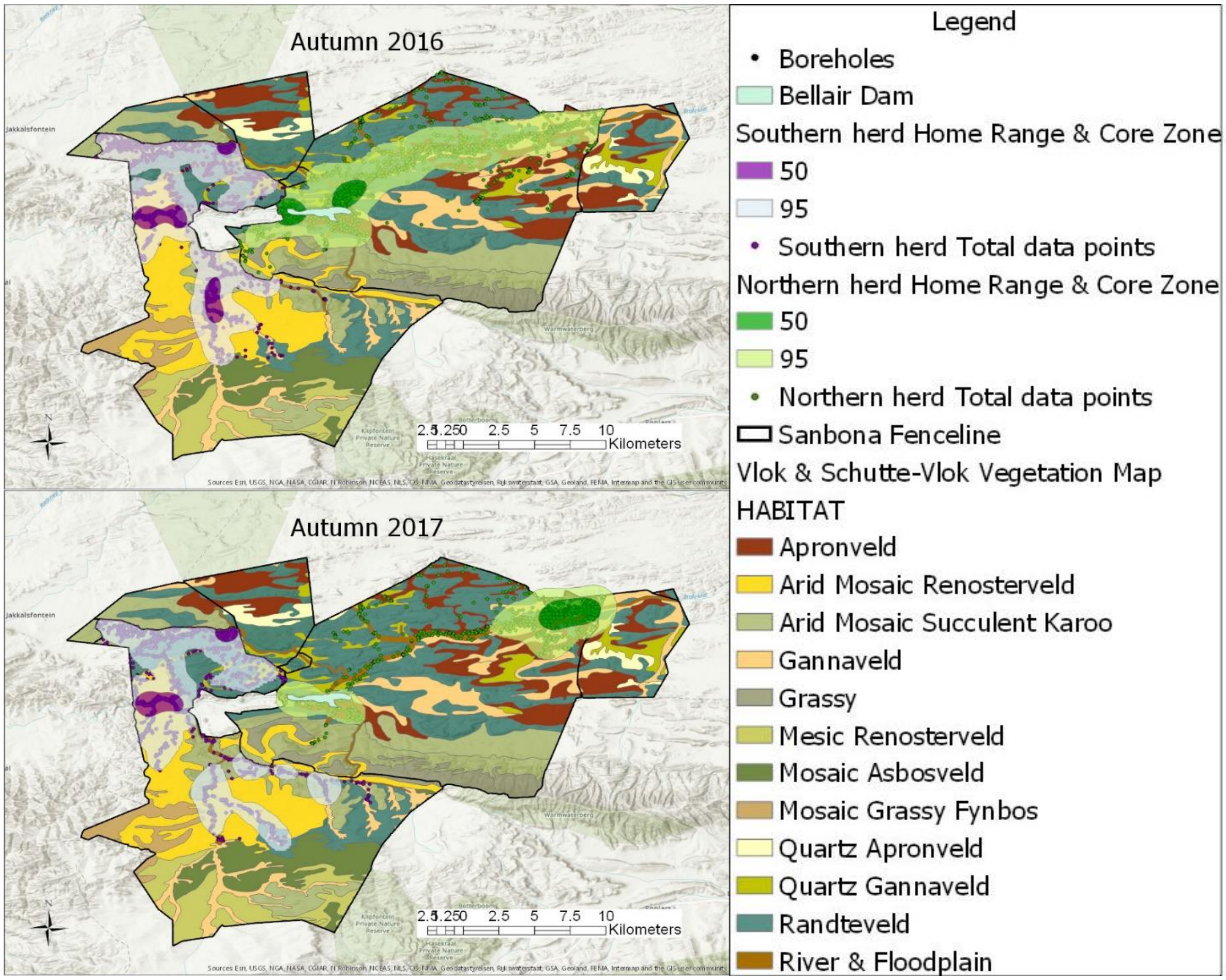

Figure 2.6. Home ranges (95% KDE) and Core zones (50% KDE) of the Northern elephant herd (green) and Southern elephant herd (purple) during the Autumn of 2016 and 2017 and the total data points recorded for each herd during this time, overlaid onto Vlok *et al*. (2005) vegetation map for the area.

River and Floodplain vegetation when compared to the summers ($p < 0.001$) and more locations recorded in the Arid Mosaic Renosterveld ($p = 0.015$) and Randteveld ($p < 0.001$) (Table 2.2, Figure 2.6).

During the cold winter months (June, July and August) cold fronts bringing rain usually approach from the west. In winter, the Northern herd spent most of their time on the western side of Sanbona North. They focused on areas to the west of Bellair dam as well as the gorges and valleys to the south-west of the dam, utilising 45 km^2, only 19% of the available space. Very little time was spent in the eastern parts of the Brak river line, as they preferred the western half as well as the valleys and open areas to the south of the river line, with only 38% of their GPS logs recorded in the River and Floodplain habitat, significantly less than summer and autumn ($p < 0.001$) (Figure 2.7). The Southern herd utilised the three major drainage lines in their home range – the Kalkoenshoek, Gatskraal and Matjiesbos river lines, as well as the open plains and valleys to the north of these drainages (Figure 2.7). The River and Floodplain habitats were used at the same percentages in winter and autumn (43% each, $p = 1$) and at similar percentage to spring, 41% (winter is not significantly different to spring, $p = 0.181$), but less than summer, 61% (summer is significantly different than winter, autumn and spring, $p < 0.001$). Interestingly, August was the only month in which the herds spent time near one another, where they were seen feeding on either side of the fence (with a dividing public access road between them) in Quartz Gannaveld and Randteveld vegetation.

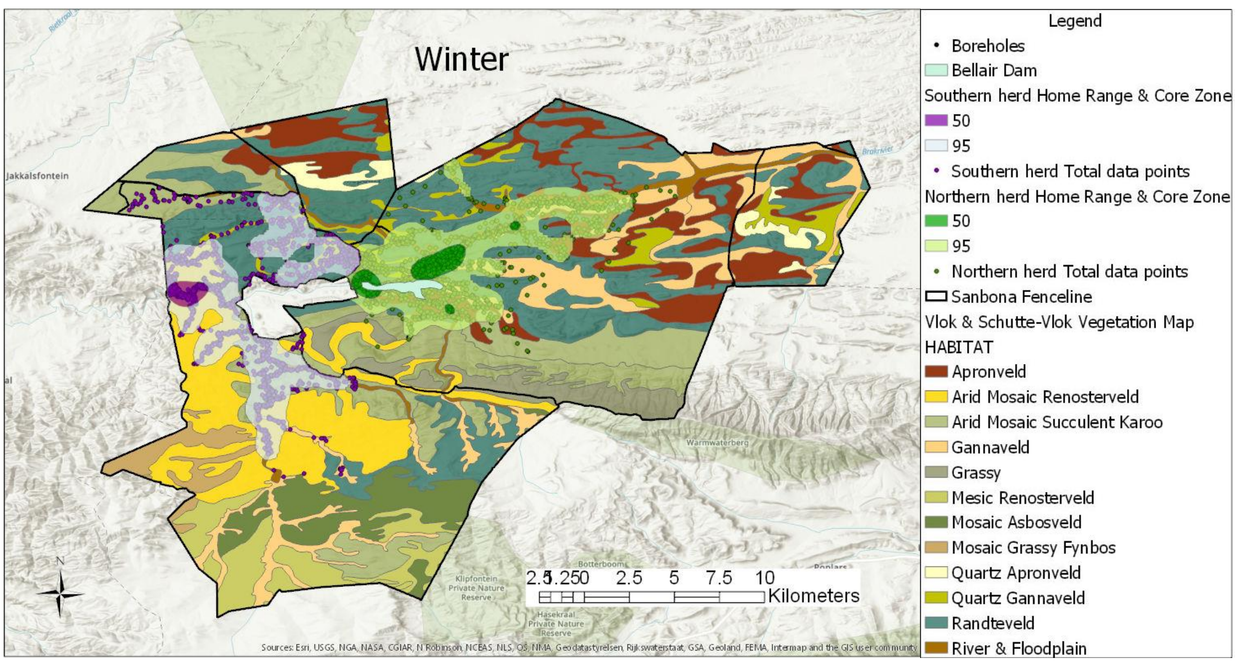

Figure 2.7. Home ranges (95% KDE) and Core zones (50% KDE) of the Northern elephant herd (green) and Southern elephant herd (purple) during Winter of 2016 and the total data points recorded for each herd during this time, overlaid onto Vlok *et al*. (2005) vegetation map for the area.

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During spring the Northern herd was more concentrated around Bellair dam (especially the western side of the dam), and the western half of the Brak river line, and were observed to occasionally utilise the valleys and open plains away from the main river line during the early hours of the morning and at night. The Southern herd's movements were very similar to their movements in autumn ($p = 0.905$), apart from increased movements into adjacent valleys and drainages from the main river line areas (Figure 2.9). They did however, have the largest seasonal home range during spring, 78 km^2, utilising 33% of their available space (slightly larger than both Autumn seasons, 68 km^2 and 70.1 km^2).

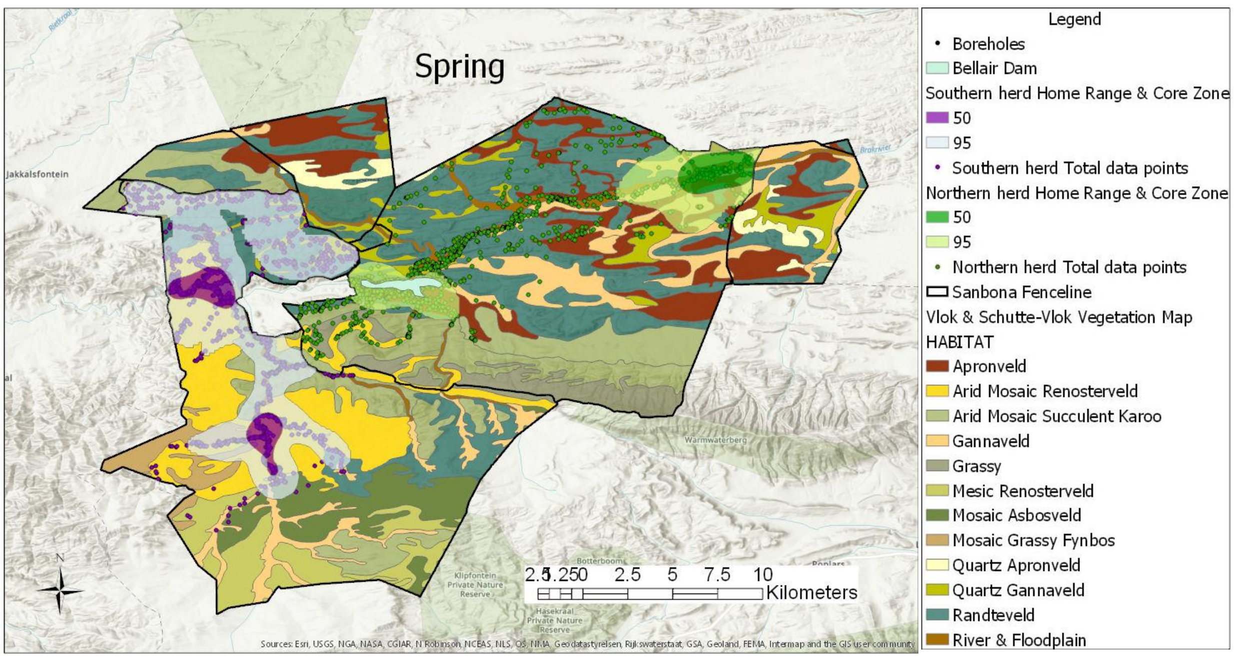

Figure 2.8. Home ranges (95% KDE) and Core zones (50% KDE) of the Northern elephant herd (green) and Southern elephant herd (purple) during Spring and the total data points recorded for each herd during this time, overlaid onto Vlok *et al*. (2005) vegetation map for the area.

Besides the distinct seasonal movements, a pattern of nocturnal movement was observed on a monthly basis during the full moon week for the Northern herd. The herd utilised the mountain slopes and valleys to the north of the main river line. Here it was observed that they fed for the night, finding signs of foraging, tracks and faeces within these areas the next morning. It is assumed that they were feeding in the area and returned to the river line in the morning, although feeding was not directly observed. These areas were only recently supplied with borehole water,

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thus during the study there was no access to water during these foraging trips. These areas consist of Randteveld vegetation, small succulent shrubs, and medium trees, such as *Euclea undulata*, *Schotia afra* and *Pappea capensis* (which is not found in the main drainage lines in which they usually feed). Nocturnal movement out of the full moon cycle was observed in other areas, such as the open plains to the South of the Brak river as well as to the South of Bellair dam.

Specific nocturnal patterns during full moon were not shown by the Southern herd, making it unique to the Sanbona Northern herd. The Southern herd did however also move out of the main drainage lines at night to feed in the adjacent valleys and open plains, returning back to the main drainage lines during the early morning.

2.4.4 The influence of artificial water points and rainfall

SWR has 17 AWPs across the reserve, 11 of which are in Sanbona North and six are situated in Sanbona South. There are also various natural pans and springs which are rainfall dependent, including Bellair dam. This brings the total number of watering points to 21 in Sanbona North and 14 in Sanbona South. Certain drainage lines also maintain pools of water after rains, such as the Kalkoenshoek river. Eight of the AWPs were constructed between March and June 2017, in preparation for the reintroduction of Black rhinoceros (*Diceros bicornis bicornis*), allowing the other animals to find food sources away from the major river lines.

Twenty three percent of both Sanbona North and South are within 2 km of watering points (Figure 2.10). The most utilised water points were in close proximity to preferred food sources, ranging from 0.4 to 8 km from water to hotspot feeding areas, with the furthest distance in the north between water sources measuring 22.5 km (as the elephant walks). Not all of the AWPs were equally utilised by the elephants. The most important sources of water for the Northern herd were Bellair Dam, six water points along the Brak river and two within the northern section. The Southern herd were more dependent on seasonal water pools and springs along the major river lines, but as these dried up they moved further afield to utilise newly provided AWPs.

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The rainfall data recorded showed that during the summer of 2016, Sanbona North received a higher rainfall (average of 29.1 mm) when compared to 2017 (6.4 mm). The opposite was seen in the South over the two summer periods. Sanbona South received an average of 11.4 mm of rain in the summer of 2016, compared to an average of 29 mm in 2017. The summer rainfall that occurred in the south in 2017 fell predominantly in the southern part of the Southern herd's home range.

In Sanbona North there was more rainfall to the east of the reserve over the summer months, with January 2016 having the highest amount of rain distributed across SWR. The autumn and winter rainfall of 2016 was spread across the Northern and Southern herd's home range, with Sanbona South receiving a higher rainfall than Sanbona North (159.5 mm and 143 mm respectively). Spring 2016 brought very little rain to the majority of the reserve with one exception in Sanbona South in November.

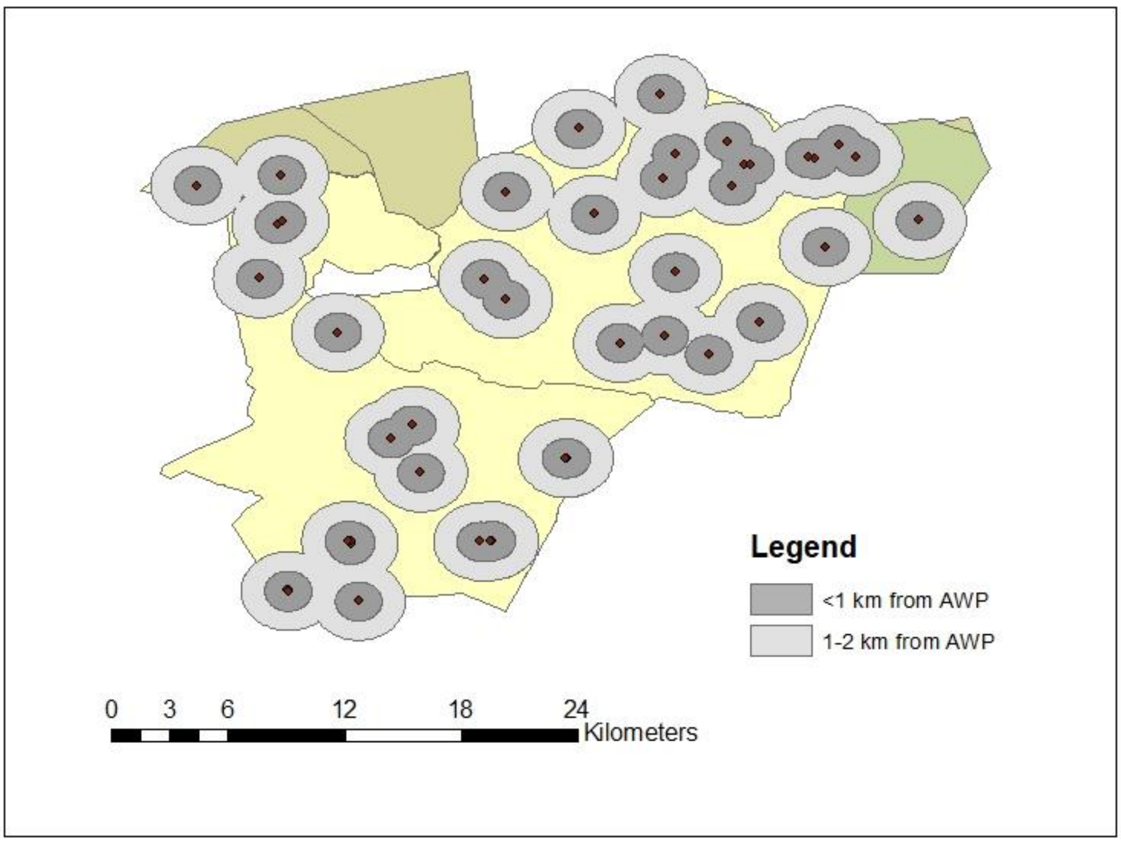

Figure 2.9. The distribution of both artificial and natural waterpoints on SWR with 1 km and 2 km buffers around each, where the management units occupied by elephants are indicated in yellow.

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2.5. Discussion

Due to elephants' foraging behaviour, smaller protected areas are at a higher risk of negative impacts on vegetation and the landscape as a whole, than larger protected areas (Lombard *et al*., 2001; Duffy *et al*., 2002). This 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). It has been recommended, that more arid reserves require larger available space for elephant populations to be viable without detrimentally impacting habitat structure and vegetation (Armbuster and Lande, 1993; Duffy *et al*.. 2011). The majority of reserves in South Africa with large herbivores such as elephant, are small, fenced reserves (Mackey *et al*., 2006). Fences restrict elephant migration patterns, thus potentially increasing the species' impact in an area (Loarie *et al.*, 2009b; Forrer, 2017). Therefore, a better understanding of the spatio-temporal movements of elephant populations in these small, fenced reserves, will allow for more effective management.

Habitat heterogeneity, local rainfall and spatial distribution of food and water all contribute to the size and structure of an elephant's home range (Lindeque and Lindeque, 1991; Leggett, 2006; von Gerhardt-Weber, 2011). Within the semi-arid to arid constraints of SWR food availability and water are expected to be two of the largest drivers of habitat selection.

2.5.1 Home ranges and Core areas

Elephant spatial usage on SWR varies between the two herds, with the Northern herd having a 60 km^2 home range and the Southern herd 74 km^2. Douglas-Hamilton (1971) calculated a 15 to 52 km^2 home range for elephants in Lake Manyara National Park and more than a 330 km^2 home range in Serengeti National Park. Leuthold and Sale (1973) recorded elephant herds in Tsavo East National Park utilising up to 1 580 km^2 as a home range and 350 km^2 in Tsavo West National Park. Elephants in Etosha National Park were found to utilise home ranges of between 2 851 km^2 and 18 681 km^2 and between 3 059 km^2 and 15 422 km^2 in the Kaokoveld (Lindeque and Lindeque, 1991). von Gerhardt-Weber (2011) found that elephants in the Caprivi, Namibia, utilised an average of 1 700 km^2 as a home range, with 9% to 14% of that being used as core areas. Therefore, in comparison to other arid areas, the herds on SWR utilised smaller areas, although they have a

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limitation due to fences. The elephants' core zones were a similar percentage of their home range to that in Namibia (von Gerhardt-Weber, 2011), with the Northern herd's core zone constituting 7% and Southern herd 10% of their home ranges.

For the duration of this study the region was in the most severe drought since the establishment of the reserve. By the onset of the 2017 summer season, many natural springs and pools had dried up completely or become very concentrated and brackish. Vegetation was also affected, with a distinct lack of new growth and a die back of many plants, thus reducing the amount of food available for the various animal species.

Similar to what Viljoen (1988) found in the arid northern Namib and as hypothesised, river lines and flood plains constituted the largest percentage of the core zones of both herds (Table 2.1). The elephants in both herds did not use their habitats randomly, and this correlates with many other studies (Douglas-Hamilton 1971; Leuthold and Sale, 1973; Ntumi *et al*., 2005). The major river line and surrounding flood plain in Sanbona North contain large amounts of preferred graze after good rains as well as dense vegetation in stretches. The main river lines in Sanbona South, as well as the minor river lines across the reserve, have dense vegetation growth due to higher quantities of available water, a shallower water table and deeper soils. Throughout these areas thick stands of woody browse occur from thicket level (such as *Euclea undulata*, *Lycium sp.* and *Carissa haematocarpa*) to taller trees (such as *Vachellia karroo*, *Searsia sp.*, *Olea europaea* and *Schotia afra*). This allows for increased browse and shelter. These areas are also often abundant in shrubby or creeping succulents. Watering holes, whether natural or man-made are often closely connected to these river lines.

Both herds' core zones correspond with many of the 'hot spots' determined as important foraging areas on SWR by Vorster (2017) through animal censusing techniques (Figure 2.2). These 'hot spots' primarily fall within the major river lines and floodplains and are areas that need to be continuously monitored as elephants and other large herbivores also utilise these areas, thus increasing the possible impact on the vegetation. According to Vorster (2017), the high intensity use areas in Sanbona North are the Brak river line and the area around Bellair dam, whilst the Kalkoenshoek and Gatskraal river lines, and the valleys to the North East of the Gatskraal, are high intensity use areas in Sanbona South. These areas correspond with the home ranges and core

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zones of both herds. The only 'hot spot' in Sanbona South that does not correspond to the Southern herd's home range is that in the south western corner.

Although river lines and flood plains are the preferred areas of utilisation (49% in Sanbona South and 44% in Sanbona North during the study), valleys and open plains away from the main river line areas were also utilised by both herds (%). The Northern herd's home range stretches into the northern and southern valleys of the reserve, crossing over ridges, feeding along valleys, over slopes and along open plains. Many of these foraging trips were observed to occur only at night and in the early hours of the morning, with the herd returning to the Brak river line in the morning. Most of the use of the valleys further north of the Brak river line coincided with the week around full moon; this is possibly due to increased visibility. This selection of open areas correlates with the findings of Kinahan *et al*. (2007) in Zambia, where breeding herds of elephants often selected for open areas at night, thus helping to release body heat, a behavioural thermoregulatory strategy. In northwest Namibia (Leggett, 2009) and in Uganda (Wyatt and Eltringham, 1974) elephants were found to be active through the evening with a rest period between 02:00 and 04:00.

Additionally, certain mountain slopes also fell within the core zones. These slopes were utilised to forage during the early mornings, late afternoons and during cooler, overcast weather when the elephants were in that particular area. This correlates with the opportunistic foraging behaviour of elephants in Namibia (Lindeque and Lindeque, 1991; von Gerhardt-Weber, 2011). Kinahan *et al*. (2007) found that ambient temperatures were one of the drivers when elephants chose certain landscapes in which to be active. At higher ambient temperatures elephants selected landscapes where the increase in temperature was slower (Kinahan *et al*., 2007). In contrast, Wall *et al.* (2006) found elephants in Kenya to avoid utilising mountain slopes entirely. As stated by the latter authors, mountaineering is more energetically expensive than feeding on flatter terrain. However, the plant species composition is different on the slopes than on the low-lying areas on SWR (Vlok *et al*., 2005). Therefore, in order to feed on these different plant species, while minimising the costs of temperature control during this exertion, the elephants utilise the slopes during cooler parts of the day, or during cooler weather. Leggett (2009) and Guy (1976) also found that elephants' peak activity was during the cooler parts of the day.

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The Southern herd also utilised valleys and plains to the north of the main river lines, crossing over ridges and spending time on mountain plateaus and in open valleys and plains (Figure 2.3). These areas consisted primarily of low browse made up of shrubs, forbs, annuals and succulents, with small clumps of trees. As with the Northern herd, much of the movement over ridges and on top of mountain plateaus occurred in the cooler times of the day or during cooler weather.

As expected, the area sizes of the home ranges and core zones differed between the Northern and Southern herds. This is not surprising as the area available to each of the herds differed substantially with regards to climate, geology, terrain and habitat types, to mention but few.

2.5.2 Seasonal movements and rainfall

Depending on the habitat and climate elephants will either find suitable vegetation to feed on in proximity to water sources or travel large distances between suitable water and vegetation (Viljoen, 1989; Loarie *et al*., 2009; Smit and Ferreira, 2010). During the cooler seasons, both herds spent more time in open areas and on slopes than during the heat of the summer months. This is likely due to the fact that elephants need to seek shelter from the heat during summer, thus spending large amounts of time in areas with a higher canopy cover, whilst being able to forage for longer in the open during the cooler months. River line areas with higher canopy cover on SWR are also areas associated with or close to watering holes. As African elephants are a water dependent species their habitat selection is influenced by water availability (de Boer *et al*., 2000; Stokke and du Toit 2002; Chamaillé-Jammes *et al*., 2007). Wittemyer *et al*. (2007) found that elephant herds in northern Kenya spent more time closer to water sources during the dry season (< 1 km) and within 100m during the hottest times of the day.

Within the core zone of the Northern herd there are nine water sources along, or within close proximity to the main river line, the Brak river. During the summer of 2016 the Northern herd spent most of their time utilising the Brak river, thus never being further than 1 to 3 km from a given water source. During the winter of 2016, the herd spent more time in the western part of their home range. This coincided with the winter rainfall that predominantly fell in that area (recorded on SWR by the ecologist) and thus possible increased vegetation growth. Based on

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observations, as the drought intensified towards the latter part of the 2017 summer, the Northern herd spent some time in the valleys away from the main river lines (54% during the summer of 2016 compared to 48% during 2017, $p < 0.0001$). It could be speculated that this could be as a result of the new AWPs that were constructed during the study period. It was observed that for the autumn of 2017, the Northern herd utilised the eastern section of the Brak river and reserve after localised showers in March filled up watering holes and created an additional green flush of grass growth as well as growth in the Gannaveld habitat (32% in autumn 2017 percent compared 14% in summer 2017 and 8% in autumn 2016).

It can be hypothesised that water availability (both natural and artificial) also influenced elephant movement within Sanbona South. Rainfall events during autumn, winter and spring of 2016, made seasonal watering holes available to the Southern herd in the northern part of their home range. Throughout most of 2016, natural pools and springs in the Kalkoenshoek river line and adjacent drainages were plentiful. This, coupled with the high food availability within these drainages, are possible reasons as to why the Kalkoenshoek, Gatskraal and adjacent valleys and river lines form part of the Southern herd's core zones. These rainfall events also created vegetation flushes, and this attracted the Southern elephants, with their more frequent movement and use of the northern valleys and open areas. However, with the prolonged drought most of these pools and springs eventually dried up or left concentrated pools, often covered in algae. It was observed that the Southern herd's movement between food and water changed throughout the study period as natural water sources dried up and were replenished with rain. As was found in Tsavo National Park, Kenya, (Leuthold and Sale, 1973) and in the Kunene Region of Namibia (Leggett, 2005), the distinct change in the area utilised between the two different summer seasons was likely caused by rainfall in the south-east of the Southern elephants' home range, increasing water availability and plant growth. Similar to Lindeque and Lindeque's (1991) observations in the northwest of Namibia, where elephants responded to distant rainfall, some of the valleys were only used when there was rain in those areas, as was noted in the summer of 2017.

Seasonal variation within each herd was noted, with certain seasons being more pronouncedly different than others. It is further speculated that rainfall influences the elephant herds' spatial usage as vegetation growth is also affected, as well as the establishment of fresh water sources within Sanbona South.

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2.5.3 Water point usage

Elephants' dependence on water varies in different habitats depending on the availability (Viljoen, 1989; Loarie *et al*., 2009a; Chamaillé-Jammes *et al*., 2007). As water resources dry up during dry seasons and droughts, elephants are expected to move further afield to find suitable water (de Boer *et al*., 2000; Chamaillé-Jammes *et al*., 2007; Loarie *et al*., 2009a; Smit and Ferreira, 2010). Many reserves utilise AWPs during dry seasons and droughts to increase dry season forage available to animals by facilitating movement away from the river lines and towards less utilised areas of the reserves and for tourism purposes (Chamaillé-Jammes *et al*., 2007; Loarie *et al*., 2009a; Smit and Ferreira, 2010).

The increase in the number of AWPs away from the main river line in Sanbona North due to the drought and in preparation for the future introduction of Black rhinoceros, allowed for less impact on the Brak River line system, which had previously been the largest animal 'hot spot' due to availability of graze, browse and water (Vorster 2017). The placement of the AWPs in and around the Brak River in Sanbona North was within 5 km of favoured vegetation (River and Floodplain vegetation habitat as well as Randteveld) and between 1 and 7 km from one another. Four of the AWPs in Sanbona North were located away from the major river lines, with two situated to the north and two to the south of the Brak River line. It was observed that the Northern elephant herd mostly utilised the AWPs along the Brak River line as well as the Bellair Dam. This implies that the dense vegetation cover along these areas as well as the vegetation available was an important driver in water hole and spatial selection. The new AWPs to the south of the river line were utilised towards the end of summer 2017 as the drought intensified, as observed through their usage of these valleys once the AWPs were constructed compared to previously. This could be attributed to the herd moving away from the preferred areas in order to access specific vegetation growth such as Arid Mosaic Succulent Karoo.

Most of the AWPs in Sanbona South were not within the Southern herd's core zone. Only two AWPs were within the herd's preferred foraging areas and these two AWPs were opened in June 2017. It appears that the Southern herd relies more on natural springs and pools along river lines.

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This results in localised feeding around these water sources and seasonal movement dependent on rainfall. The distinctive movement from one area to the next, dependent on season and weather, would thus allow areas to rest and recover. This emulates the findings in Hwange National Park, Zimbabwe, (Chamaillé-Jammes *et al*., 2007), suggesting that in SWR, water availability and the management thereof can help create more natural movements of the Southern elephant herd.

Areas around AWPs situated in historically impacted areas are more susceptible to piosphere development (Andrew, 1988). In areas where water points are within 5 km from one another there is a chance that the piospheres may merge due to high usage of elephants and other herbivores (Owen-Smith, 1996; Landman *et al*., 2012). This is more evident within the Northern elephant herd's home range than in that of the Southern elephant herd. As 89% of the water points are within at least three kilometres from another water point, the risk of piospheres merging is large. However, not all of the water points were utilised simultaneously throughout the study period as 10 of these in Sanbona North and 8 in Sanbona South were dependent on rainfall.

2.6. Conclusion

Surface water and available, quality forage are the most important factors influencing elephant spatial usage (Chamaillé-Jammes *et al*., 2007; Smit *et al*., 2007). Viljoen (1988) suggests that the major driving factor of habitat selection in desert-dwelling elephants is vegetation availability and quality over location of water. It was found that the Southern herd more readily moved larger distances between food and water sources during the day, than the Northern herd. Within fenced reserves the placement and management of surface water can affect the seasonal movement and vegetation usage of elephants by allowing them to stay within an area throughout seasons or to move between seasonal availability.

It was observed, however, that both herds chose their areas of utilisation each season according to vegetation availability more so than water. This is particularly evident in the 'exploratory' movements of the Northern herd during the last six months of this study as vegetation quantity and quality decreased due to the drought. The seasonal use of vegetation by elephants has been suggested to reduce their impact within an area (Babaasa, 2000). As SWR falls within an arid to

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semi-arid area seasonal usage is very important, as the timing and spatial dispersal of rainfall are indefinite and therefore the availability of palatable vegetation variable (Viljoen, 1989; Leggett *et al*., 2002; Leggett, 2006).

The main drainages and surrounding plains and valleys play the most important role in the elephants' spatial usage; many of these areas have estimated high values of large animal units for the Little Karoo. Although the mountain slopes are used less, these areas often have specialised vegetation (Vlok *et al*., 2005; Agenbag, 2006) that could be sensitive to prolonged feeding by elephants. This emphasises the importance of monitoring the impact on the vegetation within the core zones of both elephant herds. Only the Northern elephants showed specific nocturnal activity patterns within the week of full moon, utilising areas away from their diurnal forage areas.

As this study is a base line study for the spatial usage of elephants on SWR it is important to continue monitoring areas of high elephant usage for possible negative impacts, such as piospheres. Many of these areas are also preferred by other large herbivores and this could aggravate the impact.

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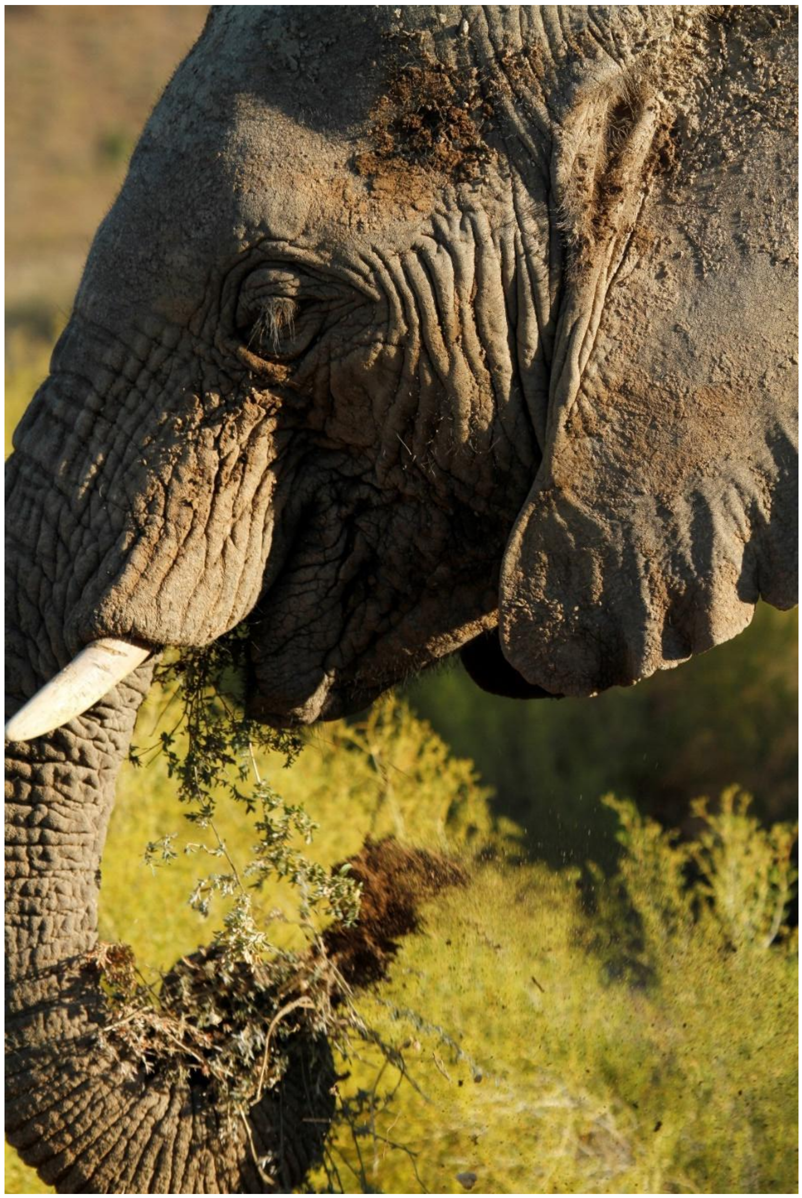
Chapter 3: Diet of elephants on Sanbona Wildlife Reserve, Little Karoo



"If elephants didn't exist, you couldn't invent one. They belong to a small group of living things so unlikely they challenge credulity and common sense." — Lyall Watson

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3.1. Abstract

As megaherbivore mixed feeders African elephants (*Loxodonta africana*) need to consume large quantities of a variety of vegetation. Elephants' diet on Sanbona Wildlife Reserve, South Africa, consisted of woody browse (C3), succulent browse (CAM) and graze (C4) as found in other succulent biomes. The impact of elephants on slow growing succulent and woody browse species, as recorded elsewhere, is a concern for the reserve. This study aims to better understand, through the use of scan sampling and isotopic faecal analysis, i) the diet of elephants on Sanbona Wildlife Reserve in the Little Karoo, ii) whether there is a difference in the diets of the two herds located on the reserve, and iii) whether there are seasonal differences in diets. Scan sampling recorded at least 94 species, from 64 genera of plants which constituted the elephants' diet, higher than previous studies indicated. Through the combination of scan sampling and isotopic faecal analysis it was made clear that the ratio of C3, C4 and CAM plants in the diet differed between the two herds and there were seasonal differences in diets. Browse (67%) constitutes the highest percentage of forage in overall diet, with graze (18%) and succulents (15%) constituting similar quantities. The results of this study will help Sanbona Wildlife Reserve to better understand the ecological requirements of elephants, as well as the impact on sensitive, slow growing plant species on the reserve. This information will allow wildlife managers to make informed decisions with regards to population management strategies.

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3.2. Introduction

Historically elephants occurred in a non-permanent capacity within the Succulent Karoo and Fynbos biomes (Ebedas *et al.*, 1995; Boshoff and Kerley, 2001). The Succulent Karoo and Fynbos biomes have some of the highest levels of plant diversity and endemism on the African continent (Van Wyck and Smith, 2001).

Elephants are megaherbivore mixed feeders feeding on both herbaceous and woody vegetation (Sinclair *et al*., 2006; Stephenson, 2007). They need to consume a variety of plant species to ensure that they absorb the necessary range of nutrients as they lack a rumen (Olivier, 1978). Due to the quantity of food they require and as a result of their digestive system, they are often seen as 'wasteful' feeders, but are in fact an important keystone species (Laws, 1970; Cumming *et al*., 1997; Selous, 2006). The balance between being a keystone species and having a negative impact on vegetation is an equilibrium that must be kept (McShea *et al*., 1997; O'Connor *et al*., 2007).

As large, generalist non-ruminant herbivores with a relatively fast digestive passage, elephants are adapted to feed on plants that are high in abundance but often of a low nutritional quality (Bell, 1971; Sukumar, 2003). The selection of plant species is therefore often dependent on availability, thus the plant species utilised more frequently or in larger proportions, is not necessarily the "preferred" food plant (Bax and Sheldrick, 1963; Field and Ross, 1976; Owen-Smith, 1988; Cerling *et al*., 2004). Guy (1976) found that the majority of plant species recorded in elephant diet was proportional to the plant's abundance, but elephants also select certain plants species and ignore others (Sukumar, 2003). Thus, due to the lack of a rumen (which would synthesise amino acids and vitamins for ruminants) elephants have to consume a variety of supplementary species to fulfil their nutritional requirements along with forage that provides for bulk feeding (Bax and Sheldrick, 1963; Oliver, 1978; Barnes, 1982).

Many studies have shown that seasonal changes influence elephant feeding ecology, usually due to the availability of forage species and nutrient availability, as well as the palatability of plants (Cooper and Owen-Smith, 1985; Holdo, 2003). One large shift is in the proportion of grass to browse in the diet between wet and dry seasons (Field and Ross, 1976). In Uganda, Field and Ross (1976) recorded grazing constituting 57% of the diet in wet months and decreasing to 29% during

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dry months, with browse of trees, shrubs and herbs making up 71% of the diet in dry months. Barnes (1982) found similar trends in Tanzania. Owen-Smith and Chafota (2012) found that elephants in the Chobe area of Botswana, shifted their diet from high percentages of leaves, shoots and grass in the wet season to high percentages of twigs, bark and roots during the hotter, drier seasons. In another study, in the Maputo Elephant Reserve, it was found that browse was more important than grass in the elephants' diets during both the wet and dry seasons (De Boer *et al*., 2000). Thus, elephant diet is directly determined by habitat, rainfall and seasonality and their foraging patterns often correlate to proximity of water (Laws, 1970; Barnes, 1982; Birkett and Stevens-Wood, 2005; Loarie *et al*., 2009).

In northern Botswana it was shown that even at high elephant population densities, there are situations in which elephants do not have a detrimental impact on tree species survival (Ben-Shahar, 1996). Duffy *et al.* (1999) found that tree abundance appeared to be the dominant reason for tree species utilisation in breeding herds, and also that even though some species were heavily browsed upon, actual destruction by elephants was low. At Mpala Research Centre it was concluded that food availability was not the sole driver of elephant diet, and that social dynamics played an important role in movement and therefore diet (Booth *et al*., 2014). Duffy *et al.* (2002) reported similar findings in Pongola Game Reserve, in that elephant impact on tree species was non-homogeneous even in regions with similar characteristics. The authors state that this could be due to population dynamics, as plant usage by bulls and cows differs.

Various methods have been utilised to determine diet of elephants, including transects, backtracking, direct animal observations, fixed point photography with respect to vegetation structure change and isotopic analysis of plants, dung, ivory and bone (Guy, 1976; Viljoen, 1989; de Beer *et al*., 2006; Minnie, 2006; Allen, 2009). Direct animal observation studies on the dietary requirements of elephants have utilised focal or scan sampling methods. In 1974, Altmann conducted a study comparing seven different monitoring methods and found focal sampling to be the most accurate when monitoring primate behaviour. Scan sampling is considered an alternative method in which all visible individuals' activities are recorded for a predetermined amount of time (Altmann, 1974; Gilby *et al*., 2010). Although focal sampling is an accurate sampling method, scan sampling is seen as a more practical alternative, especially with regards to animals that are completely habituated to human observers (Gilby *et al*., 2010).

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Guy (1976) conducted the first recorded focal sampling study of elephant diet on foot in the Sengwa Reserve in Zimbabwe in 1973 (Sukumar, 2003). Guy (1976) studied the elephants' feeding habits and found that they consumed 133 different plant species belonging to 95 genera and 4 plant families. Bax and Sheldrick (1963) recorded over a 100-plant species that were utilised by elephants in Tsavo Royal National Park (East), Kenya utilising direct animal focal sampling. Similarly, Barnes (1982) conducted an elephant diet study, utilising the Scan sampling method. In order to best identify which plant species the elephants consumed, Barnes (1982) observed the elephant herds for 4 to 8 hours, starting with the first elephant they found, and all plant species utilised were identified and recorded, recording individual bulls at 1-minute intervals and cows at 5- minute intervals. Other study methods have been utilised to analyse elephant diet. Viljoen (1989) utilised transects to identify 33 woody plant species that were eaten by elephants in the northern Namib Desert and in the Eastern Cape, South Africa, 144 plant species were found to be utilised by elephant herds in Addo Elephant National Park through the use of microhistological analysis (du Toit, 2015). Elephants therefore demonstrate a large plant diversity in their diet.

Many large herbivores, such as elephant, also actively feed throughout the night, and therefore determining diet through direct monitoring only in daylight hours can bias the study (Bax and Sheldrick, 1963). As many mammals do not fully digest their food it is possible to determine diet through faecal analysis (Van der Merwe *et al*., 1988; Landman *et al*., 2008; Booth *et al*., 2014). Isotopic analysis has been used as an effective, non-invasive method to determine diet utilising faeces (Van der Merwe *et al*., 1988; Botha and Stock, 2005; Cordon *et al*., 2005). Through faecal isotopic analysis dietary intake of graze and browse can be measured over spatial and temporal scales based on plant fractionation of $^{13}C/^{12}C$ during photosynthesis (Botha and Stock, 2005; Codron *et al*., 2011). C_3, C_4 and CAM plants each have separate photosynthetic pathways, thus showing distinct stable isotopic ratios (Smith & Epstein 1971; Vogel *et al,*. 1990). C_3 photosynthesis is found typically in plants such as forbs and shrubs and in trees and employs a photosynthetic pathway that fixes CO_2 using ribulose bisphosphate carboxylase (Bender, 1971). C_4 photosynthetic plants (grasses) have a typical Kranz leaf anatomy and utilise carboxylation of phosphoenolpyruvate to initially take up CO_2, whilst succulent plants are classified as CAM plants and utilise crassulacean acid metabolism (Smith & Epstein 1971; O'Leary, 1988; Vogel *et al.*, 1990). As elephants have a relatively poor digestive system and are estimated to deposit 10 to

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20 faecal boluses a day (Spinage, 1994). Due to the large distances elephants may travel from where food is consumed to where boluses are defecated, the contents of the faeces do not necessarily represent what the elephants were feeding on at that site (Boothe *et al*., 2014).

The majority of herbivore dietary studies in the Little Karoo region have concentrated on ungulates, such as Springbuck (*Antidorcas marsupialis*), Merino sheep (*Ovis aries*) and eland (*Tragelophus oryx*) through the use of focal sampling and rumen and vegetation analysis (Davies *et al*., 1986; Watson & Owen-Smith, 2000). By combining both field observations, such as scan sampling, and isotopic analysis of faeces, a more comprehensive understanding of elephant diet can be achieved in arid areas such as the Little Karoo.

3.3. Materials and Methods

3.3.1. Study area

Sanbona Wildlife Reserve (SWR) is approximately 57 600-hectares in size and is situated in the Little Karoo, a semi-arid area consisting of valleys and mountain ranges, with the Langeberg and Outeniqua Mountain ranges to the south and the Swartberg Mountain range to the north (Nell, 2003). SWR is located at 33°43’24’’ south and 20°36’55’’ east and is split in half by the Warmwaterberg Mountain range. The Warmwaterberg range forms part of the Table Mountain Group and primarily consists of sandstone and quartzite, whilst the lower lying hills and valleys are part of the Bokkeveld Group, consisting predominantly of sandstones and mud-rock (Almond, 2009). The eastern mountain ranges on SWR form part of the Witteberg Group (Vorster *et al.*, 2017). The Witteberg and Bokkeveld Group bedrock allows for more nutrient rich soils to form than the acidic soils derived from the Table Mountain Group (Almond, 2009). The elevation in the study area ranges from 430 m above mean sea level (a.m.s.l.) in the Brak River to 1 344 m a.m.s.l. on top of the Warmwaterberg range (Vorster *et al.*, 2017).

There are two in-situ weather stations located on SWR, one in the Sanbona South section and one in Sanbona North. Annual temperatures range from -2ºC to 41.8ºC. December, January and February (summer) are the region’s hottest months with a mean maximum ambient temperature of

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30.6 ^{o}C, and June, July and August (winter) are the coldest months with a mean minimum temperature of 4.9 ^{o}C (Vorster, *et al*., 2017). During the colder winter months clear skies can result in frost covering the ground in the early morning. Autumn (March, April and May) brings cooler weather with warm to mild days and cooler evenings (8.9 ^{o}C to 28.9 ^{o}C). Similarly, September, October and November (spring) are marked with cool to mild day temperatures and cooler evenings (7.9 ^{o}C to 27.2 ^{o}C).

The area falls within both a winter and summer rainfall region, with typically frontal (cyclonic) rainfall in winter between June and August, and summer rainfall in the form of convectional thunderstorms occurring in November, January, February and March (Vorster *et al*., 2017). Occasional droughts are common in the area, although extended droughts are rare (Desmet and Cowling, 1999).

The Warmwaterberg creates a rain shadow effect on the northern part of the reserve, which receives an average of 195 mm of rain per annum, compared to the southern part with an average of 315 mm per annum. This variation in rainfall creates a vegetation difference between the two areas, with the north being dominated by Succulent Karoo, Central Mountain Fynbos, Thickets and riverine areas, and the south consisting of Renosterveld, Central Mountain Fynbos, and Thickets. The amount of rain and the season within which it falls, fluctuates yearly with the area experiencing wet and drought cycles. The previous drought cycle occurred between 2008 and 2010, breaking in March 2011. Between 2011 and 2015 the reserve received an annual average rainfall of 224 mm (in the north) to 336 mm (in the south). In 2016, the first year of the drought cycle, only 109 mm was recorded in the North and 160.9 mm in the South. In 2017 rainfall decreased even further in Sanbona North to 98 mm but increased slightly to 177.2 mm in Sanbona South (Figure 3.2).

Surface water on the reserve is restricted to a number of small AWPs, the Bellair dam, and seasonal natural springs and rivers, which are dependent on annual rainfall (Figure 1.4). The main river courses in Sanbona South are Matjiesbos, Kalkoenshoek and Gatskraal. The Brak, Sandleegte, Wilgerbos, Bobbejaankrans and Karee Vlakte are the dominant river courses and drainage lines in Sanbona North (Figure 1.4).

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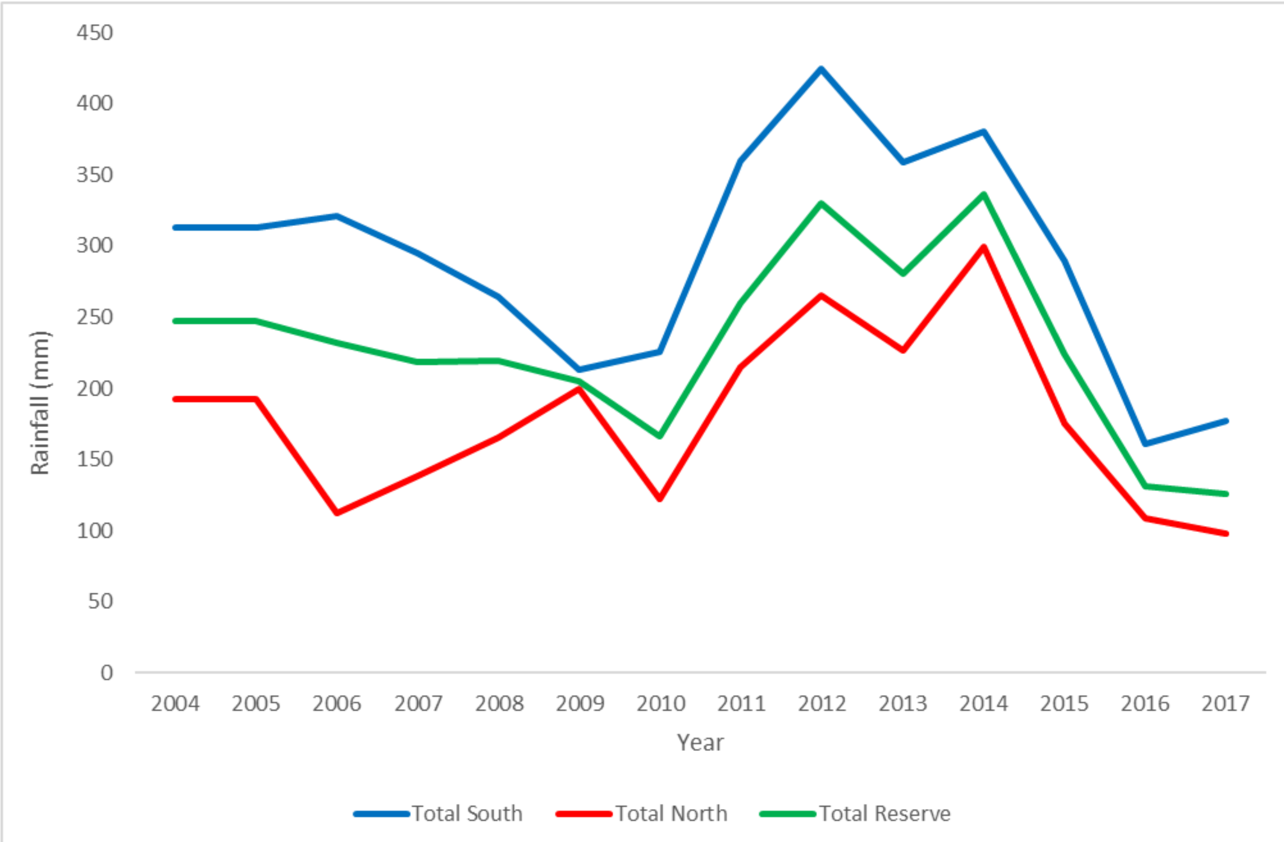

Figure 3.1. Average yearly rainfall (mm) for Sanbona North (red) and Sanbona South (blue), as well as the average across the reserve (green) from 2006 – 2017.

The low rainfall and varied geology of the area result in a high species richness of plants with 600 species occurring on SWR within 12 habitat types: Apronveld, Arid Mosaic Renosterveld, Arid Mosaic Succulent Karoo, Gannaveld, Grassy, Mesic Renosterveld, Mosaic Asbosveld, Mosaic Grassy Fynbos, Quartz Apronveld, Quartz Gannaveld, Randteveld and River line and floodplains (Vlok and Schutte-Vlok, 2015).

The internal fencing of the reserve was erected to divide the north and the south along the Warmwaterberg range, allowing for specific mammal management and tourism approaches (Vorster *et al.*, 2017). Sanbona North comprises 24 600 ha and Sanbona South 23 500 ha. The two herds are therefore separated from one another and function independently. The Southern herd consists of five individuals and the Northern herd of twelve

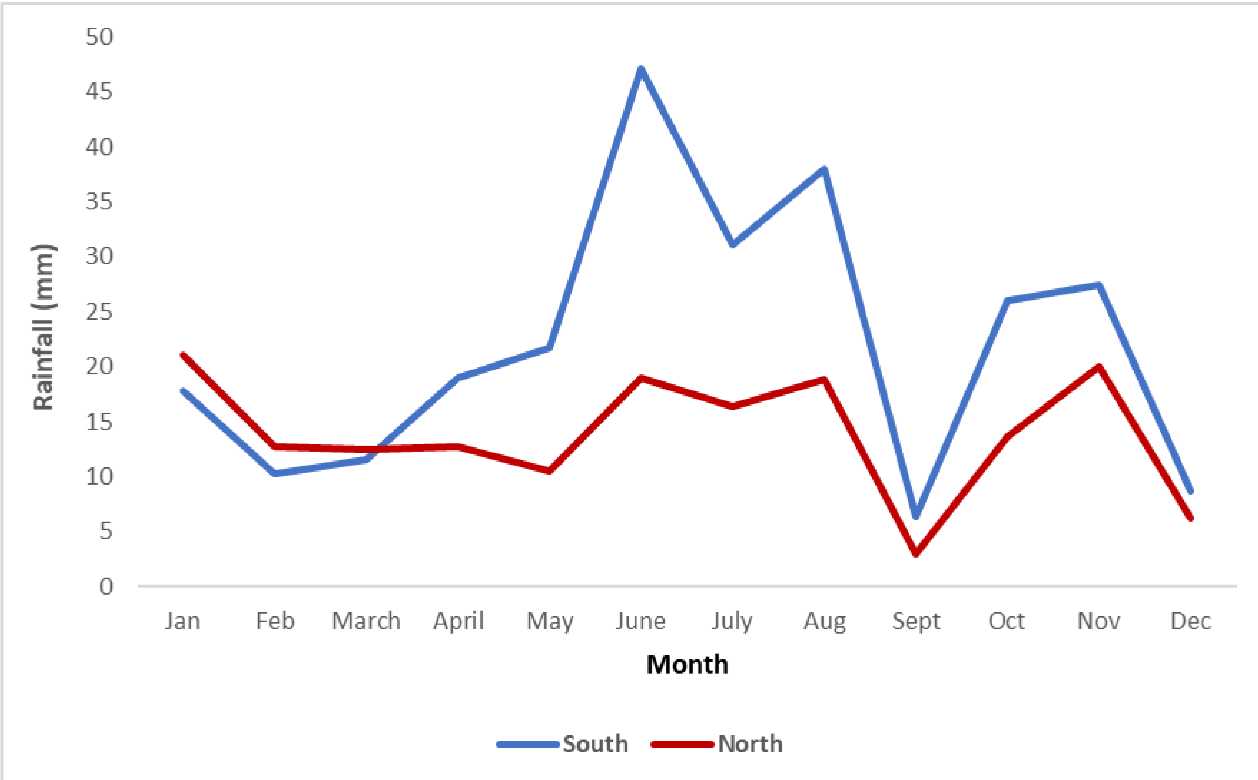

Figure 3.2. Sanbona Wildlife Reserve average monthly rainfall in Sanbona South (blue) and Sanbona North (red) of the reserve from 2005 – 2017.

3.3.2. Scan sampling

An adapted version of Barnes' (1982) scan sampling method was utilised (Gilby *et al*., 2010; Altmann, 2014). Data was collected over a period of 16 months, from December 2015 through to April 2017. Due to the small herd sizes (n=17 and n=5) compared to other scan sampling studies, each herd was monitored as a unit instead of focusing on an individual elephant. The sampling period was also adjusted to 2 hours in the morning and 2 hours in the afternoon (compared to Barnes' 4 to 8 hours) every second week, similar to Gordon *et al*. (2016). Thus, each herd was monitored for a total of 31 days, for a total of 62 monitoring sessions of 2 hours per herd. The sampling was done within a 24-hour period, either on the same day or over two days (an afternoon and the following morning).

In November 2015, the matriarch in the Northern herd and the large bull in the Southern herd were darted and immobilised from a helicopter. Both elephants were fitted with Global Positioning

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Systems (GPS) tracking collars with built-in Very High Frequency (VHF) transmitters manufactured by African Wildlife Tracking. The sampling rate was programmable and set to 1-hour intervals from the date of deployment. Herds were thus located using a combination of GPS downloads, VHF transmitters and tracking skills on the selected monitoring day.

Once the elephants were located, their movements and feeding were monitored. The herds were monitored from a vehicle or on foot depending on terrain. The elephants were calm around vehicles because of the reserve's tourism activities. Unlike other studies, such as Owen-Smith and Chafota (2012) and O'Kane *et al*. (2011), this study was not restricted to monitoring along the road network, as the elephants were often monitored from a safe location on foot. To eliminate the chances of unnecessarily disturbing the elephants, monitoring was carried out utilising 8x42 binoculars (Nikon Monarch Binoculars). Similar to the study by Gilby *et al*. (2010) conducted in Kibale National Park, Uganda, monitoring took place over a 2-hour period in the morning and in the afternoon, for 8 minutes at a time followed by a 2 min break. All plants consumed were identified to at least genus level and recorded for the herd members monitored. Behaviour, such as sleeping, dust bathing, social interaction and drinking were also noted. If visibility of the herd was lost at any stage during the 2-hour monitoring period, the time "lost" was added to the two-hour monitoring session. Additionally, if visibility of the elephants was poor, where possible backtracking was done to identify plants that were eaten during the time period. The vegetation identified that was utilised was recorded and added to the scan sampling data that was collected. A GPS location was recorded throughout the sampling period as the herds moved whilst feeding.

Correspondence analysis was used to analyse and graphically display the data collected from scan sampling of the plant species that were observed being utilised by both elephant herds and their locations (Sanbona North and Sanbona South). This was used to statistically determine which plants were more closely associated with each herd. Correspondence analysis as well as the Association Rule was further used to determine the relationship between plant species utilised and the months in which they were eaten. The Association Rule was used to determine the likelihood that a plant species will be consumed by a specific herd during a specific month.

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3.3.3. Isotopic analysis

To approximate the percentage of graze, browse and succulents in the elephants' diet on SWR, fresh faecal and vegetation samples were collected throughout the 16-month study period. Faecal samples were collected every month from both the Southern and Northern herds. Only fresh samples were collected to reduce the possibility of insect damage. Samples, a small handful size, were taken from the middle of the boluses and placed into brown paper envelopes. Each envelope was marked per herd, date, time and GPS locality. Vegetation samples were identified and thereafter all vegetation and faecal samples were air dried.

From the 378 faecal samples collected, 144 samples were randomly selected to grind and homogenize for isotopic analysis. This random sampling constituted 72 samples per herd, 18 per season, and was considered large enough to be statistically significant. The faecal samples collected during the summers of 2016 and 2017 were combined into one sample month, as were those from autumn 2016 and 2017. Each sample was ground using a mortar and pestle and then further homogenised using a Retsch ball grinder. The sample was then sifted through a 1 mm sieve and stored in a microtube for further analysis (Codron *et al*., 2011).

The vegetation sampling for comparative purposes included the 10 most prominent browse species, 9 most prominent graze species and the 10 most prominent succulent species that were utilised. Three samples were collected from each plant species consisting of 4 to 5 leaves per sample. Plant samples were oven dried, ground using a mortar and pestle, passed through a sieve and placed into micro-tubes for isotopic analysis.

All samples were taken to the University of Pretoria's Stable Isotope Laboratory at the Mammal Research Institute. Aliquots of approximately 1.0 – 1.1 mg of each homogenized sample (plant and faecal) were weighed and placed into tin capsules (RJM Systems (Pty) Ltd., Product number D1006, Tin Capsules Pressed, Standard Weight 6x4mm) that had been pre-cleaned with toluene. The capsules where then sealed for isotopic analysis. A Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system was used for the isotopic analysis (Codron *et al*., 2011; G. Hall, personal communication, 3 October 2017).

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After every eleven unknown samples, two laboratory running standards, namely Merck Gel ($\delta13C$ = -20.26‰, $\delta15N$=7.89‰, C%=41.28, N%=15.29) and DL-Valine ($\delta13C$ = -10.57‰, $\delta15N$=-6.15‰, C%=55.50, N%=11.86), and a blank sample were run. The values obtained for the Merck Gel during each run were used to correct data, whilst the DL-Valine standard values provide the ± error for each tray of samples run. These running standards are calibrated (2017) against international standards: National Institute of Standards and Technology (NIST): NIST 1557b (Bovine liver), NIST 2976 (Mussel tissue) and NIST 1547 (peach leaves).

For carbon isotope values the results were referenced to Vienna Pee-Dee Belemnite, and to air for nitrogen isotope values. Using a per mille scale (per thousand) the results were expressed in delta notation using the standard equation:

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

where X= ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$ respectively.

To determine whether there was any significant difference between the faecal samples of the Northern and Southern elephant herds in SWR an ANOVA test was performed.

3.4. Results

3.4.1 Diet of the elephants on SWR

Each herd was monitored for a total of 124 hours, during which the Northern herd (12 individuals) was observed feeding 37 650 times and the Southern herd (5 individuals) 25 185 times. The two elephant herds were observed feeding on at least 94 plant species combined, from 64 genera during the 16-month sampling period (grass species were classified together due to the lack of inflorescence during large parts of the study period, and certain succulent species were identified to only genus level) (Appendix 1, Table 3.1). Woody browse species were easy to identify and between 4 and 27 species were consumed within one day. The identification of many forb, succulent and grass species was difficult at times due to distance, obstructions, or lack of floral parts in the case of succulents and grasses. Thus, the exact number of forbs and succulent species

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may be under-represented, and no distinction was made between grass species. The total observed diet of the elephants on SWR consisted of 67% browse, 15% succulent and 18% graze. Utilising isotopic values of plant specimens collected, this equates to 73% C_3, 14% CAM, and 13% C_4 plants within their diet as some of the succulents and graze species utilise C_3 photosynthesis.

3.4.2 Difference between Northern and Southern elephant herds' diet

Plant species that were observed being consumed during the scan sampling sessions were divided into either graze, browse or succulent categories. Both the Southern and Northern herds' diets consisted predominantly of browse. The Northern herd's diet consisted of 62% browse species, 28% graze and 10% succulents (Figure 3.3), compared to 79% browse, 2% graze and 19% succulent species in the Southern herd's diet (Figure 3.4), thus the two herds diets were significantly different ($p<0.001$).

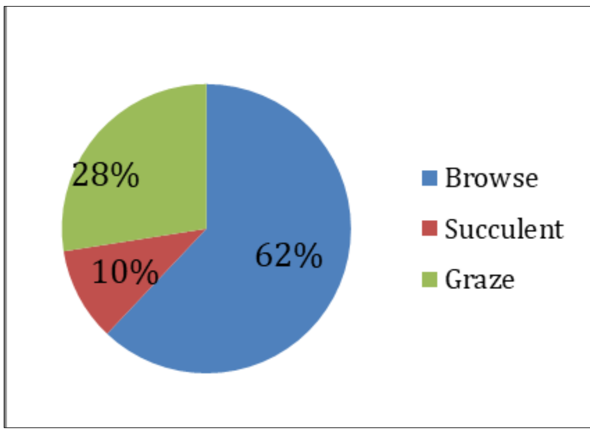

Figure 3.3. Scan sampling diet percentage of the Northern herd

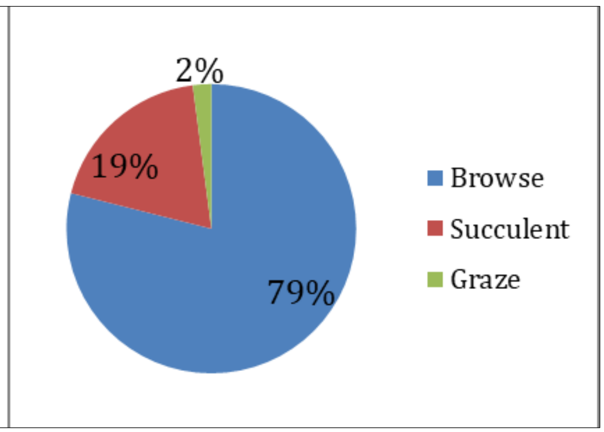

Figure 3.4. Scan sampling diet percentage of the Southern herd

When comparing the browse species utilised by the two herds, *Vachellia karroo* was the most abundant. Of the total browse eaten, *V. karroo* represented 58% of the Northern herd's browse diet, while it made up 56% of the Southern herd's. The Northern herd's diet had a lower browse ratio, but higher graze level, thus the percentage of browse within each herds' total diet differed slightly (62% compared to 79%, $p<0.001$). Of their total diet *V. karroo* constituted 44% of the Southern herd's diet while only 33% of the Northern herd's diet. Clear clustering of the species more regularly utilised can be seen in the results of the correspondence analysis conducted).

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Genera such as *Searsia* and *Euclea* were more readily browsed by the Southern herd (8% and 5% respectively of recorded diet) than the Northern herd (3% and 1% respectively), while the Northern herd utilised *Atriplex* and *Lycium sp.* (8% and 4% of observed diet) more than the Southern herd (6% and 1% respectively). Slow growing browse species such as *Schotia afra* made up only 1% of the diet in both herds, and *Carissa haematocarpa* contributed 2% to the Southern herd's diet and < 1% in the Northern herd's diet.

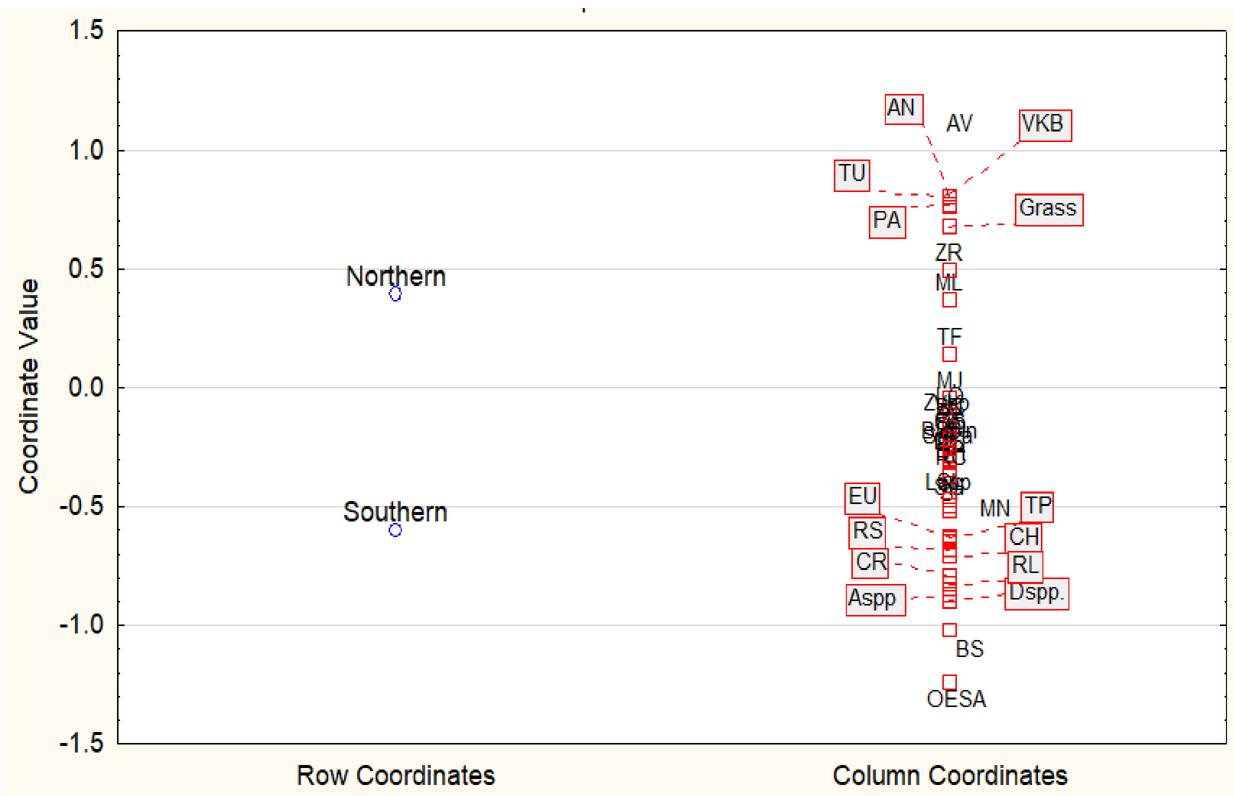

Figure 3.5. Correspondence analysis for diet of the Southern and Northern herds. The letters within the red blocks are the abbreviated plant species that were observed being utilised.

Within the succulent group, the *Mesembryanthemum* genus was the most utilised by both herds. *Mesembryanthemum junceum* was the most common succulent species consumed within the Northern herd's diet, (30% of succulent species consumed, and 3% of the total diet), whereas *M. junceum* was consumed in similar amounts to *Drosanthemum hispidum* by both the Northern and

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Southern herds (17 and 19% of succulent species consumed respectively) (Figure 3.6). *Tylecodon paniculatus,* a slow growing species, made up 7% of the Southern herd's recorded succulent diet while only 3% of the Northern herd's, making up only 1% of the Southern herd's and less than 1% of the Northern herd's total observed diet. Only the stem of *T. paniculatus* was consumed as the leaves are considered poisonous to animals (Vlok & Schutte-Vlok, 2015).

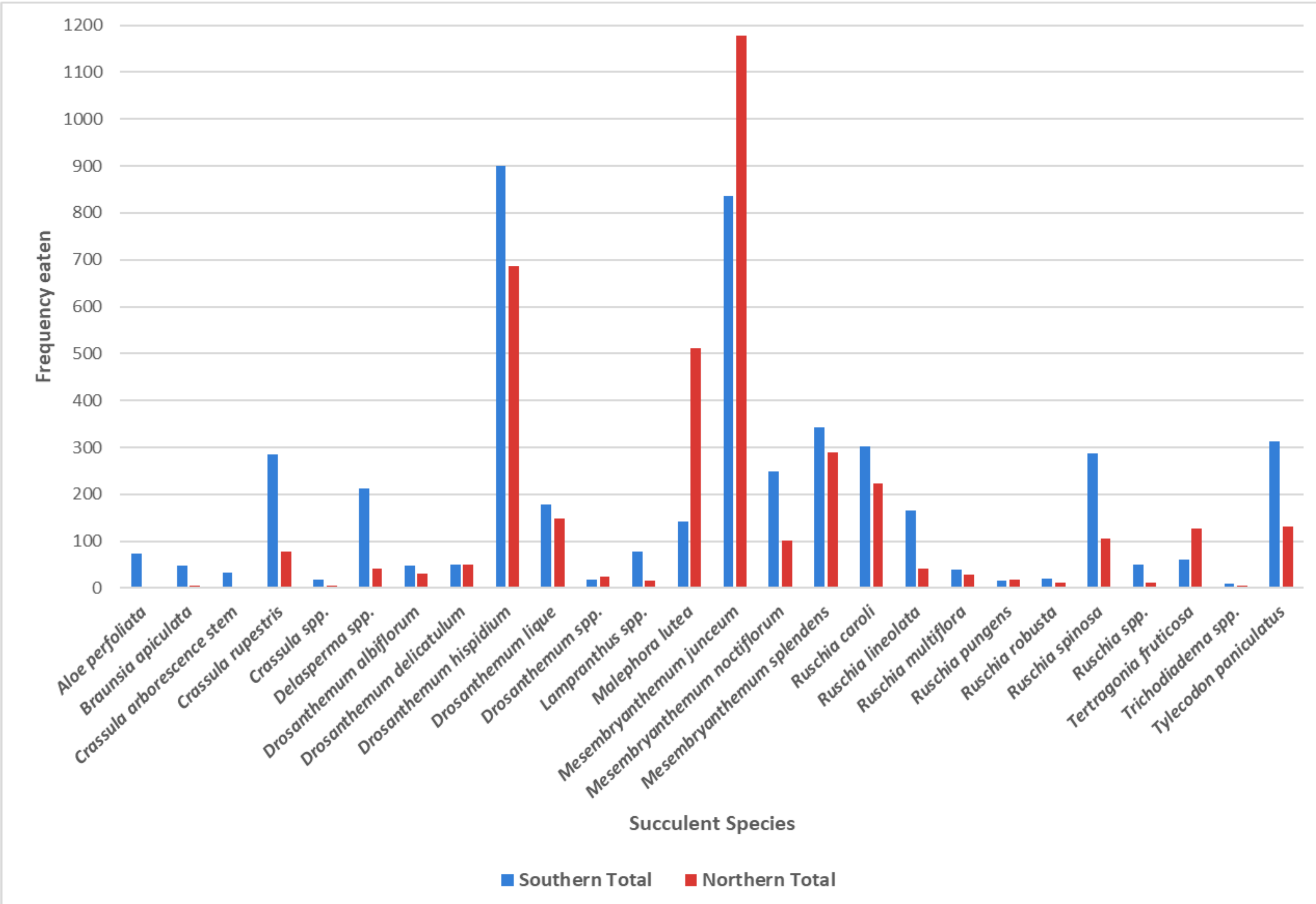

Figure 3.6. Scan Sampling: Total succulents observed being eaten during by the Northern (red) and Southern (blue) herds over the 16-month period.

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3.4.3 Seasonal difference in scan sampling of elephants' diet

Plant species recorded through scan sampling varied each season, some only occurring in the diet at certain times of the year, while other species fluctuated in the frequency that they were consumed each season. Using Correspondence Analysis plant species observed to be utilised were clustered according to month consumed, assuming that certain plant species were eaten during certain months. This was then used to determine seasonal correspondence. Succulents formed part of the elephants' diet throughout the year, however certain species were observed being utilised at a higher frequency in different seasons.

The Southern herd's diet varied across the seasons. The only seasonal significance within the Southern herd's diet (through carbon ($\delta^{13}C$) was found during spring and summer (f-ratio=7.419, p=0.01). Some species were consumed throughout the year with peaks in a specific season, while others spiked in only two seasons and yet others were only consumed during a specific season (Figure 3.7). During summer *Atriplex vestita*, *Carissa haematocarpa*, *Gymnosporia sp.* and *Searsia glauca* were consumed more than during the rest of the year. *S. lancea* was consumed throughout the year but peaked in summer. During autumn an increase was seen in the consumption of *Drosanthemum hispidum*, *Euclea undulata* and *Zygophyllum sp.*, whereas *Delasperma sp.* was almost exclusively eaten in autumn. During winter, an increase in succulents such as *Crassula rupestris*, *Malephora lutea*, *Mesembryanthemum junceum*, *Ruschia caroli*, *R. spinosa* and *Tetragonia fruticosa* were consumed. The consumption of *Berkheya sp.* and *Osteospermum sp.* also increased during winter. Grass was grazed throughout the year in different amounts, however consumption was found to be highest in spring. *Tylecodon paniculatus* was consumed throughout the year by the Southern herd but consumption thereof increased during spring.

Vachellia karroo was the species which was consumed the most. While it was consumed throughout the year, consumption thereof spiked during spring and summer. The only seasons in which *Aloe perfoliata* was seen being consumed was during spring and summer. Other browse species in Sanbona South such as *Asparagus sp.*, *Lycium sp.* and *Schotia afra* were predominantly eaten in autumn and winter. *Lampranthus sp.* consumption also increased during this time. During

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autumn and spring an increase was seen in the consumption of *R. lineolata* although it was consumed throughout the year but to a lesser degree.

The Northern herd (Figure 3.7) consumed an increased quantity of *Atriplex sp.*, *Mesembryanthemum splendens, Typha capensis,* and *Zygophyllum retrofractum* during the summer, and *T. fruticosa* during autumn. *Asparagus sp.*, both *Berkheya spp., Delosperma sp.,*

Lycium oxycarpum, R. caroli, R. spinosa, Tylecodon paniculatus and *Zygophyllum sp.* showed higher consumption rates in the winter months. *Osteospermum sinuatum* and *Ruschia multiflora* was only consumed in winter. *Tamarix usneoides* was consumed in spring whilst *Phragmites australis* was consumed during spring, followed by autumn.

Other species were also consumed in high quantities during two seasons in Sanbona North. *Drosanthemum delicatulum, D. hispidum, D. lique, E. undulata, Lycium sp, Malephora lutea, M. junceum, M. noctiflorum* and *S. lancea* were eaten throughout the year, but consumption increased during summer and winter. During summer and autumn more *S. afra,* and *S. glauca* were consumed, whilst *C. haematocarpa* was almost exclusively eaten during summer and autumn. *Hermannia sp.* were consumed only in autumn and winter, whilst the consumption of *C. rupestris* increased during these seasons. The Northern herd grazed throughout summer, autumn and winter, but less so during the spring of the study period.

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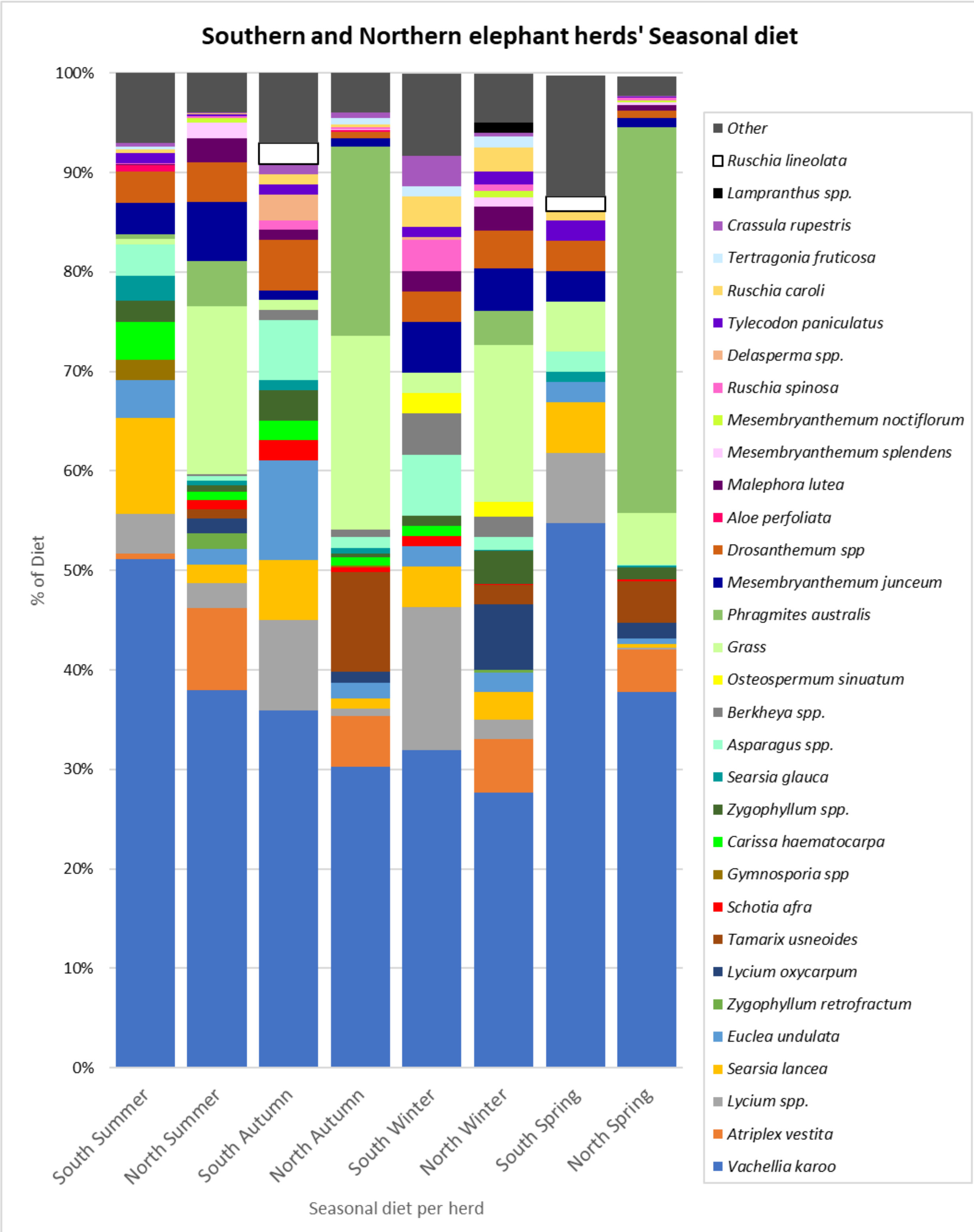

Figure 3.7. Seasonal diet of the Southern and Northern herds, showing the plant species consumed in the various seasons according to the percentage consumed within the diets.

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3.4.4 Isotopic analysis

The results of the isotopic analysis of the plant specimens collected on SWR revealed three distinct clusters of $\delta^{13}C$‰ (Figure 3.8). Table 3.2 (in Appendix 1) presents the $\delta^{15}N$‰ and $\delta^{13}C$‰ values (corrected and uncorrected) of the vegetation samples collected on SWR.

The C_3 plants on SWR tested between -24.16 and -29.77, averaging -26.56 $\delta^{13}C$‰, and C_4 plants tested between -19.84 and -13.69, averaging -15.64 $\delta^{13}C$‰. Most of the succulent (CAM) species tested on SWR fell between -19.25 and -23.72 $\delta^{13}C$‰, with a few exceptions showing a tendency towards the C_4 range such as *Mesembryanthemum junceum*, *Tylecodon paniculatus* and *Crassula rupestris*. *Ruschia caroli* and *Tetragonia fruticosa* fall within the C_3 range of -25.37 and -26.49 $\delta^{13}C$‰ with one sample of each was found to fall at -23.19 and -23.67 $\delta^{13}C$‰ respectively. Many of what are known as graze species on SWR fell into the C_3 range, with *Ehrharta sp.2* lying closer to some of the CAM plants, on the border of C_4 and C_3 (-19.30 and -19.84 $\delta^{13}C$‰). *Atriplex vestita* is a low growing shrub that provides important browse to many herbivores in the Little Karoo, and many species of the *Atriplex* genus are classified as C_4, such as *A. vestita*, with a few exceptions being C_3.

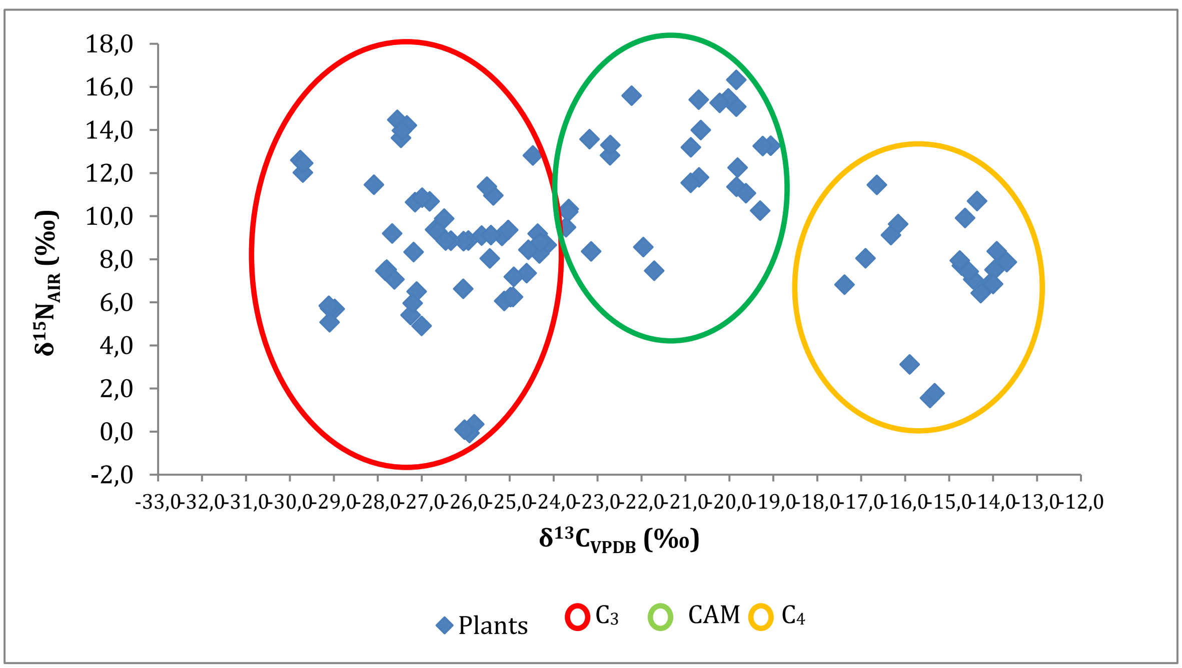

Figure 3.8. Isotopic values of vegetation samples collected on SWR. Three distinct clusters are identified containing vegetation utilising C3 (red circle), CAM (green circle) and C4 (yellow circle) photosynthetic pathways.

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A basic protein content of each plant sample is represented by the $\delta^{15}N$ values. Two plant species in particular were seen to contain low values of $\delta^{15}N$‰. These included *Vachellia karroo* (-0.06 to 0.34 $\delta^{15}N$‰) and *M. junceum* (1.56 to 3.12 $\delta^{15}N$‰). Most of the plants fell between 4.91 and 15.08 $\delta^{15}N$‰ with *Delosperma sp.* and *Drosanthemum hispidum* ranging higher between 15.26 and 16.33 $\delta^{15}N$‰.

The total faecal samples were primarily isotopically clustered towards the C_3 range (73%), with only one sample falling closer to the C_4 range (Figure 3.9and Figure 3.10). The majority of the faecal samples were between -22.59 and -27.67 $\delta^{13}C$‰. The Southern elephant herd samples had $\delta^{13}C$ values ranging between -24.9 and -27.49‰ and $\delta^{15}N$ values ranging between 3.89 and 9.97‰, thus almost exclusively within the C_3 range (Figure 3.10). The Northern herd's samples ranged from -19.06 to -28.33$\delta^{13}C$‰ with $\delta^{15}N$ values between 4.56 to 11.44‰, thus predominantly in the C_3 range with 19 samples within the CAM range and 1 within the C_4 range (Figure 3.10).

The one-way ANOVA test revealed significant differences in faecal carbon ($\delta^{13}C$) between the Northern herd and Southern herds (F-ratio=73.2, $p<0.001$).

The seasonal differences in $\delta^{13}C$ and $\delta^{15}N$ for each herd are presented in Table 3. (Appendix 1). When comparing faecal carbon ($\delta^{13}C$) between seasons, significant differences were found within the Northern herd (F-ratio=15.9, $p<0.001$), but not in the Southern herd (F-ratio=2.0, p=0.117), except during spring and summer (F-ratio=7.4, p=0.01). The Northern herd showed significant differences of $\delta^{13}C$ between spring and summer (F-ratio=25.2, $p<0.001$), autumn and spring (F-ratio=15.9, $p<0.001$), autumn and winter (F-ratio=19.9, $p<0.001$), and between winter and summer (F-ratio=29.8, $p<0.001$). There were no significant differences in faecal carbon between the summer and autumn seasons in the Southern and Northern herds', or between spring and winter in the Northern herd.

The $\delta^{13}C$ and $\delta^{15}N$ for C_3, C_4 and CAM plants as well as the elephant faecal samples collected from the Northern and Southern herds throughout the various seasons are presented in Figure 3.9 and Figure 3.10. For both herds there was a predominant, clear contribution of C_3 plants in the diet according to the $\delta^{13}C$ values. The Northern herd, however, showed some spread towards the CAM range as well (-19.25 to -23.72 $\delta^{13}C$‰) and even one sample within the C_4 range (-19.06

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$\delta^{13}C$‰). During summer and autumn, the Northern herd's faecal samples were similar in the range of values (-19.06 to 26.41 $\delta^{13}C$‰ in summer and -21.63 to -28.33 $\delta^{13}C$‰ in autumn). The range shows a greater diversity of CAM plants in the diet in summer and autumn. Winter and spring seasons in the Northern herd's diet were almost identical with -24.83 to -27.43 $\delta^{13}C$‰ values in winter and -24.20 to -27.71 $\delta^{13}C$‰ in spring. The succulents that were detected in the Southern herd's faecal samples were categorised as C_3.

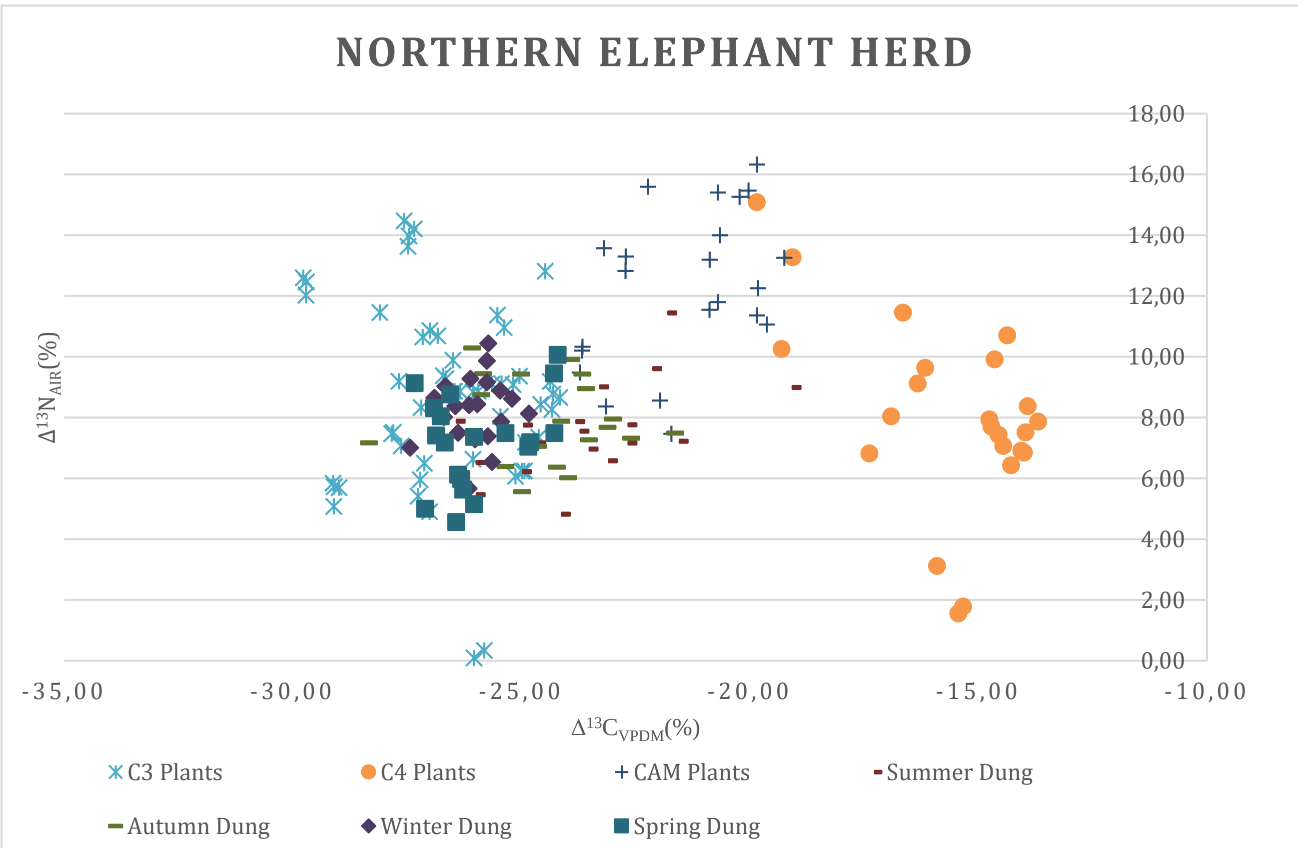

Figure 3.9. Isotopic analysis of C4, C3 and CAM vegetation, along with the isotopic values of carbon (δ13C) and nitrogen (δ15N) in the dung of the Norhern elephant (*Loxodonta africana*) herd on Sanbona Wildlife Reserve during summer, autumn, winter and spring over a 16-month period.

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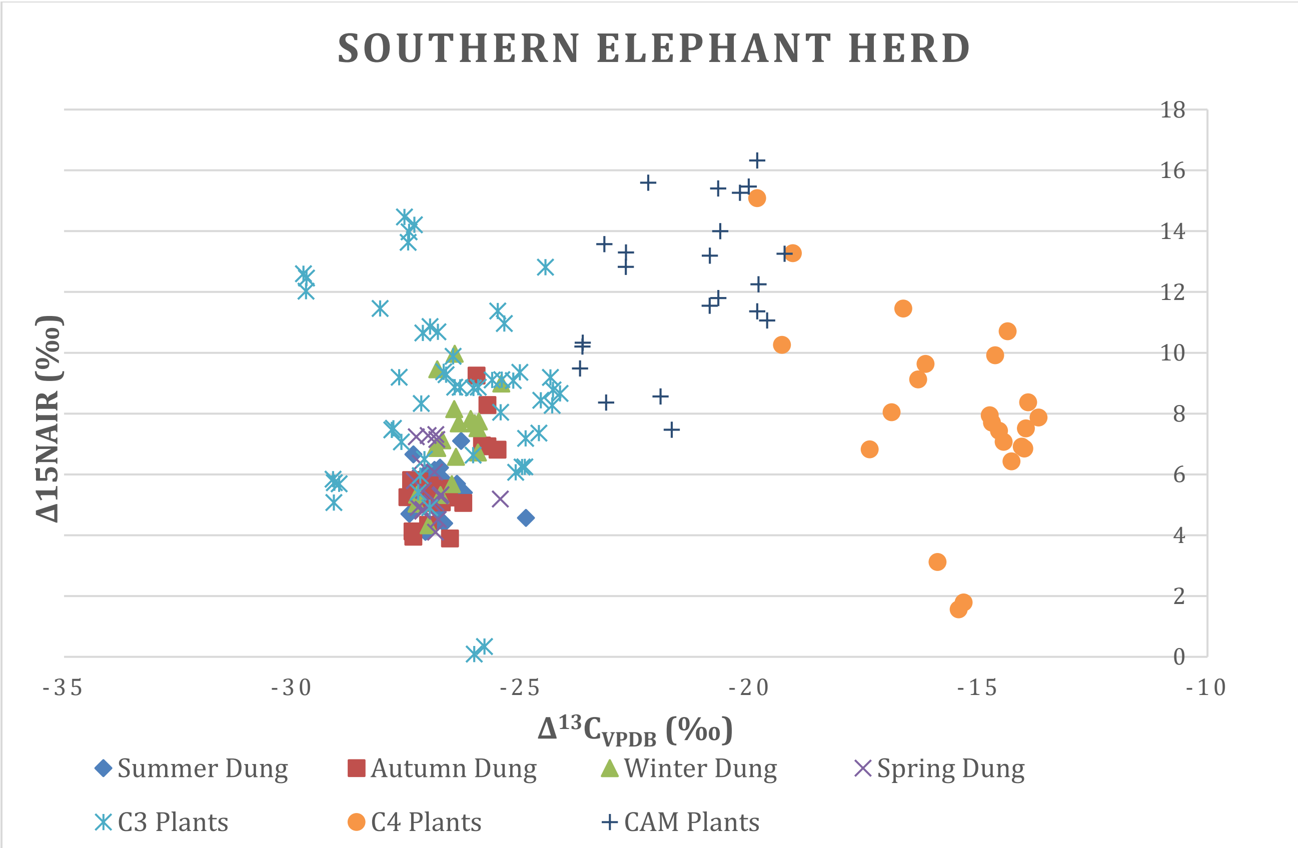

Figure 3.10. Isotopic analysis of C4, C3 and CAM vegetation, along with the isotopic values of carbon (δ13C) and nitrogen (δ15N) in the dung of the Norhern elephant (*Loxodonta africana*) herd on Sanbona Wildlife Reserve during summer, autumn, winter and spring over a 16-month period.

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3.5. Discussion

3.5.1 Observed diet

Elephants are large megaherbivore mixed feeders requiring a broad diet. The elephants were observed to consume at least 94 plant species from 64 genera, of the estimated 600 plant species on SWR (Vorster *et al*., 2017). This is similar to the findings in Addo Elephant National Park in the Eastern Cape, South Africa, where elephants were observed utilising 99 to 104 species from 67 genera (Landman *et al*., 2008). Erasmus (2008) recorded only 10-species being consumed by the original 5 elephants, only performing scan sampling over a single summer period of three months. The elephants on SWR were found to consume between 4 and 27 plant species within a day's monitoring session; this is similar to Guy's (1976) record of up to 22 plant species a day in arid savanna in Zimbabwe. The number of plant species utilised per day on SWR was dependent on the area in which the elephant herds were foraging in, the weather, and the season.

Through the isotopic analysis of succulent plants on SWR it was found that the majority had a $\delta^{13}C$‰ of between -19.25 and -23.72‰, with some succulents falling more within the range of the C_3 plant species. Plants using C_4 photosynthetic pathways fall in the range of -9 to -19 $\delta^{13}C$‰, with an average of -12.5 $\delta^{13}C$‰, whereas plants utilising C_3 photosynthetic pathways fall between -20 to – 37 $\delta^{13}C$‰, with an average of -26.5 $\delta^{13}C$‰. Van der Merwe *et* al. (1988) found that *Portulacaria afra* had an average $\delta^{13}C$ value of -17.7‰ and Sternberg, De Niro and Johnson (1984) found that CAM plants had a $\delta^{13}C$ range of -10.6 to -13.8‰ in Texas. Defining carbon isotope ratios in CAM plants has been seen as more difficult to interpret (Troughton and Card, 1975). Mooney, Troughton and Berry (1977) found that different succulent growth types displayed different photosynthetic carbon isotope ratios, with dwarf succulents being predominantly CAM and succulent shrubs ranging from CAM to C_3. It was further found that carbon isotope ratios change with a change in temperature that plants are exposed to, as well as rainfall seasons (Troughton and Card, 1975; Mooney *et al*., 1977). Many of the succulents that Mooney *et al*. (1977) looked at had similar isotope ratios to those tested on SWR.

The combined results for the observed diet of both herds consisted of 67% browse, 15% succulent and 18% graze, which equates to 73% C_3, 14% CAM, and 13% C_4. This differs from the isotopic

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analysis which showed the diet consisting solely of C_3 and CAM. This difference could be due to the fact that all grasses were grouped together during scan sampling, whereas the isotopic analysis indicated that some of the prominent graze species, such as *Themeda triandra*, *Ehrharta sp.*, *Phragmites australis*, *Scirpoides sp.*, and *Typha capensis* were C_3 species and not C_4 as per scan sampling. The lack of C_4 representation within the isotopic analysis of elephant diet could also result from the fact that the faecal samples show an average value of intake and that plant isotopes may differ between seasons and due to spatial differences (Codron *et al*., 2007; F. Radloff, personal communication, 5 December 2017). However, in other areas, such as the Kruger National Park in South Africa, Majete Wildlife Reserve in Malawi, and Samburu-Buffalo Springs National Reserves in northern Kenya, the isotopic analysis of faeces and animal tissue (hair, bone and tooth enamel) to estimate the proportion of C_3 to C_4 within elephant diet was deemed accurate (Codron *et al*., 2007; Cerling *et al*., 2009; Forrer, 2017). In comparison, Erasmus (2008) found that the elephant's diet consisted of 58% browse and 42% graze. However, as aforementioned, Erasmus' study only focussed on one summer season, and summer seasons are known to have higher grazing values (Barnes, 1982; Sukumar, 2003). The results of both the scan and isotopic techniques indicate that the majority of elephant's diet consists of woody browse species.

According to the scan sampling results, the most abundant species within the elephants' diet was found to be *Vachellia karroo* (38% of the total elephant diet on SWR). Since *V. karroo* is the most abundant tree species on SWR, this was not surprising. According to the scan sampling method *Schotia afra* makes up less than 1% of total elephant diet in SWR. Isotopically *V. karroo* and *S. afra* were found to have very similar $\delta^{13}C$, between -25.81 and -26.05 $\delta^{13}C$, thus making it difficult to differentiate between the two species. The isotopic analysis indicates that combined, *S. afra* and *V. karroo* only make up 10% of the Southern herd's diet and only 17% of the Northern herd's diet, which is far less than the observed. Allen (2009) recorded *S. afra* as one the most important browse species for elephants in Kuzuko, Addo Elephant National Park. This difference between the isotopic analysis and scan sampling results could be due to either an over- or under-representation within the isotopic sampling as both *V. karroo* and *S. afra* fall within a similar $\delta^{13}C$ range, or to an under-representation of *S. afra* in scan sampling. However, it could also be that isotopic analysis indicates that other species could make up a larger portion of the diet when compared to observations during daylight hours only. *Searsia lancea*, certain

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Lycium sp., *Euclea undulata* and *Atriplex vestita* also account for a large proportion of the diet of medium to large woody browse species. These species are common in the main drainage lines as well as surrounding plains and tributaries. *A. vestita* and the invasive *A. nummularia* fall into C_4 classification isotopically. Other important woody browse included *Asparagus sp.* and *Zygophyllum sp.* which occur in drainages, on mountain slopes, and in valleys. The second most consumed plant in Sanbona North was *P. australis*, contributing 12% of the Northern herd's total diet. Elephants in the Kruger National Park were observed to feed on *P. australis* in riverbeds (Viljoen *et al*., 2013).

Certain plants are identified as species of concern due to their slow growth rate, such as *S. afra*, *Carissa haematocarpa*, *Tylecodon paniculatus* and *Trichodiadema sp.* (S. Milton, personal communication, 24 February 2017). Within both the herds' diets, *S. afra* only made up 1% of the observed browse intake; nevertheless, damage to these trees was noticeable. Mader (2005) however, found that there was a low mortality rate in *S. afra* due to elephant utilisation on SWR between 2003 and 2006. *C. haematocarpa* is generally seen as unpalatable to many other animals (Vlok & Schutte-Vlok, 2015; Vorster, 2017), however it contributed to 2% of the Southern herd's observed woody browse diet and less than 1% in the Northern herd's diet. *T. paniculatus* would appear to be prevalent in the diet of the elephants since it is easily distinguishable by the large undigested pieces often seen in the boluses. However, results from the scan sampling study show that *T. paniculatus* contributed less than 1% to the elephants' diet. Although this may seem insignificant, it is these slow growing, less common species that could be of major concern as these plants might not be able to recover from repeated impacts (S. Milton, personal communication, 24 February 2017). *Trichodiadema sp.* were seldom utilised. However, Daves (2004) recorded *Trichodiadema bulbosum* in the diet of elephants in Addo Elephant National Park. Mooney *et al*. (2017) found that *Trichodiadema sp.* in Grahamstown, South Africa, had an average $\delta^{13}C$ value of -23.6‰. There were faecal samples with similar $\delta^{13}C$ values in the results of the isotopic analysis which could indicate the presence of this species in the diet of elephants on SWR. Thus, the difference in results between scan sampling and the isotopic analysis could be due to the size of the plants, as they are small succulents that could easily be misidentified or not observed during monitoring. Monitoring of these slow growing, less common species should take place in order to determine any negative impacts of feeding and trampling.

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Some species recorded as being eaten during scan sampling are known to be non-palatable to livestock or game, such as the *Crassula* species, and have therefore not previously been considered as possible forage for animals such as elephants (Lombard *et al*., 2008; Vlok and Schutte-Vlok, 2015). However, *Crassula rupestris*, the stem of *C. arborescens*, *C. subaphylla* and *C. tetragona* were all consumed, with *C. rupestris* consumed the most. Eland *(Taurotragus oryx)*, oryx (*Oryx gazella*) and ostrich (*Struthio camelus australis*) were also seen to favour *C. subaphylla* on SWR (Fenwick, 2008; Vorster, 2017). Thus, the elephants' diet on SWR is more diverse than previously thought, consisting of both numerous and quick growing plants, and slow growing and less prolific plant species. As expected, the most important observed component of the elephant's diet consists of browse (C_3), although succulents also form part of their diet.

3.5.2 Differences between the Northern and Southern herd's diet

The isotopic analysis of the faecal samples from the Northern and Southern herds showed significant differences, indicating that the diets varied. This is substantiated by the scan analysis since the Northern herd's diet consisted of 62% woody browse, 28% graze and 10% succulents, compared to the Southern herd's diet of 79% woody browse, 2% graze and 19% succulents. This can be expected since the habitat, and therefore vegetation types in which each herd was located, differs as was found in Chapter 2. The Northern herd had access to larger river lines forming wide flood plains, compared to the more mountainous terrain of Sanbona South. These larger flood plains as well as a higher summer rainfall pattern in Sanbona North also produces a higher grass component.

Some plant species, such as *V. karroo*, were often utilised by both the Northern and Southern herds (33% and 44% of their browse respectively), whereas certain plants were consumed more by one herd than the other. *Searsia sp.* and *Euclea undulata* were consumed in larger quantities by the Southern herd than the Northern herd (8% and 5%, versus 3% and 1%, respectively of total diet). This is likely due to the fact that Sanbona South appears to have a higher concentration of both *Searsia sp.* and *E. undulata* compared to Sanbona North. In contrast, the Northern elephants utilised higher proportions of *Atriplex vestita* than the Southern herd (6% and < 1% of their total diet respectively) as *A. vestita* is more prevalent in Sanbona North. Erasmus (2008) recorded the

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elephants consuming large amounts of *Atriplex semibaccata*, and although this was also recorded as one of the consumed *Atriplex sp.* it was not as prominent in their diet as *A. vestita*.

Although many succulent species are thought to be unpalatable, they did contribute 15% to the elephants' diet on Sanbona. Brown *et al*. (2003) recorded species from the *Mesembryanthemum* genus to be highly sought after by black rhinoceros (*Diceros bicornis*). Landman *et al*. (2008) found that succulents made up 11.4% of elephants' diet in Addo Elephant National Park in South Africa. Although succulent species, such as those in the *Mesembryanthemum* and *Drosanthemum* genera were utilised equally by both herds, the proportions of different species varied, which may also be due to their abundance in the available habitat. *M. junceum* made up a higher percentage of the Northern herd's diet, namely 30% of their succulent intake, compared to 17% for the Southern herd. *M. junceum* is not found in Fynbos areas and thus has a lower occurrence in Sanbona South than in Sanbona North. *Phragmites australis* was consumed in large amounts in Sanbona North (12% of diet) but observed less in Sanbona South. Part of the core area of the Northern elephant herd is the area around Bellair dam which has large beds of *P. australis,* and therefore explains the difference in utilisation of this species between the herds.

As expected, the observed diet differed between the two herds, with graze playing a more important role in the Northern herd due to availability, whereas the frequency at which succulents were consumed was higher in the Southern herd. The largest percentage of the Northern and Southern elephant herds diets were often the plant species which were observed to be most prominent in the areas they frequented. The largest difference between the two herds' diets with regards to frequency with which plant species were consumed could be related to the availability of those plant species within the area that each herd frequents, as seen in Chapter 2. An example of this was the frequency with which *P. australis* was consumed in Sanbona North compared to Sanbona South as a result of larger floodplain areas in Sanbona North.

3.5.3 Seasonal usage

Through the use of the Association Rule it was clear that during scan sampling certain plant species were consumed throughout the year in equal quantities, whereas other species were consumed more in certain seasons and still others only in specific seasons. The herds utilised different plant

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species in different seasons. This was most prevalent in the Northern herd, where significant differences were found between seasonal usage in the isotopic sampling results.

The Northern herd's $\delta^{13}C$ values showed a larger C_3 and CAM composition with minimal C_4 during summer, and C_3 and CAM during autumn. Winter and spring, however, showed only C_3 isotopic values. Through scan sampling it was found that graze utilization was higher during summer, autumn and winter (17%, 20% and 16% of total forage respectively) than during spring (6%). Since other studies suggest that graze intake is higher during the wet season (Field & Ross, 1976; Barnes, 1982; Sukumar, 2003; Codron *et al*., 2010; O'Kane *et al*., 2011), the results of this study correlate with these studies since average rainfall during the study was highest in autumn (46.33 mm), winter (36.28 mm), and summer (28 mm), while spring only received an average of 4.83 mm.

During spring however, the Northern herd consumed the largest quantity of *P. australis*. This is due to the new growth that occurs in this season. Furthermore, the area around the Bellair dam (Sanbona North) was burnt in the late winter as part of the alien clearing project, in an effort to reduce the invasive *Tamarix usneoides* in that area. Burning stimulates the re-growth of *P. australis* as well as reduces the moribund material, making new growth more accessible in the spring. This resulted in a large quantity of soft bulk feed that was high in nitrogen, potassium and manganese (Köbbing *et al*., 2013). The Northern herd consumed *V. karroo* in larger quantities during spring and summer than autumn and winter. *T. usneoides* and *V. karroo* both produce new leaves during spring, forming important browse. Similarly, Gordon *et al*. (2016) found that giraffe (*Giraffa camelopardalis giraffa*) utilise other browse during winter when *V. karroo* browse decreases. During the summer months *V. karroo* flowers, producing seed pods in late summer and early autumn, increasing the browsing value of the species. Similarly, *S. afra* are predominantly browsed in summer by the Northern herd when seed pods are produced, increasing the protein content of the tree. In Augrabies Falls National Park, South Africa, Buk (2004) classified *S. afra* as a low palatability browse species only utilised when more palatable species decrease in availability. Buk (2004) further recorded black rhinoceros (*Diceros bicornis bicornis*) only feeding on *S. afra* during summer and autumn. *Atriplex sp.* were consumed throughout the year but primarily during summer. Likewise, many of the succulent plants were consumed throughout the year, with consumption increasing during summer and peaking in winter, with *Ruschia sp.*

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being consumed predominantly in winter. This could be due to the fact that there is increased nutrient storage in these plants during these times as they prepare to flower in spring. Plants such as *Osteospermum sinuatum* and both *Berkheya cuneata and B. spinosa* were consumed exclusively during winter, which coincides with the flowering season for these species. *Tylecodon paniculatus* was also only consumed by the Northern herd during winter. This could be due to increased water content and growth of the stems after autumn and winter rains. However, other species such as *Hermannia sp.* that were only consumed in autumn and winter, may only be consumed because the elephants were feeding in the area in which they grow. This could also be the reason for the increased consumption of *Crassula rupestris* during autumn and winter as results indicate that Northern elephants' foraging behaviour on slopes was found to occur predominantly during autumn and winter (as found in Chapter 2).

These findings closely correlate the findings of the isotopic analysis for the Northern herd during spring, summer and autumn, but not for winter, when large amounts of CAM plants were consumed. During winter the Northern herd utilised mountain slopes and valleys away from the thicker river line areas more so than during other seasons. This could explain why there was an increase in CAM plants consumed during this time. However, Allen (2009) found that a larger quantity of succulents were consumed by elephants in Kuzuko Contractual Park, Greater Addo Elephant National Park, during summer than winter (making up an average of 23.8% and 19.5% of their diet during summer and winter, respectively).

Spring is predominantly the flowering season for many plants after winter rains, and with the increase in temperatures in summer there is an increase in leaf production in various C_3 species (Esler *et al*., 2006). The Southern herd's diet showed a cluster towards C_3 vegetation in all four seasons. This however does not correlate with the scan sampling data. Through scan sampling it was found that the Southern herd also consumed higher quantities of succulents such as *C. rupestris*, *Malephora lutea*, *Mesembryanthemum junceum*, *Ruschia caroli, Ruschia spinosa* and *Tetragonia fruticosa* in winter. During this study the south received the highest rainfall with an average of 78 mm in winter. This would have increased growth and nutrient storage within succulents. This higher rainfall combined with cooler temperatures allowed the Southern herd to feed more in open valleys and on mountain slopes where these succulents occur. Other succulent species such as *Drosanthemum hispidum* were consumed throughout the year, but primarily in

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autumn. This differs from the Northern herd where few *D. hispidum* were consumed in autumn, primarily peaking in winter and summer. Also differing from the Northern herd is the Southern herd's consumption of *T. paniculatus* throughout the year, peaking in spring. This could be because growth is usually most rigorous in arid systems after winter rainfall, therefore in Sanbona South in spring (winter rainfall being highest) and in Sanbona North in winter (autumn rainfall being highest) (Ogle & Reynolds, 2004; Esler *et al*., 2006; Yan *et al*., 2015). Grass was utilised at low quantities throughout the year but increased during winter with the highest observed intake occurring during spring. This correlates with higher winter rainfall and the increase in temperatures in spring (Esler *et al*., 2006).

Rainfall in Sanbona South was lowest in spring and summer. There was an increased usage of woody browse in the Southern herd's diet in summer, such as a higher utilisation of *Searsia glauca* and *Atriplex vestita*. Akin to the Northern herd, *V. karroo* was consumed throughout the year but more so in spring and summer, correlating with new leaf production, flowering and low rainfall. *V. karroo* is thus likely consumed at such high levels due to its high abundance along drainage lines and almost year-round availability. *Searsia lancea* was also consumed throughout the year, with utilisation increasing in summer, decreasing in autumn, and at its lowest in winter before increasing again in spring. This decrease in utilisation in autumn and winter correlates with the flowering season. During autumn *Euclea undulata* produce berries, which were observed to be eaten by both elephant herds, correlating with an increase in utilisation during autumn. Autumn also saw an increase in the utilisation of *Zygophyllum sp.* which increase leaf production during this time. Utilisation of *Asparagus sp.* and *Lycium sp.* by the Southern elephants increased in autumn and winter. This increase in utilisation of these browse species correlates with a decrease in utilisation of *V. karroo*. However, *Lycium sp.* only produce leaves after substantial rainfall events. Since rainfall occurred in autumn and winter it would appear that the elephants were able to utilise this increase in leaf production, thus decreasing the use of *V. karroo*. As within Sanbona North, the Southern herd also consumed higher quantities of *Berkheya* and *Osteospermum sp.* in winter.

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3.5.3 Differences between scan and isotopic data

Differences between the results of the scan sampling and the isotopic analysis were noted. The main difference was the low percentage of *V. karroo* in the isotopic results compared to the scan sampling results, where *V. karroo* forms a large portion of both elephant herds' diets. There was also a difference in seasonal use. This contradiction between sampling methods is reason for further observation to determine which method(s) would be best to utilise in the Little Karoo ecosystem. *Mesembryanthemum junceum*, *Tylecodon paniculatus*, *Crassula rupestris* and *Atriplex vestita* were also not recorded as part of the diet range through isotopic analysis as they were all classified as C_4 plants. The large differences between the browse:graze:succulent ratios of the observed diets and that of the C_3:CAM: C_4 ratios of the isotopic analysis were largely due to the fact that many of the graze species were classified as C_3 and not C_4. This could be the result of the dry conditions and warm temperatures experienced when grass samples were collected and consumed. Additionally, the isotopic representation of C_4 plant species has been found to be under-represented due to inefficient metabolism (Van der Merwe *et al*., 1988). Additionally,it may not show the full spectrum of diet, as it is only a fraction of the entire bolus. Bax and Sheldrick (1963) stated that faecal analysis alone was not sufficient to base a dietary study of elephants on, but rather the combination of scan sampling and faecal analysis is needed.

3.6. Conclusion

Understanding elephant diet within an area is critical to understanding the spatial requirements of a population and the impact they may have on an ecosystem (Holechek *et al*., 1982). An estimated 600 plant species occur on SWR, of which at least 94 were utilised by the two elephant herds. Both herd's diets consisted of large percentages of browse, but the percentage of graze and succulents consumed varied between herds. Although the diet of both the Southern and Northern herds consisted of similar forage species, the frequency at which each of the species was utilised differed due to availability to each herd.

According to scan sampling, the most important browse species is *V. karroo*, which is abundant throughout the majority of the drainage lines within the herds' home ranges and does not seem to

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be vulnerable to the browsing impact of elephants. *P. australis* also forms an important forage source for the Northern herd that is not impacted by heavy utilisation. Both herds' diets consisted of the same basic core forage species (*V. karroo*, *Lycium* species and *Searsia* species) throughout the year, however seasonal dietary changes were recorded as vegetation quality and quantity were observed to be affected by the change in seasons and intensifying drought conditions.

The downfall of scan sampling was that nocturnal foraging behaviour could not be observed and diurnally, smaller plants were possibly misidentified. Smaller succulent species were more difficult to identify from a distance, especially when not in flower. Scan sampling also only covers a few hours of feeding each month, which could add biases to the results. For instance, species such as *P. australis* could have been eaten by the Southern herd as the spatial analysis indicated that the herd utilised areas where pockets of *P. australis* grew, however, this was not observed regularly during scan sampling. In order to improve on our knowledge of the feeding ecology of elephants in semi-arid areas such as SWR, it is vital that further and continued studies be conducted. Although isotopic analysis was helpful in understanding the diet classification with regards to plant photosynthetic pathways, it did not align with the results from the scan sampling. This was possibly due to the change in photosynthetic pathways of succulent plant species and some grasses due to the dry conditions experienced during the study, as well as the small sample of each bolus that is tested. Some plant species were also more difficult to grind for faecal analysis. However, since scan sampling only covers a fraction of the total feeding time, perhaps scan sampling is more representative of the true feeding ecology. To better understand the feeding ecology, it would be beneficial to create a plant epidermal library for SWR and to conduct microhistological studies on the elephant dung samples.

Through this study we were able to better understand how elephants survive in this section of the Little Karoo. However, it is important for further studies to be conducted in order to fully understand the feeding ecology of elephants in semi-arid areas such as SWR.

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3.8. Appendix 1

Table 3.1. Total number of each of the 94 plant species foraged on by both herds and the percentage within their diet.

Browse species	Total	Total % of browse diet
Asparagus sp.	1376	3.2
Atriplex nummularia	667	1.5
Atriplex vestita	2613	6.0
Barleria pungens	7	< 0.1
Berkheya cuneata	336	0.8
Berkheya spinose	236	0.5
Blepharis capensis	15	< 0.1
Braunsia apiculata	53	0.1
Buddleja saligna	168	0.4
Carissa haematocarpa	572	1.3
Diospyros lycioides	26	0.1
Elytropappus rhinocerotis	49	0.1
Euclea undulata	1792	4.1
Euryops sp.	6	< 0.1
Felicia sp.	20	< 0.1
Galenia secunda	89	0.2
Galenia africana	10	< 0.1
Gazania lichtensteinii	6	< 0.1
Gloveria integrifolia	14	< 0.1
Gomphocarpus fruticosus bark	33	0.1
Gymnosporia buxifolia	67	0.2
Gymnosporia szyszylowiczii	85	0.2
Helichrysum sp.	1	< 0.1
Hermannia althaefolia	62	0.1
Hermannia cuneifolia	27	0.1
Hirpicium sp.	16	< 0.1
Limeum aethiopicum	24	0.1
Lycium oxycarpum	1903	4.4
Lycium sp.	1800	4.2
Manochlamys albicans	4	< 0.1
Medicago sativa	6	< 0.1
Microloma sagittatum	6	< 0.1

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Monechema sp.	13	< 0.1
Monsonia crassicaule	38	0.1
Muraltia spinosa	2	< 0.1
Nymania capensis	3	< 0.1
Olea europaea subs. africana	102	0.2
Oncosiphon piluliferum	6	< 0.1
Osteospermum sinuatum	241	0.6
Osteospermum sp.	11	< 0.1
Pelargonium tetragonum	9	< 0.1
Pentzia incana	14	< 0.1
Pteronia oblanceolata	19	< 0.1
Pteronia pallens	31	0.1
Salsola aphylla	112	0.3
Schotia afra	375	0.9
Searsia glauca	582	1.3
Searsia lancea	2434	5.6
Searsia longispina	280	0.6
Tamarix usneoides	1195	2.8
Vachellia karroo	23915	55.3
Vachellia karroo burnt	680	1.6
Viscum rotundifolium	10	< 0.1
Zygophyllum retrofractum	201	0.5
Zygophyllum sp.	872	2.0
Total	43234	100

Graze species	**Total**	**Total % of graze diet**
Grass species	5613	54.2
Phragmites australis	4677	45.2
Scirpoides sp.	8	0.1
Typha capensis	56	0.5
Total	10354	100

Succulent species	**Total**	**Total % of succulent diet**
Aloe perfoliata	74	0.9
Bulbine succulenta	4	< 0.1
Crassula arborescens stem	33	0.4
Crassula rupestris	362	4.2
Crassula subaphylla	10	0.1

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Crassula tetragona	13	0.1
Cephalophyllum curtophyllum roots	7	0.1
Delosperma sp.	254	2.9
Drosanthemum albiflorum	78	0.9
Drosanthemum bicolor	6	0.1
Drosanthemum crassum	17	0.2
Drosanthemum delicatulum	100	1.2
Drosanthemum giffenii	8	0.1
Drosanthemum hispidum	1587	18.3
Drosanthemum lique	326	3.8
Drosanthemum micans	5	0.1
Drosanthemum speciosum	5	0.1
Drosanthemum sp.	21	0.2
Haworthia viscosa	4	< 0.1
Lampranthus sp.	92	1.1
Malephora lutea	652	7.5
Mesembryanthemum junceum	2013	23.2
Mesembryanthemum noctiflorum	350	4.0
Mesembryanthemum resurgens	10	0.1
Mesembryanthemum splendens	632	7.3
Ruschia caroli	524	6.0
Ruschia lineolate	207	2.4
Ruschia multiflora	68	0.8
Ruschia polita	9	0.1
Ruschia pungens	33	0.4
Ruschia robusta	32	0.4
Ruschia spinose	394	4.5
Ruschia spp.	96	1.1
Tetragonia fruticosa	187	2.2
Trichodiadema sp.	14	0.2
Tylecodon paniculatus	443	5.1
Total	8670	100

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Table 3.2. δ15N and δ15C values (‰) of C4, CAM and C3 vegetation samples used as a reference in the stable isotopic analysis of the diet of elephant in SWR, South Africa. The %N and %C were determined by the Isotope Laboratory, Mammal Research Institute, University of Pretoria.

C3/C4/CAM	Type	Species	$\delta^{15}N$ (‰)	%N	δ^{13C} (‰)	%C	C/N
C3	Browse	*Asparagus sp.*	6.25	2.31	-24.93	44.98	22.72
		Asparagus sp.	6.24	2.39	-24.98	45.38	22.13
		Asparagus sp.	6.07	2.31	-25.13	44.72	22.58
		Carissa haematocarpa	6.63	0.84	-26.06	49.27	68.55
		Carissa haematocarpa	8.33	1.00	-27.19	51.02	59.5
		Carissa haematocarpa	9.2	0.94	-27.67	47.72	58.97
		Euclea undulata	4.91	0.71	-27	48.43	79.76
		Euclea undulata	6.5	0.66	-27.12	49.75	87.83
		Euclea undulata	5.96	0.74	-27.21	49.60	78.34
		Euclea undulata	5.41	0.75	-27.26	49.00	76.56
		Lycium oxycarpum	12.82	2.77	-24.48	34.89	14.7
		Lycium oxycarpum	14.21	2.26	-27.34	32.82	16.93
		Lycium oxycarpum	14.47	2.21	-27.56	30.63	16.19
		Schotia afra	9.1	1.38	-25.64	49.00	41.36
		Schotia afra	8.87	1.42	-25.94	48.34	39.82
		Schotia afra	8.84	1.38	-26.05	49.88	42.3
		Searsia lancea	8.86	1.80	-26.34	46.08	29.81
		Searsia lancea	9.28	1.75	-26.65	46.14	30.71
		Searsia lancea	9.38	1.74	-26.7	46.34	30.99
		Tamarix	9.36	2.99	-25.04	34.51	13.48
		Tamarix	9.08	3.14	-25.18	34.16	12.7
		Tamarix	9.12	2.33	-25.43	29.89	14.96
		Tamarix	8.04	2.61	-25.45	33.28	14.86
		Vachellia karroo	0.34	1.45	-25.81	44.24	35.71
		Vachellia karroo	-0.06	1.37	-25.92	42.63	36.2
		Vachellia karroo	0.09	1.33	-26.03	41.68	36.51
		Zygophyllum sp.	10.69	3.12	-26.83	35.38	13.25
		Zygophyllum sp.	10.86	3.24	-27	35.33	12.73
		Zygophyllum sp.	10.65	2.94	-27.15	35.25	13.98
		Ehrharta sp. 1	12.46	1.41	-29.7	42.22	34.91

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	Graze	*Ehrharta sp. 1*	12.02	1.50	-29.71	41.91	32.61
		Ehrharta sp. 1	12.6	1.48	-29.77	42.12	33.1
		Phragmites australis	13.98	1.38	-27.45	41.15	34.7
		Phragmites australis	13.63	1.71	-27.48	41.22	28.08
		Phragmites australis	11.46	1.75	-28.09	39.95	26.59
		Scirpoides sp1	8.66	1.03	-24.16	42.86	48.37
		Scirpoides sp1	8.27	1.01	-24.33	42.45	48.88
		Scirpoides sp1	9.19	1.32	-24.36	44.01	38.89
		Scirpoides sp1	8.44	0.95	-24.58	43.49	53.68
		Scirpoides sp2	8.78	0.77	-24.31	44.12	66.68
		Scirpoides sp2	7.36	0.82	-24.62	45.06	64.32
		Scirpoides sp2	7.18	0.63	-24.91	45.29	83.87
		Themeda triandra	7.07	1.82	-27.63	41.25	26.37
		Themeda triandra	7.52	1.82	-27.8	41.21	26.44
		Themeda triandra	7.47	1.66	-27.83	41.08	28.94
		Typha capensis	5.69	0.34	-28.98	23.63	80.73
		Typha capensis	5.73	0.34	-29.09	25.81	89.1
		Typha capensis	5.08	0.35	-29.1	23.20	76.58
		Typha capensis	5.84	0.33	-29.12	23.52	83.15
	Succulent	*Ruschia spinosa*	10.96	2.05	-25.37	34.34	19.56
		Ruschia spinosa	8.87	1.59	-26.46	34.06	25.01
		Tetragonia fruticosa	11.37	2.64	-25.52	30.75	13.57
		Tetragonia fruticosa	9.89	3.92	-26.49	31.67	9.43
C4	Browse	*Atriplex vestita*	7.07	3.25	-14.45	35.36	12.71
		Atriplex vestita	9.91	2.21	-14.64	30.08	15.88
		Atriplex vestita	11.45	3.21	-16.65	32.31	11.75
	Graze	*Cynodon dactylon*	9.63	0.79	-16.16	41.54	61.26
		Cynodon dactylon	9.12	0.64	-16.33	41.90	76.46
		Cynodon dactylon	8.04	1.06	-16.91	40.21	44.46
		Cynodon dactylon	6.82	1.00	-17.38	41.48	48.17
		Ehrharta sp. 2	13.27	0.34	-19.06	36.22	124.33
		Ehrharta sp. 2	10.26	0.44	-19.3	38.97	104.52
		Ehrharta sp. 2	15.08	0.33	-19.84	40.63	143.94
		Stipagrostis obtusa	7.87	0.80	-13.69	33.08	48.44
		Stipagrostis obtusa	8.37	0.69	-13.92	22.33	37.9

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		Stipagrostis obtusa	7.51	0.72	-13.97	29.88	48.36
	Succulent	*Crassula rupestris*	6.85	0.37	-14	41.74	131.27
		Crassula rupestris	6.91	0.28	-14.06	40.66	171.35
		Crassula rupestris	6.43	0.29	-14.28	41.44	165.79
		Mesembryanthemum junceum	1.79	1.23	-15.33	33.64	31.9
		Mesembryanthemum junceum	1.56	1.41	-15.44	34.66	28.71
		Mesembryanthemum junceum	3.12	1.58	-15.9	33.10	24.51
		Tylecodon paniculatus	10.7	0.90	-14.37	35.79	46.45
		Tylecodon paniculatus	7.43	0.50	-14.56	22.62	52.71
		Tylecodon paniculatus	7.7	0.89	-14.71	37.75	49.22
		Tylecodon paniculatus	7.94	0.93	-14.76	37.67	47.43
CAM	Succulent	*Delosperma sp.*	16.33	1.59	-19.84	30.18	22.07
		Delosperma sp.	15.47	1.63	-20.03	29.56	21.17
		Delosperma sp.	15.26	1.50	-20.22	30.22	23.47
		Drosanthemum hispidum	14	1.78	-20.65	34.37	22.51
		Drosanthemum hispidum	15.41	2.15	-20.7	32.74	17.74
		Drosanthemum hispidum	13.19	1.82	-20.88	33.93	21.77
		Drosanthemum hispidum	15.59	1.62	-22.23	33.95	24.49
		Malephora lutea	13.26	1.22	-19.25	25.57	24.49
		Malephora lutea	12.25	0.96	-19.82	25.07	30.52
		Malephora lutea	8.56	1.32	-21.96	26.51	23.39
		Mesembryanthemum splendens	11.36	1.85	-19.84	32.54	20.48
		Mesembryanthemum splendens	11.8	1.74	-20.69	34.20	22.96
		Mesembryanthemum splendens	11.55	2.03	-20.88	34.33	19.78
		Mesembryanthemum splendens	13.3	1.57	-22.71	24.51	18.24
		Mesembryanthemum splendens	12.83	1.80	-22.72	25.77	16.7
		Mesembryanthemum splendens	10.33	2.45	-23.66	33.63	16.03
		Mesembryanthemum splendens	9.49	2.19	-23.72	33.58	17.91
		Ruschia spinose	10.21	0.93	-23.67	35.64	44.91
		Ruschia caroli	11.06	0.86	-19.63	39.79	53.82
		Ruschia caroli	7.47	1.38	-21.71	40.71	34.48
		Ruschia caroli	8.37	1.08	-23.15	40.38	43.77
		Tetragonia fruticosa	13.57	4.25	-23.19	33.55	9.2

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Table 3.3. δ15N and δ13C values (‰) of faecal samples representing the diet of elephant in summer, autumn, winter and spring 2016-2017 in Sanbona Wildlife Reserve, South Africa. The standard corrected values were determined by laboratory technicians at the Stable Isotope Lab, Mammal Research Institute, University of Pretoria

Season	Southern herd faecal samples					Northern herd faecal samples				
	δ^{15}N (‰)	%N	δ^{13C} (‰)	%C	C/N	δ^{15}N (‰)	%N	δ^{13C} (‰)	%C	C/N
Summer	4.57	1.47	-24.9	45.64	36.32	8.99	1.54	-19.06	43.24	32.75
	5.4	1.27	-26.26	45.14	41.32	7.22	1.73	-21.53	44.6	30.07
	7.1	1.76	-26.32	42.88	28.49	11.44	1.5	-21.78	44.37	34.5
	5.48	0.92	-26.37	42.12	53.2	9.61	1.44	-22.11	44.1	35.62
	5.69	1.37	-26.41	45.1	38.54	7.16	1.69	-22.65	43.98	30.3
	4.39	1.45	-26.69	44.77	36.04	7.76	1.69	-22.65	44.99	31.08
	5.89	1.62	-26.75	42.58	30.59	6.58	1.13	-23.08	43.87	45.47
	6.22	1.54	-26.78	44.38	33.7	9.01	1.59	-23.27	43.89	32.23
	4.9	1.18	-26.78	41.81	41.51	6.96	1.78	-23.5	44.01	28.79
	4.49	1.32	-26.8	46.73	41.38	7.55	1.64	-23.7	43.94	31.31
	4.87	1.36	-26.86	44.76	38.4	7.87	1.77	-23.79	45.24	29.77
	6.15	1.37	-26.9	41.65	35.52	4.82	1.34	-24.11	45.5	39.57
	4.39	1.22	-26.9	46.53	44.43	7.17	1.12	-24.65	44.76	46.65
	4.38	1.13	-26.92	44.65	46.1	7.75	1.06	-24.94	43.48	47.99
	5.7	1.43	-27	40.59	33.1	6.22	1.45	-24.96	42.67	34.3
	6.04	1.77	-27.09	41.26	27.2	8.81	1.9	-25.44	44.41	27.2
	4.11	1.62	-27.1	44.73	32.29	5.46	1.3	-25.97	45.69	41.06
	4.27	1.64	-27.12	45.59	32.39	6.52	1.29	-25.97	48.55	43.81
	6.66	1.86	-27.36	42.18	26.51	7.88	1.23	-26.41	41.85	39.72
	4.7	1.55	-27.45	43	32.26					
Autumn	6.81	0.87	-25.52	43.94	58.91	7.49	1.33	-21.63	44.03	38.75
	6.92	1.11	-25.74	44.73	46.93	7.32	1.51	-22.59	42.64	32.91
	8.28	1.26	-25.74	43.92	40.54	7.95	1.22	-22.99	44.37	42.33
	6.95	1.15	-25.86	46.16	46.88	7.68	1.51	-23.11	43.99	34
	9.25	1.36	-25.98	45.33	38.75	7.27	1.26	-23.52	43.21	40.15
	5.06	0.86	-26.27	47.81	65.16	8.95	1.19	-23.58	38.38	37.51
	3.89	1.5	-26.56	44.76	34.73	9.43	1.58	-23.66	41.83	30.79
	5.24	1.19	-26.58	46.87	46.01	9.91	1.62	-23.9	41.46	29.83

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	5.08	1.83	-26.74	45.36	28.98	6.02	1.39	-23.97	44.54	37.38
	5.53	0.88	-26.76	44.24	58.67	7.88	1.28	-24.12	44.7	40.84
	5.64	1.21	-27	45.81	44.32	6.37	1.4	-24.22	46.13	38.57
	4.34	1.44	-27.04	47.35	38.34	7.05	1.52	-24.63	44.64	34.34
	5.07	1.54	-27.04	46.11	34.88	5.56	1.22	-24.98	44.34	42.37
	5.06	1.43	-27.14	43.56	35.54	9.43	1.98	-25	45.06	26.58
	5.77	1.25	-27.23	43.94	41.06	6.39	1.5	-25.34	45.99	35.88
	3.95	1.27	-27.36	46.3	42.61	9.44	1.5	-25.83	45.61	35.54
	4.12	1.25	-27.38	45.74	42.59	8.75	1.57	-25.87	43.58	32.31
	5.81	1.33	-27.41	45.9	40.36	10.29	1.2	-26.07	44.91	43.6
	5.25	1.29	-27.49	45.18	40.97	7.17	1.79	-28.33	48.15	31.43
Winter	7.46	0.84	-25.44	45.66	63.33	8.13	1.39	-24.83	44.75	37.6
	8.99	1.46	-25.93	45.26	36.21	8.62	1.32	-25.2	45.07	39.87
	7.74	1.27	-25.95	43.67	40.22	7.87	1.31	-25.44	46.25	41.14
	6.72	1.22	-25.96	43.88	41.91	8.89	1.32	-25.46	45.2	40.03
	7.52	1.14	-26.02	43.92	44.75	6.54	1.1	-25.64	41.47	44.1
	7.68	1.17	-26.11	45.85	45.79	10.44	1.03	-25.72	40.96	46.48
	7.82	1.56	-26.37	44.08	32.87	7.39	1.23	-25.73	44.92	42.55
	7.68	1.75	-26.43	45.14	30.11	9.87	1.42	-25.75	45.52	37.33
	6.58	1.34	-26.46	44.32	38.5	9.16	1.47	-25.75	45.01	35.62
	9.97	1.09	-26.47	46.1	49.42	8.44	1.27	-25.96	45.33	41.63
	8.15	1.36	-26.52	44.6	38.23	7.29	1.66	-26.01	45.55	32
	5.68	1.29	-26.73	46.2	41.88	9.28	1.11	-26.11	45.75	48.11
	7.12	1.46	-26.77	46.68	37.33	8.41	1.3	-26.14	44.66	40.03
	5.32	1.31	-26.84	46.54	41.51	5.67	1.53	-26.15	48.82	37.23
	9.46	1.33	-26.84	44.73	39.24	7.5	1.8	-26.38	44.82	28.99
	6.87	1.43	-26.87	45.04	36.8	8.38	1.32	-26.44	46.4	40.98
	6.91	1.55	-27.03	44.95	33.88	9.03	1.28	-26.66	44.69	40.63
	4.33	1.26	-27.28	45.3	42.04	8.02	1.25	-26.69	44.15	41.32
	5.33	1.41	-27.29	45.39	37.61	8.65	1.27	-26.9	40.56	37.13
	5.04	1.46	-27.47	45.54	36.45	7.01	1.35	-27.43	46.19	40.06
Spring	5.19	1.09	-25.46	47.4	50.62	10.06	1.84	-24.2	41.82	26.46
	5.33	1.46	-26.76	46.42	37.03	7.49	1.31	-24.27	46.16	41.21
	5.29	1.19	-26.78	46.1	45.28	9.45	1.36	-24.28	43.62	37.29

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	4.52	1.24	-26.82	44.91	42.21	7.19	1.4	-24.8	44.67	37.33
	7.15	1.18	-26.85	45.54	44.97	7.04	1.67	-24.84	46.16	32.3
	5.08	1.12	-26.87	45.97	47.91	7.49	1.43	-25.34	45.19	36.77
	7.31	1.42	-26.87	46.42	38.25	7.36	1.47	-26.03	44.91	35.74
	4.1	1.28	-26.88	45.1	41.15	5.15	1.32	-26.03	45.8	40.48
	6.08	1.42	-26.9	45.53	37.3	5.63	1.66	-26.27	41.18	28.87
	5.06	1.12	-26.96	45.22	47.29	5.98	1.78	-26.31	42.9	28.18
	7.28	1.22	-27.04	43.81	41.99	6.12	1.89	-26.38	44.1	27.24
	5.47	1.65	-27.14	45.87	32.48	4.56	1.34	-26.42	43.35	37.74
	4.85	1.4	-27.15	46.44	38.7	8.76	1.14	-26.55	46.34	47.38
	4.79	1.17	-27.16	45.3	45	7.18	1.33	-26.67	46.18	40.48
	6.37	1.11	-27.21	46.68	49.01	8.04	1.75	-26.76	44.32	29.62
	4.91	1.33	-27.26	43.35	38	7.41	1.76	-26.86	44.39	29.43
	7.24	1.35	-27.3	46.19	39.9	8.31	1.87	-26.91	43.43	27.05
	5.79	1.28	-27.34	46.24	42.22	5	1.37	-27.1	44.53	37.87
	6.72	0.95	-27.44	48.23	59.2	9.13	1.87	-27.33	41.94	26.22
						9.03	2.32	-27.71	45.48	22.86

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Table 3.4 Plant species abbreviations utilised in Chapter 3

Species	**Abbreviated species name**
Atriplex nummularia	*A. nummularia*
Atriplex vestita	*A. vestita*
Berkheya cuneata	*B. cuneata*
Berkheya spinosa	*B. spinosa*
Carissa haematocarpa	*C. haematocarpa*
Crassula arborescence	*C. arborescence*
Crassula rupestris	*C. rupestris*
Crassula subaphylla	*C. subaphylla*
Crassula tetragonia	*C. tetragonia*
Drosanthemum hispidium	*D. hispidium*
Euclea undulata	*E. undulata*
Mesembryanthemum junceum	*M. junceum*
Mesembryanthemum noctiflorum	*M. noctiflorum*
Phragmites australis	*P. australis*
Ruschia caroli	*R. caroli*
Ruschia lineolata	*R. lineolate*
Ruschia spinosa	*R. spinosa*
Schotia afra	*S. afra*
Searsia glauca	*S. glauca*
Searsia lancea	*S. lancea*
Tamarix usneoides	*T. usneoides*
Tylecodon paniculatus	*T. paniculatus*
Vachellia karoo	*V. karroo*

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Table 3.5. Plant species list recorded on Sanbona Wildlife Reserve

Acanthopsis disperma	*Euphorbia burmannii*	*Othonna filicaulis*
Acrodon sp.	*Euphorbia clandestina*	*Othonna osteospermoides*
Adromischus filicaulis	*Euphorbia mauritanica*	*Othonna retrofracta*
Adromischus maculatus	*Euphorbia multiceps*	*Othonno sp.*
Adromischus triflorus	*Euphorbia multifolia*	*Oxalis ciliaris*
Agathosma ovata	*Euphorbia rhombifolia*	*Oxalis obtusa*
Agathosma sp.	*Euryops lateriflorus*	*Oxalis pes-caprae*
Aizoon karooicum	*Euryops nodosus*	*Oxalis sp.*
Albuca sp.	*Euryops rehmannii*	*Pachypodium succulentum*
Aloe microstigma	*Euryops spp.*	*Panicum sp.*
Aloe perfoliata	*Euryops subcarnosus*	*Pappea capensis*
Aloe striata	*Euryops tenuissimus*	*Paspalum sp.*
Aloe variegata	*Exomis microphylla*	*Passerina obtusifolia*
Anacampseros lanceolata	*Felicia filifolia*	*Pegolettia baccaridifolia*
Anacampseros ustulata	*Felicia muricata*	*Pelargonium abrotanifolium*
Anginon difforme	*Felicia ovata*	*Pelargonium alternans*
Anisodontea dissecta	*Felica sp.*	*Pelargonium crispum*
Anisodontea reflexa	*Fingerhuthia africana*	*Pelargonium crithmifolium*
Anisodontea triloba	*Fockea capensis*	*Pelargonium sp.*
Antegibbaeum fissoides	*Freesia refracta*	*Pelargonium tetragonum*
Anthospermum sp.	*Freylinia undulata*	*Pelargonium triste*
Aptosimum indivisum	*Galenia africana*	*Peliostomum leucorrhizum*
Arctopus sp.	*Galenia cymosa*	*Pennisetum sp.*
Arctotis sp.	*Galenia fruticosa*	*Pentaschistis airoides*

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Argyrolobium sp.
Aristida congesta
Asclepias fruticosa
Aspalathus angustifolia
Aspalathus spp.
Asparagus aethiopicus
Asparagus africanus
Asparagus burchellii
Asparagus capensis
Asparagus mucronatus
Asparagus oliveri
Asparagus retrofractus
Asparagus striatus
Astroloba corrugata
Astroloba smutsiana
Athanasia sp.
Atriplex lindleyi subsp inflata
Atriplex nummularia
Atriplex semibaccata
Atriplex vestita
Augea capensis
Avonia papyracea (Anacampseros papyracea)
Babiana karooica
Ballota africana
Barleria pungens

Galenia sarcophylla
Galenia secunda
Galium tomentosum
Garuleum bipinnatum
Gasteria brachyphylla
Gazania krebsiana
Gazania lichtensteinii
Gibbaeum geminum
Gibbaeum heathii
Gibbaeum nuciforme (Gibbaeum cryptopodium)
Gibbaeum pachypodium
Gibbaeum pilosulum
Gibbaeum pubescens
Gibbaeum shandii
Gibbaeum velutinum
Gladiolus sp.
Glottiphyllum depressum
Glottiphyllum surectum
Glottiphyllum carnosum
Gloveria integrifolia
Gnidia deserticola
Gomphocarpus fruticosus
Gymnosporia buxifolia
Gymnosporia szyszylowiczii
Haemanthus sanguineus

Pentzia incana
Phragmites australis
Phylica sp.
Phyllopodium rustii
Phymaspermum sp.
Piaranthus parvulus
Picris echioides
Plagiochloa unicolor
Plumbago tristis
Podalyria sp.
Pollichia campestris
Polygala asbestina
Polygala microlopha
Polygala scabra
Polygala sp.
Portulacaria afra
Prismatopcarpus sp.
Protea humiflora
Protea laurifolia
Protea repens
Psilocaulon simile
Psilocaulon spp.
Psilocaulon utile
Pteronia adenocarpa
Pteronia empetrifolia

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Bartholina etheliae
Berkheya cuneata
Berkheya spinosa
Blepharis capensis
Boophane disticha
Braunsia apiculata
Bromus sp.
Brunsvigia josephinae
Brunsvigia striata
Buddleja saligna
Buddleja salviifolia
Bulbine frutescens
Bulbine mesembryanthemoides
Bulbine succulenta
Bulbinella trinervis
Cadaba aphylla
Calobota spp (Lebeckia)
Carissa haematocarpa
Carpobrotus deliciosus
Cassytha ciliolata
Cenchrus ciliaris
Cephalophyllum curtophyllum
Cephalophyllum purpureo-album
Cerochlamys pachyphylla
Chaenostoma sp. (Sutera sp)
Chlorophytum crispum

Haworthia arachnoidea
Haworthia viscosa
Helichrysum rosum
Helichrysum sp.
Helichrysum zeyheri
Heliophila cornuta
Heliophila sp.
Hemimeris gracilis
Hereroa aspera
Hermannia althaefolia
Hermannia cuneifolia
Hermannia filifolia
Hermannia flammula
Hermannia multiflora
Hermannia odorata
Hermannia spp.
Hirpicium alienatum
Hirpicium integrifolium
Holothrix spp.
Hoodia gordonii
Hoodia pilifera
Hordeum sp.
Hueria barbata
Hyobanche glabrata
Hyobanche sanguinea
Hyparrhenia hirta

Pteronia fasciculate
Pteronia flexicaulis
Pterona glauca
Pteronia hirsuta
Pteronia incana
Pteronia oblanceolata,
Pteronia oppositifolia
Pteronia ovalifolia
Pteronia pallens
Pteronia paniculata
Pteronia robusta
Pteronia sordida
Pteronia staehelinoides
Pteronia succulenta
Pteronia viscosa
Rafnia spp.
Restio spp.
Rhigozum obovatum
Rhinephyllum muirii
Romulea sp.
Rosenia sp.
Ruschia caroli
Ruschia robusta
Ruschia spinosa
Ruschia sp.
Salix mucronata

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Chrysocoma ciliata	*Hypertelis salsoloides*	*Salsola aphylla*
Cissampelos capensis	*Ifloga glomerata*	*Salsola glabrescens*
Citrullus lanatus	*Indigofera heterophylla*	*Salsola tragus*
Clutia tomentosa	*Indigofera spp.*	*Salsola smithii*
Colchium coloratum sp. burchellii (Androcymbium burchelii)	*Ixia sp.*	*Salsola tuberculata*
Colchium longipes (Androcymbium longipes)	*Justicea cuneata*	*Salvia sp.*
Colchium volutare (Androcymbium volutare)	*Kniphofia sp.*	*Sarcostemma viminale*
Conophytum minimum	*Lachenalia karooica*	*Scabiosa columbaria*
Conophytum piluliforme	*Lachenalia sp.*	*Schotia afra*
Convolvulus sagittatus	*Lampranthus spp.*	*Scirpoides sp.*
Conyza scabrida	*Lapeirousia pyramidalis*	*Searsia glauca*
Cotula sp.	*Leipoldtia schultzei*	*Searsia lancea*
Cotyledon orbiculata	*Lessertia frutescens (Sutherlandia frutescens)*	*Searsia longispina*
Crassula arborescens	*Lessertia lanata*	*Selago albida*
Crassula barbarta	*Leucodendron tinctum*	*Selago distans (Walafrida distans)*
Crassula capensis	*Leucodendron uliginosum*	*Selago geniculata (Walafrida geniculata)*
Crassula capetella	*Leucospermum pluridens*	*Selago spp.*
Crassula columnaris	*Leucospermum sp.*	*Senecio acaulis*
Crassula congesta	*Leysera gnaphalodes*	*Senecio articularis*
Crassula cultrata	*Leysera tenella*	*Senecio haworthii*
Crassula deltoidea	*Limeum aethiopicum*	*Senecio pauciflosculosus*
Crassula expansa	*Linum sp.*	*Senecio radicans*
Crassula hemispherica	*Liparia sp.*	*Senecio scaposus*

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Crassula muscosa
Crassula orbicularis
Crassula perforata
Crassula pyramidalis
Crassula rupestris
Crassula subaphylla
Crassula tecta
Crassula tetragona
Crassula umbella
Crassula vaillantii
Cullen obtusifolia
Cullumia sp.
Cyanella lutea
Cylindrophyllum comptonii
Cymbopappus adenosolen
Cynodon dactylon
Cyperus sp.
Cysticapnus vesicaria
Delosperma sp.
Dianthus basuticus
Dianthus bolusii
Dianthus thunbergii
Diascia sp.
Dicerothamnus rhinocerotis
Digitaria sp.

Lobelia sp.
Lobostemon sp.
Lotononis pumila
Lotononis venosa
Lotononis sp.
Lycium cinereum
Lycium ferocissimum
Lycium hirsutum
Lycium oxycarpum
Lycium pumilum
Lyperia tristis
Macledium spinosum (Dicoma spinosa)
Malephora lutea
Manochlamys albicans
Massonia depressa
Maytenus oleoides
Medicago sativa
Melianathus comosus
Mellilotus indica
Melolobium candicans
Merxmuellera sp.
Mesembryanthemum archeri (Sceletium rigidum)
Mesembryanthemum crystallinum
Mesembryanthemum guerichianum
Mesembryanthemum ladismithiense (Sceletium strictum)

Senecio sp.
Septulina glauca
Sericocoma avolans
Setaria sp.
Silene sp.
Sisymbrium sp.
Solanum sp.
Solanum tomentosum
Spiloxene sp.
Stachys aethiopica
Stapelia hirsuta
Stipagrostis ciliata
Stipagrostis namaquensis
Stipagrostis obtusa
Strumaria sp.
Struthiola eckloniana
Struthiola sp.
Suaeda fruticosa
Syncarpha sp.
Syringodea sp.
Tamarix usneoides
Tetragonia fruticosa
Tetragonia sarcophylla
Themeda triandra
Thesium lineatum

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Dimorphotheca cuneata
Dioscorea elephantipes
Diospyros austro-africana
Diospyros lycioides
Dodonaea viscosa
Dorotheanthus bellidiformis
Drimia sp.
Drosanthemum archeri
Drosanthemum bicolor
Drosanthemum delicatulum
Drosanthemum hispidum
Drosanthemum micans
Drosanthemum speciosum
Duvalia caespitosa
Duvalia parviflora
Ehrharta sp.
Enneapogon sp.
Eragrostis sp.
Erica cerinthoides
Erica plukenetii
Erica sp.
Erigaron sp.
Eriocephalus africanus

Mesembryanthemum noctiflorum (Aridaria noctiflora)
Mesembryanthemum resurgens (Phyllobolus resurgens)
Mesembryanthemum subtruncatum
Mesembryanthemum tortuosum (Sceletium tortuosum)
Metalasia sp.
Microloma tenuifolium
Microloma sagittatum
Monechma incanum
Monechma spartoides
Monsonia crassicaule (Sarcocaulon crassicaule)
Montinia caryophyllacea
Moquiniella rubra
Moraea spp.
Muraltia heisteria
Muraltia spinosa
Muraltia sp.
Nemesia fruticans
Nemesia ligulata
Nenax sp.
Nerine humilis
Notobubon sp.
Nymania capensis
Oedera squarrosa

Thesium sp.
Trachyandra revoluta
Tribulus terrestris
Trichodiadema sp.
Trichogyne polycnemoides
Tridentea gemmiflora
Trifolium burchellianum
Tritonia sp.
Tulbaghia sp.
Tylecodon cacalioides
Tylecodon paniculatus
Tylecodon reticulatus
Tylecodon ventricosus
Tylecodon wallichii
Typha capensis
Ursinia sp.
Vachellia karroo
Viscum capense
Viscum continuum
Viscum rotundifolium
Wahlenbergia gutheriei
Wahlenbergia nodosa (Lightfootia nodosa)
Watsonia sp.

Eriocephalus brevifolius
Eriocephalus ericoides
Eriocephalus grandiflorus
Eriospermum alcicorne
Eriospermum capense
Eriospermum ericoides
Eriospermum paradoxum
Euclea crispa
Euclea undulata
Euphorbia atrispina

Oldenburgia paradoxa
Olea europea subsp. africana
Oncosiphon piluliferum
Ornithogalum sp.
Ornithoglossum undulatum
Osteospermum incanum (Chrysanthemoides incana)
Osteospermum moniliferum (Chrysanthemoides monilifera)
Osteospermum sinuatum (Tripteris sinuata)
Osteospermum sp.
Othonna cylindrica

Wiborgia sp.
Wurmbea variabilis
Xenoscapa fistulosa
Zaluzianskya minima
Zeuktophyllum calycinum
Zygophyllum foetidum
Zygophyllum lichtensteinianum
Zygophyllum morgsana
Zygophyllum pygmaeum
Zygophyllum retrofractum
Zygophyllum sp.

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Chapter 4: Research findings, conclusion and management recommendations for Sanbona Wildlife Reserve

"The question is, are we happy to suppose that our grandchildren may never be able to see an elephant except in a picture book?" David Attenborough

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4.1. Overview

Diet and water provision determine the spatial usage of elephants within a landscape (Laws *et al.*, 1975; Loarie *et al*., 2009a; Smit and Ferreira, 2010). This study investigated the spatial and feeding ecology of elephants on Sanbona Wildlife Reserve (further referred to as SWR) in the semi-arid Little Karoo. Spatial analysis of the herds was done through the use of Global Positioning System (GPS) satellite collars attached to an elephant in each of the two herds, thus tracking their spatial use and allowing us to calculate home ranges and core zones. Within these high use areas (home ranges and core zones), feeding ecology was determined by means of the scan sampling method and isotopic analysis of faeces, providing a more in-depth understanding of the elephants' forage composition. In addition, by looking at water point placement and use, it is possible to better understand the influence of water points on seasonal movements of elephants. The findings of this research will provide baseline data to aid SWR, as well as other reserves in similar semi-arid succulent areas, in developing strategies to monitor and manage elephant impact on vegetation. It will also help to compile an elephant management plan. The findings of this study also provide a better insight into the importance of succulents within elephants' diet in the Little Karoo as well as the limitations of isotopic and scan sampling methods within semi-arid to arid environments. In this report, the key study findings are summarised, and the management implications of these findings are discussed in detail.

4.2. Research findings

Chapter 2: The spatial usage of elephants on Sanbona Wildlife Reserve

- The Northern elephant herd on SWR utilised 60.4 km^2, 25% of the area available to them, as their home range. Within this area, they utilised 4 km^2, 7.0% of the determined home range (according to Kernel Density method) and 20.8 km^2, 25.2% of the determined home range (according to the Grid Square method), as their core zone.
- The Southern elephant herd utilised 73.9 km^2, 26.0% of their available area home range. Of this, they used 7.3 km^2, 10.0% of the determined home range (according to

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Kernel Density method), and 16.1 km^2, 26.0% of the home range (according to the Grid Square method), as their core zone.

- As hypothesised, river lines and flood plains contributed the largest percentage of the core zones of both herds (44% for the Northern herd and 49% for the Southern herd).
- Valleys and open plains away from the main river line areas were utilised by both herds within their home range.
- The Northern herd's home range stretches into the northern valleys of the reserve, crossing over ridges, feeding along valleys, over slopes and along open plains (Randteveld and Apronveld). Spatial usage also spreads to open plains and valleys to the south of the Brak river line (Randteveld, Apronveld and Gannaveld).
- The foraging trips to the north and south of the Brak river line by the Northern herd were observed to occurr at night and in the early hours of the morning, with the herd returning to the river line during the morning.
- The Northern elephant herd were observed to utilise the northern most valleys only on clear nights during the week around full moon. These foraging trips occurred once to several times during this week every month. This is possibly due to increased visibility.
- Certain mountain slopes fall within the core zones of the Northern herd, such as the slopes to the north and south of the Bellair dam, and those of the hills around the main river lines. The Northern herd was observed feeding on these slopes during the early mornings, late afternoons and during cooler, overcast weather.
- The Southern herd also utilised valleys and plains to the north of the main river lines, crossing over ridges and spending time on mountain plateaus and in open valleys and plains. These areas consist primarily of low browse made up of shrubs, forbs, annuals and succulents, with small clumps of trees in between (Randteveld, Arid Mosaic Renosterveld and Arid Mosaic Succulent Karoo). As with the Northern herd, much of the movement over ridges and on top of mountain plateaus occurred in the cooler times of the day or during cooler weather. However, no specific pattern of movement was observed during the week of full moon as with the Northern herd.
- During the cooler seasons, herds spent more time in open areas and on slopes during the day than during the heat of the summer months.

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- During the summer of 2016 the Northern herd spent the majority of the time utilising the Brak river, thus never being further than 1 to 3 km from a given water source. These areas also provided the best shelter during the heat of the day.
- Towards the latter part of the summer of 2017, as the drought intensified, the Northern herd spent some time utilising valleys away from the main drainages in the Arid Mosaic Succulent Karoo vegetation habitat, thus utilising some of the new water sources (AWPs constructed by management).
- Throughout most of 2016, the Southern herd utilised the Kalkoenshoek, Gatskraal and adjacent valleys and tributaries, always within proximity of the plentiful natural pools and springs within the Kalkoenshoek and Gatskraal river lines.
- Seasonal watering holes were available to the Southern herd in the northern part of the home range during autumn, winter and spring of 2016, due to rainfall within that section of the home range in autumn and winter. This correlates with the herds more frequent movement and use of the northern valleys and open areas as water availability and new plant growth increased together with new plant growth.
- A distinct change in the area utilised by the Southern herd during the summer of 2017 compared to the previous summer was likely caused by rainfall to the south-east of their home range, increasing water availability and plant growth.
- The placement of the AWPs in and around the Brak River in Sanbona North are within 5 km of favoured vegetation and from 1 - 7 km from one another.
- The majority of the AWPs in Sanbona South were not within the Southern herd's core zone. The Southern herd relied mostly on natural pools and springs.

Chapter 3: Diet preferences of elephants on Sanbona Wildlife Reserve

- At least 94 plant species from 64 genera were utilised by the elephants over the 16-month study period.
- Between 4 and 27 different species were consumed within a day's monitoring sessions.
- Both the Southern and Northern herds' diet consisted predominantly of browse, with the Northern herd's diet consisting of 62% browse, 28% graze and 10% succulent species, compared to 79% browse, 2% graze and 19% succulent species in the Southern herd's diet.

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- *Vachellia karroo* was the dominant browse species for both Southern and Northern herds, 44% in the Southern herd and 33% in the Northern herd, making up 38% of total elephant diet on the reserve.
- *Searsia spp.* and *Euclea undulata* were more readily browsed by the Southern herd (8% and 5% of recorded diet) than the Northern herd (3% and 1% respectively).
- The Northern herd utilised other species such as *Atriplex*- and *Lycium* species more (8% and 4% of observed diet) than the Southern herd, (6% and 1% respectively of their total observed diet). *Atriplex spp*. were more prevalent in Sanbona North.
- *Phragmites australis* was consumed predominantly by the Northern herd and was their second highest utilised forage (12% of total diet). They utilised *P. australis* the most during spring, followed by autumn. This correlates with growth after rainfall.
- During scan sampling, succulents belonging to the *Mesembryanthemum* genus were most consumed by both herds. *Mesembryanthemum junceum* was the most consumed species within the genus and made up 30% of succulent species consumed by the Northern herd (only 3% of total diet). The Southern herd utilised both *M. junceum* and *Drosanthemum hispidum* in similar proportions (17% and 19% of succulent species consumed, 3% and 4% of total diet respectively).
- Slow growing species were recorded at low percentages in both herds' diets. For example: *Schotia afra* (1% of diet for both herds), *Carissa haematocarpa* (<1% and 2% of diet for Northern and Southern herd) and *Tylecodon paniculatus* (3% and 7% of succulent diet, and 1% and <1% of total diet for Northern and Southern herd). Large amounts of *T. paniculatus* were however found in faeces samples during winter and spring.
- Results indicate that there is a statistical certainty that certain plant species are eaten throughout the year in equal quantities, whereas other species are eaten more in certain seasons, and some only in certain seasons.
- Increases in utilisation of plant species reflects flowering and growing seasons of different plants as well as availability.
- The results of the isotopic analysis of the plant specimens collected on SWR revealed three distinct clusters of $\delta^{13}C$‰.

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- Most of the succulent (CAM) species tested on SWR fell between -19.25 and -23.72 $\delta^{13}C$‰, with a few exceptions showing a larger tendency towards the C_4 range, such as *Mesembryanthemum junceum*, *Tylecodon paniculatus* and *Crassula rupestris*. *Ruschia caroli* and *Tetragonia fruticosa* fall within the C_3 range of -25.37 and -26.49 $\delta^{13}C$‰ with one sample of each falling at -23.19 and -23.67 $\delta^{13}C$‰ respectively.
- Results from the faecal samples from the Northern herd were isotopically clustered together towards the C_3 range, with only one sample falling closer to the C_4 range. This differs from the observed diet. The majority of the faecal samples fell between -27.67 and -22.59 $\delta^{13}C$‰. The Southern elephant herd samples had $\delta^{13}C$ ranging between -24.9 and -27.49‰, and $\delta^{15}N$ values ranging between 3.89 and 9.97‰. The Northern herd's samples ranged from -19.06 to -28.33$\delta^{13}C$‰ with $\delta^{15}N$ values between 4.56 to 11.44‰.
- There were significant differences found between seasonal usage in the isotopic sampling within the Northern herd, in particular between spring and summer, autumn and spring, autumn and winter, and winter and summer. Thus, the species consumed and the quantity thereof varied between seasons.
- The Northern herd's faecal $\delta^{13}C$ values showed a larger C_3 and CAM composition, with minimal C_4 representation during summer, and C_3 and CAM during autumn. Winter and spring, however, showed only C_3 isotopic values.
- Differences were noted when comparing scan sampling and the isotopic analysis results. A lack of C_4 within the isotopic results does not necessarily indicate that the elephants do not graze, because in arid environments some grasses utilise the C_3 photosynthetic pathways. The lack of CAM species within the Southern herd's faecal samples could be for similar reasons.

4.2. Limitations of the study

Elephants are large, potentially dangerous animals and need to be treated with caution when monitoring them in the field. Due to this, four main limitations were identified and considered during this project.

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i. Access: The road network is concentrated mostly in Sanbona North, with limited or no road network in the Wilderness section of Sanbona South. This meant that much of the data collection in Sanbona South was done on foot. Some of the areas that had to be reached were far away and thus time spent monitoring was limited to daylight hours for safety reasons.

ii. Observation distance: When the elephants were viewed from a distance, either by vehicle or on foot, the data collection for the scan sampling part of the dietary analysis was conducted using binoculars. This undoubtedly makes identification of plant species consumed difficult, especially with regards to succulents when not in flower, thus influencing data collected. The elephants' dietary preferences at night were also not studied.

iii. Random sampling of elephant faeces for the isotopic analysis study: The small sample size (in comparison to the total bolus size) that is collected and then further resampled for analysis increases the possibility of not sampling the full range of vegetation consumed.

iv. Drought conditions: The severity of the drought experienced during the time of this study could naturally affect the elephants' diet and spatial usage, which would differ during wetter years. Further studies would be beneficial in monitoring the impact of the elephants on sensitive plant species as well as indicator species across years with higher rainfall.

4.3. Conclusion

Elephants are seen as an important keystone species as they have an influence on other animal and plant species, through effecting canopy cover, seed dispersal, nutrient recycling, habitat structural changes and influencing biopedturbation processes (Styles and Skinner, 2000; Kerley and Landman, 2006; Kerley *et al*., 2008). However, as elephants are megaherbivores, needing large amounts of nutrients to sustain them on a daily basis, it is important for elephant populations to be preserved whilst maintaining biodiversity (Owen-Smith, 1988; van Aarde and Jackson, 2007). In small fenced reserves the impact of large herbivores, such as elephants, on vegetation and habitat structure is more concentrated than on larger reserves (Lombard *et al*., 2001; Duffy *et al*., 2002; Loarie *et al*., 2009; Duffy *et al*., 2011). This impact is the result of a lack of space and therefore a lack of seasonal movement and plant refuges (Shannon *et al*., 2006; Loarie *et al*., 2009). Although it is important to remember that vegetation structures are not stochastic, changing with climatic

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changes (such as droughts and floods), fires and herbivore influences (Ben-Shahar, 1993; Barnes, 2001; Owen-Smith *et al*., 2006). Within arid habitats elephant populations should be managed according to the driest times, such as during droughts, therefore allowing landscapes to prosper during wet years.

Rainfall, vegetation growth, water availability and population size all influence how elephants utilise their landscape, and therefore their potential impact on vegetation (Viljoen, 1988; Guldemond & van Aarde 2008). In a semi-arid environment such as the Little Karoo, rainfall events and patterns are a major driving force influencing the way elephants utilise the space available to them, as this influences vegetation growth, cover and water availability (Viljoen, 1989b; Leggett *et al*., 2002).

Through this study it was observed that both herds only utilise a fraction of the available space as home ranges (Northern herd 25% and the Southern herd 31%) and core zones (Northern herd 7% and the Southern herd 10% of home range, KDE). The preferred areas primarily consisted of the River and Floodplain habitat (an annual mean of 44% of the Northern herd's time, and 49% of the Southern herd's time), where the highest quantity of forage and available water was located. The size of home ranges and core zones utilised is far smaller than in other arid areas, although it amounts to a similar percentage of available space to that utilised in Namibia (Douglas-Hamilton, 1971; Lindeque & Lindeque, 1991; Von Gerhardt-Weber, 2011). Parts of the home ranges were only utilised during specific weather conditions, correlating with changes in season. These areas include mountain slopes and ridge lines, and open valleys away from major river lines. These areas consist of Randteveld, Gannaveld, Apronveld and Arid Mosaic Succulent Karoo in Sanbona North (16%, 15%1 10% and 9% of the Northern herd's time respectively), and Arid Mosaic Succulent Karoo, Arid Mosaic Renosterveld and Randteveld in Sanbona South (14%, 13% and 12% of the Southern herd's time respectively). The finding thus shows that although the herds prefer river lines and flood plains as hypothesised, mountain slopes and open valleys were utilised seasonally.

Elephants utilise space according to availability and quality of forage and water, forming two of the important drivers of elephant habitat use, thus naturally utilising landscapes seasonally (Laws, 1970; Barnes, 1982; Lindeque and Lindeque, 1991; Leggett, 2006; Chamaillé-Jammes *et al*., 2007a, b; Smit *et al*., 2007). Within SWR the Northern elephant herd's spatial usage was observed

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to be within 5 km from water when utilising the River and Floodplain, Randteveld, Gannaveld, Apronveld and Arid Mosaic Succulent Karoo. When water is available throughout the year through the use of AWPs seasonal movement is often reduced. Thus, the Northern elephants' seasonal movement might be able to be influenced by the management of AWP's, as was seen by Chamaillé-Jammes *et al*. (2007a, b) in Hwange National Park, Zimbabwe, and Smit *et al*. (2007) in Kruger National Park, South Africa. The Southern elephant herd's spatial usage was observed to be less restricted to areas AWPs, however the majority of habitats utilised were in areas where natural water sources were observed to be replenished by rain showers throughout the study period. For this reason, as naturally filled water points and springs are replenished, management can close nearby AWP's, thus allowing animals to utilise the refreshed water points. This will allow areas, and the plant species in those areas, to rest and enforce more seasonal movement.

Through scan sampling an estimated 94 of the 600-plant species occurring on the reserve were utilised by the two elephant herds. The findings show that certain species, such as *Vachellia karroo* and *Phragmites australis* (in Sanbona North) form important bulk forage. These species are less impacted than others as they coppice after being browsed upon (Barnes *et al*., 1996). Grazing forms an important part of the Northern herd's diet after seasonal rains but was not always a reliable forage source due to the drought. A variety of browse and succulent species make up a large quantity of important forage for both herds but in low percentages. As hypothesised, the herds' diets fluctuated seasonally, with C3 (browse) being the most important source of food throughout the year. The diets of each herd, however, did differ in percentages consumed, with the Northern herd's diet consisting of 62% browse species, 28% graze and 10% succulents, compared to 79% browse, 2% graze and 19% succulent species utilised by the Southern herd. Thus, the fourth hypothesis was also correct, with succulent plants playing a more important role in the Southern herd's diet than in the Northern herd. Scan sampling should also be conducted through a wet period when the drought has broken to determine how this has affected diet selection.

Through this study, areas of utilisation, as well as species utilised have been identified. To better understand the impact that elephants may have in these identified areas it is important for further management through ongoing monitoring of the elephant herds as well as vegetation monitoring.

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Managing large herbivores within a fenced semi-arid reserve has its unique challenges. The more we understand how these animals survive in these landscapes and what their impact is on the specialised vegetation, the better reserves can maintain the balance within this delicate landscape.

4.4 Management Recommendations for Sanbona Wildlife Reserve

4.4.1 Recommended Vegetation Monitoring Methods

Monitoring vegetation growth, and in particular slow growing species utilised by elephants, is very important to help assess the long-term impact of elephants in the Little Karoo. Through the findings of Chapters 2 and 3 we can better understand which areas are heavily utilised by elephants and which slow growing or vulnerable plant species are utilised and thus at risk of possible trampling. Vorster (2017) found that the vegetation on SWR very likely does not have a large buffering capacity despite the slow increase in cover and abundance. To monitor the impact of herbivory by elephants (Figure 4.1), and other large herbivores, it is important to continue with the adapted wandering quadrat method established by Erasmus (2008) and adapted by the Sanbona Wildlife Team (Vorster *et al*., 2017). Through this method woody browse such as *Schotia afra*, *Pappea capensis*, *Searsia spp.*, *Carissa haematocarpa* and *Euclea undulata* (although abundant it is slow growing) can be monitored for impacts by measuring growth and damage annually. A GPS point and photo are taken at the start tree, with each transect named and recorded according to the existing methodology. The species name, height and diameter of trees along the transect are measured and a rating is given, between 0 – 10, for the damage done to the shoots, branches, bark or roots (Vorster *et al*. 2017). Notes are also made as to whether the tree has died or is coppicing after utilisation. When the transect occurs along a river line, one side of the drainage is chosen and followed, whereas if the transect runs along a line of trees, the wandering quadrant method is used until 50 trees have been recorded (Vorster *et al*., 2017). However, utilising the spatial information from this study, the current transect locations may need to be adjusted. To ensure that

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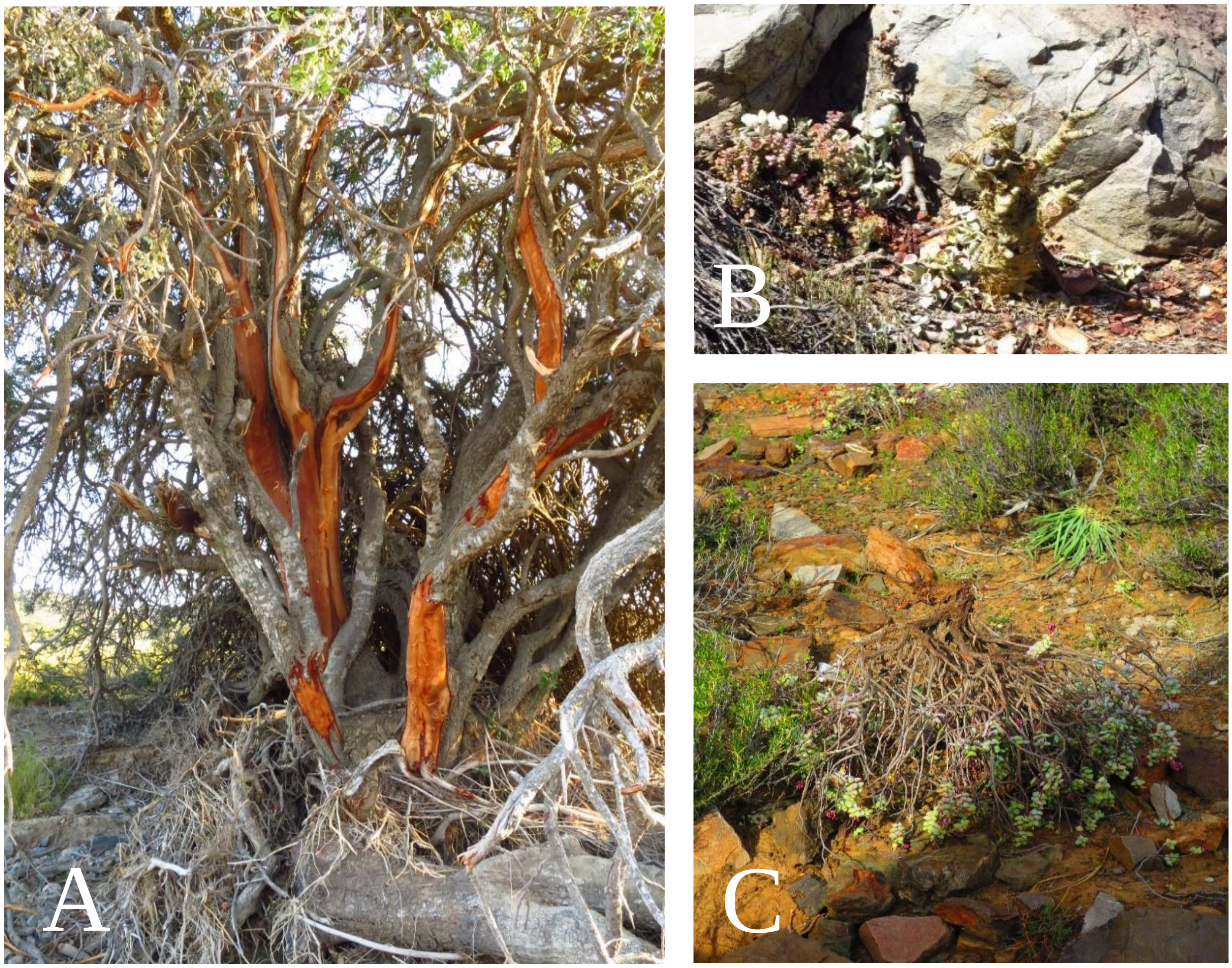

Figure 4.1. Damage done on three plant species during foraging. A) debarking and breaking of branches of *Schotia afra*, B) braking of *Tylecodon paniculatus*, and C) uproated bush of *Crasulla rupestris*.

this monitoring is continued on an annual basis it is important that the process is achievable for the conservation managers. This would reduce the statistical significance over a short time period, but as this would need to be long term monitoring this would allow for data collected to be statistically tested. The original number of transects could be reduced to 28, focusing on the areas with the highest impact. Since *Vachellia karroo* is fast growing and resilient, the river lines where it is dominant can be excluded.

Smaller woody- and succulent browse should also be monitored, and these mostly occur along south facing slopes, floodplains, valleys and ridges within Randteveld. Randteveld and Apronveld habitat types have been identified by Kraaij and Milton (2006) as areas which are often first to show signs of over utilisation by herbivores. Species identified as indicator species as well as

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species possibly vulnerable to impacts of large herbivores in these areas are *Tylecodon paniculatus*, *Aloe perfoliata*, *Tetragonia fruticosa*, *Trichodiadema spp*., *Berkheya cuneata* and *Berkheya spinosa* (Vorster, 2017), as these species all display traits suggested by Connor *et al*. (2007) which could cause plant species to be vulnerable to elephant herbivory. Furthermore, Aloe species have been recorded to be sensitive to elephant impact even when herbivory is low, as was found in the Addo Elephant National Park (Lombard *et al*., 2001; Landman *et al*., 2008).

The method suggested to monitor vegetation along Randteveld, Apronveld, Arid Mosaic Succulent Karoo, Arid Mosaic renosterveld and along southern facing slopes is quadrats along a 200m transect. The width of the quadrats should measure 1m by 4m, ensuring minimal disturbance within a quadrat, as well as decreasing errors. Once the transect start point is noted by a GPS point and photograph, the transect line is established. Every 20m a quadrat is created perpendicular to the transect ensuring a better representation over a gradient (Elzinga *et al*. 2001). Thus, each transect consists of 10 quadrats. Within each quadrat plants are identified to species level where possible, otherwise to genus, and counted. The plants' canopy cover is measured, and notes made on damage due to foraging or trampling. According to core zones and areas of utilisation where sensitive species occur, 8 sights have been identified.

Statistically, four transects in each of the identified areas in Sanbona North and South should be monitored, thus a combined 32 transects. However, to ensure that conservation management and science merge, monitoring must be adapted to be time- and cost effective, easily replicated, and scientifically sound (Vorster, 2017). Thirty-two quadrant and 30 line transects would not be time effective for a small ecological management team. It would therefore be more effective to reduce the quadrants to 2 per selected area, thus halving the sample size to a more manageable 16-quadrants.

Furthermore, to ensure easier identification of succulents via the flowers, and therefore more accurate species identification, both vegetation monitoring methods will be carried out once a year during spring. As a control, transects for both trees and smaller browse should be conducted in similar vegetation types within areas devoid of large herbivores such as elephants.

Due to trampling and foraging around waterpoints, sacrifice areas known as piospheres are created (Lange, 1969). These piospheres are at risk of merging when waterpoints are too close together,

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creating homogeneous landscapes (Lange, 1969; Owen-Smith, 1996; Chamaillé-Jammes *et* al., 2009). It is therefore important to monitor the impact of piospheres within an area and to ensure that they do not merge by managing AWP placement and usage.

Piospheres around AWP should be monitored to ensure to monitor impact from herbivores. In order to do this the size and changes of piospheres should be monitored. Image-based methods have been found to be a more cost- and time-effective methods of monitoring long term changes around piospheres (Booth & Cox 2008). A method such as fixed photo points is recommended to be utilised to monitor possible changes by comparing photos taken from the same angle yearly (Elzinga *et al*., 2001). Although fixed point photography is already being implemented on the reserve it has not looked at piospheres specifically. Each AWP must be photographed numerous times from the same elevated angle, filling the same amount of space per frame, allowing photos to be replicated and therefore compared over years (Elzinga *et al*., 2001). In order to capture the piosphere from an aerial point, a drone can be utilised, or the photo can be taken from a raised position. The size of the piosphere (width and breadth) must be measured on the photos, as well as the size of ground cover captured in the photographs. These measurements can then be compared yearly, thereby noting any changes. The predominant growth form and vegetation type around water points should also be noted to monitor whether there is any change in species cover.

4.4.2 Further Population management recommendations

Due to the potential impact in fragmented landscapes created by a small fenced reserve, it is also important to manage population growth to ensure long-term sustainability. This can be achieved through GnRH (Gonadotropin Releasing Hormone) vaccination of bulls or Porcine Zona Pellucida (PZP) vaccination of cows as a form of immunocontraception (Delsink *et* al. 2006; Druce *et al*. 2011). GnRH vaccination (Improvac) of elephant bulls was implemented in 2012 as a means to control population growth on SWR (Vorster *et al*., 2017). The production of sperm cells and the release of sex steroids is combated by the bull's immune system because of the vaccination (Lueders *et al*., 2017). This prevents the sexually mature bulls' breeding behaviour, with a non-invasive, reversible effect similar to castration (Vorster *et al*., 2017). Vaccination takes place twice a year, in November and May and has proven successful over the past three years. As non-sexual bulls mature, the ratio of male to females will lead to possible changes of treatment from bulls to cows (PZP) (Vorster *et al*., 2017).

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The current immunocontraception should be continued with the possibility of removing a group of bulls in the future to reduce numbers. Currently this would be disruptive to the rest of the herd as the bulls do not yet break away from the herds. However, if the space available to the herds was increased, by removing the dividing fence between Sanbona North and South, the herds could merge. According to elephant social behaviour, this would allow for the older bulls to break apart once more as nomads or to from the herd and form bachelor groups, making it easier and less disruptive to the family herd to remove individuals. This would allow management to cease Improvac treatment on some bulls thereby allowing some breeding to take place every few years, resulting in a more natural social structure and resultant population dynamics.

If the internal dividing fence was removed, larger seasonal movements and habitat utilisation will be possible, not only for the elephants but for all the animals, including predators. This increase in size and envisaged seasonal migration would be beneficial in relieving pressure during dry season as animals will be able to move according to where rain falls. By increasing the preferred habitat of the elephants (and other large herbivores), pressure on more vulnerable vegetation will be relieved. Using the maximum population estimations of Gough and Kerley (2006), 0.5 elephants per km^2, and Erasmus (2008) 0.8 km^2 of preferred habitat, I suggest that the stocking rate should not exceed 20 elephants with the increase in seasonal movement through the removal of the internal dividing fence. However, the removal of the fence line could have an effect on the SWR business model, and this would need to be taken into consideration.

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