

**THE EFFECT OF ELEPHANTS**  
*(Loxodonta africana, BLUMENBACH, 1797)*  
**ON**  
**XERIC SUCCULENT THICKET**

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

Master  
Of  
Science  
Of  
Rhodes University

by

**EDWARD JOSEPH KNOTT**

**July 2007**

---

## Abstract

---

This study looks at the impact of elephant feeding on the Xeric Succulent Thicket component of Eastern Cape Subtropical Thicket (ECST) in Addo Elephant National Park (AENP). Observations of elephant feeding were carried out and vegetation transects were surveyed for impact of elephant feeding. The results indicated that the Nyati elephants spent the majority of their time grazing (nearly 90%), particularly the cow-young herds, and especially when the herd gathered in larger numbers. Browsing events were concentrated on *Acacia karroo* (81%) and there was no significant difference between the sexes in their preference for this species. Despite being subjected to most of the browsing, the majority of *A. karroo* trees were undamaged and the effect of elephants was generally light. It appears unlikely that, three years after re-introduction to Nyati, the elephants have had an effect on community structure of the vegetation.

Surveys were conducted on stands of the alien invasive weed prickly pear *Opuntia ficus-indica*, and it was recorded that elephants in Nyati have had a dramatic effect on prickly pear, utilising all adult plants assessed and destroying 70% of them. This level of destruction in such a short period of time suggests that prickly pear is a highly favoured species. The results from the present study suggest that elephants can play a role in the control of prickly pear.

Results are discussed in terms of elephants as both megaherbivores and keystone species, and as agents of intermediate disturbance.

---

## TABLE OF CONTENTS

---

Title page	i
Abstract	ii
Table of contents	iii
Acknowledgements	viii
Preface	ix

**CHAPTER 1:** General introduction to the African elephant (*Loxodonta africana*), with particular reference to the Eastern Cape Province, South Africa

The behavioural ecology of the African elephant	1
Social organisation and herd size	1
Habitat selection	3
Movement	4
The history of elephants in the Eastern Cape Province	5
The Addo elephants	6
The Nyati herd	7
Broad aims	7

**CHAPTER 2:** The study area

General introduction	9
Geology	11
Vegetation of the Eastern Cape Province	11

The Albany Hotspot	11
Eastern Cape Subtropical Thicket (ECST)	12
The vegetation of the AENP	14
Vegetation of the study sites	15

**CHAPTER 3: The feeding biology of African elephant *Loxodonta africana* in Xeric**

**Succulent Thicket**

Introduction	18
Elephant nutrition	18
Elephants as keystone herbivores	21
The effects of elephants on vegetation	22
The influence of water	24
Other factors influencing the relationship between elephants and vegetation	24
Effects of elephant feeding in East Cape Subtropical Thicket (ECST)	26
Positive effects of elephant feeding	22
Aims	29
Materials and methods	30
The importance of grass in the diet: observations of elephant feeding behaviour	30
Data manipulation and analysis	30
The effect of elephants on abundance and biodiversity of woody plants and the effect of browsing on selected tree species	33

Data analysis	34
Elephant Importance Value (ELEVI)	35
Results	36
The importance of grass in the diet:	36
The effect of elephants on abundance and biodiversity of woody plants	40
Transect results	40
Plant community structure at Nyati and Addo Heights	40
Plant abundance	41
The effect of browsing on selected tree species	43
Plant utilisation	43
The effect of elephants on target species	45
ELEVI	47
Discussion	48
The importance of grass in the diet of elephants in Nyati	48
The effect of elephants on the abundance and biodiversity of woody plants	50
The effect of browsing on selected tree species	51

**CHAPTER 4: Elephants as possible biological control agents of prickly pear (*Opuntia ficus-indica*)**

Introduction	53
The ecology of prickly pear	54
Distribution and reproduction	54

Prickly pear as a valuable resource	55
Control of invasive weeds	55
Control of prickly pear	56
Materials and methods	59
Quantification of the impact of elephants on the prickly pear stands in Nyati	59
Data collection	59
Sampling	59
Results	60
General, qualitative description of utilisation	60
Quantification of damage to prickly pear	61
Indigenous plant utilisation	65
Discussion	68
<b>CHAPTER 5: General discussion</b>	
Elephants, disturbance and biodiversity	70
The role of complex, interacting factors	71
Density-dependence and time exposure duration	72
<b>CHAPTER 6: Recommendations for management</b>	
Monitoring at Nyati	74
Monitoring at Addo Heights	74
Prickly pear ( <i>Opuntia ficus-indica</i> )	75
Population density	75

<b>REFERENCES</b>	76
<b>APPENDICES</b>	104
<b>Appendix 1:</b> Plant list of species sampled on the transects	104

---

## ACKNOWLEDGEMENTS

---

I thank my wife, Liesl, for her assistance in the field, for her support and her encouragement. My thanks to my supervisor, Ric Bernard, for his guidance, patience, time and effort. My thanks to Hugo Bezuidenhout, Lucius Moolman and John Adendorff of SANParks for permission to study at Addo Elephant National Park. Thanks to Holly Dublin for her insights and points of clarity. Thank you to Pierre Beukes for opening the doors of intermediate disturbance. And my thanks to God, for daughters and elephants and inspiration.

---

## PREFACE

---

This thesis is structured as follows:

**Chapter 1** is primarily a review of the behaviour and ecology of elephants, and the history of elephants in the Eastern Cape Province.

**Chapter 2** details the two study sites, Nyati and Addo Heights. It includes descriptions of the vegetation.

**Chapter 3** is the first research chapter, dealing with the feeding effects of elephants on vegetation.

**Chapter 4** is a second research chapter, which explores the relationship between elephants and prickly pears.

**Chapter 5** is a theoretical discussion of various theories relating to elephant-vegetation dynamics.

**Chapter 6** consists of various management recommendations.

## CHAPTER 1

### **General Introduction to the African Elephant (*Loxodonta africana*), with particular reference to the Eastern Cape Province of South Africa**

---

The aim of this chapter is to provide a brief introduction to relevant aspects of the biology of the African elephant (*Loxodonta africana*) Blumenbach, 1797, and to the history of elephants in the Eastern Cape Province.

#### **BEHAVIOURAL ECOLOGY OF THE AFRICAN ELEPHANT**

The behavioural ecology of elephants is very strongly shaped by their very large size, the habitat that they occupy and their reliance on water (Owen-Smith, 1992; de Longh *et al.*, 1999; Mpanduji *et al.*, 2002; Shoshani *et al.*, 2004; Guldemond *et al.*, 2005; Leggett, 2006; Morley, 2006; Sam *et al.*, 2006). Their size (5-6 tonnes for males; 3-3,5 tonnes for females) requires very high daily food intake, which, depending on the quality, abundance and patchiness of food sources, determines time spent feeding and moving between food sources. The sex differences in adult size similarly affect aspects of feeding, patterns of movement and habitat selection of males and females (Shannon, 2005).

#### Social organisation and herd size

Elephant herds are multi-tiered, complex societies comprising differing levels of cohesion, with the social bonds within clans being the weakest, whilst the mother-offspring unit is strongest (Wittemyer *et al.*, 2005). Elephant society is organised into matriarchal family groups and independent mature males (Moss & Poole, 1983; Moss,

1988; Owen-Smith, 1992; Poole, 1994), the basic unit consisting of a mother with her dependent offspring, grown daughters with their offspring (Owen-Smith, 1992; Poole, 1994) and including males up to puberty (Mubalama, 2000). These mixed herds of adults and young elephants, called clans (Douglas-Hamilton, 1972; Viljoen, 1989), are most common (Mpanduji *et al.*, 2002) with the mother-offspring unit the most frequent family unit (Owen-Smith, 1992; Poole, 1994; Mubalama, 2000). A female usually remains within her natal family for life, and the bonds between her and the other female members of her group are strong and long-lasting (Anderson, 1994; Whitehouse *et al.*, 2002). Adult males live separately from females, either alone or in bachelor herds (Owen-Smith, 1992; Poole, 1994). Male elephants leave the family group when they reach sexual maturity (at approximately 12-14 years; Owen-Smith, 1992; Shannon, 2005). Thereafter they are found alone, in small bachelor groups, or temporarily associating with females (Owen-Smith, 1992). Once on their own, bulls alternately wander alone and associate with other bulls (Owen-Smith, 1992), and groups consisting of an old mature bull accompanied by two or three much younger males are not uncommon. Subadults tend to associate and interact in peer groups, but bachelor herds usually include various ages (Galanti *et al.*, 2006). Bulls wander further than cows (Leggett, 2006) but during periods of sexual inactivity most stay in small retirement areas, often with one or more regular companions (Poole & Moss, 1981; Poole, 1989; Galanti *et al.*, 2006). Bulls are generally more widely dispersed, especially around the periphery of the range (Gibson *et al.*, 1996). Herd size is determined by factors other than random aggregations based on habitat preference (Dublin, 1996). In general, herd size is correlated with season, with larger herds forming in the wet season when availability of preferred forage is greater (Dublin,

1996) and during movements or during the mating season (Namibia - Jachmann, 1987; Tanzania – Galanti *et al.*, 2006). Large herds tend to split into smaller groups (bond groups) but continue to occupy the same home range and associate at least half the time (Owen-Smith, 1992). These bond groups usually stay less than a mile apart, staying in touch through rumbling calls (Owen-Smith, 1992).

### Habitat selection

Elephants are highly adaptable, occurring throughout the African continent in a variety of habitats. For example, in Mago National Park, Ethiopia, elephants live in semi-arid bush and riverine forests (Demeke & Bekele, 2000). In Virunga National Park, DRC, elephants are localised in bushland (Mubalama, 2000) and occur in the swamps, but never in the mountains (de Long *et al.*, 1999). Elephants in Namibia occur from true desert to subtropical forests (Lindeque, 1995), and in South Africa they are widespread, due to an extensive metapopulation management strategy, from the coastal belt to the Succulent Karoo, and the subtropical thicket of the Eastern Cape Province, to the woodlands of the Kruger National Park.

The resource most crucial to an elephant's survival is water and the availability and distribution of water are major factors determining the habitat use of elephants (Owen-Smith, 1992; de Longh *et al.*, 1999; Mpanduji *et al.*, 2002; Shoshani *et al.*, 2004; Guldemon *et al.*, 2005; Leggett, 2006; Morley, 2006; Sam *et al.*, 2006). For example, most of the elephants in Namibia have inhabited, and continue to inhabit the areas along drainage lines, as they are often the only sources of subterranean water or springs (Lindeque, 1995) and serve as linear oases (Lindeque, 1995; Leggett, 2006). In Botswana, family groups of elephants have slightly different ranges from bull groups and

tend to occur in habitats with easier access to water than do bulls (Gibson *et al.*, 1996). The tendency of breeding herds to concentrate along the river-lines probably relates to their larger group sizes, relatively higher mass-specific energy demands (owing to a smaller body size) and the need for better quality food for themselves for lactation and pregnancy (Knight *et al.*, 1994) and for their dependent calves (Barnes, 1982). By contrast, elephant bulls remain within the interior, away from riverfronts, where limited food and water are available, by virtue of their smaller herd sizes and the need for only enough food to meet maintenance requirements (Knight *et al.*, 1994; Ben-Shahar, 1999; Pers. obs). Similar differences in habitat use by male and female elephants have been described in Tembe Elephant Park (Morley, 2006) and elsewhere in KwaZulu-Natal (Shannon, 2005).

### Movement

In Northern Botswana, in an area of 80 000 km<sup>2</sup> (Ben-Shahar, 1997), the resident elephant population is large (between 65 000 and 100 000 elephants; Blanc *et al.*, 2005) due to natural recruitment and immigration from the adjacent areas of Zambia, Namibia and Zimbabwe (Melton, 1985; Calef, 1988). These elephants tend to converge around water sources and reach high densities (7-10 elephants/km<sup>2</sup>) (Melton, 1985; Craig, 1990) where they may reduce the abundance of cover of preferred plant species (Ben-Shahar, 1993; Pickup, 1994). During the dry season, when seasonal pans and steams dry up, the herds concentrate around the major rivers in northern Botswana, bringing the densities close to 4/km<sup>2</sup>, along the Chobe riverfront (Gibson *et al.*, 1998). When pans persist into the dry season as a result of a good rainy season, then elephants remain widespread (Gibson *et al.*, 1998). Another result of an extended, good rainy season in Botswana is

the long-distance movements of individuals (Gibson *et al.*, 1998), which may travel up to 1000 km to the Kalahari Desert and reach areas not normally inhabited by elephants (Gibson *et al.*, 1998; Nagafela, 1998 in Gibson *et al.*, 1998). Elsewhere in Africa, elephants travel long distances in response to season (Thouless & Dyer, 1992; Thouless, 1995; Leggett, 2006). For example, during Cameroon's dry season elephants stay in Waza and Kalamaloue National Parks because of water availability, and move out during the rains when there is also less perennial grass available inside the parks (Tchamba, 1993). The elephants in Mago National Park migrate seasonally to Omo National Park, Sudan (Demeke & Bekele, 2000). In Nigeria, there is a seasonal migration of forest elephants (*Loxodonta africana cyclotis*) between the rainforest of Cross River National park in Nigeria and Cameroon's Takamanda Forest Reserve (Obot *et al.*, 2005). Elephants in Namibia are amongst the most migratory-nomadic of any elephants on the continent, primarily as a result of scarce surface water resources (Jachmann, 1995; Lindeque, 1995). Patterns of movement are often reflected in changes in diet (Osborn, 2002). The elephants of Cameroon migrate to the swamps in the SE for riparian vegetation in the dry season, then migrate northwards again to feed on the ripening fruit during the wet season (Turkalo & Fay, 1996).

## **THE HISTORY OF ELEPHANTS IN THE EASTERN CAPE PROVINCE**

The formal archaeological record indicates that the African elephant *Loxodonta africana* has been present in Southern Africa from at least 30 000 years before present. This record gives evidence of pre-historical occurrence in thicket and thicket-associated habitats in the Eastern Cape Province (Boshoff *et al.*, 2002).

By 1920, relict herds of elephants were present only in the impenetrable scrub-thickets of Addo and the densely forested foothills of the Outeniqua Mountains around Knysna. By 1930 there were 22 surviving within the entire region: 11 in the Addo bush and 11 in the Knysna forest. On 13<sup>th</sup> June 1931, the Strathmore/Mentone Forest Reserve officially became the Addo Elephant National Park (AENP) and in 1997 it was proposed that AENP be expanded to accommodate the increasing populations of elephant, black rhino (*Diceros bicornis bicornis*) and buffalo (*Syncerus caffer*). The proposal was accepted by South African National Parks (SANParks) and is in the process of being implemented.

### **THE ADDO ELEPHANTS**

The initial Addo population stems from a small remnant population of 11 elephants. This herd consisted of a large bull; a younger bull; six adult females; 2 subadult females; and a male calf (Trollope, 1931 in Kerley *et al.*, 2001). The population reached a size of 25 by the end of 1938 (Whitehouse, 2001). This decreased to 18 over the next 9 years, following a hiatus in recruitment, due to the death of the founder males (Whitehouse, 2001). Recruitment resumed in 1948, once male calves born some years earlier had reached sexual maturity (Whitehouse, 2001). The population's growth was also hindered by the lack of adequate fencing, as break-outs resulted in the responsible elephants being shot (Whitehouse, 2001). In 1954 the Armstrong fence was built, and the population increased dramatically hereafter, with a doubling time of 13.6 years (Whitehouse, 2001). The total population size by the end of 2001 was 336 individuals (Whitehouse, 2001). Female fecundity of the Addo population is reported as being high, with a mean age of first calving of 13 years and a mean inter-calf interval of 3.8 years (Whitehouse & Hall-

Martin, 2000). There was an equal number of immature elephants of each sex, but the adult sex ratio was biased towards females, due to higher male mortality (Whitehouse, 2001). This was primarily due to intraspecific fighting, with 70-90% of all male deaths (20) since 1954 attributable to this (Whitehouse, 2001). This relatively high incidence (Hanks, 1979) of fighting is because of the confinement of the population (Whitehouse, 2002) and the resultant unusually high density of elephants ( $> 2.5/\text{km}^2$  - Whitehouse & Irwin, 2002).

### **THE NYATI HERD**

On the 13<sup>th</sup> May 2003, part of the family group B, which was the largest of the matriarchal groups in AENP, was passively translocated to the Nyati Section of the Park. Two days prior to this, four elephant bulls from Kruger National were translocated to a boma in Nyati and released on the same day that the Addo herd was translocated. Currently the herd numbers 67 individuals, comprising five bulls, with the rest of the herd consisting of females, their young and bachelors. Since their relocation, six young have been born, including twins in January 2005. So far, all have survived.

### **BROAD AIMS**

Within AENP, previous studies have concentrated on the 11 700 ha section of the park that was inhabited by elephants and on the effect of elephants in Spekboom Succulent Thicket. With the introduction of elephants to the Nyati section, the opportunity was created to study elephants from introduction and importantly, in a different vegetation type (Xeric Succulent Thicket). This study has used two sites, Nyati as the treatment site

(with elephants), and Addo Heights, as the control area and which has been set aside for future elephant introductions. The detailed aims, questions and hypotheses of the research are described in each of the research chapters, but broadly the research examined the feeding biology of elephants in Xeric Succulent Thicket, looking at the effect of sex and group structure on the amount of time spent browsing and grazing, food selection and the effect of elephant feeding on selected plant species.

## CHAPTER 2

### The Study Area

---

#### GENERAL INTRODUCTION

The AENP (33°31' S, 25°45' E) is situated in the Sunday's River Valley basin, some 25kms from the coast, and 60kms north of Port Elizabeth (Hall-Martin & van der Walt, 1979 in Lombard *et al.*, 2001; Fig. 2.1). In the last 13 years, the AENP has increased in size through the addition of adjacent land; the Zuurberg National Park was amalgamated into AENP in 1994; Nyati was incorporated into AENP in 2000; and Addo Heights is the most recently incorporated area. Elephants were initially restricted to an area of 11 708 ha in the original park (Hall-Martin, 1992), were introduced into Nyati in May 2003, and may be introduced to Addo Heights in 2008 (J. Adendorff, Regional Section Ranger, pers. comm.).

Topographically AENP is characterised by a series of low undulating hills. Numerous small pans occur throughout the original elephant enclosure but, except in years of abnormally high rainfall, they are dry for the greater part of the year. Permanent water is provided by artificial water holes and dams (Paley & Kerley, 1998). The Nyati section has the seasonal Coerney River meandering through its lower reaches.

The region in which AENP falls is considered to be semi-arid (Stuart-Hill, 1992). The mean daily temperature for January is 32.4° C and 13.5° C for July; however, temperatures in excess of 40° C frequently occur in summer (Stuart-Hill, 1992). The mean annual rainfall for the period 1960 to 1989 was 445mm (range 245 – 665), with rainfall occurring throughout the year, but peaking in late summer (February-March) and

spring (October-November) while prolonged droughts occur regularly (Hall-Martin & Barratt, 2001).

The Eastern Cape Province is characterised by a great complexity of floras and vegetation types converge in the region as a result of the transitional nature of the climate, geomorphology and geology (Lubke & de Moor, 1998).

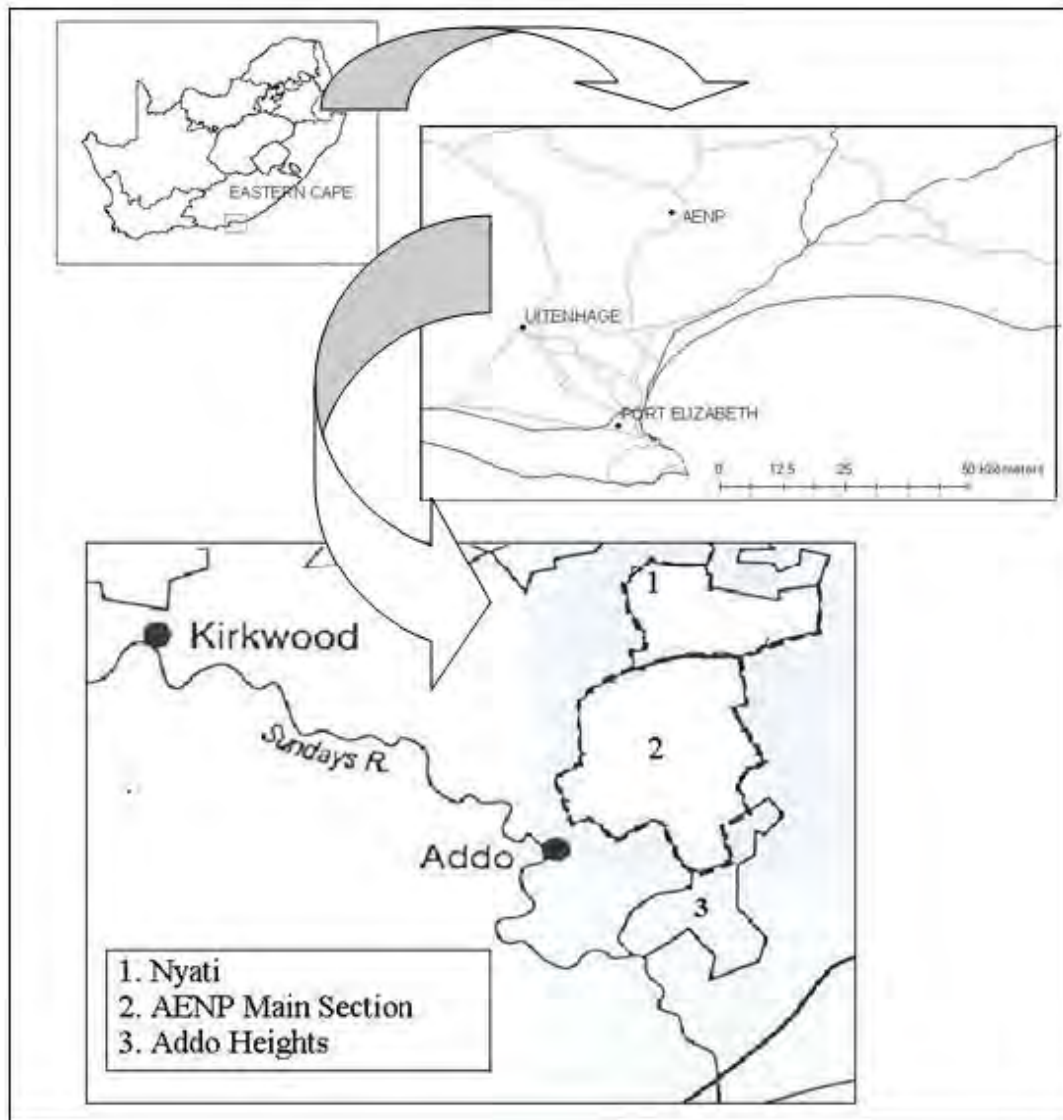


Figure 2.1: The location of the study area. (Adapted from Johnson, 1998).

## **GEOLOGY**

The coastal zone of the southern parts of the Eastern Cape Province is dominated by three great sedimentary deposits: the Cape Supergroup; the Karoo Supergroup; and the Uitenhage Group (Rust, 1998). The rocks are largely composed of the Karoo Supergroup in the northern half of AENP and of the Cape Supergroup and Uitenhage Group in the southern half. The Karoo rocks are all sedimentary in origin and represent a continuous deposition of sediment extending from the end of the carboniferous period some 300 million years ago to the Jurassic about 180 million years ago (Rust, 1998). The Cape Supergroup rocks are also sedimentary and were formed between the Cambrian and Ordovician periods about 505 million years ago (Rust, 1998). Rocks of the Dwyka and Ecca groups of the Karoo Supergroup underlie much of the AENP. Towards the north of AENP, the broken terrain of the Karoo rocks stops against the rocks of the Cape Supergroup, giving rise to the Zuurberg, which lie across the Park (Coetzee & Vlok, 2001). The study sites, Nyati and Addo Heights, are dominated by rocks of all three sedimentary deposits - the Uitenhage Group, the Cape Supergroup and the Karoo Supergroup.

## **VEGETATION OF THE EASTERN CAPE PROVINCE**

### The Albany Hotspot

The Albany Hotspot, or Albany Centre, in the Eastern Cape Province was recognised as an important phytogeographical centre by Nordenstam (1969) in his study on speciation and endemism in the genus *Euryops*. This area has become recognised as an area of such botanical importance that it is now referred to as the 'Albany Hotspot' (Cowling and

Hilton-Taylor, 1994). The Albany Hotspot stretches from the Baviaanskloof and the Gamtoos River to the Kei River and is bounded by the escarpment of the Amatole and Winterberg ranges (Phillipson, 1995). Cowling and Hilton-Taylor (1994) estimate the flora of the Albany hotspot to comprise at least 2000 vascular plant species. The area is regarded as a transitional centre for many genera centred in the Maputoland-Pondoland, Cape and Karoo-Namib regions (Cowling, 1984).

An important vegetation type in the region and in AENP is the Thicket Biome and this is described in more detail below.

#### Eastern Cape Subtropical Thicket (ECST)

The Thicket Biome in the Albany Centre is represented by Eastern Cape Subtropical Thicket and it is the dominant vegetation type in the south-eastern part of the Eastern Cape Province, covering an estimated 22 500 km<sup>2</sup>, or 30-35% of the Albany Centre (Johnson, 1998). The flora of ECST comprises an estimated 600 vascular plant species with a level of endemism of approximately 10% (Cowling, 1984). While there are no endemic families or genera restricted to ECST, many genera are centred here in terms of species numbers and endemism (Cowling, 1984). Van Jaarsveld (1987) notes that this is a region of active succulent speciation due to the diversity in local terrain combined with climatic transition between the subtropical east coast and the temperate Cape. ECST is regarded as a transitional vegetation type because its floristic components are shared with many other phytochoria (Low & Rebelo, 1996). ECST is floristically and structurally heterogenous (Midgley *et al.*, 1991) and varies from a closed scrubland to low forest dominated by a mixture of evergreen sclerophyllous and succulent shrubs (Low & Rebelo, 1996). It is dense, spiny and often impenetrable and is usually unistratal (Lubke

*et al.*, 1987). In arid forms, the field layer is sparse, composed mainly of succulents, dwarf shrubs and geophytes, while in more mesic forms, a herbaceous layer of shade-loving grasses and forbs becomes more prominent (Everard, 1987).

ECST is ecologically restricted by several factors (Johnson, 1998). It grows on moderately deep, mainly orange-red, well-drained soils of the dry river valleys of the Eastern Cape Province. This vegetation rarely occurs above 800 metres above sea level, which correlates closely to rainfall totals, and these two factors appear to be the most critical in influencing the distribution of ECST (Marker, 1991 in Johnson, 1998). Stuart-Hill (1992) gives an estimate of 225-500mm rainfall per annum, but rainfall may be erratic due to the convergence of four rainfall regimes in the area. Totals may thus be deceptive, and at times are inflated by periodic phenomena such as three-day rains (Marker, 1991 in Johnson, 1998). However the Addo Basin, an area that covers AENP and its surrounds, benefits from the moderating coastal influence, so although rainfall is low, it is reasonably predictable (Hoffmann, 1989). This predictable rainfall has been linked to the high incidence of succulence in the area, which decreases sharply with the increasing aridity further north (Hoffmann & Cowling, 1990). Temperature appears to have little effect on ECST, except in bottomlands and inland areas where frost occurs, as many succulent species such as *Portulacaria afra* are frost-sensitive (Johnson, 1998). ECST is not fire-prone (Midgley *et al.*, 1991) but is highly sensitive to overgrazing due to the slow growth rates of the main fodder plants (Moolman & Cowling, 1994), and low levels of recruitment of the dominant shrubs (Stuart-Hill & Danckwerts, 1988). Succulent thicket is thus being rapidly eliminated by poor farming practices in the Eastern Cape Province (Hoffmann & Cowling, 1990).

Low and Rebelo (1996) have divided the Thicket Biome into five vegetation types: Dune Thicket, Valley Thicket, Xeric Succulent Thicket, Mesic Succulent Thicket and Spekboom Succulent Thicket.

## **THE VEGETATION OF AENP**

The vegetation of the original AENP was considered to be Xeric Succulent Thicket (Lubke *et al.*, 1987), however, it is not uniform across the park, largely owing to varied historical land use practices. Archibald (1955) described five plant communities within the original AENP, the most extensive being Spekboom Succulent Thicket, in which spekboom (*Portulacaria afra*) is the dominant species, but which also contains *Euclea undulata*, *Rhus pterota*, *Azima tetracantha*, *Schotia afra* and *Capparis sepiaria*. With the inclusion of new land, other vegetation types are now present including Mesic Succulent Thicket, Eastern Thorn Bushveld, Acacia karroo Thicket and Coastal Forest. The Mesic vegetation is found in the south of the park where it covers the rolling hills, to the steep north-facing slopes of the Zuurberg Mountains. It stops abruptly at the base of the mountain, where it is replaced by Acacia karroo Thicket which grows along stream lines and which has a diverse composition of tree and shrub species (Coetzee & Vlok, 2001). Spekboom Succulent Thicket occurs from the very southern sections of the Park up to the zone where the foothills of Zuurberg's northern slopes open onto the Karoo plains in the extreme north. Xeric Succulent Thicket occurs throughout the Park, dominating from the centre of the Park northwards. Eastern Thorn Bushveld is found scattered in patches throughout the Park. Acacia karroo Thicket grows along all the main water drainage areas of the plains.

## VEGETATION OF THE STUDY SITES

Nyati is dominated by Xeric Succulent Thicket, which stretches across Nyati and is found wherever the floodplain grasses and Acacia karroo Thicket do not occur. Nyati is criss-crossed by the Coerney River, and consequently the area contains the associated riparian vegetation that is dominated by *Acacia* thicket. Grassland floodplains abound throughout the lower reaches of Nyati, dominated by *Cynodon dactylon* grass, interspersed with infestations of Jointed cactus (*Opuntia aurantiaca*). Prickly pear (*Opuntia ficus-indica*) stands occur throughout this section of AENP. As the low-lying areas give way to the Zuurberg mountains, the vegetation becomes dominated by euphorbia trees (*Euphorbia grandidens*).

Addo Heights is a mosaic of vegetation types, with dense stands of Mesic and Xeric Succulent Thicket giving way to expanses of grassland. Infestations of *O. ficus-indica* and *O. aurantiaca* also occur here, often at high densities. There is no river in this section of AENP and as a result, there is substantially less Acacia karroo Thicket.

These two study sites are effectively separated by the central portion of the park (Fig. 2.1), and so form a continuous system bounded in the north by the Zuurberg mountains and in the south by the Alexandria Dunefield. The vegetation along this gradient gradually shifts from exclusively Xeric Succulent Thicket in the far north, to Mesic Succulent Thicket in the south of AENP, (before the Dune thicket and Coastal forest of the Woody Cape Section is reached). Addo Heights is the area where the xeric and mesic vegetation types converge.

Brief descriptions of the important vegetation types in the study areas are given below, with details taken from various sources (see Tinley, 1975; Cowling, 1984; Low and

Rebelo, 1996; Midgley et al., 1991; Lubke & van Wijk, 1998; Lubke & De Moor, 1998; Coetzee & Vlok, 2001; Vlok *et al.*, 2003).

Xeric Succulent Thicket – This thicket occurs mainly in dry areas of the Fish and Sundays River valleys. There is a high proportion of succulents and the flora is transitional from Tongaland-Pondoland to Karoo-Namibian. It includes leaf-and stem-succulent shrubs, trees and lianas and small- and large-leaved sclerophyllous shrubs and trees, succulent herbs, grasses and forbs. This low, relatively sparse thicket has a shrub canopy 2 to 2.5m in height. The number of succulents and endemics is high, although species richness is low compared to other thicket types. Characteristic tree species are *Grewia robusta*, *Brachyleana ilicifolia*, *Maytenus capitata* and *Lycium campanulatum*. Succulent species include *Euphorbia coerulescens*, *Portulacaria afra* and *Euphorbia bothae*. There are few herbs and grasses such as *Pentzia incana*, *Chrysocoma ciliata* and *Cynodon dactylon*. The plants obtain their moisture from valley mists in the drier regions. Xeric Succulent Thicket is invasive into savanna and grassland and the absence of large browsers, such as rhino and kudu, to contain the larger plants is resulting in its spread into neighbouring vegetation types (Everard, 1987).

Acacia karroo Thicket - this narrow band of vegetation consists of dense stands of *Acacia karroo* trees, which grow along all the main water drainage areas of the plains. This vegetation unit is not very rich in species (Coetzee & Vlok, 2001), (but it may include several grasses, lianas and other trees in the form of *Diospyros lycioides* and *Rhus* species).

Both Nyati and Addo Heights were previously subjected to agricultural practices, in the form of pastoral farming of goats and cattle. Prior to its incorporation into AENP though,

Nyati formed part of the Riverbend Concession, and contained small populations (<20) of extralimital and rare species, such as sable antelope (*Hippotragus niger*), waterbuck (*Kobus ellipsiprymnus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*). These species no longer occur in Nyati. Addo Heights has not been used for any ecotourism or hunting ventures.

## CHAPTER 3

### The Feeding Biology of African elephant *Loxodonta africana* in Xeric Succulent Thicket

---

#### INTRODUCTION

##### Elephant nutrition

The diet of elephants is shaped primarily by their very large size. Jarman (1974) and Bell (1969; 1971) observed that while the relative metabolic rate of African ungulates decreases with increasing body size, the digestive tract size remains a fixed proportion of adult size. Based on this, larger herbivore species should be able to tolerate a diet of lower quality than smaller species (= the Jarman-Bell Principle of Geist (1974)). The absolutely larger gut size of larger species is important because it results in a longer retention time (Illius & Gordon, 1992) and therefore a more complete digestion of plant material (Demment & Van Soest, 1985). However, while the longer gut retention times of the larger species (or sex) allows the use low quality food, it does not require it, and larger species can be expected to use high quality food when it is abundant (Owen Smith, 1988; Van Soest, 1996). Based on the above, elephants are expected to have a very long gut retention time and a high digestive coefficient, however neither is the case (Clauss *et al.*, 2003; O'Connor *et al.*, 2007). In very large species, the gut retention time represents a trade off between allowing as complete digestion as possible and not allowing development of methanogenic bacteria, which convert acetic acid to methane and carbon dioxide and reduce available energy. Consequently, Clauss *et al.* (2003) have proposed that very large herbivores, such as elephants, would need to evolve adaptations to speed

up throughput of material through the gut and reduce the development of methanogenic bacteria. In elephants, total gut length is shorter than expected and the diameter of components such as the small intestine is greater, and these together result in a reduced gut retention time (Clauss *et al.*, 2003). The very large size of the elephant results in high absolute daily energy requirements for maintenance, which must be met through extraction of energy from a large volume of plant material. This need for an abundant food source is exaggerated by the reduced gut retention time and low digestive coefficient. Indeed, elephants spend up to 75% of their time feeding (Owen-Smith, 1992; Whitehouse *et al.*, 2002) and an adult elephant consumes in excess of 150kg of plant material per day (Ben-Shahar, 1999).

The diet of elephants is composed of many plant species and plant components (Paley & Kerley, 1998), because it is more economical to include suboptimal species than to take time to discriminate (Crawley, 1983 in Mwangi *et al.*, 2004). However, the diet may also be dominated by certain plant species which are both nutritious enough to meet energy requirements and also available in abundance (*e.g. Portulacaria afra*, Boshoff *et al.*, 2001; *Mopane colophospermum*, Lagendijk *et al.*, 2005; Danquah & Oppong, 2006).

In many habitats, grass is abundant and nutritious and the ratio between browse and graze differs seasonally and from region to region. Grass forms an important component of the diet for many elephant populations in savanna habitats, particularly during the wet season when it is abundant (see O'Connor *et al.*, 2007 for theoretical explanation of this). For instance, in KwaZulu-Natal, South Africa (Bowland & Yeaton, 1997) and in Kruger NP, South Africa (Codron *et al.*, 2006) grass constitutes as much as 45% of the elephants' diet, reaching a peak in autumn and nadir in late winter. For similar examples from

Cameroon, Ethiopia, Eritrea, Gabon, Kenya, Uganda and Zambia see Field (1971); Field & Ross (1976); Guy (1976); Barnes (1982); Lindsay, (1982); Western & Lindsay (1984); Dublin (1986); Owen-Smith (1992); Jachmann (1995); Tchamba (1993); White *et al.* (1993); Dublin (1995); Turkalo & Fay (1996); Cerling *et al.* (2004); Shoshani *et al.* (2004).

By contrast, forest elephants are often highly frugivorous (van Wyk & Fairall, 1969; Alexandre, 1977 (in Turkalo & Faye, 1996); Short, 1981; Dudley *et al.*, 1992; White *et al.*, 1993; Muoria *et al.*, 2001; Theuerkauf *et al.*, 2001; Danquah & Oppong, 2006), and tend to rely more on woody plant species than monocots (Sam *et al.*, 2006). Not all studies of forest elephants have reported the same results and forest elephants in western Cameroon feed extensively on grass in a mixed forest-savanna habitat (Tchamba, 1993). In the Knysna forest, only 11 of more than 35 species of forest trees and shrubs available were eaten while most of the common genera of shrubs and grasslike plants of fynbos were routinely eaten (Milewski, 2002).

Because of their very large size, elephants are often forced to feed on large amounts of low-quality forage (Jachmann, 1988) and the quantity of available forage is probably a more important limiting factor than quality. Food quantity may be particularly problematic in areas of high elephant density (Dublin, 1996).

There are significant differences between the sexes with regard to feeding duration, plant species selection, plant parts selected, amount of forage intake and the effects of feeding on the vegetation (Shannon, 2005). These differences may be explained in terms of the sexual dimorphism of elephants and also the tendency of males to form smaller groups than females. Female elephants in Pongola Game Reserve, Pilanesberg National Park,

Phinda Private Game Reserve, Tembe Elephant Park and Hluhluwe imfolozi Park tend to be more selective, have shorter feeding bouts and exhibit less destructive feeding behaviour than males (Shannon, 2005) and just shorter feeding bouts have been reported in Chobe (Stokke & Du Toit, 2000). Elsewhere, female elephants also tend to consume more forage than males (Owen-Smith, 1992).

O'Connor *et al.* (2007) argue that the diet of elephants in summer, when grass is green and abundant, should comprise mostly of grass and, because of the much larger size of males, that this will be most evident in bulls.

#### Elephants as keystone herbivores

Species that play a disproportionately large role in maintaining the links in a food web, to the extent that their extermination would cause a cascade of change or extinctions in an ecosystem are called keystone species (Western, 1990). Elephants determine the rate, scale and direction of habitat change (Waithaka, 1993) and are keystone herbivores whose activities profoundly influence the structure, composition and productivity of vegetation communities (Laws *et al.*, 1975, Eisenberg, 1981; Owen-Smith, 1992; 1992; Kerley *et al.*, 1995; Boshoff *et al.*, 2001; Waithaka, 2001; Usongo, 2003; McKnight, 2004). Elephants play a prominent role in the regulation of ecological processes within any ecosystem that they inhabit due to their size; their forage intake; low digestive coefficient; and their population densities (Owen-Smith, 1992; Ben-Shahar, 1999; Hawthorne & Parren 2000; Boshoff *et al.*, 2001; Mwangi *et al.*, 2004; Whyte, 2004). Elephants are important seed dispersal agents (Waithaka, 2001; Fisher, 2005) and their disappearance would result in a reduction of biological diversity and an increase in species extinction rates (Waithaka, 2001).

### The effects of elephants on vegetation.

The effects of elephant feeding are varied and numerous across the African continent. A range of interacting factors determine the extent of these effects including biotic factors such as the densities of elephants and the effect of other browsing herbivores, and abiotic factors such as soil type and fire. Too many researchers however, have viewed the elephant-vegetation relationship from a narrow point of view, neglecting the array of factors influencing this relationship. Consequently, conflicting findings are reported.

The interaction of woodlands and elephants is thought to be cyclic (Caughley, 1976) or to reach equilibrium at low densities of elephants and trees (Laws *et al.*, 1975) as it is assumed that elephants reduce tree density and therefore reduce their own food availability (McShane, 1987). A woodland-density gradient (Western, 1990; Birkett *et al.*, 2000) persists, where tree density and elephant density is inversely correlated – high tree densities exist where elephant densities are lowest.

In many areas with prolonged exposure to high elephant densities, habitat degradation has resulted. For example, in Zimbabwe, areas with high densities of elephants undergo a decrease in the density of canopy trees and a decline in woody biomass (Ford, 1987 in Osborn, 2002; Guy, 1989; Osborn, 2002). (See the following references for further examples: Botswana - Child, 1968; Croze, 1974; Thomson, 1975; Spinage, 1990; Knight *et al.*, 1994; Ben-Shahar, 1996; Gibson *et al.*, 1998; Kenya – Dublin, 1991; Poole, 1993; Waithaka, 1993; Dublin, 1996; Gakami, 1996 in Waithaka, 1997; Mwathe, 1997 in Waithaka, 2003; Waithaka, 1997; Mubalama, 2000; Pamo & Tchamba, 2001; Litoroh,

2002; Ogola & Omondi, 2005.) This habitat degradation is characterised by low biological diversity, reduced habitat heterogeneity and weakened structural complexity (Waithaka, 1993) and often results in landscape change. For example in Kenya a tropical mountain forest has been converted to high shrub land (Waithaka, 1993). By contrast, areas of low elephant density experience less extensive effects of elephant browsing on the vegetation (Owen-Smith, 1992; Bowland & Yeaton, 1997; Hiscocks, 1999; Damiba & Ables, 1994; Milewski, 2002) and, for example, very low tree mortality has been recorded in Burkina Faso (Nazinga Game Ranch; 0.1 elephants/km<sup>2</sup>; Christenson in McShane, 1989). Some studies in areas of high elephant densities have failed to detect high levels of damage. For example, in Chobe National Park, Botswana, elephant densities are high but heavy damage, attributable to elephants, was only recorded in 5.3% of scans (Knight *et al.*, 1994 and see Ben-Shahar, 1997; 1999; Spinage, 1994 for further examples). Some authors have suggested that elephants control their utilisation of plant species (Jachmann, 1986; 1989) and utilise trees on a sustainable basis (Bell, 1985; the minimal damaging trait of Jachmann, 1987). Whilst feeding decisions may be made for reasons of sustainability, it is perhaps more likely that they should be interpreted in relation to optimal foraging theory, food density, distribution and giving up time, taking into account the very large size of the species (e.g. Searle *et al.*, 2005).

The impact of elephants on the vegetation varies from overbrowsing to the inhibition of regeneration and the death of mature trees (Viljoen, 1989; Tchamba & Mahamat, 1992; Damiba & Ables, 1994; Höft & Höft, 1995; Cumming *et al.*, 1997; Mwathe *et al.*, 1997 in Waithaka, 2003). Trees that are utilised by elephants inhabiting forests are lightly

utilised (Alexandre, 1977, in Turkalo & Fay, 1996) and simply shaken and butted until the fruits fall off (Feer, 1995; Maisels *et al.*, 2002).

Much attention has focused on the removal of the savanna tree component by elephants (Pellew, 1983; Owen-Smith, 1992; Kerley *et al.*, 1995) throughout their ranges but elephants are also grazers. However, there have been few studies of the effect of elephants on the grass layer.

#### The influence of water

Elephants tend to converge around water sources where they may reach very high densities. Consequently elephant damage to woody plants, including trampling of seedlings; scratching against the bark of mature trees; and the killing of trees through ringbarking, is often confined to a distance of several hundred metres from the water (Melton, 1985; Craig, 1990; Spinage, 1990; Ben-Shahar, 1993; Spinage, 1994; Ben-Shahar, 1999; Brits *et al.*, 2002; De Beer *et al.*, 2006). The elephant-vegetation relationship in Etosha National Park, Namibia clearly demonstrates this, where woody plant survival increases as the distance from a water source increases (De Beer *et al.*, 2006). The influence of elephants in the riverine habitats is lessened when rains are good, enabling the elephants to spend less time near the riverfront, and exaggerated when rains are poor (Melton, 1985; Craig, 1990; Ben-Shahar, 1993; Pickup, 1994).

#### Other factors influencing the relationship between elephants and vegetation

A variety of factors may either lessen or exaggerate the effects of elephants. These include soil nutrients; mineral availability; water drainage; drought; flooding; intense browsing by large herbivore species other than elephants; climate; geology; topography; human influences; and the frequency of fire and frost (Jachmann, 1985; McShane, 1987;

Guy, 1989; Martin *et al.*, 1989; Dublin *et al.*, 1990; Jachmann, 1987; Spinage, 1990; Lewis, 1991; Owen-Smith, 1992; Jones & Tafangenyasha, 1994 in Tafangenyasha, 2001; Spinage, 1994; Ben-Shahar, 1997; Tafangenyasha, 1997; Tafangenyasha, 2001; Omondi *et al.*, 2002a; De Beer *et al.*, 2006).

Soil nutrient availability is important, as it affects the growth form of the tree species, and subsequently determines that tree's ability to withstand elephant impact. Woodland response to elephants may differ over a range of soil conditions (McShane, 1987). On sandy well-drained sites, trees respond to elephant utilisation by coppice regrowth and increasing browse density. By contrast, on clayey poorly-drained sites, the same species are killed by elephant utilisation, thus reducing tree density (McShane, 1987).

Various characteristics of the tree species will influence the way in which the tree responds to elephant browsing (McShane, 1987). Coppice is a common response to elephant browsing over a range of soil conditions (Jachmann & Bell, 1985; McShane, 1987) and makes trees and shrubs resistant to elephant browsing. Shade intolerant tree species will select for height growth rather than strength and longevity, resulting in a relatively thin stem and heavy canopy in mature trees making them easy to push over (Jachmann, 1987). Also, high densities of browsers, a minimal coppicing rate and slow regeneration in a number of tree species may be major factors contributing to a shift of a large part of the tree canopy to levels above the feeding range for elephants, necessitating tree felling to bring the biomass within reach (Jachmann, 1987).

Fire and elephants both play pivotal roles in the dynamics of certain woodland types in northern Botswana but these effects differ between woodland habitats dominated by specific plant species (Ben-Shahar, 1997). Woodland vegetation in the region can be

viewed as a mosaic of three states characterised by low elephant utilisation and high fire damage; high elephant impact and low fire damage; and minor elephant utilisation and/or minor fire damage (Ben-Shahar, 1993).

#### Positive effects of elephant feeding

Elephants facilitate browsing by mesoherbivores by making additional foliage available and by generating browsing lawns for animals such as kudu and impala (*Aepyceros melampus*) which prefer to browse on trees that have experienced elephant impact (Maisels *et al.*, 2002; Shoshani *et al.*, 2004; Makhabu *et al.*, 2006). Elephants are important seed dispersal agents for several plant species (Barnes, 2001; Waithaka, 2001; 2003).

In the Hluhluwe/imfolozi Complex the long-term absence of elephants from the area was a major reason for vegetation succession towards thicket and closed woodland (Anderson, 1994) which resulted in the local extinction of three grazers and a sharp reduction of several others to vulnerable levels (Owen-Smith, 1987).

#### Effects of elephant feeding in East Cape Subtropical Thicket (ECST)

Research into the effects of elephants in ECST has been concentrated in the AENP and spans a period of about 50 years. The published papers have focused on the architectural changes to the vegetation induced by elephant grazing, and not on the effects on biodiversity (Moolman & Cowling, 1994). There is some disagreement between researchers about the effects that elephants have on ECST. The major discrepancy revolves around the reduction in biodiversity; earlier studies in AENP reported a 45% reduction in biomass but no negative influence on species diversity (Penzhorn *et al.*, 1974). However, as the vegetation's exposure to elephant utilisation increased with time,

and consequently intensity, this changed and there is consensus that elephant-affected areas show a reduction in canopy height, volume, plant density, and species diversity (Barrat & Hall-Martin, 1991; Moolman & Cowling, 1994; Johnson, 1998). The reduction in species diversity includes a loss of *Aloe africana* (Archibald, 1955; Penzhorn *et al.*, 1974; Barrat & Hall-Martin, 1991; Stuart-Hill, 1991) and a loss or absence of the mistletoes (*Moquinella rubra*, *Viscum crassulae* and *V. rotundifolium*) despite a high frequency of their host plants (Penzhorn *et al.*, 1974; Midgley & Joubert, 1991). The frequency of *Crassula ovata* was reduced by 50% (Stuart-Hill, 1992).

The components most affected by the feeding regime of elephants were the small succulents and geophytes (Moolman & Cowling, 1994; Cowling & Kerley, 2002).

Crassulaceae were the only group of succulents that were not adversely affected by elephants (Moolman & Cowling, 1994), due to the fact that they regenerate so well through vegetative reproduction. Elephant browsing did not affect species richness and frequency in the large shrub and tree component of succulent thicket in AENP with the exception of *Euphorbia mauritanica* and *Rhigozum obovatum* (Stuart-Hill, 1991).

However, canopy cover was reduced significantly (Stuart-Hill, 1992).

Spekboom (*P. afra*) benefits from some forms of browsing (Johnson, 1998; Cowling & Kerley, 2002) and the top-down browsing pattern of elephants encourages the production of a skirt and thus ramets, which is the plant's primary means of reproduction (Von Maltitz, 1991).

By virtue of the broad diet, large volume of forage, limited mastication and relatively poor digestion, elephants have the potential to be important agents of seed dispersal in ECST (Cowling & Kerley, 2002). Elephants have been shown to disperse the widest

variety of plant species in thicket, and these seeds have an extremely high viability (Mendelson, 1999).

Unlike other regions of Africa, where elephants can drive dramatic change to savannas and forest, ECST appears to be resistant to elephant browsing and various authors have suggested that elephants maintain succulent thicket in a relatively uniform state (Barratt & Hall-Martin, 1991 in Moolman & Cowling, 1994; Stuart-Hill, 1991; Johnson, 1998). Although this may appear to be contradicted by the extreme elephant-driven change in the original AENP, this is probably the result of a prolonged period of overstocking (Cowling & Kerley, 2002). Through most of the history of AENP, elephant populations have remained in excess of the carrying capacity, ranging from 1.6-3.8 per km<sup>2</sup> (Penzhorn *et al.*, 1974; Barratt & Hall-Martin, 1991 in Moolman & Cowling, 1994; Moolman & Cowling, 1994). Unlike savanna systems, where fire is an important driver of change, fire plays little role in ECST (Cowling *et al.*, 1997; Vlok *et al.*, 2003). By contrast, water is important and elephant damage is much greater in close proximity to water (Knight *et al.*, 2002) than at a distance.

A major limitation of earlier studies in the Eastern Cape Province is that the focus was primarily on one component of ECST, Spekboom Succulent Thicket, which dominates the elephant-inhabited area of AENP. The expansion of AENP, and the reintroduction of elephants to areas from which they have been absent for many years, has created an opportunity to study their effects from first introduction in a vegetation types (Xeric Succulent Thicket) that have not been studied and in a landscape that has not been altered through the creation of artificial water sources.

## Aims.

The broad aim of this research was to contribute to a better understanding of the feeding biology of elephants in Xeric Succulent Thicket and to provide information that can be used by the managers of AENP. However, the research and data analysis have focussed on three specific questions.

1. *The importance of grass in the diet of elephants in Nyati.* Previous studies have shown that grass is eaten more by elephants in savanna habitats than in forests and that there is a sex difference in the occurrence of grazing. Since Xeric Succulent Thicket is characterised by a relatively poorly developed grass layer it is hypothesised that elephants will browse more than graze. Furthermore, as has been previously reported, it is hypothesised that bulls will graze more than herds.
2. *The effect of elephants on biodiversity of woody plants.* Studies in Spekboom Succulent Thicket have suggested that the feeding of elephants has resulted in a reduction in density of trees but no change in species richness (of trees). Thus, it is hypothesised that tree density will be significantly lower in Nyati than the control areas but that there will be no significant reduction in species richness.
3. *The effect of browsing on selected tree species.* There is ample evidence that elephants will damage trees during feeding and that this damage is greatest where elephant densities are high and sustained. Since elephants have been present in Nyati for a short period of time and at low densities, it is hypothesised that damage will be mostly light. In addition, it was decided to focus on a highly preferred tree species (*A. karroo*) and invasive weed (*O. ficus-indica*) where the likelihood of detecting an effect of elephants would be greatest.

## MATERIALS AND METHODS

### 1. The importance of grass in the diet: observations of elephant feeding behaviour

Because of the unpredictable nature of elephant activity and distribution, observations were made on an opportunistic basis over a period of 18 months (Table 3.1). Whenever the herd or an individual was seen, observations were made for as long as the animals remained visible. For all observations, the interval scan method was used (Van Aarde & Skinner, 1975; Rose, 2000; Jones & Pillay, 2004) with observations being made every minute. At each observation, the activity of every visible elephant was recorded and the activity of each elephant is termed an activity event. During the observation period, the following were noted: the time of day; the locality where the elephants were first seen; the number of elephants counted; the age and sex of each elephant; whether the unit was the herd or one or more bulls; the activity of all visible elephants. Age and sex were identified using the method of Moss (1988), but using only two age groups, namely adult and young (0-12 years) (Shannon, 2005). Due to the difficulty of assessing sex in young elephants, only the sex of adults was assessed. Although the question asked related to feeding only, information on a range of other activities was collected. The types of activity noted were feeding; foraging (defined as the process of searching for food); drinking; travelling (defined as the movement from one place to another as opposed to wandering around in search of food items) and other (including bathing and various social activities). If the elephants were feeding, the following was recorded; whether the elephant was grazing or browsing and what plant the elephant was feeding on.

### Data manipulation and analysis

Elephants were observed on 33 occasions (termed observation periods) for a total of 1600 minutes during which 32117 individual observations of elephants (activity events) were made (Table 3.1). Data have been analysed in two separate ways, firstly at an individual activity event level where all data from all observation periods have been pooled and results expressed as a percentage of the 32117 observations. Since none of the hypotheses includes a seasonal component, the pooling of data was deemed to be acceptable. These data have been used in a descriptive way and have not been analysed statistically.

Secondly, at an observation period level ( $n=3$ ) where data from that period have been pooled and results expressed as a percentage of the total number of observation events in that period. Where one type of behaviour comprised more than 50% of all observations for that period, the period was recognised as being dominated by that behaviour (e.g. grazing dominated period). To allow further analysis, each of the 33 observation periods was characterised by group size (large, greater than 10 elephants, and small, less than 10) and structure (herd, typically 20 or more elephants with adult females, young and sometimes accompanied by one or more adult males; and bulls, a small group of adult and subadult males with no females). Clearly, there is a link between group size and structure and all large groups were the herd, and most small groups were bulls. Two small groups were small family units. Two way ANOVAs were then used to explore the relationship between categorical variables (group size, large/ small; group structure, herd/ bulls; feeding, grazing/ browsing; elephant behaviour, feeding/ foraging/ drinking/ travelling/ other) and the dependent variable (proportion of events in each category). Percentages and proportions were arcsine transformed before statistical analysis.

Table 3.1: Monthly occurrence of observation periods including the number of activity events per month.

YEAR	MONTH	NO. OF OBSERVATION PERIODS	ACTIVITY EVENTS
2004	January	1	1530
2004	February	2	1187
2004	March	3	2508
2004	April	3	1378
2004	May	2	1576
2004	June	1	1001
2004	August	1	9
2004	September	7	7954
2004	October	2	5384
2004	November	6	4634
2004	December	1	971
2005	January	1	1049
2005	March	1	1314
2005	June	2	1622
Total		33	32117

2. The effect of elephants on abundance and biodiversity of woody plants and the effect of browsing on selected tree species; Quantification of the impact of elephants on the vegetation

The line transect method (Buckland *et al.*, 2007) was employed to determine the effect of elephants in the study area. The transects (for details see below) were located in Nyati (with elephants) and Addo Heights, which served as the control site. In Nyati, transects were positioned at random in two areas of Xeric Succulent Thicket, one that had been used by elephants and one that had not yet been used. Because of the very short history of elephants in Nyati, it was decided to target areas that had been used by elephants so as to increase the chance of detecting elephant induced change. The second set of transects in Nyati then serve as a control to test if elephants were selecting specific vegetation associations within Nyati. Elephant use was established by direct observation of elephants or through the presence of dung, by signs of trampling or by visible signs of elephant feeding (uprooted trees, broken trunks and the height at which the tree is browsed). The latter is the least reliable as both Black rhino *Diceros bicornis bicornis* and Kudu *Tragelaphus strepsiceros* occupy the same area. These indicators do not necessarily all exist within an area occupied by elephant and preference has been given to the first two means of confirming elephant utilisation of vegetation. In Addo Heights, transects were located at random in regions of Xeric Succulent Thicket.

Ten, 100 m long transects were randomly located within each study site, resulting in 30 transects. Along each transect, at 1m intervals, a peg was dropped to the ground and the object located (plant, rock, soil, water, dung) was recorded. Whenever a plant was hit the species was recorded and the nature and degree of elephant utilization assessed. Plant

species that could not be identified in the field were sampled and identified later using several field guides (Shearing, 1997; Vanderplank, 1999; van Oudtshoorn, 1999; Manning, 2001; Coates-Palgrave, 2002). Any samples that could not be identified hereafter were taken to the Schonland Herbarium at Rhodes University. Elephant utilization was assessed according to the following utilisation categories: no use; light intensity (defined as minimal defoliation, with no broken branches or bark stripping); medium intensity (consisting of a combination of defoliation, bark stripping, and broken branches); and heavy intensity (comprising broken branches, a broken trunk, a trampled or uprooted plant).

#### Data analysis

Within each transect, total plant abundance was determined; and presence (present/absent), frequency and utilisation of each plant species was calculated. Plant abundance in two Nyati sites and Addo Heights has been compared using ANOVAs. Percentages were arcsine transformed before analysis.

Plant species diversity at Nyati and Addo Heights was calculated using the Shannon-Wiener Index. This measurement (H) takes into account species richness (S – the total number of plant species present) and the proportion of each species (P).

$$H = -\sum (P \ln[P]).$$

Using species richness (S) and the Shannon-Wiener Index (H), a measure of evenness (E) is then calculated, defined as follows:

$$E = H/\ln(S).$$

### Elephant Importance Value (ELEVI)

Danckwerts *et al.* (1992) developed what is known as a plant's Ecological Importance Value (EIV). I have adapted his method to create what I term a plant's Elephant Value of Importance (ELEVI) which incorporates presence, frequency and degree of utilisation for each species. Presence is calculated as the percentage across the 10 transects and is given a maximum score of 100. That is to say, if a plant occurs in five of the transects, it has a 50% presence and is allocated 50 points. Frequency is the mean of the 10 values calculated for each transect per species and is also given a maximum score of 100. (If species N occurs 10 times of 40 plants in transect 1, the frequency is 25%.). Utilization is scored on a presence or absence basis. If species N is utilized in a transect, it is given a score of 100. If it is not utilized the score is zero. In calculating ELEVI, the utilization value is a mean of the values for the 10 transects. These figures are then added to give the plant's elephant value of importance (ELEVI; Table 3.2).

Table 3.2: A theoretical ELEVI calculation.

Species	Presence	Frequency	Utilization	ELEVI
<i>Acacia</i>	60	15	33	108
<i>karroo</i>	(present in 6 of 10 transects)	(mean frequency of occurrence for the species in 10 transects)	(mean for 10 transects)	

## RESULTS

### 1. The importance of grass in the diet: observations of elephant feeding behaviour

In 16012 (49.9%) of the individual elephant observations (activity events), animals were feeding and of these, 14305 (89.3%) were grazing events (Table 3.3). A similar pattern was seen at the observation period level and, of the 33 observation periods, 22 (67%) were dominated by feeding activity of which 18 were dominated by grazing and 4 by browsing (Table 3.3).

Table 3.3: Percent occurrence of different behaviours of elephants in Nyati. Percentages of grazing and browsing are of total feeding events; all other percentages are of the total number of observations. One observation period was not dominated by a particular behaviour and numbers in that column do not total 33.

	Observations			
	Activity events	%	Observation periods	%
Total	32117		33	
Feeding	16012	49.9	22	66.5
Grazing	14305	89.3	18	82
Browsing	1707	10.7	4	18
Foraging	2259	7	0	0
Travelling	12705	39.6	9	27
Drinking	823	2.6	1	3
Other	318	0.9	0	0

The interaction between group size or herd structure and time spent grazing and browsing (Table 3.4) was examined using two way ANOVAs. A two way ANOVA, with group structure (herd/bulls) and feeding mode (grazing/browsing) as categorical variables, and proportion of all feeding events (arcsine transformed) in the 33 observation periods as the dependent variable detected a significant effect of feeding mode and no significant effect of group structure (Table 3.5). Post Hoc Tukey HSD tests showed that herds spent significantly more time grazing than browsing ( $P < 0.001$ ) while there was no significant difference for the bulls ( $P > 0.05$ ).

Table 3.4: The effect of group size and structure on behaviour. Data are mean ( $\pm 1$ sd) percent observations for each type of behaviour in the 33 observation periods. Percentages of grazing and browsing are of total feeding events; all other percentages are of the total number of observations. \* = significant difference ( $P < 0.05$ ).

	Group size		Group structure	
	Small	Large	Bulls	Herd
Feeding	65.3 $\pm$ 20.3	50.2 $\pm$ 30.3	62.5 $\pm$ 21.6	51.9 $\pm$ 30.0
Grazing	50.8 $\pm$ 39.2	82.9 $\pm$ 25.7*	64.2 $\pm$ 35.4	77.6 $\pm$ 31.5
Browsing	49.2 $\pm$ 39.2	17.0 $\pm$ 25.7*	35.7 $\pm$ 35.4	22.4 $\pm$ 31.5
Foraging	10.2 $\pm$ 7.3	8.2 $\pm$ 5.7	11.8 $\pm$ 7.2	8.0 $\pm$ 5.7
Travelling	15.8 $\pm$ 10.8	37.6 $\pm$ 30.4	15.7 $\pm$ 9.5	36.0 $\pm$ 30.0
Drinking	6.3 $\pm$ 17.7	3.2 $\pm$ 7.6	8.3 $\pm$ 20.4	3.0 $\pm$ 7.4

Table 3.5 Results table from a two way ANOVA with categorical variables group structure (herd/bull) and feeding (graze/browse).

effect	SS	df	MS	F	P
intercept	16.26	1	16.27	73.55	<0.0001
Herd/bull	0.0061	1	0.0061	0.027	0.869
Graze/browse	3.17	1	3.173	14.35	0.00035
interaction	0.47	1	0.48	2.15	0.148
error	13.71	62	0.221		

A second two way ANOVA, with group size (large/small) and feeding mode as categorical variables and proportion of all feeding events (arcsine transformed) in the 33 observation periods as the dependent variable, showed that groups size did not have a significant effect but that feeding did and there was a significant interaction between the variables (Table 3.6).

Table 3.6 Results table from a two way ANOVA with categorical variables group size (large/small) and feeding (graze/browse).

effect	SS	df	MS	F	P
intercept	20.14	1	20.14	108.3	<0.0001
Large/small	0.0091	1	0.009	0.049	0.82
Graze/browse	2.646	1	2.647	14.23	0.00036
interaction	2.66	1	2.66	14.29	0.00035
error	11.53	62	0.18		

Post Hoc Tukey HSD tests showed that large groups of elephants grazed significantly more than they browsed ( $P < 0.001$ ) and grazed significantly more than small groups either grazed or browsed ( $P < 0.05$  for both). Small groups spent equal amounts of time grazing and browsing ( $P > 0.05$ ).

Similarly, two way ANOVAs were used to explore the relationship between group size or group structure and the five behaviour categories as categorical variables, and proportion of behaviours (arcsine transformed) in the 33 observation periods as the dependent variable. Neither group size nor structure had a significant effect on the proportion of observations of time spent in the different behaviours (Tables 3.4; 3.7 & 3.8). In both cases, elephants spent significantly more time feeding than in any other activity (Post Hoc Tukey HSD tests;  $P < 0.05$  for all).

Table 3.7 Results table from a two way ANOVA with categorical variables group structure (herd/bull) and behaviour(feeding, foraging, travelling, drinking or other).

effect	SS	df	MS	F	P
intercept	4.75	1	4.75	90.17	<0.0001
Herd/bull	0.00056	4	0.00056	0.010	0.92
behaviour	5.29	4	1.32	25.12	<0.0001
interaction	0.385	1	0.096	1.83	0.12
error	8.165	155	0.052		

Table 3.8 Results table from a two way ANOVA with categorical variables group size (large/small) and behaviour (feeding, foraging, travelling, drinking or other).

effect	SS	df	MS	F	P
intercept	5.90	1	5.90	115.29	<0.0001
Large/small	0.00029	4	0.00029	0.0058	0.94
Graze/browse	6.81	4	1.70	3.29	<0.0001
interaction	0.61	1	0.153	3.00	0.020
error	7.93	155	0.051		

2. *The effect of elephants on abundance and biodiversity of woody plants.*

**Transect results**

Plant Community Structure at Nyati and Addo Heights

In Nyati, the lowest number of species on a transect was four and the maximum was 24 plant species. The Nyati Control transects yielded a minimum of three plant species and a maximum of 18 plant species. Addo Heights had a minimum of six plant species on a transect and a maximum of 19 plant species (Table 3.9). Total species richness was higher at Nyati (63 plant species), lower at Addo Heights (51 plant species) and lowest at the Nyati Control (49 plant species) (Table 3.9) (Appendix 1 for full species lists).

Biodiversity was very similar at Nyati (Shannon-Wiener Index = 1.45) and at Addo Heights (Shannon-Wiener Index = 1.49) but higher at the Nyati control sites (Shannon-Wiener Index = 2.57; Table 3.9). At all sites, certain species were dominant (*A. karroo* at Nyati; *Cynodon dactylon* at Nyati control and Addo Heights; and *O. ficus-indica* at Addo

Heights; Table 3.10). Evenness at Nyati ( $E = 0.55$ ) was similar to that at Addo Heights ( $E = 0.56$ ) and was higher at Nyati control (0.66). The higher biodiversity value for Nyati control cannot be attributed to a greater number of species (Table 3.9) and is probably then due the higher evenness value. The three sites shared 39 species in common, with 24 being unique to Nyati, 12 unique to Addo Heights and 2 unique to Nyati control (Appendix 1; Table 3.9).

Table 3.9: Comparison of plant community structure at Nyati and Addo Heights.

	Nyati	Nyati Control	Addo heights
Species Richness – Total	63	49	51
Species Richness per transect (Mean; max; min)	12.8; 24; 4	7.8 ;18; 3	11.5; 19; 6
Shannon-Wiener Index	1.45	2.57	1.49
Evenness	0.55	0.66	0.56
Number of unique species	24	2	12
Total as % of all plant species observed (73)	83.5	67	70

#### Plant abundance

There was no significant difference in mean abundance of all plants at the three sites ( $F = 1.66$ ;  $df = 2$ ;  $P > 0.05$ ; Table 3.10). However, at a species level, *A. karroo* was significantly more abundant at Nyati than at Nyati control or Addo Heights ( $F = 3.8$ ;  $df =$

2;  $P < 0.05$ ; Table 3.10). There was no significant difference in abundances of the other tree species although this was in many cases due to the high levels of variability.

### *3. The effect of browsing on selected tree species*

#### Plant utilisation

The mean number of trees per transect in Nyati was  $33.2 \pm 24.5$  of which the majority were unbrowsed ( $20.9 \pm 23.6$  trees per transect; Table 3.11). There was a significant effect of level of browse (no browse, light medium and heavy browse) on the arcsine transformed proportion (ANOVA,  $F = 8.4$ ;  $df = 3$ ;  $P < 0.001$ ). The Post Hoc Tukey HSD test showed that there were significantly more unbrowsed trees than all categories of browsed trees ( $P < 0.001$  for all) and no significant differences between any of the levels of browsing. Nevertheless, the impact of elephant browsing was mostly light (89 of 123 browse events were light) with low levels of medium (18 browse events) and high (16 browse events; Table 3.11).

Various forms of utilization that fall under medium and heavy browsing have been analysed separately and all were quite rare. Bark stripping occurred in 3 transects, broken branches in 4 transects, broken trunks in 3 transects and uprooted trees were not observed (Table 3.12). Broken branches occurred most often (21 instances), bark stripping less frequently (16 instances) and broken trunks least often (5 instances) (Table 3.12). There was no significant difference between mean occurrence of any of the categories of medium and heavy browsing (ANOVA,  $F = 1.20$ ;  $df = 2$ ;  $P > 0.05$ ).

Table 3.10: The presence and mean abundance of the most abundant tree species and the most abundant grass (*C. dactylon*) at Nyati and Addo Heights. Presence is the number of transects in which the species was recorded. Abundance is the number of a particular species as a percentage of all plants in that transect. The first row shows the mean abundance (n=10 transects per site) for all plants.

Species	Presence			Abundance		
	Nyati	Nyati control	Addo	Nyati	Nyati control	Addo
Mean (all species)	N/A	N/A	N/A	75.8±14.7	83.2 ± 18.0	87.8± 11.0
<i>Acacia karroo</i>	7	5	5	22.3±27.4	3.1± 5.6	2.3±3.4
<i>Cussonia spicata</i>	0	0	4	0	0	2.9±4.8
<i>Cynodon dactylon</i>	5	8	9	14.8 ±17.8	28.0± 27.7	31.2 ±35.6
<i>Euclea undulata</i>	2	2	3	0.8 ±1.7	0.2± 0.4	0.7 ±0.8
<i>Euphorbia grandidens</i>	0	0	2	0	0	2.4 ±5.5
<i>Maytenus heterophyllus</i>	2	2	0	3.1 ±9.0	0.5± 0.9	0
<i>Opuntia ficus-indica</i>	2	3	7	1.1 ±2.2	3.2± 8.7	20.1 ±22.0
<i>Pappea capensis</i>	2	0	3	4.0 ±7.7	0	0.3 ±0.5
<i>Portulacaria afra</i>	0	0	1	0	0	0.2 ±0.7
<i>Ptaeroxylon obliquum</i>	0	0	2	0	0	0.2 ±0.5
<i>Putterlickia pyracantha</i>	2	1	3	3.0 ±8.9	0.1± 0.3	1.0 ±1.6
<i>Rhus undulata</i>	3	2	4	0.8 ±2.7	1.1± 2.6	1.8 ±3.0
<i>Schotia afra</i>	1	1	4	0.3 ±0.8	0.1± 0.3	1.1 ±1.6
<i>Sideroxylon inerme</i>	2	1	2	0.1 ±0.4	0.1± 0.3	0.3 ±0.8

Table 3.11: Summary of levels of browsing in Nyati. Data are presented as numbers of plants in each category of damage and their percentages (total column) and as means for the ten transects at each site. Where two percentage values are given for light, medium and heavy damage, the first is of all trees (332) and the second, of browsed trees (123).

	total	Mean $\pm$ 1sd/transect
All trees	332	33.2 $\pm$ 24.5
unbrowsed	209	20.9 $\pm$ 23.6
unbrowsed %	62.9	61.9 $\pm$ 39.0
browsed	123	12.3 $\pm$ 15.0
browsed %	37.1	38.0 $\pm$ 39.0
light	89	8.9 $\pm$ 10.3
light %	26.8 (72.4)	34.2 $\pm$ 28.8 (73.0 $\pm$ 19.7)
medium	18	1.8 $\pm$ 3.1
medium %	5.4 (14.6)	9.0 $\pm$ 12.5 (14.5 $\pm$ 17.2)
heavy	16	1.6 $\pm$ 4.0
heavy %	4.8 (13.0)	4.3 $\pm$ 10.2 (12.4 $\pm$ 18.9)

Table 3.12: The occurrence of medium and heavy browsing in the form of bark stripping, broken branches and trunks, and uprooted trees. The number in brackets is the number of transects in which damage was observed. The mean is the mean occurrence per transect.

Defoliation category	bark stripped	branches broken	trunk broken	plant trampled	plant uprooted
Total per category	16 (3)	21 (4)	5 (3)	0	0
Mean $\pm$ sd	1.6 $\pm$ 2.6	2.1 $\pm$ 3.0	0.5 $\pm$ 1.0	0	0

Only *A.karoo* occurred often enough in the transects to allow an analysis of levels of damage at a species level and this is reported in the next section.

#### The effect of elephants on target species.

##### Observations of feeding on target species

*Opuntia ficus-indica* was eaten at least once in five (19%) of the 33 observation periods and was the only food plant in one observation period. *Acacia karroo* was eaten in 23 (85%) of the observation periods and was the only food source in 9 (33%) of the observation periods. Of the 1707 observed browsing events, all could be allocated to a specific species and of these, 3% were on *O. ficus-indica* and 81% were on *A. karroo*. A two way ANOVA was used to test the effect of target species and group structure as categorical variables on percentage of feeding events on the target species (arcsine transformed) per observation period as the dependent variable. There was no significant difference between herds and bulls in their use of either *A. karroo* (herds,  $84.2 \pm 26.9$ ;

bulls,  $50.2 \pm 46.9$ ; data are mean % of browsing events  $\pm$  1sd ) or *O. ficus-indica* (herds,  $6.0 \pm 2.2$ ; bulls  $1.7 \pm 4.9$ ) but both social groups used significantly more *A. karroo* than *O. ficus-indica* (Table 3.13 for ANOVA results).

Table 3.13. Results table from a two way ANOVA with categorical variables target plant species (*A. karroo* or *O. ficus-indica*) and group structure (herd/ bull).

effect	SS	df	MS	F	P
intercept	10.22	1	10.22	48.87	<0.0001
Target species	7.97	1	7.97	38.12	<0.0001
Herd/ bull	0.66	4	0.66	3.15	0.08
interaction	0.31	1	0.31	1.48	0.22
error	10.45	50	0.21		

#### Browsing damage on target species in the transects

*Acacia karroo* trees were recorded in 70% of Nyati's transects and had the highest abundance of all plants (Table 3.10). The majority of trees (186, 83%) were ignored (Table 3.14) and where browsing was recorded, it was mostly light. Only 16% (37) of all *A.karroo* trees were browsed and of these, browsing was light on 32 trees (Table 3.14). Significantly more trees were unbrowsed than were browsed and there was no significant difference between the levels of browse (Kruskal-Wallis ANOVA on ranks; data not normally distributed;  $H= 15.1$ ;  $df = 3$ ;  $P<0.005$ ).

*Opuntia ficus-indica* was only found on two of Nyati's transects and was only subjected to light intensity browsing.

Table 3.14: Utilisation of *A. karroo* at Nyati. Data are presented as total numbers (total row with percentage of all trees in brackets) and as mean values per transect with percentages in brackets. Three transects had no *A.karroo* and n=7 for all calculations of mean values except for abundance where n=10.

	<i>Acacia karroo</i>			Browse level		
	Abundance	ignored	browsed	light	medium	Heavy
total	223	186 (83.4%)	37 (16.6%)	32 (14.3%)	2 (0.9%)	3 (1.3%)
transect	22.3±27.4	26.6± 25.9 (83.9±26.1)	5.3± 6.3 (16.1±. 26.1)	4.5± 5.9	0.3± 0.4	0.4± 0.5

## ELEVI

The most important plant species, in terms of their utilisation by elephant; presence across the surveyed transects; and overall abundance were *A. karroo*, *C. dactylon* and *Putterlickia pyracantha* (Table 3.15). Other important species for the Nyati herd included the succulent Spekboom (*Portulacaria afra*), and the woody species *Euclea undulata*, *Pappea capensis* and *Schotia afra*; and the shrubs *Maytenus heterophyllus* and *Rhigozum obovatum* (Table 3.15). It was not possible to determine the use of the grass species *C. dactylon* but it had a high presence and abundance hence its dominance.

Table 3.15: The most important browse plant species for the Nyati elephant herd, according to their ELEVI rating. The grass species *Cynodon dactylon* has a rating of 93, but is absent from the table as it is grazed.

Species	Presence	Frequency	Utilization	ELEVI
<i>Acacia karroo</i>	70	9	38	117
<i>Euclea undulata</i>	20	1	10	31
<i>Maytenus heterophyllus</i>	20	1	17	38
<i>Opuntia ficus-indica</i>	20	2	3	25
<i>Pappea capensis</i>	20	1	17	38
<i>Putterlickia pyracantha</i>	20	1	30	51
<i>Rhus undulata</i>	30	1	10	41
<i>Schotia afra</i>	10	1	3	14
<i>Sideroxylon inerme</i>	20	1	17	38

## DISCUSSION

*The importance of grass in the diet of elephants in Nyati.*

Contrary to the hypothesis, the results for the present study indicate that grass is a very important component of the diet, with grazing comprising about 90% of all feeding observations. The importance of grazing is more marked in the herd than with the bulls, and herds spent significantly more time grazing than browsing. The degree to which elephants graze varies. In Uganda (Field, 1971; Owen-Smith, 1992), and Zambia (Jachmann, 1995) for instance, elephants feed primarily on grass but in KwaZulu-Natal, South Africa, grass constitutes only 45% of elephants' diet (Bowland & Yeaton, 1997) whilst Kenya's Tsavo elephant population's diet comprises less than 25% grass per year on average (Cerling *et al.*, 2004). Previous studies in the Spekboom Succulent Thicket of

Addo have reported that the grass *Cynodon dactylon* is a primary forage species (Novellie *et al.*, 1991) forming 50 % of the diet in winter (Paley & Kerley, 1998). The elephants in Nyati feed on grass more than most other populations. A seasonal change in the consumption of grass has been reported in some studies (Dublin, 1997; Paley & Kerley, 1998) and the very high consumption of grass by the elephants in Nyati might be the result of a seasonal bias in observations (i.e. more observations at a time of year when grass is eaten than when it is not). However, observations were made throughout the year and this is an unlikely explanation.

Contrary to the hypothesis that bulls would use more grass than herds, in Nyati, herds grazed significantly more than browsed while the bulls spent equal amounts of time grazing and browsing. A number of studies have reported a sex difference in feeding behaviour of elephants. For example, female elephants in KwaZulu-Natal tend to be more selective, have shorter feeding bouts and exhibit less destructive feeding behaviour than males (Shannon, 2005); females in Chobe have shorter feeding bouts (Stokke & Du Toit, 2000); and elsewhere, female elephants also tend to consume more forage (Owen-Smith, 1992). The probable explanation for the unexpected prevalence of grazing in Nyati is that grass was more abundant than expected in Xeric Succulent Thicket, with a single grass species (*C. dactylon*) comprising about 15% of all plants in the transect and being the second most abundant plant species. The region is close to the coast and rain falls throughout the year with peaks in late summer and spring. Although not assessed in this study it is likely that grass quality and quantity does not decline significantly during winter and remains a preferred food source for the elephants.

*The effect of elephants on the abundance and biodiversity of woody plants*

Plant biodiversity was highest at Nyati control and lower and similar at Addo Heights and the Nyati transects that had been used by elephants. Clearly these differences cannot be attributed to the presence of elephants and it more likely that within Nyati, the elephants have selected specific areas and avoided others thus creating the differences between Nyati and Nyati control. The key differences between the two Nyati sites was the Evenness scores (higher in Nyati Control than Nyati) with the vegetation of Nyati being dominated by *Acacia karroo*.

Observations of elephants feeding on Nyati revealed a predominance of *A. karroo* in the diet (81% of all browsing events were on *A. karroo*) and this was supported by the transects in which the same species was frequently browsed. A number of other studies have reported a similar preference for members of the genus *Acacia* (Spinage, 1994; Shoshani *et al.*, 2004, Birkett *et al.*, 2000 in Omondi *et al.*, 2002b, Jachmann, 1985, Osborn, 2005, and see O'Connor *et al.*, 2007 for review).

The results for Nyati do not support either of the hypotheses (that there would be no reduction in plant biodiversity and that there would be a reduction in abundance of woody plants in the presence of elephants) and it appears that elephants have not had a pronounced effect. Elephants had been at Nyati for two years when the observations were made and the results are similar to those previously reported for AENP in the early years after elephant introduction (Penzhorn *et al.*, 1974) and elsewhere in Africa (Botswana - Ben-Shahar, 1999). This is in contrast to later studies in AENP (Barratt & Hall-Martin, 1991 in Moolman & Cowling, 1994; Moolman & Cowling, 1994) and elsewhere in Africa (Kenya - Waithaka, 1993; Zimbabwe – Osborn, 2002) which indicate that species

richness is highest in the areas that had been excluded from elephant activity. A reduction in the density of trees is a common effect of elephant feeding and has been reported in a number of studies (Damiba & Ables, 1994; Ben-Shahar, 1999 and in AENP, Penzhorn *et al.*, 1974). Another primary target of elephant browsing activity in Nyati was prickly pear *Opuntia ficus-indica*, an alien invasive species and this is the topic of Chapter 4.

#### *The effect of browsing on selected tree species*

The degree of utilisation of the vegetation in Nyati varied from nibbling ends of branches (classified as light defoliation) to total destruction of the trunk, but it was predominantly light intensity browsing and there were no observations of tree species uprooted. In her study of vegetation impact by elephant following their reintroduction to the Sabi Section of Kruger National Park, South Africa, Hiscocks (1999) reports that most observations were of light browsing, with no major impact on the woody vegetation which was dominated by *Acacia burkei* and *Combretum apiculatu*. Other studies in AENP have similarly reported that elephant utilisation had minimal affect on the woody plant component but the sub-dominant portion of the vegetation, consisting mainly of small succulents and geophytes (Moolman & Cowling, 1994; Cowling & Kerley, 2002) was negatively affected. Elephant damage to vegetation elsewhere varies, from trampling of seedlings (Chobe National Park, Botswana – Ben-Shahar, 1993) and light browsing and debarking (Knysna, South Africa – Milewski, 2002) to death of tree species by toppling and uprooting (Kenya - Höft & Höft, 1995). A further indication of the relatively light impact that elephants have had in Nyati is that, for even the preferred species, *A. karroo*, the majority of specimens in the transects were not browsed. It is likely that various

factors have combined to produce the low levels of damage to trees. These are the low elephant density and their short history in Nyati, and the high prevalence of grass in the diet.

There is ample evidence that high densities of elephants lead to habitat degradation (Botswana - Knight *et al.*, 1994; Ben-Shahar, 1996; Cameroon - Pamo & Tchamba, 2001; Kenya - Poole, 1993; Waithaka, 1997; Mubalama, 2000; Ogola & Omondi, 2005). Low densities have the opposite effect, with elephants seemingly having very little effect on the vegetation, such as in Burkina Faso (Christenson in McShane, 1989), Zimbabwe (Martin *et al.*, 1989) or in the arid areas of Namibia (Jachmann, 1987). However, because damage is cumulative, it is not just the density of elephants but the number of years for which they have been present and whether or not their movements are restricted. The prolonged stay of an increasing number of elephants has a detrimental effect on the vegetation, as reported in both Cameroon (Tchamba, 1993) and AENP (Johnson, 1998; Lombard *et al.*, 2001) and it should be expected that the same pattern of increasing change will be seen at Nyati.

## CHAPTER 4

### **Elephants (*Loxodonta africana*) as possible biological control agents of prickly pear (*Opuntia ficus-indica*) in Addo Elephant National Park.**

---

The prickly pear (*Opuntia ficus-indica*) is an alien invasive weed that is common in the Nyati section of AENP. Previous studies have suggested that it is a preferred food plant of elephants and that elephants have been responsible for its eradication in AENP (Chavez-Ramirez *et al.*, 1997; Urquhart & Klages, 1997). The objectives of this chapter were to quantify the effects of elephants, two years after re-introduction, on prickly pear in the Nyati region of the Addo Elephant National Park.

### INTRODUCTION

Alien species pose a significant threat to global biodiversity, second only to habitat loss (Holmes & Cowling, 1997; Schmitz & Simberloff, 1997; Walker & Steffen, 1997). Alien plants are able to displace indigenous plants (Frankel *et al.*, 1995; Groves & Willis, 1999), change the structure and composition of ecological communities (Woods, 1993; Mullet & Simmons, 1995; Fogarty & Facelli, 1999), and alter ecosystem processes (Vitousek, 1990; Mack & D'Antonio, 1998). Several methods exist for the control of alien invasive species including manual removal, chemical poisoning and biological control (Hosking & du Preez, 1999; Zimmerman *et al.*, 2001; Willis & Memmott, 2005). With the development of ecotourism in the Eastern Cape Province of South Africa, land that had previously been used for livestock is being converted into game reserves. Often this land is infested with weeds such as prickly pear (*Opuntia ficus-indica*) and jointed

cactus (*Opuntia aurantiaca*) and an important part of the rehabilitation process is the removal of these plants.

## **THE ECOLOGY OF PRICKLY PEAR**

### Distribution and reproduction

Undesirable, exotic plant species that invade vegetation and landscapes are called environmental weeds (Groves, 1991). Early colonists in South Africa considered indigenous species to be of little value and exotics were introduced for various reasons (Goodall & Naude, 1997) especially for fodder for their livestock. *Opuntia ficus-indica* was introduced for this purpose (Stirton, 1983 in Hoffmann, 1991). Prickly pear is found throughout South Africa, having been introduced from Mexico (Zimmermann, 1981; Bromilow, 1995) after which it spread throughout the country. Initially it infested an area of approximately 900 000 ha, mainly in the Eastern Cape Province and Karoo (Zimmermann, 1981). Today, dense populations of prickly pear occupy less than 100 000 ha of South Africa and are confined mostly to the coastal areas of the Eastern Cape Province and to isolated pockets in the Karoo and to the north of the country (Zimmermann *et al.*, 1986). The primary reason for the success of this plant is the fact that it reproduces so well vegetatively (Grant & Grant, 1971a; Mandujano *et al.*, 1996) by means of both seeds and cladodes. Elephants are amongst a number of animals that act as dispersal agents for the related species, *O. stricta* (Kruger National Park, South Africa - Chavez-Ramirez *et al.*, 1997; Hoffmann *et al.*, 1998).

### Prickly pear as a valuable resource

*Opuntia ficus-indica* is an important crop in agricultural economies throughout arid and semi-arid parts of the world (Griffith, 2004). Prickly pears are utilised as feed for stock and for fodder during droughts (De Kock & Aucamp, 1970 in Zimmerman & Moran, 1991) and is also widely utilised for its succulent fruits (Bromilow, 1995; Wiemeler, 1988 in Zimmerman & Moran, 1991). It is also utilised widely by wild animals, from Africa (Double Drift Nature Reserve, South Africa - Chavez-Ramirez *et al.*, 1997) to the arid areas of the US and Mexico (Theimer & Bateman, 1992; Hoffmann *et al.*, 1993; Ruthven *et al.*, 1994). Prickly pear is particularly valuable as a fodder and food resource in arid regions, such as Ethiopia, as it can withstand prolonged periods of drought and nutrient shortage; it is easily propagated; it is a persistent plant in these conditions; it has a high dry matter yield; it is highly digestible; and is an important source of Nitrogen (Tegene *et al.*, 2005).

### **CONTROL OF INVASIVE WEEDS**

There are serious shortcomings in the control of alien invasive plants, due mostly to a lack of resources to conduct research on their control (Goodall & Naude, 1997).

Chemical control is achieved with the injection of MSMA (metsulfuron-methyl) or glyphosate, but it is time-consuming and costly (Bromilow, 1995). Furthermore, the economic constraints on landowners to successfully clear their lands are great (Goodall & Naude, 1997).

Alien invasive control is also a complex undertaking (Goodall & Naude, 1997), requiring different strategies for different densities; different habitats; different ages and varying

sizes of plants. Conventional control – that is, the use of labour-intensive methods, may take several years. The process usually consists of an initial clearing followed by however many follow-up operations are required until the plant either ceases to exist (which is unlikely), or the plant can be controlled with minimal resources. The duration of the operation will depend on the method utilised; the effectiveness of the clearing operation; and the density of the weed. However, many plants have seed banks that persist for many years, hereby extending the treatment period for a much longer duration (Goodall & Naude, 1997).

In order for clearing operations to be as successful as possible, rehabilitation needs to occur within the cleared area, to facilitate regeneration of the habitat and prevent re-invasion. Rehabilitation implies that the area is returned as close as possible to its former natural state and further degradation is stopped (Goodall & Naude, 1997).

Where infestations are sparse, many natural growth forms remain and succession quickly fills the gaps left by alien species (Goodall & Naude, 1997). In dense infestations however, the soil surface is exposed making the site prone to erosion and re-invasion (Goodall & Naude, 1997). Rehabilitation methods are many and varied, from sowing the cleared site with seed; stacking brush over the cleared area; re-planting the area with indigenous plants or using a combination of methods, but these methods are costly and time-consuming.

#### Control of prickly pear

Only about 2% of alien invasive plant species have been certified for biological control (Hoffmann, 1991) and most environmental weeds can only be controlled using herbicides and/or mechanical control (Goodall & Naude, 1997). Biological control of environmental

weeds is limited to *Opuntia* species and a few other plant species (Hoffmann, 1991). Due to the limited effectiveness of biological control on prickly pear, infestations most often need to be treated chemically (Zimmermann & Moran, 1991). This chemical control method entails injecting the stem with a herbicide, which combined with felling allows control of the infestation (Zimmermann, 1989) but this is time-consuming and costly. At one time, due to prickly pear's high forage value, there was a call for the control of the biological control agents themselves (Pretorius, 1989 in Zimmerman & Moran, 1991) by farming associations who perceived them as pests (Zimmermann & Moran, 1991). The success of biological control of prickly pear in South Africa with the cactus moth *Cactoblastis cactorum* and cochineal *Dactylopius opuntiae* has varied from partial (Bromilow, 1995) to very successful (Zimmermann, 1989). The varying degree of success depends largely on the efficacy of the primary control agent cochineal. This agent is reportedly less effective in higher rainfall areas (Goodall & Naude, 1997; Zimmermann *et al.*, 1986) and it is also used on infestations of *Opuntia aurantiaca*, where its effectiveness is limited by mass die-offs of the agent in cold winter conditions. The other known biological control agent of prickly pear, the phyticid moth or cactus moth, fails to kill large prickly pears (Goodall & Naude, 1997) but is effective against isolated, small plants (Annecke & Moran, 1978). Annecke & Moran (1978) reported that in Australia the cochineal, aided by hand-felling, contributed most to the clearance of nearly 75% of an infested area, including most of the densest infestations. In addition to the limitations imposed on the cochineal by high rainfall and cold temperatures, their effectiveness has also been inhibited by coccinellid predators (Geyer, 1946, 1947 in Zimmerman & Moran, 1991; Pettey, 1948 in Zimmerman & Moran, 1991; Annecke *et*

*al.*, 1969; Morrison, 1984). According to Robertson (1985), predation by at least 6 species of ants accounted for egg losses of about 55%. A similar situation occurred in Mountain Zebra National Park where ants preyed on the cochineal released for control of *O. aurantiaca*. Host plant incompatibility also contributes to ineffectiveness of the control agent, as reported by Robertson (1985; 1988) who found that first instars of the cochineal failed to penetrate *O. ficus-indica* cladodes because the cuticle was too thick and because of gum exudations.

It has been reported that biological control carries with it certain risks, particularly with regards to its non-target effects (Zimmermann *et al.*, 2001). For example, the cactus moth arrived in America, where it is damaging native cactus species, including the critically endangered semaphore cactus *O. corallicola* (Stiling *et al.*, 2000).

Large wild herbivores have a largely unexplored potential as agents for the control of invasive exotic trees and shrubs (for example in forest and fynbos in conservation areas in the south-western Cape Province) and appear capable of reducing populations of invasive exotics without doing corresponding damage to ecologically similar indigenous plants (Milewski, 2002). In AENP, the prickly pear is a problem weed and interestingly, it appears to be a favoured food of elephants, which have taken on the role of biological control agents. Due to the various potential problems with biological control, it has been recommended that an analysis of the food web in which the agent would feature, be conducted to assess the safety of post-release control (Willis & Memmott, 2005).

However, elephants were not introduced into Nyati with the exclusive intent of controlling prickly pear, and as opposed to other introduced control agents, elephants are indigenous to South Africa. However, there is a need to determine the impact of

biological control agents on the growth and population dynamics of target weeds (Hoffmann *et al.*, 1998) and the aim of this chapter is to assess the effect of elephants on prickly pear and the effect that their prickly pear utilisation has on the rest of the plant community. The hypotheses tested are that elephants will have a detrimental effect on stands of prickly pear and may serve as a natural control agent for the weed, and that the indigenous vegetation in the areas surrounding these stands will also be adversely affected.

## **MATERIALS AND METHODS**

### Quantification of the impact of elephants on the prickly pear stands in Nyati

#### Data collection

Thirteen sites (= plots) of varying size containing prickly pear were selected randomly across the study site to determine the extent and degree of elephant impact. Plot size, which ranged from about 10 – 100m<sup>2</sup>, and shape were determined by the distribution of prickly pear plants. Utilisation of the plots by elephants was confirmed by direct observation of elephants or through the presence of dung, trampled plants or visible signs of feeding. Signs of utilisation consisted of broken prickly pear trunks; dispersed and flattened cladodes on the ground; and large pathways leading to infestations of prickly pear. The indigenous vegetation with trunks within the plot was also analysed for visible signs of elephant feeding (branch tips lightly browsed, uprooted trees, broken trunks and trees that had experienced bark-stripping).

### Sampling

All plants within each plot, regardless of the size of the plot, were counted and assessed. For prickly pear plants, the height was measured, the nature and degree of utilization was recorded and the dispersed cladodes in the plot counted. Height was measured using a 3m measuring stick. Plants were assumed to be adult if height was greater than 1m.

Utilisation was classified as no utilization; standing (living plants that were slightly damaged); browsed to the ground; knocked over; and uprooted. All cladodes on the ground were counted and classified as either new (new cladodes capable of regrowth), old (usually colourless but still alive), dead (decomposing) or trampled (flattened, usually into a mulched form). For indigenous plant species, all plants were recorded and assessed for the level of utilisation. Elephant utilization was classified as no use; light intensity (defined as minimal defoliation, with no broken branches or bark stripping); medium intensity (which consists of a combination of defoliation, bark stripping, and broken branches); and heavy intensity (comprising broken branches, a broken trunk, a trampled or uprooted plant).

### Data manipulation and analysis

The relative abundance of different forms of damage to whole prickly pear plants and different categories of the cladodes have been compared using one way ANOVAs – or the non-parametric equivalent.

## **RESULTS**

### General, qualitative description of utilisation

When utilising prickly pear, the Nyati elephants most often destroyed the plants, removing most cladodes and either left them strewn on the ground or trampled them (Fig.

4.1). Furthermore, the trunks were most often browsed down to the ground or close to the ground, if not knocked over or uprooted. Pathways were opened up to get to prickly pear stands (Fig. 4.2).



Figure 4.1: Typical indications of elephant utilisation in a prickly pear plot showing scattered cladodes.



Figure 4.2: Large open pathways leading to the prickly pear infestations are also indicative of elephant utilisation.

#### Quantification of damage to prickly pear.

The 13 plots contained variable numbers of intact and damaged adult plants and cladodes scattered on the ground (Table 4.1). Of 37 adult plants, 26 were browsed to the ground, knocked over or uprooted, 11 were standing and lightly browsed, and no adult plants were undamaged (Table 4.1).

Table 4.1: Prickly pear structure and abundance within the sampled plots (n=13). Data are total numbers in all 13 plots and mean and sd per plot.

	Total number	Mean per plot
Adult plants		
No damage	0	/
Standing	11	0.8±0.9
Browsed to ground	17	1.3±1.1
Knocked over	7	0.5 ±1.2
Uprooted	2	0.2±0.4
Total heavy damage	26	2.0±1.6
Cladodes		
new	75	5.8±3.7
old	461	35.4±24.7
dead	399	30.7±22.4
trampled	228	17.5±23.1
Old, dead & trampled	1088	83.7±53.2

A one way ANOVA with category of damage as the categorical variable and number of plants in each category as the dependent variable indicated a significant effect (F= 5.03;

df = 4;  $P < 0.05$ ; Figure 4.3). A Post Hoc Tukey HSD test showed that there were significantly more plants in the browsed to the ground category than in the uprooted and no damage categories ( $P < 0.05$  for both). For further analysis, the three categories of dead adult plants (browsed to the ground, knocked over and dead or uprooted) were combined, and a one way ANOVA used to compare the occurrence of dead, standing, and untouched plants. Although there was a significant effect of category of damage ( $F = 3.3$ ;  $df = 2$ ;  $P < 0.05$ ), no pairs were significantly different (Figure 4.3).

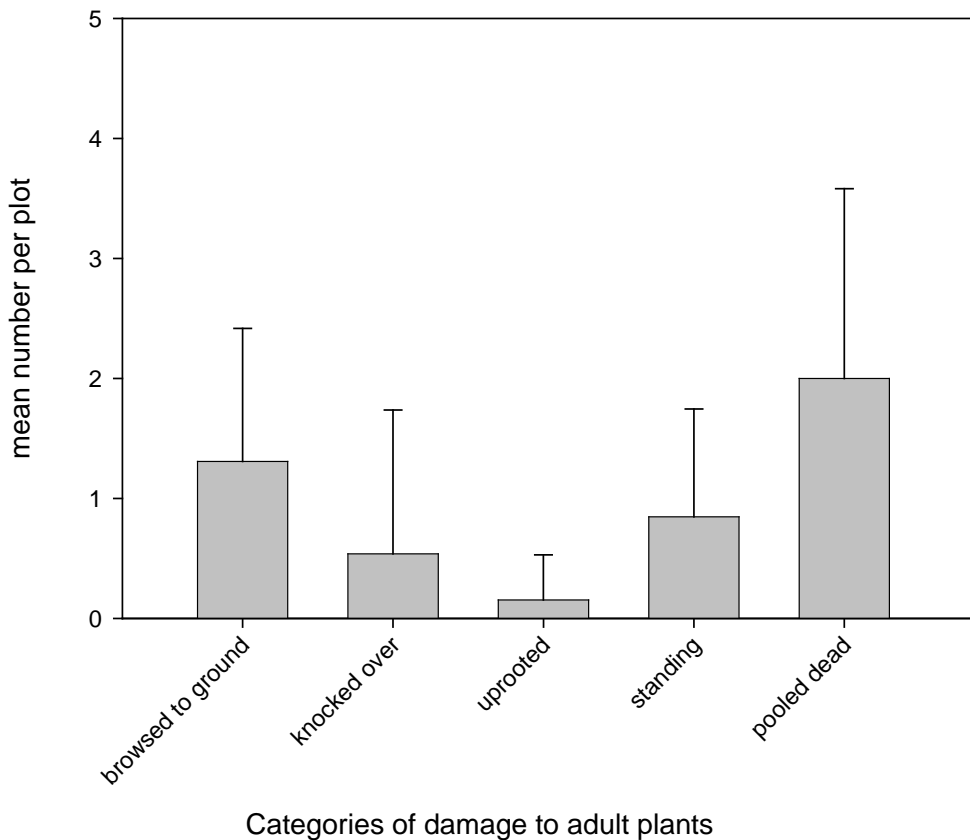


Figure 4.3. Occurrence of adult plants in different states of damage in 13 plots. Data are mean numbers per plot with 1 sd.

While the plots included a small number of adult plants, there were large numbers of cladodes in various conditions on the ground. A one way ANOVA with condition of the cladodes as the categorical variable and number in each condition as the dependent variable revealed a significant effect of cladode condition ( $F= 5.64$ ;  $df= 3$ ;  $P<0.005$ ). A Post Hoc Tukey HSD test showed that there were significantly fewer new cladodes than old or dead cladodes ( $P<0.05$  for both; Figure 4.4 ). To allow further analysis, the categories of cladodes that were not capable of regrowth (old, dead and trampled) were pooled and compared with new cladodes from which regrowth was possible. Data were not normally distributed and a Mann-Whitney Rank Sum Test revealed significantly fewer new cladodes than those capable of regrowth ( $T= 91$ ;  $n=13$ ;  $P<0.001$ ; Figure 4.4).

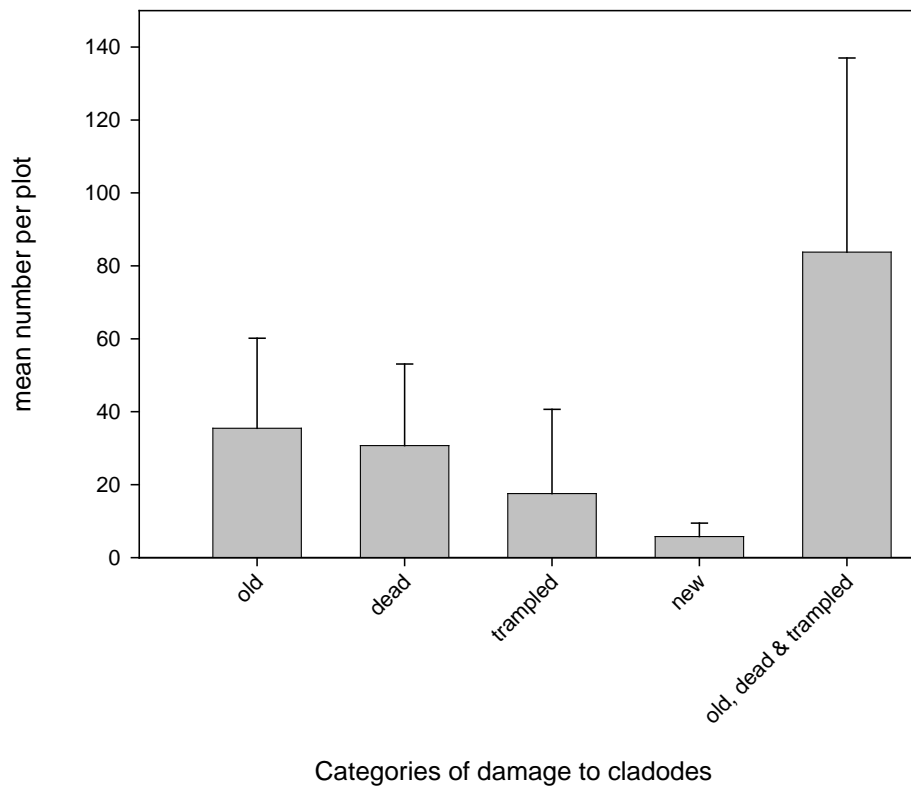


Figure 4.4: The occurrence of cladodes of prickly pear in different conditions in 13 plots. Data are mean numbers per plot with 1 sd.

### Indigenous plant utilisation

Due to the dense nature of Eastern Cape Subtropical Thicket (ECST), the elephants have to go to substantial effort to reach the prickly pear. As a result, much of the impact on the indigenous vegetation is due to a trampling effect (Table 4.3). The impact of elephant browsing on indigenous vegetation within the prickly pear plots was mostly heavy (48%) with similar levels of low (28%) and medium (24%) impact (Table 4.2). A one way ANOVA with category of damage as the categorical variable gave a significant effect of damage ( $F=5.1$ ;  $df=3$ ;  $P<0.005$ ). A Post Hoc test (Student-Newman-Keuls Method) showed that there were significantly fewer undamaged trees than those heavily damaged ( $P<0.05$ ) and that no other pairs were different ( $P>0.05$ ).

Table 4.2: Summary of levels of browsing on indigenous plant species in prickly pear plots in Nyati. Data are numbers of plants in each category of damage.

	Levels of utilisation			
	no utilisation	light	medium	heavy
Total per browsing category	4	20	17	34
% Of total browsing events	5	27	23	45
Mean browsing events per plot	0.2±0.4	1.5±1.3	1.3±0.8	2.6±2.7

Various forms of utilisation that fall under light, medium and heavy browsing were analysed separately, trampling (a form of heavy utilisation) was most common, followed by varying degrees of defoliation (Kruskal-Wallis ANOVA  $H=14.4$ ;  $df=4$ ;  $P<0.01$ ; Table 4.3).

Table 4.3: The effect of elephants on indigenous plant species within the prickly pear plots. Numbers in brackets are the number of plots in which the level of damage occurred.

Defoliation category	defoliation only	bark stripped	branches broken	trunk broken	plant uprooted	trampling
Total	20 (10 plots)	4 (4 plots)	13 (9 plots)	2 (2 plots)	0	32 (6 plots)
Mean per plot	$1.5 \pm 1.3$	$0.3 \pm 0.6$	$1.0 \pm 1.0$	$0.2 \pm 0.4$	0	$2.5 \pm 2.9$

Different plant species were subjected to different levels of browsing with eight species subjected to light browsing, nine to medium and eight to heavy browsing (including trampling). Certain species such as *Schotia afra* were utilised across the spectrum of browsing intensity, whilst other species were only utilised in a certain way (for example *Rhus undulata* was primarily lightly browsed) (Table 4.4).

Table 4.4: The levels of browsing experienced by different plant species. Data are numbers of plants per species for which different levels of browsing were recorded.

	no browsing	light	medium	heavy
<i>Acacia karroo</i>	0	1	3	6
<i>Azima tetracantha</i>	2	4	2	3
<i>Cynodon dactylon</i>	0	0	0	17
<i>Diospyros simii</i>	0	0	0	1
<i>Euclea undulata</i>	1	0	0	0
<i>Euphorbia mauritannica</i>	0	0	0	1
<i>Maytenus heterophylla</i>	0	3	4	1
<i>Olea africana</i>	0	0	1	0
<i>Pappea capensis</i>	0	2	1	1
<i>Portulacaria afra</i>	0	1	3	0
<i>Putterlickia pyracantha</i>	0	2	1	0
<i>Rhus undulata</i>	1	6	1	0
<i>Schotia afra</i>	0	1	1	4

## DISCUSSION

It is assumed in this chapter that damage to prickly pear was caused by elephants only. Although black rhino are present in Nyati, there were only 4 when the observations were made and they were never seen feeding on prickly pear. Although elephants have only been in the Nyati section of AENP for 3 years, they have had a dramatic effect on the prickly pears. In 13 stands, with 37 adult plants, 26 had been destroyed and all of those that remained standing had been browsed to some extent. This level of utilization, in such a short period of time, suggests that prickly pear is a highly favoured species. Elephants in the original AENP have successfully eradicated prickly pear from the Park (Urquhart & Klages, 1997) although it is not known how rapidly this occurred. It is thus not surprising that the Nyati elephants, having been relocated from Addo to Nyati, have continued to show this apparent preference for prickly pear. Although in Nyati, prickly pear was browsed similarly by the herd and the bulls that originated from Kruger National Park (see Chapter 3), there is no record of Kruger elephants feeding on this *Opuntia* species (Chavez-Ramirez *et al.*, 1997; Hoffmann *et al.*, 1998). It seems likely therefore that the Kruger bulls have learnt this feeding behaviour from the herd members that originated from the original AENP.

The very high level of utilization of adult prickly pear plants might suggest that elephants are good biological control agents. However, many more cladodes were left lying on the ground than the number of adult plants and since these cladodes may take root and generate a new plant, re-infestation is possible. Although not possible within the confines of this study, it would be important to revisit the 13 sites and establish the extent of re-infestation. It is also possible that elephants may disperse the seeds of *O. ficus-*

*indica* in their faeces however this seems not to have occurred in the original elephant camp at Addo where the species has been eliminated.

Whilst feeding on prickly pear, indigenous vegetation was affected. Indigenous trees within the prickly pear stands were subjected to intense browsing pressure and nearly half of all browsing events were heavy. Interestingly, this level of browsing was greater than that detected in the transects where most trees were unbrowsed and the most common level of browsing was light. Although these data were collected in different ways and cannot be compared statistically, the difference is pronounced. A parallel may be drawn between water holes and prickly pear stands since both attract elephants and are focal points for damage (the piosphere of Owen-Smith, 1996). However, while water holes will continue to attract elephants unless the source is closed down, prickly pear stands are probably only attractive for a short period of time, which should allow the indigenous vegetation to recover. Unfortunately, not all the *Opuntia* species in AENP are targeted by elephants, with jointed cactus *O. aurantiaca* remaining a problem in the area.

## CHAPTER 5

### General Discussion

---

The effect of elephants on the environment is often perceived as damage and destruction, however, there are several reasons why this may not always be the case. Some of these are briefly discussed below.

#### Elephants, disturbance and biodiversity

There can be no doubt that elephants have an effect on the habitat which they occupy, by virtue of their size alone. It is the degree of this impact though that has given rise to much concern for ecosystems throughout Africa. The degree depends on many variables, most notably the density of the elephant population and the role that water sources play within the habitat and includes other factors such as the effects of fire. While this impact is often seen as negative, it is possible that, by creating small pockets of disturbance, elephants will cause an increase in biodiversity. A theoretical framework for this is found in the Intermediate Disturbance Hypothesis (Connell, 1978) which proposes that the highest diversity in communities is attained, and maintained, at intermediate levels of disturbance. The highest diversity should occur at an intermediate stage in succession after a large disturbance or with smaller disturbances that are neither very frequent or infrequent (Connell, 1978). Without disturbance, there is a tendency towards loss of diversity (Lindsay, 1993), because dominant species can out-compete and replace other species through competitive exclusion (Gause, 1934). At the other extreme, there is a tendency towards loss of diversity with too much disturbance (Gillson & Lindsay, 2003). However, intermediate levels of disturbance can prevent competitive exclusion for

instance by affecting the abundance, spatial distribution, and resource usage of a competitor (Connell, 1978; Padisák *et al.*, 1993). According to the non-equilibrium paradigm, disturbance and change are normal, particularly to savanna ecosystems (McNaughton *et al.*, 1988) and enhance the diversity, stability and resilience of an ecosystem (Walker, 1989; Scholes & Walker, 1993; Gillson & Lindsay, 2003). Based on this, elephants, as primary agents of disturbance, should promote an increase in biodiversity, or conversely, in the absence of elephants, biodiversity will decline. An example of this is seen in Hluhluwe/imfolozi Complex where the long term absence of elephants has resulted in the local extinction of three grazers and a sharp reduction of several others to vulnerable levels (Owen-Smith, 1987). Elephants play an essential role in creating gaps in forests and, in the process, open up a more productive and varied ground layer to a range of other vertebrates (Western, 1987).

The Intermediate Disturbance Hypothesis may serve as a useful theoretical framework for future studies in the Greater AENP where different regions have been subjected to different levels of elephant driven disturbance.

#### The role of complex, interacting factors

There are various reasons why the impact of elephants on their environment should not be viewed in isolation. Firstly, other herbivores utilise the same resources as elephants (Dublin *et al.*, 1990; Owen-Smith, 1992; Ben-Shahar, 1997) and may contribute to habitat change. Fire is a primary agent of change that works hand-in-hand with elephants to affect ecosystems (Ben-Shahar, 1993; Tafangenyasha, 2001). Soil nutrient availability is another limiting factor to consider (Jachmann, 1987) and a factor that is commonly overlooked, specifically by the proponents of elephant culling, is the physiology and

physiognomy of plant species (McShane, 1987; Jachmann, 1987). Different plant species – and plants of that species – have differing reproductive strategies for survival; different growth forms; varying defences to herbivory; different regenerative qualities; differences in forage quality; different responses to fire, low rainfall, frost and drought. Thus, it is important, where possible, that studies of elephant-vegetation interactions take a holistic view of the entire system.

#### Density dependence and duration of exposure

Much of the impact that an elephant population has on its environment is linked to the size of the population and the size of the area that the population inhabits (the population density) (Owen-Smith, 1992; Cumming *et al.*, 1997; Mwathe *et al.*, 1997 in Waithaka, 2003). The larger the population and the greater the population density, the greater will be the effect on the ecosystem (Pamo & Tchamba, 2001). Since much of the damage caused by elephants is cumulative, the duration of exposure is an important factor (Hiscocks, 1999). The longer an area is exposed to the effects of elephants, particularly in high numbers, the greater will be the impact for that area. It thus becomes important to develop a measure that combines both density of elephants and a measure of time over which the region has been exposed to elephants. Such a measure, which could take the form of elephant years (elephant density multiplied by years of exposure), would allow comparison between different systems. The results from the present study showed very little effect of elephants on ECST in Nyati except for the alien invasive *Opuntia ficus-indica*. However, this needs to be viewed in the light of the short period for which elephants have been present and their low density.

The size of the area available to elephants is limited in most cases by fences, which concentrate elephant feeding and prevent natural movement. This increases the likelihood that elephant will drive visible change in a relatively short period of time and fuel the perception that elephants are destructive. It is however important to remember that these are Man-made, un-natural systems which prevent the normal long distance elephant movements that would have created long periods of reduced elephant density and reduced pressure on the habitat.

## CHAPTER 6

### Management Recommendations

---

#### Monitoring at Nyati.

Although the present study detected little effect of the elephants in Nyati, it is expected that the effects of their feeding will be cumulative and monitoring must continue.

Monitoring of the woody component of the vegetation could use the method used in this study, which would ensure that future results are comparable with those presented in the thesis. Monitoring must also incorporate the non-woody component to detect changes brought about by elephants grazing.

Direct observations of elephants should also continue giving two different, but comparable sources of information on the diet of elephants and their effects on the vegetation.

#### Monitoring at Addo Heights

The proposed introduction of elephants to Addo Heights provides an ideal opportunity to study the effects of elephants. In this instance it is important to collect robust pre-release information and this could be done using a transect method similar to that used in this study. A vegetation map should be developed and transects carried out in each vegetation type. In view of the importance of grass in the diet of elephants in Nyati, the non-woody component of the vegetation must be carefully assessed. In addition, botanical reserves (or elephant exclosures) should be created to serve as control sites.

### Prickly pear (*Opuntia ficus-indica*)

The results from the present study indicate that elephants are attracted to stands of prickly pears and will break off cladodes and browse adult plants to the ground. However, because prickly pear can reproduce vegetatively, there is the possibility of regrowth. It is therefore essential that in both Nyati and Addo Heights, stands of prickly pear are visited annually and the extent of regrowth assessed. If regrowth does occur, then another method should be used to destroy the cladodes. The fact that the elephants have eliminated prickly pear in the Main Camp at Addo might suggest that regrowth is unlikely and monitoring unnecessary. However, the density of elephants is lower in Nyati and the browsing pressure on prickly pear may be low enough to allow regrowth.

### Population Density

The maintenance of stable elephant populations, both for conservation and tourism, is a major concern (Ruess & Halter, 1990; Knight *et al.*, 2002). In stark contrast to the Main Camp at Addo, where elephants have driven considerable change to the vegetation, particularly in the vicinity of waterholes, at Nyati, the current elephant population has had little effect. It would be in the Park's best interest to maintain the current population level and to curb reproduction within the population and this is an opportune time to implement contraception.

## References

---

- Alexandre, D. (1977). Role disseminateur des elephants en foret Tai (Cote d'Ivoire). *Terre et Vie*. **32**: 47-72.
- Anderson, J.L. (1994). The Introduction of Elephant into Medium-sized Conservation Areas. *Pachyderm*. **18**: 35-38.
- Annecke, D.P., Karny, M. & Burger, W.A. (1969). Improved biological control of the prickly pear, *Opuntia megacantha*, in South Africa through the use of an insecticide. *Phytophylactica*. **1**: 9-13.
- Annecke, D.P. & Moran, V.C. (1978). Critical reviews of biological pest control in South Africa. 2. The prickly pear, *Opuntia ficus-indica*. *Journal of the Entomological Society of Southern Africa*. **41**: 161-188.
- Archibald, E.E.A. (1955). An ecological survey of the Addo Elephant National Park. *South African Journal of Botany*. **20**: 137-154.
- Barnes, R.F.W. (1982). Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology*. **20**: 123-126.
- Barnes, M. E. (2001). Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments*. **49**: 541-554.
- Bell, R. H. V. (1969). The use of herbaceous layers by grazing ungulates in the Serengeti. In: Watson, A. (ed.) *Animal populations in relation to their food resources. Symposium of the British Ecological Society*. Blackwell, Oxford, pp 111-124.
- Bell, R. H. V. (1971). A grazing system in the Serengeti. *Scientific American*. **225**: 86-93.

- Bell, R. H. V. (1985). Elephants and woodlands – a reply. *Pachyderm*. **5**: 17-18.
- Ben-Shahar, R. (1993). Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*. **65**: 249-256.
- Ben-Shahar, R. (1996). Woodland dynamics under the influence of elephants and fire in northern Botswana. *Vegetatio*. **123**: 153-163.
- Ben-Shahar, R. (1997). Elephants and woodlands in Northern Botswana: How many elephants should there be. *Pachyderm*. **23**: 41-43.
- Ben-Shahar, R. (1999). Elephants and their woodland Habitats in Northern Botswana. *Pachyderm*. **27**: 101-104.
- Birkett, A., Musyoki, C. & Bitok, E. (2000). An ecological assessment of Sweetwaters Rhino Sanctuary. Report to Kenya Wildlife Services. *Unpublished*.
- Blanc, J.J., Barnes, R.F.W., Craig, G.C. Douglas-Hamilton, I., Dublin, H.T., Hart, J.A. & Thouless, C.R. (2005). Changes in elephant numbers in major savanna populations in eastern and southern Africa. *Pachyderm*. **38**: 19-28.
- Boshoff, A., Kerley, G. I. H., Cowling, R. M. & Wilson, S. L. (2001). The potential distributions, and estimated spatial requirements and population sizes, of the medium- to large-sized mammals. *TERU report No 33, University of Port Elizabeth*. Pp 44.
- Boshoff, A., Skead, J. & Kerley, G.I.H. (2002). Elephants in the broader Eastern Cape Province. In *Workshop Proceedings of Elephant conservation and management in the Eastern Cape Province*, ed. G. Kerley, S. Wilson & A. Massey. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa, pp. 3-16.

- Bowland, J.M. & Yeaton, R.I. (1997). Impact of domesticated African elephants *Loxodonta africana* on Natal bushveld. *South African Journal of Wildlife Research*. **27** (2): 31-36.
- Brits, J., van Rooyen, M.W. & van Rooyen, N. (2002). Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*. **40**: 53-60.
- Bromilow, C. (1995). Problem Plants of South Africa. *Briza Publications, Arcadia, South Africa*.
- Buckland, S. T., Borchers, D. L., Johnston, A., Henrys, P. A. & Marques, T. A. (2007). Line transect methods for plant surveys. *Biometrics*. Online Early Articles. *Published online*. [10.1111/j.1541-0420.2007.00798.x](https://doi.org/10.1111/j.1541-0420.2007.00798.x).
- Calef, G.W. (1988). Maximum rate of increase in the African Elephant. *African Journal of Ecology*. **26**: 323-327.
- Caughley, G. (1976). The elephant problem – an alternative hypothesis. *East African Wildlife*. **14**: 265-283.
- Cerling, T. E., Passey, B. H., Ayliffe, L. K., Cook, C. S., Ehleringer, J. R., Harris, J. M., Dhidha, M. B. & Kasiki, S. M. (2004). Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **206**: 367-376.
- Chavez-Ramirez, F., Wang, X., Jones, K., Hewitt, D. & Felker, P. (1997). Ecological Characterization of *Opuntia* clones in South Texas: Implications for Wildlife

- Herbivory and Frugivory. *Journal of the Professional Association for Cactus Development*. **2**: 9-19.
- Child, G. (1968). An ecological survey of northeastern Botswana. *FAO Publishers*. No TA2563, Rome.
- Christenson, B. (1976). Tree utilization by African elephant in Po National Park, Upper Volta. *East African Wildlife Journal*. **14**: 265-283.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rossner, G.E. & Streich, W.J. (2003). The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*. **136**: 14-27.
- Coates-Palgrave, K. (2002). Trees of Southern Africa. *Struik, Cape Town*.
- Codron, J., Lee-Thorp, J., Sponheimer, M., Codron, D., Grant, R.C. & De Rutter, D.J. (2006). Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy*. **87**: 27-34.
- Coetzee, K. & Vlok, J. (2001). Reserve Management Plan for Kwazuka Game Reserve. *Unpublished*.
- Cowling, R.M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. *Bothalia*. **15**: 175-227.
- Cowling, R.M., Kirkwood, D., Midgley, J.J. & Pierce, S.M. (1997). Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone coastal fynbos. *Journal of Vegetation Science*. **8**: 475-488.

- Cowling, R.M. & Kerley, G.I.H. (2002). Impacts of elephants on the flora and vegetation of subtropical thicket in the Eastern Cape Province. In *Workshop Proceedings of Elephant conservation and management in the Eastern Cape Province*, ed. G. Kerley, S. Wilson & A. Massey. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa, pp. 55-72.
- Craig, C.G. (1990). Present population and distribution of elephants in Botswana. In *The future of Botswana's elephants. Proceedings of the Kalahari Conservation Society*, Gaborone, 9-12 November 1990.
- Crawley, M.J. (1983). Herbivory: the dynamics of animal plant interactions. *Blackwell Scientific Publications*. London.
- Croze, H. (1974). The Serona bull problem. 1. The trees. *East African Wildlife Journal*. **12**: 29-47.
- Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M. Ford, A.G., Hovorka, M.D., Johnston, D.S., Kalcounis, M., Mahlangu, Z. & Portfors, C.V.R., (1997). Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science*. **93**: 231-236.
- Damiba, T.E. & Ables, E.D. (1994). Population characteristics and impacts on woody vegetation of elephants on Nazinga Game Ranch, Burkina Faso. *Pachyderm*. **18**: 46-53.
- Dankwerts, J. E., O'Reagain, P. J. & O'Connor, T. G. (1992). Range management in a changing environment: a South African perspective. *Proceedings of Australian Rangeland Society Conference*, Cobar. Unpublished.

- Danquah, E. & Oppong, S.K. (2006). Food plants of forest elephants and their availability in the Kakum Conservation Area, Ghana. *Pachyderm*. **40**: 51-60.
- De Beer, Y., Killian, W., Versfeld, W. & van Aarde, R.J. (2006). Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments*. **64**: 412-421.
- De Kock, G.C. & Aucamp, J.D. (1970). Spineless cactus. The farmer's provision against drought. Agricultural Institute of the Karoo Region, Leaflet No. 37. *Department of Agricultural Technical Services, South Africa*. p11.
- de Longh, H., Tchamba, M., Tamis, W. Van't Zelfde, M. Prins, H., de Haes, H.U., Bauer, H. & Tiawoun, S. (1999). Results of Four Years' Satellite Tracking of Elephants in Northern Cameroon. *Pachyderm*. **27**: 62-65.
- Demeke, Y. & Bekele, A. (2000). Study on the elephants of Mago National Park, Ethiopia. *Pachyderm*. **28**: 32-43.
- Demment, M.W. & Van Soest, P.J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*. **125**: 641-672.
- Douglas-Hamilton, I. (1972). *On the ecology and behaviour of the African elephant*. Unpublished Thesis, Oxford University, Oxford.
- Dublin, H. T. (1986). *Decline of the Mara Woodlands: the Role of Fire and Woodlands*. Ph.D. thesis. Unpublished. The University of British Columbia.
- Dublin, H. T. (1991). Dynamics of the Serengeti-Mara Woodlands: an historical perspective. *Forest and Conservation History*. **35**: 169-178.

- Dublin, H. T. (1995). Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire and other factors. In Sinclair, A.R.E. & Arcese, P. *Serengeti II: Dynamics, management and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Dublin, H. T. (1996). Elephants of the Masai Mara, Kenya: seasonal habitat selection and group size patterns. *Pachyderm*. **22**: 25-35.
- Dublin, H. T. (1997). Chairman's report: African Elephant Specialist Group. *Pachyderm*. **24**: 1-3.
- Dublin, H. T., Sinclair, A. R. E & McGlade, J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti-Mara Woodlands. *Journal of Animal Ecology*. **59**: 1147-1164.
- Dudley, J., Mensah-Ntiamoah, A. & Kpelle, D. (1992). Forest elephants in a rainforest fragment: preliminary findings from a wildlife conservation project in Southern Ghana. *African Journal of Ecology*. **30**: 116-124.
- Eisenberg, J. F. (1981). *The Mammalian Radiations*. University of Chicago Press, Chicago.
- Everard, D.A. (1987). A classification of the subtropical thicket in the Eastern Cape Province, based on syntaxonomic and structural attributes. *South African Journal of Botany*. **53**: 329-340.
- Feer, F. (1995). Morphology of fruits dispersed by African forest elephants. *African Journal of Ecology*. **33**: 279-284.
- Field, C.R. (1971). Elephant ecology in the Queen Elizabeth National Park, Uganda. *East African Wildlife Journal*. **9**: 99-123.

- Field, C.R. & Ross, I. C. (1976). The savanna ecology of Kidepo Valley National Park. II. Feeding ecology of elephant and giraffe. *East African Wildlife Journal*. **14**: 1-16.
- Fisher, F. (2005). Elephants in Cote d'Ivoire – a warning for West African conservation. *Pachyderm*. **38**: 64-75.
- Fogarty, G. & Facelli, J. M. (1999). Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. *Plant Ecology*. **144**: 27-35.
- Ford, A.G. (1987). Changes in vegetation structure and soil conditions in miombo woodland in the Sengwa region, Zimbabwe. MSc Thesis, University of Zimbabwe. *Unpublished*.
- Frankel, O. H., Brown, A. D. H., & Burdon, J. J. (1995). The Conservation of Plant Biodiversity. *Cambridge University Press, Cambridge*.
- Gakami, N. (1996). The impacts of elephant on the vegetation of Samburu National reserve. MPhil thesis, Moi University, Kenya. *Unpublished*.
- Galanti, V., Preatoni, D., Martinoli, A., Wauters, L. A. & Tosi, G. (2006). Space and habitat use of the African elephant in the Tarangire-Manyara ecosystem, Tanzania: Implications for conservation. *Mammalian Biology*. **2**: 99-114.
- Geyer, J.W.C. (1946). A study of the biology and ecology of *Exochumus flavipes* Thunb. (Coccinellidae, Coleoptera). Part I. *Journal of the Entomological Society of South Africa*. **9**: 219-234.
- Geyer, J.W.C. (1947). A study of the biology and ecology of *Exochumus flavipes* Thunb. (Coccinellidae, Coleoptera). Part II. *Journal of the Entomological Society of South Africa*. **10**: 64-108.

- Gibson, D.St.C., Dudley, J. P. Craig, G. C., Haynes, G. & Klimowicz, J. (1996). Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*. **39**: 187-194.
- Gibson, D.St.C., Craig, G.C. & Masogo, R.M. (1998). Trends of the elephant population in northern Botswana from aerial survey data. *Pachyderm*. **25**: 14-27.
- Gillson, L. & Lindsay, K. (2003). Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy*. **6**: 411-419.
- Goodall, J.M. & Naude, D.C. (1997). An ecosystem approach for planning sustainable management of environmental weeds in South Africa. *Agriculture, Ecosystems and Environment*. **68**: 109-123.
- Grant, V. K. & Grant, A. (1971a). Dynamics of clonal microspecies in cholla cactus. *Evolution*. **25**: 144-155.
- Griffith, M. P. (2004). The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *American Journal of Botany*. **91**:1915-1921.
- Groves, R.H. (1991). Control of environmental weeds. *Plant Protection Quarterly*. **6**: 95-98.
- Groves, R. H. & Willis, A. J. (1999). Weeds and loss of native plant biodiversity: some Australian examples. *Australian Journal of Environmental Management*. **6**: 156-163.
- Guldmond, R. A. R., Lehman, E. R., Ferreira, S. M. & van Aarde, R. J. (2005). Elephant numbers in Kafue National Park, Zambia. *Pachyderm*. **39**: 50-56.
- Guy, P.R. (1976). The feeding behaviour of elephant (*Loxodonta africana*) in the Segwa area, Rhodesia. *South African Journal of Wildlife Research*. **6**: 55-63.

- Guy, P. (1989). The influence of elephants and fire on a *Brachystegia-Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology*. **5**: 215-226.
- Hall-Martin, A.J. (1992). Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe*. **35**: 65-88.
- Hall-Martin, A.J. & Barratt, D.G. (2001). The effect of elephants *Loxodonta africana* on thicket vegetation in the Addo Elephant National Park. Internal Report, SANParks. Pretoria. *Unpublished*.
- Hall-Martin, A.J. & van der Walt, P.T. (1979). Conservation Management Plan: Addo Elephant National Park. Internal Report, SANParks, Kimberley. *Unpublished*.
- Hanks, J. 1979. *A struggle for survival: The elephant problem*. Struik, Cape Town.
- Hawthorne, W.D. & Parren, M.P.E. (2000). How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology*. **16**: 133-150.
- Hiscocks, K. (1999). The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe*. **42** (2): 47-55.
- Hoffmann, J.R. (1991). Biological control of weeds in South Africa. *Agriculture Ecosystems & Environment*. **37**: 1-255.
- Hoffmann, M.T. (1989). Vegetation studies and the impact of grazing in the semi-arid Eastern Cape Province. *Unpublished Ph.D thesis*, University of Cape Town.
- Hoffmann, M.T. & Cowling, R.M. (1990). Desertification in the lower Sundays River Valley, South Africa. *Journal of Arid Environments*. **19**: 105-117.

- Hoffmann, M.T., James, C.D., Kerley, G.I.H. & Whitford, W.G. (1993). Rabbit herbivory and its effect on cladode, flower and fruit production of *Opuntia violaceae* var *macrocentra* (Cactaceae) in the northern Chihuahuan Desert, New Mexico. *Southwestern Naturalist*. **38**: 309-315.
- Hoffmann, J.H., Moran, V.C. & Zeller, D.A. (1998). Long-term population studies and the development of an integrated management programme for control of *Opuntia stricta* in Kruger National Park, South Africa. *Journal of Applied Ecology*. **35**,156-160.
- Höft, R. & Höft, M. (1995). The Differential effects of elephants on rain forest communities in the Shimba Hills, Kenya. *Biological Conservation*. **73**: 67-79.
- Holmes, P.M. & Cowling, R.M. (1997). The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology*. **34**: 317-332.
- Hosking, S.G. & du Preez, M. (1999). A cost-benefit analysis of removing alien trees in the Tsitsikamma mountain catchment. *South African Journal of Science*. **95**: 442-446.
- Illius, A.W. & Gorrdon, I.J. (1992). Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia*. **89**: 428-434.
- Jachmann, H. (1985). Estimating age in African elephants. *African Journal of Ecology*. **23**: 199-202.
- Jachmann, H. (1986). Notes on the population dynamics of the Kasungu elephants. *African Journal of Ecology*. **24**: 215-226.
- Jachmann, H. (1987). Elephants and woodlands II. *Pachyderm*. **8**: 11-12.

- Jachmann, H. (1988). Numbers, distribution and movements of the Nazinga elephants. *Pachyderm*. **10**: 16-21.
- Jachmann, H. (1989). Food Selection by Elephants in the Miombo Biome, in Relation to Leaf Chemistry. *Biochemical Systematics and Ecology*. **17**: 15-24.
- Jachmann, H. (1995). Survey experiments and aerial survey of elephants in the South Luangwa National park and the Lupande Game Management Area, Zambia, 1993. *Pachyderm*. **19**: 81-86.
- Jachmann, H. & Bell, R.H.V. (1985). Utilisation by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*. **23**: 245.
- Jarman, P.J. (1974). The social organization of antelope in relation to their ecology. *Behaviour*. **48**: 215-266.
- Johnson, C.F. (1998). *Vulnerability, irreplaceability and reserve selection for the elephant-impacted flora of the Addo Elephant National Park, Eastern Cape Province, South Africa*. Unpublished MSc. Thesis. Rhodes University, Grahamstown.
- Jones, M. A. & Tafangenyasha, C. (1994). Gonarezhou Park Plan, Zimbabwe. Department of National Parks and Wildlife Management, Harare. . *Unpublished Report*.
- Jones, M. & Pillay, N. (2004). Foraging in captive hamadryas baboons: implications for enrichment. *Applied Animal Behaviour Science*. **88**: 101–110.
- Kerley, G.I.H., Knight, M.H. and de Kock, M. (1995). Desertification of subtropical thicket in the Eastern Cape Province, South Africa: are there alternatives? *Environmental Monitoring and Assessment*. **37**: 211-230.

- G. Kerley, S. Wilson & A. Massey. (2001). *Workshop Proceedings of Elephant conservation and management in the Eastern Cape Province*. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa.
- Knight, M.H., Hitchins, P. & Erb, K.P. (1994). An Aerial Survey of Rhinoceros and Elephant in a Portion of the Chobe National Park and Surrounding Areas, Northern Botswana, September 1992. *Pachyderm*. **18**: 64-74.
- Knight, M., Castley, G., Moolman, L. & Adendorff, J. (2002). Elephant Management in Addo Elephant National Park. In *Workshop Proceedings of Elephant conservation and management in the Eastern Cape Province*, ed. G. Kerley, S. Wilson & A. Massey. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa, pp.32-40.
- Legendijk, D.D.G., de Boer, W.F. & van Wieren, S.E. (2005). Can African elephants survive and thrive in monostands of *Colophospermum mopane* woodlands? *Pachyderm*. **39**: 43-49.
- Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1975). *Elephants and their Habitats*. Clarendon Press, Oxford.
- Leggett, K. (2006). Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. *Pachyderm*. **40**: 24-34.
- Lewis, D.M. (1991). Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology*. **29**: 207-221.

- Lindeque, M. (1995). Conservation and management of elephants in Namibia. *Pachyderm*. **19**:49-53.
- Lindsay, W. K. (1982). *Habitat Selection and Social Group Dynamics of African elephants in Amboseli, Kenya*. MSc. thesis. Unpublished. University of British Columbia.
- Lindsay, K. (1993). Elephants and habitats: the need for clear objectives. *Pachyderm*. **16**: 34-40.
- Litoroh, M.W. (2002). Aerial elephant count in the Shimba Hills ecosystem, Kenya. *Pachyderm*. **32**: 55-63.
- Lombard, A.T., Johnson, C.F., Cowling, R.M. & Pressey, R.L. (2001). Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*. **102**: 191-203.
- Low, A.B. & Rebelo, A.G. (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- Lubke, R. A., Everard, D. A. & Jackson, S. (1987). The biomes of the Eastern Cape Province with emphasis on their conservation. *Bothalia*. **16**: 251-261.
- Lubke, R. & de Moor, I. (1998). *Field Guide to the Eastern and Southern Cape Coasts*. University of Cape Town Press. Rondebosch, Cape Town.
- Lubke, R. & van Wijk, Y. (1998). Terrestrial plants and coastal vegetation. In: *Lubke, R. & de Moor, I. (1998). Field Guide to the Eastern and Southern Cape Coasts*. University of Cape Town Press. Rondebosch, Cape Town. pp.289-294.
- Mack, M.C. & D'Antonio, C.M. (1998). Impacts of biological invasions on disturbance regimes. *Trends in Ecological Evolution*. **13**: 195-198.

- Maisels, F., Blake, S. & Turkalo, A. K. (2002). Wild forest elephants shake down fruit and leaves from trees. *Pachyderm*. **33**: 88-90.
- Makhabu, S.W., Skarpe, C. & Hytteborn, H. (2006). Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica*. **30**:136-146.
- Mandujano, M. C. C., Montaña I. & Mendez, L. E. (1996). Reproductive ecology and inbreeding in *Opuntia rastera* (Cactaceae) in the Chihuahuan Desert: why are sexually derived recruitments so rare? *American Journal of Botany*. **83**: 63-70
- Manning, J. (2001). *South African Wild Flower Guide 11*. Eastern Cape Province. Botanical Society of South Africa. Cape Town.
- Marker, M. E. (1991). Environmental variables acting on Valley Bushveld. In Zacharias, P. J. E. & Stuart-Hill, G. C. Proceedings of the First Valley Bushveld/Subtropical thicket Symposium. *Grassland Society of South Africa*, Howick.
- Martin, R. B., Craig, G. C. & Booth, V. R. (1989). *Elephant Management in Zimbabwe*. Internal Report. Department of National Parks and Wildlife Management, Harare. *Unpublished*.
- McKnight, B. L. (2004). Elephant numbers, group structure and movements on privately owned land adjacent to Tsavo East National Park, Kenya. *Pachyderm*. **36**:44-51.
- McNaughton, S. J., Ruess, R. W. & Seagle, S. W. (1988). Large mammals and process dynamics in African ecosystems. *Bioscience*. **38**: 794-800.
- McShane, T. O. (1987). Elephant-fire relationships in *Combretum/Terminalia* woodland in south-west Niger. *African Journal of Ecology*. **25**. 79-94.

- McShane, T.O. (1989). Some Preliminary Results of the Relationship Between Soils and Tree Response to Elephant Damage. *Pachyderm*. **11**:29-32.
- Melton, D.A. (1985). The status of elephants in northern Botswana. *Biological Conservation*. **31**: 317-333.
- Mendelson, S. S. (1999). *The role of thicket herbivores in seed dispersal within restoration sites in Valley Bushveld*. MSc. Thesis. Unpublished. University College, London.
- Midgley, J.J. & Joubert, D. (1991). Mistletoes, their host plants and the effects of browsing by large mammals in Addo Elephant National Park. *Koedoe*. **34**: 149-152.
- Milewski, A.V. (2002). Elephant diet at the edge of the Fynbos Biome, South Africa. *Pachyderm*. **32**: 29-38.
- Morley, R. C. (2006). *The demography of a fragmented population of the savanna elephant (Loxodonta africana) in Maputoland*. PhD thesis, University of Pretoria, Pretoria. Unpublished.
- Moolman, H.J. & Cowling, R.M. 1994. The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation*. **68**: 53 – 61.
- Morrison, J.F. (1984). *Protection from beetle-predation in cochineal insects (Dactylopidae: Homoptera)*. MSc Thesis, Rhodes University, Grahamstown. Unpublished.
- Moss, C.J. 1988. *Elephant Memories*. William Morrow Publishers, New York.
- Moss, C.J. & Poole, J.H. (1983). Relationships and social structure of African elephants. In Hinde, R.A. *Primate Social Relationships: An Integrated Approach*. Blackwell Scientific Publications, Oxford.

- Mpanduji, D.G., Hofer, H., Hilderbrandt, T.B., Goeritz, F. & East, M.L. (2002). Movements of elephants in the Selous-Niassa wildlife corridor, southern Tanzania. *Pachyderm*. **33**: 18-31.
- Mubalama, L. (2000). Population and distribution of Elephants (*Loxodonta africana africana*) in the Central Sector of the Virunga National Park, Eastern DRC. *Pachyderm*. **28**: 44-55.
- Mullet, T. & Simmons, D. (1995). Ecological impacts of the environmental weed sweet pittosporum (*Pittosporum undulatum*) in dry sclerophyll forest communities. *Victoria Plant Protection Quarterly*. **10**: 131-138.
- Muoria, P.K., Gordon, I. & Oguge, N.O. (2001). Elephants as seed dispersal agents in Arabuko-Sokoke Forest, Kenya. *Pachyderm*. **30**: 75-80.
- Mwangi, P.N., Milewski, A. & Wahungu, G.M. (2004). Chemical composition of mineral licks used by elephants in Aberdares National Park, Kenya. *Pachyderm*. **37**: 59-67
- Mwathe, K. (1997). Elephant-habitat studies in Shimba Hills National Reserve. KWS-WWF Report. *Unpublished*.
- Mwathe, K., Mungai, P. & Ngoru, S. (1997). The impacts of confined elephant populations on their habitats. The Mt. Kenya example. KWS Report. *Unpublished*.
- Nagafela, N. V. (1998). Annual report of Kgalagadi District. Internal Report, Department of Wildlife and National Parks, Botswana. *Unpublished*.
- Nordenstam, B. (1969). Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica*. **23**: 1-77.

- Novellie, P., Hall-Martin, A. J. & Joubert, D. (1991). The problem of maintaining large herbivores in small conservation areas: deterioration of the grassveld in the Addo Elephant National Park. *Koedoe*. **34**: 41-50.
- Obot, E., Edet, C., Ogar, G. & Ayuk, J. (2005). Population survey of elephants in Okwangwo Division, Cross River National Park, Nigeria. *Pachyderm*. **38**: 59-63.
- O'Connor, T. G., Goodman, P. S. & Clegg, B. (2007). A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*. **136**: 329-345.
- Ogola, P. O. & Omondi, P. O. (2005). Demography of a confined elephant population and the potential consequence of translocation: the case of Sweetwaters Game Reserve, Kenya. *Pachyderm*. **39**: 57-62.
- Omondi, P., Bitok, E. & Mayienda, R. (2002a). Decline of elephants and other wildlife in the Nasolot-Kamnarok conservation areas, Kenya. *Pachyderm*. **33**: 69-73.
- Omondi, P., Wambwa, E., Gakuya, F., Bitok, E., Ndeere, D., Manyibe, T., Ogola, P. & Kanyingi, J. (2002b). Recent translocation of elephant family units from Sweetwaters Rhino Sanctuary to Meru National Park, Kenya. *Pachyderm*. **32**: 39-48.
- Osborn, F.V. (2002). Elephant-induced change in woody vegetation and its impact on elephant movements out of a protected area in Zimbabwe. *Pachyderm*. **33**: 50-57
- Osborn, F.V. (2005). Habitat selection by bull elephants in central Zimbabwe. *Pachyderm*. **39**: 63-67.
- Owen-Smith, N. (1987). Pleistocene extinctions: the pivotal role of Megaherbivores. *Paleobiology*. **13**: 351-362.

- Owen-Smith, R.N. (1992). *Megaherbivores: The influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Owen-Smith, N. (1993). Woody plants, browsers and tannins in southern African savannas. *South African Journal of Science*. **39**: 128-133.
- Owen-Smith, N. (1996). Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*. **26**: 107-112.
- Padisák, J., Reynolds, C. S. & Sommer, U. (1993). Intermediate disturbance hypothesis in phytoplankton ecology. *Aquatic Botany*. **51**: 341-342.
- Paley, R.G.T. & Kerley, G.I.H. (1998). The winter diet of elephant in Eastern Cape Subtropical Thicket, Addo Elephant National Park. *Koedoe*. **41**: 37-45.
- Pamo, E. T. & Tchamba, M. N. (2001). Elephants and vegetation change in the Sahelo-Soudanian region of Cameroon. *Journal of Arid Environments*. **48**: 243-253.
- Pellew, R.A. (1983). The impact of elephant, giraffe and fire upon the Acacia tortillas woodlands of the Serengeti. *African Journal of Ecology*. **21**: 241-67.
- Penzhorn, B.L., Robertse, P.J., & Olivier, M.C. (1974). The influence of the African elephant on the vegetation of the Addo Elephant National Park. *Koedoe*. **17**: 137-158.
- Pettey, F.W. (1948). The biological control of prickly pears in South Africa. *Scientific Bulletin for the Department of Agriculture and Forests of the Union of South Africa*. **271**: 1-163.
- Phillipson, P. B. (1995). What is the Albany Hotspot? *The Naturalist*. **39**: 14-19.

- Pickup, G. (1994). Modelling patterns of defoliation by grazing animals in rangelands. *Journal of Applied Ecology*. **31**: 231-246.
- Poole, J.H. (1989). Mate, guarding, reproductive success and female choice in African elephants. *Animal Behaviour*. **37**: 842-849.
- Poole, J. H. (1993). Kenya's initiatives in Elephant Fertility Regulation and Population Control Techniques. *Pachyderm*. **16**: 62-65.
- Poole, J. H. (1994). Sex differences in the behaviour of African elephants. In: *The Differences Between the Sexes*. R. Short & E. Balaban (Eds.). Cambridge University Press, Cambridge: pp. 331-346.
- Poole, J. H. & Moss, C.J. (1981). Musth in the African elephant *Loxodonta africana*. *Nature*. **292**: 830-831.
- Pretorius, M.W. (1989). *Cactoblastis* en cochenille op doringlose turksvy. Boerdery in Suid Afrika, Aangeplante weidings en Voergewasse. Report A.3/1989. Government Printer, Pretoria. *Unpublished*.
- Robertson, H.G. (1985). The ecology of *Cactoblastis cactorum* (Lepidoptera: Phycitidae) in relation to its effectiveness as a biological control agent of prickly pear and jointed cactus in South Africa. PhD Thesis, Rhodes University, Grahamstown. *Unpublished*.
- Robertson, H.G. (1988). Spatial and temporal patterns of predation by ants on eggs of *Cactoblastis cactorum*. *Ecology and Entomology*. **13**: 207-214.
- Rose, L.M. (2000). Behavioural sampling in the field: continuous focal versus focal interval sampling. *Behaviour*. **137**: 153-180.

- Ruess, R.W. & Halter, F.L. (1990). The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *African Journal of Ecology*. **28**: 259-75.
- Rust, I.C. (1998). Geology and geomorphology. In: Lubke, R. & de Moor, I. *Field Guide to the Eastern and Southern Cape Coasts*. University of Cape Town Press. Rondebosch, Cape Town. 10.
- Ruthven, D.C., Hellgren, E.C. & Beasom, S.L. (1994). Effects of root plowing on white-tailed deer condition, population, status and diet. *Journal of Wildlife Management*. **58**: 59-70.
- Sam, M.K., Danquah, E., Oppong, S.K. & Bosu, E.D. (2006). Elephant survey in the Bia Conservation Area, western Ghana. *Pachyderm*. **40**: 41-50.
- Scholes, R. J. & Walker, B. H. (1993). *An African Savanna – Synthesis of the Nylsvly Study*. Cambridge University Press, Cambridge.
- Schmitz, D.C. & Simberloff, D. (1997). Biological invasions: a growing threat. *Issues in Science and Technology*. **13**: 33-40.
- Searle, K.R., Vandervelde, T., Thompson Hobbs, N. & Shipley, L.A. (2005). Gain functions for large herbivores: tests of alternative models. *Journal of Animal Ecology*. **74**: 181-189.
- Shannon, G. (2005). *The effects of sexual dimorphism on the movements and foraging ecology of the African elephant*. Unpublished PhD thesis. University of KwaZulu-Natal, Durban.

- Shearing, D. (1997). *South African Wild Flower Guide 6 – Karoo*. Botanical Society of South Africa. Kirstenbosch, Cape Town.
- Short, J. (1981). Diet and feeding behaviour of the forest elephant. *Mammalia*. **45**: 177-185.
- Shoshani, J., Hagos, Y., Yacob, Y., Ghebrehiwet, M. & Kebrom, E. (2004). Elephants (*Loxodonta africana*) of Zoba Gash, Eritrea: Part 2. Numbers and distribution, ecology and behaviour, and fauna and flora in their ecosystem. *Pachyderm*. **36**: 52-68.
- South African National Parks (SANParks), 1997. Draft Management Plan for Addo Elephant National Park. *Unpublished*.
- Spinage, C.A. (1990). Botswana's Problem Elephants. *Pachyderm*. **13**: 14-19.
- Spinage, C.A. (1994). *Elephants*. T and AD Poyser Ltd., United Kingdom.
- Stiling, P., Rossi, A. & Gordon, D. (2000). The difficulties in single factor thinking in restoration: replanting a rare cactus in the Florida Keys. *Biological Conservation*. **94**: 327-333.
- Stirton, C.H. (1983). *Plant invaders: beautiful, but dangerous*. Report by Botanical Research Institute, Department of Agricultural Technical Services, Cape Town. *Unpublished*.
- Stokke, S. & du Toit, J. (2000). Sex and size-related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*. **23**: 70-80.
- Stuart-Hill, G.C. (1991). Elephants, the rightful conservators of the Valley Bushveld. *Veld and Flora*. **77**: 9-11.

- Stuart-Hill, G.C. (1992). Effects of elephants and goats on the Kaffrarian succulent thicket of the Eastern Cape Province, South Africa. *Journal of Applied Ecology*. **29**: 699-710.
- Stuart-Hill, G.E. & Danckwerts, J.E. (1988). Influence of domestic and wild animals on the future of Succulent Valley Bushveld. *Pelea*. **7**: 45-56.
- Tafangenyasha, C. (1997). Tree loss in the Gonarezhou National Park, Zimbabwe. *Journal of Environmental Management*. **49**: 355-366.
- Tafangenyasha, C. (2001). Decline of the mountain acacia *Brachystegia glaucescens* in Gonarezhou National Park, southeast Zimbabwe. *Journal of Environmental Management*. **63**: 37-50.
- Tchamba, M.N. (1993). Number and Migration Patterns of Savanna Elephants (*Loxodonta africana africana*) in Northern Cameroon. *Pachyderm*. **16**: 66-71.
- Tchamba, M. & Mahamat, H. (1992). Effects of elephant browsing on the vegetation in Kalamaloue National Park, Cameroon. *Mammalia*. **92**: 35-42.
- Tegegne, F., Kijora, C. & Peters, K. J. (2005). Cactus pear (*Opuntia ficus-indica*): A strategic crop in combating food and feed insecurity and desertification in Tigray, Northern Ethiopia. *Proceedings of the Society for Nutritional Physiology*. **14**: p 60
- Theimer, T. C. & Bateman, G. C. (1992). Patterns of prickly pear herbivory by collared peccaries. *Journal of Wildlife Management*. **56**: 234-240.
- Theuerkauf, J., Ellenberg, H., Waitkuwait, W. E. & Mühlenberg, M. (2001). Forest elephant distribution and habitat use in the Bossematié Forest Reserve, Ivory Coast. *Pachyderm*. **30**: 37-45.

- Thomson, P.J. (1975). The role of elephants, fire and other agents in the decline of *Brachystegia boehmii* woodland. *Journal of the Southern African Wildlife Management Association*. **51**: 11-18.
- Thouless, C.R. (1995). Long distance movements of elephants in Northern Kenya. *African Journal of Ecology*. **33**: 321-334.
- Thouless, C. R. & Dyer, A. (1992). Radiotracking of elephants in Laikipia District, Kenya. *Pachyderm*. **15**: 34-39.
- Tinley, K.L. (1975). Habitat physiognomy, structure and relationships. *University of Pretoria Publications New Series*. **97**: 67-77.
- Trollope, S. (1931). *Ranger's report on the Addo Elephant National Park, 1<sup>st</sup> November, 1931*. Internal report, National Parks Board, Pretoria. *Unpublished*.
- Turkalo, A. & Fay, J.M. (1996). Studying forest elephants by direct observation. *Pachyderm*. **21**: 45-54.
- Urquhart, C. & Klages, N. (1997). *Addo – more than just elephants*. Bluecliff Publishing.
- Usongo, L. (2003). Preliminary results on movements of a radio-collared elephant in Lobeke National Park, south-east Cameroon. *Pachyderm*. **34**: 53-58
- van Aarde, R.J. & Skinner, J.D. (1975). The food and feeding behaviour of the giraffe *Giraffa camelopardis* in the Jack Scott Nature Reserve. *Publications of the University of Pretoria. New Series*. **97**: 59-68.
- Van Jaarsveld, E. (1987). The succulent riches of South Africa and Namibia. *Aloe*. **24**: 45-92.

- Vanderplank, H.J. (1999). *Wildflowers of the Port Elizabeth Area: Gamtoos to Swartkops Rivers*. Bluecliff Publishing. South Africa.
- Van Oudtshoorn, F. (1999). *Guide to grasses of Southern Africa*. Briza Publications. Pretoria, South Africa.
- Van Soest, P.J. (1996). Allometry and ecology of feeding behaviour and digestive capacity of herbivores: a review. *Zoo Biology*. **15**: 455-479
- Van Wyk, P. & Fairall, N. (1969). The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*. **12**: 57-89.
- Viljoen, P.J. (1989). Habitat selection and preferred food plants of a desert dwelling elephant population in the northern Namib Desert, SWA/Namibia. *African Journal of Ecology*. **27**: 227-240.
- Vitousek, P.M. (1990). Biological invasions and ecosystem processes – towards an integration of population biology and ecosystem studies. *Oikos*. **57**: 7-13.
- Vlok, J.H.J., Euston-Brown, D.I.W. & Cowling, R.M. (2003). Acock's Valley Bushveld 50 years on: new perspectives on the delimitation, characterisation and origin of subtropical thicket vegetation. *South African Journal of Botany*. **69**: 27-51.
- Von Maltitz, G. P. (1991). Spekboom dynamics. In; *Proceedings of the First Valley Bushveld/Subtropical Thicket Symposium*. (eds: P. J. K. Zacharias & G. C. Stuart-Hill) Grassland Society of Southern Africa, Howick.
- Waithaka, J. (1993). The impact of Elephant Density on Biodiversity in Different Ecoclimatic Zones in Kenya. *Pachyderm*. **16**: 86-95.

- Waithaka, J. (1997). Management of elephant populations in Kenya – what have we learnt so far? *Pachyderm*. **24**: 33-36.
- Waithaka, J. (2001). Elephants as seed dispersal agents in Aberdare and Tsavo National Parks, Kenya. *Pachyderm*. **30**: 70-74.
- Waithaka, J. (2003). The Impact of Elephant Density on Biodiversity in Different Ecoclimatic Zones in Kenya. *Pachyderm*. **16**: 86-87.
- Walker, B. (1989). Diversity and stability in ecosystem conservation. In *Western, D. & Pearl, M. (Eds.). (1989). Conservation for the 21<sup>st</sup> Century*. Oxford University Press, Oxford. Pp 121-130.
- Walker, B. & Steffen, W. (1997). An overview of the implications of global change for natural and managed terrestrial ecosystems. 1, URL: <http://www.consecol.org/voll/iss2/art2>.
- Western, D. (1987). Africa's elephants and rhinos: flagships in crisis. *Trends of Ecological Evolution*. **2**: 343-346.
- Western, D. (1990). The Ecological Role of Elephants in Africa. *Pachyderm*. **12**: 42-45.
- Western, D. & Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant herd population. *African Journal of Ecology*. **22**: 229-244.
- White, L. J. T., Caroline, E., Tutin, G. & Fernandez, M. (1993). Group composition and diet of forest elephants *Loxodonta africana cyclotis* in the Lope Reserve, Gabon. *African Journal of Ecology*. **31**: 181-199.
- Whitehouse, A.M. (2001). *The Addo Elephants: conservation biology of a small, closed population*. PhD thesis, University of Port Elizabeth, Port Elizabeth.

- Whitehouse, A.M. (2002). The Addo population: population history and present status. In *Workshop Proceedings of Elephant conservation and management in the Eastern Cape Province*, ed. G. Kerley, S. Wilson & A. Massey. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa, pp. 16-19.
- Whitehouse, A. & Hall-Martin, A.J. (2000). Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. *Oryx*. **34**: 46-55.
- Whitehouse, A. & Irwin, P. (2002). *A field guide to the Addo Elephants*. Rhodes University Environmental Education Unit.
- Whyte, I. J. (2004). Ecological basis of the new elephant management policy for Kruger National Park and expected outcomes. *Pachyderm*. **36**: 99-108.
- Wiemeler, P. (1988). Nutzungsmöglichkeiten von *Opuntia ficus-indica*. Miller im Raum Uitenhage, Sudafrica. Thesis, Justus Liebig University, Giessen. *Unpublished*.
- Willis, A.J. & Memmott, J. (2005). The potential for indirect effects between a weed, one of its biocontrol agents and native herbivores: A food web approach. *Biological Control*. **35**: 299-306.
- Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*. **69**: 1357-1371.
- Woods, K.D. (1993). Effects of invasion by *Lonicera tatarica* on herbs and tree seedlings in 4 New-England forests. *American Midland Naturalist*. **130**: 62-74.
- Zacharias, P. J. E. & Stuart-Hill, G. C. (1991). *Proceedings of the First Valley Bushveld/Subtropical thicket Symposium*. Grassland Society of South Africa, Howick.

- Zimmermann, H.G. (1981). *The ecology and control of Opuntia aurantiaca in South Africa in relation to the cochineal insect Dactylopius austrinus*. PhD Thesis. Rhodes University, Grahamstown. *Unpublished*. Pp 154.
- Zimmermann, H.G. (1989). Control of Prickly Pear. Farming in South Africa. *Weeds B.1.1/1989*. Government Printer, Pretoria, 2pp.
- Zimmermann, H.G. & Moran, V.C. (1991). Biological control of prickly pear, *Opuntia ficus-indica* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment*. **37**: 29-35.
- Zimmerman, H.G., Moran, V.C. & Hoffmann, J.H. (2001). The renowned Cactus moth *Cactoblastis cactorum* (Lepidoptera: Pyralidae): its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Florida Entomologist*. **84**: 543-551.

## APPENDICES

**Appendix 1:** Plant list of species sampled on the transects, per site.

<u>Plant species</u>	<u>Nyati</u>	<u>Nyati Control</u>	<u>Addo Heights</u>
<i>Acacia karroo</i>	yes	yes	yes
<i>Aloe ferox</i>	yes	yes	yes
<i>Aloe longistyla</i>	no	no	yes
<i>Anacampseros arachnoides</i>	yes	no	no
<i>Aristida congesta</i>	no	no	yes
<i>Aristida adscensionis</i>	yes	no	yes
<i>Andropogon eucomus</i>	no	no	yes
<i>Asparagus capensis</i>	yes	yes	yes
<i>Asparagus mucronatus</i>	yes	yes	yes
<i>Asparagus retrofractus</i>	yes	no	yes
<i>Atriplex semibaccata</i>	yes	yes	yes
<i>Azima tetracantha</i>	yes	yes	no
<i>Carissa bispinosa</i>	yes	yes	yes
<i>Carissa macrocarpa</i>	yes	no	no
<i>Carpobrotus deliciosus</i>	yes	yes	no
<i>Cenchrus ciliaris</i>	yes	yes	yes
<i>Chloris virgata</i>	yes	yes	yes
<i>Chrysocoma ciliata</i>	yes	yes	yes
<i>Crassula obovatum</i>	no	no	yes
<i>Cussonia spicata</i>	no	no	yes
<i>Cymbopogon plurinodis</i>	yes	yes	no
<i>Cynodon dactylon</i>	yes	yes	yes
<i>Digitaria eriantha</i>	yes	yes	yes
<i>Diospyros simii</i>	yes	yes	no
<i>Ehrharta calycina</i>	yes	yes	yes
<i>Eragrostis aethiopica</i>	yes	no	yes
<i>Eragrostis capensis</i>	yes	yes	no
<i>Eragrostis curvula</i>	yes	yes	yes
<i>Eragrostis habrantha</i>	no	no	yes
<i>Eriocephalus ericoides</i>	yes	yes	yes
<i>Euclea undulata</i>	yes	yes	yes

<i>Euphorbia grandidens</i>	no	no	yes
<i>Euphorbia mauritannica</i>	no	yes	no
<i>Fingerhuthia africana</i>	yes	yes	no
<i>Grewia occidentalis</i>	yes	yes	no
<i>Heteropogon contortus</i>	no	no	yes
<i>Hyparrhenia hirta</i>	yes	yes	no
<i>Hypoestes aristata</i>	yes	yes	no
<i>Lycium cinereum</i>	yes	no	no
<i>Lycium ferosissimum</i>	no	no	yes
<i>Maytenus heterophyllus</i>	yes	yes	no
<i>Merxmuellera disticha</i>	no	no	yes
<i>Mesembryanthemum aitonis</i>	yes	yes	yes
<i>Olea africana</i>	yes	no	yes
<i>Opuntia aurantiaca</i>	yes	yes	no
<i>Opuntia ficus-indica</i>	yes	yes	yes
<i>Opuntia imbricata</i>	no	yes	no
<i>Oxalis smithiana</i>	yes	yes	no
<i>Panicum ecklonii</i>	yes	no	no
<i>Panicum maximum</i>	yes	no	yes
<i>Panicum schinzii</i>	yes	no	no
<i>Pappea capensis</i>	yes	yes	yes
<i>Pennisetum setaceum</i>	yes	no	yes
<i>Pentzia incana</i>	yes	yes	no
<i>Phragmites australis</i>	yes	yes	no
<i>Plumbago auriculata</i>	yes	yes	no
<i>Portulacaria afra</i>	no	no	yes
<i>Psilocaulon junceum</i>	no	no	yes
<i>Ptaeroxylon obliquum</i>	yes	yes	no
<i>Pteronia glauca</i>	yes	yes	no
<i>Rhigozum obovatum</i>	yes	yes	yes
<i>Ruschia sp.</i>	yes	yes	yes
<i>Putterlickia pyracantha</i>	yes	yes	yes
<i>Rhus undulata</i>	yes	yes	yes
<i>Schotia afra</i>	yes	yes	yes
<i>Senecio sp.</i>	yes	yes	yes
<i>Setaria verticillata</i>	yes	no	yes
<i>Sideroxylon inerme</i>	yes	yes	no

<i>Sporobolus africanus</i>	yes	yes	yes
<i>Sporobolus fimbriatus</i>	yes	yes	yes
<i>Stipagrostis obtusa</i>	yes	no	yes
<i>Themeda triandra</i>	yes	yes	yes
<i>Tribolium uniolae</i>	yes	no	yes
<i>Tristachya leucothrix</i>	yes	no	yes
<i>Viscum rotundifolium</i>	yes	no	no

---