MEGAHERBIVORES IN SUCCULENT THICKET: RESOURCE USE AND IMPLICATIONS

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This study aims to develop a predictive understanding of the resource use, impacts and interactions of elephant *Loxodonta africana* and black rhinoceros *Diceros bicornis* in the succulent thickets of the Eastern Cape, South Africa. While these megaherbivores typically dominate the biomass, elephant are more abundant, such that their impacts off-set that of all other herbivores. Consequently, this thesis has three main foci: first, developing a mechanistic understanding of the influences of elephant; second, developing predictive insights into elephant impacts on plant communities; finally, an understanding of the knock-on-effects of the impacts for coexisting rhinoceros. Thus, by documenting the diet and dietary preferences of elephant, I firstly show that only about 18% of the species previously thought vulnerable to herbivory, occur in the diet. This refutes the generally held belief that elephant herbivory is the primary driver of decline among plants, and emphasizes the likely contribution of other mechanisms (e.g. trampling, knock-on-effects, etc.). Thus, the accurate prediction of the impacts caused by elephant requires an understanding of previously marginalized mechanisms. From here, I quantify >50 years of impacts on the thicket shrub community and test their spatial and temporal extent near water. I confirm the vulnerability of thicket to transformation (particularly near water) as the accumulated influences of elephant reduce community composition and structure, and predict that these impacts will eventually bring about landscape-level degradation and a significant loss of biodiversity. Importantly, results show an uneven distribution of effects between elements of this community: from community composition and structure, to the structure of individual canopy species and ecological functioning. While these findings confound our interpretation of the extent of the impacts, it demonstrates the importance of explicitly recognizing biodiversity and heterogeneity for the conservation management of elephant. Finally, I test the consequences of the impacts for coexisting rhinoceros. While I show that this causes rhinoceros to change their foraging strategies in the presence of elephant at high densities, I also show that elephant may facilitate access to food for rhinoceros at reduced densities. These findings indicate the importance of elephant in driving the structure and composition of the thicket shrub community and the consequences of this for coexisting large herbivores. Thus, developing a predictive understanding of the spatial and temporal variations of elephant impacts between elements of biodiversity and the mechanisms driving these changes are key to their management. This implies that the effective conservation management of elephant can only be achieved through the careful, scientific design of monitoring programmes.
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*I never did a day's work in my life. It was all fun.*

Thomas E. Edison
CHAPTER ONE

General Introduction

The ecological importance of a species is often dependent on body size, particularly as this determines both the relative use and transfer of energy (Peters 1983; Schmidt-Nielsen 1984). In African large herbivore assemblages, megaherbivores (i.e. species weighing > 1000 kg as adults, comprising elephant *Loxodonta africana*, rhinoceroses *Diceros bicornis* and *Ceratotherium simum*, hippopotamus *Hippopotamus amphibius* and giraffe *Giraffa camelopardalis*) typically dominate the biomass and utilize the greatest share of the available resources through their enhanced tolerance of lower-quality food (Owen-Smith 1988). Consequently, they are considered a separate trophic guild that play a key role in the abundance and structure of herbivore communities (Fritz 1997; Fritz et al. 2002, 2011), and hence ecosystem functioning (*sensu* Duffy et al. 2007). Specifically, at high densities megaherbivores monopolize resources and limit herbivore abundances through competition, while at low densities these herbivores are unable to compensate fully (Fritz 1997; Fritz et al. 2002). These trophic interactions are particularly significant for elephant and mediated mostly by powerful effects on vegetation structure and composition; the latter exceeding that of other large herbivores in both magnitude and extent (Owen-Smith 1988; Kerley et al. 2008). However, despite the key role of megaherbivores in shaping the composition and structure of ecological systems, our understanding of their interactions with resources and each other is surprisingly poor. This often reflects a lack of information, such that these interactions are readily inferred by virtue of the features of megaherbivores. In the case of black rhinoceros, for example, there exists little more than a few handfuls of published records of their diet (e.g. Hall-Martin et al. 1982; Ganqa et al. 2005; Parker et al. 2009; Van Lieverloo et al. 2009; Buk & Knight 2010) and even fewer of their influences on plants (Birkett 2002; Heilmann et al. 2006; Luske et al. 2009). Where extensive records exist (e.g. the effects of elephant on plant communities – reviewed in Owen-Smith 1988, Conybeare 2004, Skarpe et al. 2004, Kerley & Landman 2006, Kerley et al. 2008), our understanding is confounded as the emphasis is on descriptive studies with little predictive power. Amongst the megaherbivores there exists a particular need to develop such predictive insights for elephant, as they are often the most abundant and influence a greater range of ecological patterns and processes through robust impacts (Kerley & Landman 2006; Kerley et al. 2008).
The notion that elephant influence ecological systems has been part of their scientific study for nearly 60 years (Kerley et al. 2008). The initial focus emerged as local population numbers increased and dense woodlands were converted to open savannas and treeless grasslands - the so-called elephant problem (reviewed in Laws 1970; Caughley 1976). In an attempt to reduce the apparently adverse impacts, early management approaches (e.g. culling, provision of artificial water points; Pienaar 1983) aimed to stabilise populations at levels that were thought to maintain vegetation dynamics, and presumably associated biological diversity (Caughley 1983; Pienaar 1983). However, amid much controversy, these interventions probably achieved little more than detract from the primary objective that was to reduce the impacts (Van Aarde et al. 2006; Van Aarde & Jackson 2007 and references therein). Moreover, there existed only sparse evidence that elephant influenced ecosystems negatively. Cumming et al. (1997) focused new attention on the elephant-biodiversity debate as they demonstrated significant declines in the richness of tall trees, birds, mantises and ants with the conversion of tall miombo woodlands to shrub-thickets – ultimately, the effects intensified at elevated densities, raising both conservation and management concerns.

Developing in parallel to this debate was the understanding that ecosystems are not stable, but rather function across a spatio-temporal hierarchy of patterns and processes (Wu & Loucks 1995; Pickett et al. 1997). Specifically, disturbance is an integral part of these systems that modifies both resilience and resistance (Walker 1989; Gillson et al. 2005). Thus, modern thinking considers elephant a part of biodiversity and their effects fundamental to generating and maintaining this diversity. For these reasons, management focus has shifted from manipulating population numbers to identifying the extent and intensity of the impacts (Whyte et al. 1999; Owen-Smith et al. 2006; Van Aarde et al. 2006). This change brought with it the recognition that elephant influence a range of ecological patterns and processes at various spatial and temporal scales: from the composition and structure of plant and animal communities, to soil resources, litter production and nutrient dispersal (reviewed in Owen-Smith 1988, Conybeare 2004, Skarpe et al. 2004, Kerley & Landman 2006, Kerley et al. 2008). Importantly, elephant often contribute positively to biodiversity by dispersing seeds (Lewis 1987; Cochrane 2003; Babweteera et al. 2007) and nutrients (Paley 1997; Treydte et al. 2007), and creating habitat and foraging opportunities for coexisting fauna (Makhabu et al. 2006; Pringle 2008; Valeix et al. 2011). While concerns of the adverse consequences for vegetation remain a primary focus, it is also recognized that it is not the local severity of such disturbances that is important, but rather the spatial extent (Owen-Smith 1996; Owen-Smith et al. 2006). Thus, it is widely thought that vegetation structure may be homogenised across
landscapes with consequences for ecosystem processes and resilience as seasonal and long-term movements are constrained by fences (created through physical or figurative barriers – Hayward & Kerley 2009; Van Aarde & Jackson 2007) or modified by artificially manipulating the availability of limiting resources (e.g. surface water - Chamaillé-Jammes et al. 2007; Smit et al. 2007; Loarie et al. 2009). However, despite the apparent advances in our understanding of the role of elephant (documented in roughly 270 peer-reviewed studies), there are few empirical studies that specifically address either the spatial or temporal extent of the effects, or demonstrate how this may vary between elements of biodiversity.

Our inability to predict the impacts reflects mostly a lack of long-term quantitative studies (as is the case throughout ecology - Carpenter 2002; Hastings 2004), but also the traditional approach of contrasting communities in the presence and absence of elephant using exclosure treatments. These contrasts show dramatic changes and raise significant concerns: for example, in the Addo Elephant National Park (AENP), South Africa, a roughly 55% decline in plant biomass and the local extinction of plant species at treatments with elephant, necessitated the expansion of the area on several occasions to reduce the impacts (Penzhorn et al. 1974; Moolman & Cowling 1994; Lombard et al. 2001; Kerley & Landman 2006). However, the approach of using exclosure treatments as controls against which to measure the effects, assumes that the changes are due to elephant. While elephant typically dominate herbivore biomass, this assumption may not be realistic due to the presence of other large herbivores, often at high densities (Cowling & Kerley 2002; Kerley & Landman 2006). For example, Odadi et al. (2011) showed that the influences of plains zebra Equus burchelli at increased abundances outweigh that of elephant (at lower abundances) in driving large herbivore community structure. At another level, these contrasts are often used to infer the mechanisms of elephant impact. Specifically, most plant-based studies are used to infer the diet, assuming that declines between treatments are the result of herbivory (Laws 1970; Penzhorn et al. 1974; Midgley & Joubert 1991; Stuart-Hill 1992; Moolman & Cowling 1994; Trollope et al. 1998; Lombard et al. 2001). Knowing the diet, and particularly the food preferences of elephant, may be particularly important as it provides a tool with which to predict the impacts. Thus, for example, preferred items (i.e. items utilized more frequently when alternative foods are available on an equal basis - Johnson 1980) may experience accelerated impacts as they are selectively removed, providing advance warning of the effects. However, the impacts on plant communities are not only a function of elephant food requirements, particularly as more than half of their daily requirements are discarded during feeding (Paley 1997). The assumption that elephant herbivory is the primary driver of
community structure (e.g. Laws 1970; Conybeare 2004; Kerley & Landman 2006; Kerley et al. 2008) has resulted in other mechanisms being understudied. Thus, an urgent need exists to develop predictive insights of the mechanisms of elephant impact on biodiversity and ecosystem functioning to understand the impacts.

Identifying alternative mechanisms of elephant impact may be particularly challenging, given that many of the direct impacts have not been quantified and have a range of potential knock-on effects (Kerley & Landman 2006). Few studies have investigated the consequences of the impacts of elephant for other large herbivores (Kerley et al. 2008). Surprisingly, where this information exists, the emphasis has been on demonstrating that elephant facilitate herbivore access to habitat and increase the availability and quality of food (Owen-Smith 1988; Makhabu et al. 2006; Valeix et al. 2011). This is despite clear evidence that elephant limit herbivore abundances across ecosystems through their ability to monopolise resources (Fritz et al. 2002, 2011; Valeix et al. 2008). Identifying the consequences of such effects for another megaherbivore may be particularly useful as there exists little empirical evidence on how resources are shared within this trophic guild (e.g. Lamprey 1963; Jarman 1971; Leuthold 1978; Makhabu 2005). Furthermore, understanding the role of competition may be particularly important for this guild, which is relatively invulnerable to top-down processes (e.g. predation – except that imposed by man, disease; Owen-Smith 1988, Sinclair et al. 2003).

The fundamental aim of this study was, therefore, to develop a predictive understanding of the resource use, impacts and interactions of megaherbivores using the succulent thickets of the Eastern Cape, South Africa. While elephant and black rhinoceros dominate the biomass in this system, elephant are by far the most abundant and utilise the greatest share of the available resources. Consequently, I focused mostly on the role of elephant as their effects were expected to off-set that of rhinoceros through high population densities. The study was focused exclusively within the succulent thickets of the AENP for four important reasons. First, nearly 90% of South Africa’s elephant populations (but not numbers) are currently confined to small enclosed areas similar to the AENP (in particular the Addo Main Camp section that encloses the majority of the elephant population; Mketeni 2012). Thus, the findings from this study may have wide application in areas where the impacts are known to intensify and accelerate, raising both conservation and management concerns. Second, a review of the effects of elephant on biodiversity in the AENP indicates a clear declining trend at all levels investigated: from soils to plant richness and biomass to insect, bird and large herbivore abundances (Kerley & Landman 2006). In particular, AENP represents the only
example where elephant are driving the extinction of rare and endemic plant taxa (Moolman & Cowling 1994; Lombard et al. 2001). This suggests that managing these effects in succulent thicket is a priority. Third, despite extensive evidence of the consequences of elephant for biodiversity (Conybeare 2004; Skarpe et al. 2004; Kerley & Landman 2006; Kerley et al. 2008), the focus has been on savanna systems that respond strongly to other drivers of ecosystem change (e.g. rainfall variability, fire frequencies, and the impacts of other large herbivores – Dublin et al. 1990; Trollope et al. 1999; Eckhardt et al. 2000; Gillson 2004; Hayward & Zawadzka 2010) and confound our understanding of the role of elephant. In succulent thicket, elephant are the dominant herbivores and principal drivers of ecological patterns and processes (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995). Finally, while most studies on elephant effects are spatially and/or temporally limited (which excludes the possibility of detecting trends), the incremental expansion of the Addo Main Camp section may be used to establish a gradient of effects on the basis of the time the area was utilised. Thus, by substituting space for time and assuming an even distribution of elephant, this provides a unique opportunity to determine broad trends in relation to the intensity of utilization (an approach analogous to that of Barratt & Hall-Martín 1991 and Lombard et al. 2001).

With the above in mind, I tested the following as a series of discreet studies and present these in the form of Chapters (2-5):

In **Chapter Two**, I first document the diet and dietary preferences of elephant to investigate the role of elephant herbivory (as opposed to other mechanisms) in driving the impacts. Specifically, I test the extent of utilization of Important Plants, a group with high conservation value identified by Lombard et al. (2001) as apparently being particularly vulnerable to elephant browsing in the AENP. I argue that because elephant herbivory is assumed the primary mechanism responsible for plant extinction, other mechanisms have been understudied. **Chapters Three and Four** use a 31 year data-set and the incremental expansion of the Addo Main Camp section to develop a long-term perspective of the effects of elephant on the thicket shrub community. In **Chapter Three** I test the localised effects of elephant near water and predict that these show a classic piosphere pattern. With time and increasing elephant numbers this pattern may expand and cause a loss in ecological functioning as the shrub community is gradually transformed. I hypothesize that this pattern can be interpreted in terms of a state-and-transition model and show that elephant have the
ability to expand the alternative grassland-state across the landscape, causing severe transformation. **Chapter Four** expands on nearly 40 years of research in thicket to develop a predictive understanding of the effects of elephant on thicket at a landscape-level, contrasting the impacts between elements of the community; i.e. from community composition and structure, to the structure of individual canopy species. Despite the importance of the canopy shrub community in ecological functioning and resilience and evidence of the impacts of elephant, no clear understanding has emerged regarding its long-term responses to elephant. Neither is it clear how the effects may be distributed within this community, which confound our understanding of the extent of the effects. Finally, in **Chapters Five and Six** I test the consequences of the effects of elephant on plant communities for coexisting large herbivores. Specifically, I expect these effects to limit food availability for browsers, thus increasing the potential for competition (**Chapter Five**). I test this specifically for black rhinoceros by (1) describing the seasonal diet and dietary preferences of elephant and rhinoceros to determine how resources are shared within this guild, (2) assessing the degree of diet separation in relation to the seasonal availability of resources, and (3) contrasting the diet and preferences of rhinoceros in the presence and absence of elephant (using adjacent sites). Finally, I measure the nutritional costs of the predicted shift in resource use in the presence of elephant with faecal quality descriptors and discuss the results in terms of the potential consequences for coexisting megaherbivores in small enclosed areas. However, because it is also likely that elephant may facilitate access to resources for rhinoceros, I finally quantify potential browsing opportunities for rhinoceros along a gradient of elephant utilization (**Chapter Six**). With this I demonstrate the dual role of elephant for rhinoceros foraging in succulent thicket. **Chapter Seven** sums up my understanding of the role of elephant, their interactions with resources and with black rhinoceros and provide pointers for future research directions.

The five central chapters of this thesis have been submitted for publication in journals, and are therefore stand-alone units that follow the style of journal articles.
CHAPTER TWO

Relevance of elephant herbivory as a threat to Important Plants in the Addo Elephant National Park.¹²

INTRODUCTION

Much controversy surrounds the conservation management of southern Africa’s burgeoning elephant *Loxodonta africana* population (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006). While numerous studies document the changes to biodiversity and community structure caused by elephant (reviewed in Conybeare 2004, Kerley & Landman 2006, Kerley *et al.* 2008), the mechanisms driving these changes are rarely determined, poorly understood or simply inferred. Moreover, elephant effects are often associated with many other factors (e.g. rainfall variability, fire frequencies, and the impacts of other large herbivores – Dublin *et al.* 1990; Gillson 2004) that play equally important roles as drivers of community change. Thus, an urgent need exists to develop a predictive understanding of the mechanisms of elephant impact on biodiversity and ecosystem functioning.

Because elephant influence a range of ecological processes, the mechanisms of impact vary considerably: in the succulent thickets of the Addo Elephant National Park (AENP), South Africa, elephant play a key role in 14 of 19 processes identified (Kerley & Landman 2006). Although it is generally assumed that herbivory is the primary driver of community structure (e.g. Laws 1970; Conybeare 2004; Kerley & Landman 2006; Kerley *et al.* 2008), elephant also influence ecosystems through trampling (Plumptre 1994; Kerley *et al.* 1999a), zoochory (Lewis 1987; Cochrane 2003; Babweteera *et al.* 2007) and nutrient cycling (Paley 1997; Treydte *et al.* 2007), all of which may have a range of knock-on effects. For example, Kerley *et al.* (1999a) hypothesized that trampling and path formation may facilitate access to habitat for other herbivores in otherwise impenetrable thicket. Herbivory in the AENP is

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*Author contributions: ML conceived and designed the experiment, performed the experiment, analysed the data and wrote the papers; GIHK and DSS provided guidance during the conception and analyses phases of the experiment, respectively.*
attributed primarily to elephant because they contribute the bulk (c. 80%) of total vertebrate herbivore biomass (South African National Parks Unpublished data), and have been stocked at densities (1.0–4.1 elephants.km$^{-2}$) believed to far exceed ecological carrying capacity (Kerley & Landman 2006). However, this assumption may not be realistic due to the presence of many other large herbivores (e.g. black rhinoceros *Diceros bicornis*, kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus*), often at high densities (Cowling & Kerley 2002). This highlights the need to demonstrate appropriate cause-and-effect relationships when ascribing changing patterns to elephant.

Traditionally, the impact of elephant on the plant communities of the AENP is examined by contrasting elephant-occupied areas with areas that exclude elephant. The effects are striking and significant declines in plant richness, density and biomass have been recorded (reviewed in Kerley & Landman 2006). These plant-based studies are frequently used to infer elephant diet, assuming that such declines are the result of herbivory. As examples, the tree succulent, *Aloe africana*, and the epiphyte, *Viscum rotundifolium*, have long been assumed to be absent from the elephant area due to elephant herbivory (Penzhorn et al. 1974; Midgley & Joubert 1991). Plants assumed most vulnerable to elephant browsing (hereafter collectively termed Important Plants) are the regionally rare and endemic small succulent shrubs and geophytes (Moolman & Cowling 1994; Lombard et al. 2001), which from a conservation perspective, are the most important components of succulent thicket (Cowling & Hilton-Taylor 1994). Thus, Moolman & Cowling (1994) showed that the richness, density and cover of these groups were significantly lower in elephant-browsed sites than exclosures. Moreover, Important Plant richness and abundance decreased exponentially, presumably due to increasing length of exposure to elephant browsing (Lombard et al. 2001).

The assumption that elephant herbivory is responsible for plant extinction in the AENP (Penzhorn et al. 1974; Moolman & Cowling 1994; Lombard et al. 2001) has resulted in other mechanisms being understudied. We argue that these mechanisms should be included in assessments of elephant impact, to predict and manage the effects. We describe the diet and dietary preferences of elephant in succulent thicket to investigate the extent of utilization of Important Plants, and identify the species most vulnerable to local extinction through elephant herbivory. Finally, we distinguish potential alternative mechanisms responsible for the decline of Important Plants.
STUDY AREA

AENP (33°31’S, 25°45’E) is situated 60 km north-east of Port Elizabeth in the Eastern Cape Province, South Africa. At the time of the study (November 2002–June 2003), the majority of the elephant population (c. 380 individuals) was restricted to the Addo Main Camp section (AMC; 120 km²), representing c. 7.5% of the area of the park (Fig. 2.1).

![Map of Addo Elephant National Park](image)

Fig. 2.1 Extent of the Addo Elephant National Park, South Africa, showing the location of the Addo Main Camp section (study area).

The region in which the AENP falls is semi-arid, with 260–530 mm annual rainfall. Mean maximum temperatures are hot in summer (c. 30 °C) and mild in winter (c. 22 °C), with temperatures in excess of 40 °C occurring frequently in summer. AENP is situated in the endemic-rich succulent thicket of the Albany Centre (Van Wyk & Smith 2001). Nearly 70% of AMC is covered with Sundays Thicket, a diverse, dense, thorny and evergreen type, 2–4 m high, and dominated by the tree succulent *Portulacaria afra* (Mucina & Rutherford 2006). Succulent thicket generally comprises a high diversity of growth forms, including succulents, evergreen shrubs, lianas, herbs, geophytes and grasses. Typical co-dominant shrubs and low
trees are *Azima tetracantha*, *Capparis sepiaria*, *Carissa bispinosa*, *Euclea undulata*, *Gymnosporia* spp., *Schotia afra* and *Searsia* spp. Other plant communities present, include Coega Bontveld, Albany Coastal Belt and Albany Alluvial vegetation (Mucina & Rutherford 2006), while some sections comprise large areas of grassland with a high incidence of *Cynodon dactylon*.

**METHODS**

**Microhistological dietary determination**

Elephant diet was determined by the microhistological analysis of faecal material. The technique followed Sparks and Malechek (1968) in assessing the relative proportions of plant fragments from their epidermal characteristics. Accuracies and biases of the technique are outlined in Holechek *et al.* (1982).

Fresh faecal samples were collected opportunistically from family groups during November 2002 (spring), January 2003 (summer), April 2003 (autumn) and June 2003 (winter). Faeces (c. 200 g DM) were oven-dried, ground over a 2 mm screen and stored until analysis. The procedure was modified from McAllister and Bornman (1972) and involved the digestion of faecal samples (c. 5 g DM per sample) in 55% nitric acid for 2 min., followed by the dilution of the mixture and boiling for a further 5 min. Samples were passed through a 250 µm sieve (MacLeod *et al.* 1996) and stored in FAA until analysis. From each faecal sample, two sub-samples were drawn, placed on a gridded microscope slide and the identity of the first 50 identifiable fragments per sub-sample recorded (for a total of 100 fragments per sample).

**Relative food availability**

The relative availability of potential food items for elephant was expressed as estimated plant cover, determined using the canopy line–intercept method (Barbour *et al.* 1987). Twenty 50 m transects were located randomly (based on map references), and in proportion to the occurrence of plant communities in AMC, during spring (November 2002, high rainfall) and winter (June 2003, low rainfall). The occurrence, and hence availability and utilization, of many thicket plants respond primarily to the incidence of rain and frost (Hoffman 1989), and thus the need for the seasonal approach.
Utilization of Important Plants

Lombard et al. (2001) identified 77 Important Plants with high conservation value (i.e. Albany Centre Endemics, Red Data Book species, species rare within the AENP, and indicators of elephant browsing intensity) that are apparently particularly vulnerable to elephant browsing in the AENP. Sixty of these plant species were subsequently observed (the remainder having been either extirpated or reduced to very small populations) within AMC (Lombard et al. 2001), and were therefore considered to be potentially available to elephant. The occurrence of these Important Plants in the diet of elephant was assessed by reference to checklists from Johnson (1998). The analysis included reference to the winter diet of elephant in AMC quantified by Paley and Kerley (1998), and the diet of elephant recently (2003) introduced to the Nyathi concession area (NCA; Fig. 2.1), quantified by Davis (2004). Because elephant have not been present in the NCA since the mid-1900s (Kerley & Landman 2006), all 77 Important Plants were assumed potentially available to elephant at this site.

Data analysis

Elephant diet composition was quantified in terms of plant species and by grouping all species into broad growth form categories (i.e. grasses, woody shrubs, succulents, forbs, lianas, geophytes and epiphytes). Results are reported as mean diet composition ($n = 41$) and mean relative food availability ($n = 40$).

EstiMateS Ver. 8.2 (Colwell 2009) was used to produce an accumulation curve (mean ± SD; 50 randomized iterations) of plant species recorded per faecal sample. The asymptote of this curve was used to assess sampling efficiency. Because the accumulation curve did not reach a steady asymptote (although characterized by small increases in species richness and small SD), total species richness was further estimated using the nonparametric incidence-based coverage estimator (ICE; Foggo et al. 2003). ICE estimates species richness based on the relative proportions of common, infrequent and unique species, respectively.

Principal dietary items (PDI), defined by Petrides (1975) as those foods consumed in the greatest quantities, were identified as the plant species that contributed to more than 2% of the diet of elephant. Plant species and growth forms that were proportionately more frequent in the diet than the available environment were considered preferred, and were estimated by Jacobs’ index (Jacobs 1974):

$$D = (u - a)*(u + a - 2ua)^{-1}$$
where \( u \) is the proportional utilization of the food item and \( a \) is its proportional availability. The index ranges from +1 to -1, where +1 indicates maximum preference and -1 maximum avoidance. Many alternative preference measures (e.g. forage ratio, electivity index) are subject to several limitations (e.g. bias for rare food items, non-linearity) that are minimized by Jacobs’ index (Jacobs 1974; Krebs 1989).

A \( \chi^2 \) goodness-of-fit tested the null hypothesis that growth forms were utilized in proportion to their relative availability (Quinn & Keough 2002). Differences between the relative availability and utilization of plant species and growth forms were further assessed by calculating 95% confidence intervals for the mean utilization of each species and category (Neu et al. 1974). Data were arcsine-transformed to satisfy assumptions of normality (Quinn & Keough 2002). In principle, preference/avoidance is considered significant if the confidence interval does not overlap the relative availability. Following the arguments of Moran (2003), confidence intervals were not adjusted using the sequential Bonferroni correction. Kruskal–Wallis ANOVA on Ranks (Tukeys’ multiple-comparison test) was used to test differences in species richness and abundance between growth form categories.

**RESULTS**

**Relative food availability**

A total of 121 plant species, dominated by woody shrubs (40 spp.) and forbs (27 spp.), were recorded in AMC and considered potentially available to elephant. The observed species richness is considerably less than the 581 vascular plants listed for the area (Johnson 1998), possibly due to the limited sampling effort (sample size and sample period) of the current study relative to the patchy distributions of many plant species. Woody shrubs (39.9%) and grasses (38.5%) contributed the bulk of available food. Eight Important Plants were recorded in AMC during our study; these included *Albuca schoenlandii*, *Asparagus crassicladus*, *Asparagus subulatus*, *Calobota psiloloba*, *Delosperma ecklonis*, *Euphorbia clava*, *Gymnosporia capitata* and *Viscum* sp. We assumed that the relative availability of the remaining Important Plants recorded by Lombard et al. (2001) was less than the minimum (c. 0.01%) recorded for any plant species.

**Diet composition**

The sampling efficiency curve clearly approached an asymptote, with little variation in
dietary information at the upper limit of sampling effort (Fig. 2.2). This confirms that our sample size \( n = 41 \) were adequate to describe the diet of this elephant population.

![Accumulation curve](image)

**Fig. 2.2** Accumulation curve (mean ± SD of 50 randomized iterations) of plant species recorded per elephant faecal sample.

Ninety plant species, from 67 genera and 40 families, were identified in 41 elephant faecal samples (Appendix 2). ICE estimated 104 plant species in the diet after the analysis of these samples, suggesting that up to 14 additional species potentially occur in the diet, but was not encountered because they were particularly rare.

Woody shrubs (47.2%), grasses (34.1%) and succulents (11.4%) contributed the bulk of the diet (Fig. 2.3), being significantly more abundant \( H_6 = 222.75; P < 0.001 \) than forbs (2.7%), geophytes (2.1%), lianas (1.8%) and epiphytes (0.7%). Woody shrubs were also the most diverse group (40 spp.; \( H_6 = 214.87; P < 0.001 \), with geophytes and epiphytes represented by only two species each (Appendix 2). Growth forms were not utilized in proportion to their relative availability \( \chi^2_6 = 33.17; P < 0.001 \), but this deviation could be attributed entirely to epiphytes \( \chi^2_5 = 7.78; P = 0.25 \). Epiphytes were utilized in proportions significantly greater than their relative availability \( P < 0.05 \), and were preferred by elephant \( D = 0.95; \) Fig. 2.3).

Thirteen plant species identified as PDI occurred in 85% of the faecal samples and contributed 66.5% of the diet (Fig. 2.4). Sixty-seven (74%) of the 90 plant species browsed by elephant contributed < 1% each to the diet (Appendix 2). Many may be incidentally
Fig. 2.3 Utilization (mean ± 95% confidence interval; shaded bars) and mean relative availability (clear bars) of growth forms identified in the diet of elephant. Jacobs’ index values (shaded squares) indicate preference ($D > 0$) and avoidance ($D < 0$). Preference/avoidance was considered to be significant if the confidence interval did not overlap with the mean relative availability.

browsed (e.g. lianas and epiphytes) as parts of larger mouthfuls. However, no correlation was observed between the utilization of lianas ($r_s = 0.19; n = 41; P = 0.224$) or epiphytes ($r_s = 0.06; n = 41; P = 0.719$) and their associated host plants, suggesting selection for these groups.

More than 30% of the diet of elephant comprised plant species that were not encountered during the food availability assessments, further suggesting selective foraging. PDI were characterized by grasses (29.8%), woody shrubs (27.4%) and the succulent $P. \text{afra}$ (9.3%). The grass, $C. \text{dactylon}$ (19.6%), was the dominant plant species identified in the diet, followed by $P. \text{afra}$ and the spinescent woody shrub, $C. \text{bispinosa}$ (6.1%). Four PDI ($Eragrostis \text{obtusa}, Searsia \text{longispina}, Putterlickia \text{pyracantha}$ and $Grewia \text{robusta}$) were utilized in proportions significantly greater than their relative availability ($P < 0.05$) and were preferred by elephant ($D > 0$; Fig. 2.4). Woody shrubs dominated the preferred dietary species, with $G. \text{robusta}$ the most preferred PDI ($D = 0.99$; Fig. 2.4).

Elephant avoided 58 (47.9%) of the 121 plant species recorded as potentially available within AMC. Forbs (mainly Asteraceae and Fabaceae) and low-growing succulents mainly
Crassulaceae, Euphorbiaceae and Mesembryanthemaceae) dominated the avoided plants. Six geophytic species (mainly Asphodelaceae and Hyacinthaceae) were avoided.

**Utilization of Important Plants**

Only 10 (c. 17%) of the 60 Important Plants identified as having high conservation value and apparently being particularly vulnerable to elephant browsing occurred in the diet of elephant in AMC (Table 2.1). Davis (2004) identified an additional four species (*Salvia scabra, Euphorbia inermis, Euphorbia ledienii* and *Trichodiadema intonsum*) in the diet of elephant from the recently occupied NCA.

Twelve of the Important Plants utilized were Albany Centre Endemics (Table 2.1). The remaining species was the epiphyte, *Viscum* sp., recognized as an indicator of elephant browsing intensity (Midgley & Joubert 1991); *Bulbine* sp. was included in the analysis because it was one of the few geophytes identified in the diet that (depending on the species) has high conservation value. None of the Important Plants utilized had any Red Data Book status.
Table 2.1 The percentage of Important Plants (mean ± SD) identified in the diet of elephant in the Addo Main Camp section (current study, Paley & Kerley 1998) and Nyathi concession area (Davis 2004).

<table>
<thead>
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<tr>
<td>Woody shrubs</td>
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<tr>
<td>Asparagaceae</td>
<td><em>Asparagus crassiclades</em></td>
<td>ACE</td>
<td>0.50 ± 0.84</td>
<td>0.98 ± 1.17</td>
<td>0.33</td>
<td>-</td>
<td>0.17 ± 0.38</td>
</tr>
<tr>
<td>Asparagaceae</td>
<td><em>Asparagus subulatus</em></td>
<td>ACE</td>
<td>0.26 ± 0.35</td>
<td>1.71 ± 2.12</td>
<td>0.74</td>
<td>-</td>
<td>0.66 ± 1.40</td>
</tr>
<tr>
<td>Celastraceae</td>
<td><em>Gymnosporia capitata</em></td>
<td>ACE</td>
<td>&lt; 0.01 ± 0.03</td>
<td>1.95 ± 2.79</td>
<td>1.00</td>
<td>0.97</td>
<td>0.21 ± 0.57</td>
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<tr>
<td>Euphorbiaceae</td>
<td><em>Jatropha capensis</em></td>
<td>ACE</td>
<td>&lt; 0.01</td>
<td>0.73 ± 1.18</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Lamiaceae</td>
<td><em>Salvia scabra</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Asphodelaceae</td>
<td><em>Aloe africana</em></td>
<td>ACE</td>
<td>&lt; 0.01</td>
<td>0.10 ± 0.30</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td><em>Euphorbia inermis</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.02 ± 0.14</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td><em>Euphorbia ledienii</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.04 ± 0.19</td>
</tr>
<tr>
<td>Mesembryanthemaceae</td>
<td><em>Aptenia haeckeliana</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.56</td>
<td>-</td>
</tr>
<tr>
<td>Forbs</td>
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<td></td>
<td></td>
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<tr>
<td>Asteraceae</td>
<td><em>Senecio linifolius</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.18</td>
<td>0.17 ± 0.38</td>
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<tr>
<td>Geophytes</td>
<td></td>
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<tr>
<td>Asphodelaceae</td>
<td><em>Bulbine sp.</em></td>
<td>Unknown</td>
<td>&lt; 0.01</td>
<td>1.39 ± 2.15</td>
<td>1.00</td>
<td>-</td>
<td>0.11 ± 0.32</td>
</tr>
<tr>
<td>Dracaenaceae</td>
<td><em>Sansevieria aethiopica</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.18</td>
<td>-</td>
</tr>
<tr>
<td>Mesembryanthemaceae</td>
<td><em>Trichodiadema intonsum</em></td>
<td>ACE</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.75 ± 1.45</td>
<td>-</td>
</tr>
<tr>
<td>Epiphytes</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Viscaceae</td>
<td><em>Viscum sp.</em></td>
<td>Indicator sp.</td>
<td>0.02 ± 0.07</td>
<td>0.63 ± 0.86</td>
<td>0.95</td>
<td>-</td>
<td>6.89 ± 5.19</td>
</tr>
</tbody>
</table>

+ significantly preferred; - significantly avoided; ACE = Albany Centre Endemic; Indicator sp. = Indicator of elephant browsing intensity (Midgley & Joubert 1991). Jacobs’ index values indicate preference ($D > 0$) and avoidance ($D < 0$) of Important Plants identified in the current study.
Important Plants contributed 8.5% (current study), 6.9% (Paley & Kerley 1998) and 9.1% (Davis 2004) to the diet, and were dominated by woody shrubs (6.4% – current study), succulents (5.6% – Paley & Kerley 1998) and epiphytes (6.9% – Davis 2004). No single plant family dominated (in terms of either species richness or abundance) the Important Plants identified in the diet. *Aptenia haeckeliana* (5.6%) and *Viscum* sp. (6.9%) were recognized as PDI in AMC (Paley & Kerley 1998) and the NCA (Davis 2004), respectively.

Preference/avoidance of Important Plants identified by Paley & Kerley (1998) and Davis (2004) could not be determined, because we had no corresponding estimates of relative food availability. The current study indicated that Important Plants were utilized (with the exception of *A. crassicladus* and *A. subulatus*) in proportions significantly greater than their relative availability (*P* < 0.05) and may, therefore, be considered to be preferred by elephant (*D* > 0; Table 2.1). *A. crassicladus* and *A. subulatus* were utilized in proportion to their relative availability.

**DISCUSSION**

The large body size, large food volume requirements and robust feeding style of elephant facilitate a broad diet, and 146 plant species (90 spp. – current study; 70 spp. – Paley & Kerley 1998; 104 spp. – Davis 2004) have been identified in their diet in the AENP (AMC and NCA). Thus, elephant herbivory may influence the fate of a large number of plant species (Kerley & Landman 2006), particularly those that are preferred. This provides key insights into the plants that could be monitored to measure elephant effects (see Chapters 3, 4 & 6). However, only 14 of the 77 (c. 18%) Important Plants were encountered in the diet and could therefore be shown to be vulnerable to local extinction through elephant herbivory. An additional 6% of these species were avoided by elephant; i.e. those plant species encountered during the food availability assessments, but not in the diet. Thus, elephant herbivory is unlikely to be driving their status. In total, this represents 23% of the Important Plants for which we have use and/or availability data. The remaining Important Plants that were not encountered in the diet, or during the food availability assessments, may be avoided by elephant, or their availability may have been reduced through either past herbivory or other mechanisms. However, Lombard *et al.* (2001) showed that at least a proportion of these plant species are present in AMC. The limited utilization of Important Plants in the recently occupied NCA (with an abundance of these species), suggests that alternative mechanisms of
elephant impact, not previously recognized (cf. Moolman & Cowling 1994; Lombard et al. 2001), are likely to be responsible for their decline.

Important Plants utilized by elephant contributed a large proportion to their diet (6.9–9.1%) and were dominated by woody shrubs (species richness – current study, Davis 2004) and epiphytes (species abundance – Davis 2004). Although geophytes and low succulents are overrepresented among the Important Plants thought to be vulnerable to elephant browsing (Moolman & Cowling 1994; Lombard et al. 2001), these two categories were underrepresented in the diet. Moolman & Cowling (1994) have shown that geophytes and many low succulents are little affected by elephant herbivory, possibly because of the ephemeral availability or toxicity of some species. In fact, it is thought that elephant, through their large bite size and robust feeding style, promote the vegetative reproduction of many small succulents (especially members of the Crassulaceae – Moolman & Cowling 1994). The disappearance of *A. africana* from the AENP has long been assumed a result of elephant herbivory (Penzhorn et al. 1974). By demonstrating that elephant consume *A. africana*, we provide the first evidence that this assumption might be true. Similarly, Penzhorn et al. (1974) hypothesized that the disappearance of epiphytes from AMC could be a result of preference for either the host or epiphyte. In contrast, our results support Midgley & Joubert’s (1991) suggestion that epiphytes are selected by elephant (rather than the host being selected), possibly due to their high nutritional status.

Identifying alternative mechanisms responsible for the decline of Important Plants is particularly challenging, given that many of the direct impacts (e.g. herbivory, trampling, zoochory and nutrient cycling) have not been quantified and may have a range of knock-on effects (Kerley & Landman 2006). Furthermore, it is likely that no single mechanism will determine the fate of all plants. Although the decline of many Important Plants may not be attributed to herbivory *per se*, selective herbivory by elephant on palatable species changes the composition and structure of plant communities (e.g. Jachmann & Croes 1991). These changes may influence the competitive interactions between plants (Huntly 1991). Elephant are also responsible for extensive trampling and path formation in otherwise impenetrable thicket (Plumptre 1994; Kerley et al. 1999a). Although many Important Plants may be vulnerable to trampling by elephant, the changes in vegetation associated with path formation have a range of knock-on effects, including altering microclimates (Kerley & Landman 2006), and presumably plant physiology. Path formation by elephant may further facilitate access for other herbivores, thereby allowing them the opportunity to encounter plants that
were not previously available, as Kerley et al. (1999a) hypothesized for tortoises that selectively browse on geophytes and succulents.

Although elephant are recognized as having key roles in a range of ecological processes (Kerley & Landman 2006), the mechanisms of elephant impact responsible for the decline and/or loss of Important Plants in the AENP cannot be inferred from available information. An understanding of the knock-on-effects associated with such impacts will be critical to understanding, and possibly predicting, the changes to plant communities and ecosystems caused by elephant. It is only by demonstrating appropriate cause-and-effect relationships between elephant and ecosystem change that we will have confidence in the assumption that elephant are responsible for the observed changes. This is particularly important as more than 20% of succulent thicket flora is endemic to the Eastern Cape (Vlok et al. 2003), and the AENP is the only reserve where plant species are currently vulnerable to global extinction as a result of elephant impacts (Kerley & Landman 2006). In the absence of a predictive understanding, conservation management interventions (which by virtue of involving elephant are costly and attract significant public attention, and even litigation) may fail in their objectives.
CHAPTER THREE

Understanding long-term variations in an elephant piosphere effect to manage impacts

INTRODUCTION

Herbivores influence vegetation dynamics at a range of spatial and temporal scales, with the intensity and heterogeneity of these effects determined by a spatio-temporal hierarchy of foraging decisions. At a landscape scale, foraging decisions made at finer-scales are constrained by both biotic and abiotic factors, including proximity to water, topography and the availability and quality of food (Senft et al. 1987). For elephant *Loxodonta africana*, surface water availability is a key limiting resource that influences population dynamics, movement and range-use patterns (Chamaillé-Jammes et al. 2007; Smit et al. 2007; Loarie et al. 2009), and hence impacts on biological diversity. Consequently, much of the debate around managing the impacts of southern Africa’s elephant population has focused on the management of surface water, particularly when supplemented (e.g. through boreholes) away from natural permanent water (Owen-Smith et al. 2006; Van Aarde et al. 2006). Where elephant movements are modified by the provision of artificial water points (Smit et al. 2007; Loarie et al. 2009), effects on vegetation dynamics become more widespread, and intensify in areas that previously functioned as seasonal refuges for plant regeneration (Owen-Smith 1996). Conservation areas with abundant water supply and elevated elephant numbers are therefore vulnerable to degradation as the utilization gradients that develop around water coalesce and vegetation structure is homogenized across the landscape (Owen-Smith 1996; Pickup et al. 1998; Gaylard et al. 2003). These changes have severe implications for other herbivores (e.g. Walker et al. 1987; Grant et al. 2002) and presumably other elements of biodiversity, with consequences for ecosystem processes and resilience (Owen-Smith 1996). Thus, developing a predictive understanding of the spatial and temporal variations of elephant impacts in relation to water is key to managing these impacts. This comes at a time


Author contributions: ML conceived and designed the experiment, performed the experiment, analysed the data and wrote the paper; GIHK, AJH and DSS provided guidance during the conception and analyses phases of the experiment.
when conservation managers use water availability as a tool to manipulate elephant
distributions in an attempt to maintain landscape heterogeneity (Pienaar et al. 1997; Gaylard
et al. 2003; Owen-Smith et al. 2006).

The (foraging and trampling) impacts of herbivores on vegetation dynamics and soil
resources in relation to water, creating a piosphere effect (i.e. a radial pattern of attenuating
impact), are well documented, particularly for rangelands (reviewed in James et al. 1999).
Descriptive models of these spatial patterns are expected to show sigmoid responses, which
are intuitively attractive as tools to estimate the extent of the piosphere effect (on the basis of
the distance from water at which the asymptote of the curve is reached), and thus to
determine the location of water points (allowing for areas of imperceptible impacts) across
the landscape (Graetz & Ludwig 1978; Thrash & Derry 1999). For herbaceous communities
these distances vary with rainfall, herbivore numbers and the proximity of neighbouring
watering points (e.g. Parker & Witkowski 1999; Thrash 2000), but this has not been tested for
woody communities that may be less dynamic; neither is it clear how the extent of the
piosphere effect contrasts between communities or features within a community (e.g. biomass
vs. abundance) that may differ in their sensitivity to impacts. Our understanding of these
variations is confounded by a lack of long-term quantitative studies on spatio-temporal
variations in piospheres (e.g. Adler & Hall 2005), while conceptual models were developed
for open (i.e. non-fenced) rangelands (Graetz & Ludwig 1978). In these systems, sigmoid
models are expected to show increasing displacement of asymptotes away from water (allied
with declining curve steepness) as the piosphere pattern expands with continuous utilization
(Graetz & Ludwig 1978; Pickup et al. 1998). However, many wildlife systems, and
particularly those with elephant, are more complex (i.e. fenced, multiple water points,
seasonal water availability, varying population densities) such that the predicted spatio-
temporal variations may not always hold (Chamaillé-Jammes et al. 2009), thus questioning
the reliability of these models as management tools.

Despite the documented changes in vegetation structure and dynamics caused by
elephant (reviewed in Kerley et al. 2008) and the fact that these impacts intensify near water
(e.g. Mosugelo et al. 2002; Chamaillé-Jammes et al. 2007, 2009; Loarie et al. 2009), elephant
piosphere effects are poorly described or simply inferred. Moreover, these descriptions are
largely restricted to savanna habitats and most focus on herbaceous communities that appear
to be resilient to impacts (e.g. Thrash 1998; Parker & Witkowski 1999; Thrash 2000); these
communities also respond strongly to other environmental drivers (e.g. drought, rainfall
variability), such that our understanding of the impacts may be confounded (Kerley et al.
2008; Chapter 2). Thus, despite concerns that vegetation structure may be homogenized across landscapes with consequences for ecosystem processes, few studies (Thrash et al. 1991; Brits et al. 2002; Mosugelo et al. 2002; Chamaillé-Jammes et al. 2009; Smith 2012) have considered the components of the vegetation that are likely to show long-term responses (i.e. woody shrubs and trees) and are vulnerable to elephant effects. This highlights the need to demonstrate elephant piosphere effects across a range of habitats, focusing on the woody components.

Using 31 years of data on shrub structure in the succulent thickets of the Addo Elephant National Park, South Africa, we test spatial and temporal variations in elephant impacts at a single water point. We predict that shrub structure increases rapidly to an asymptote with distance from water, a classic piosphere effect, but that the extent of the effect varies depending on the sensitivity of the structural feature to elephant impacts (Graetz & Ludwig 1978). With time and increasing elephant numbers, we expect the piosphere effect to expand (characterized by an increasing displacement of asymptotes away from water and declining curve steepness - Graetz & Ludwig 1978; Pickup et al. 1998) as the shrub community is gradually replaced with a community of grasses. Because shrub structure is important for ecological functioning (sensu Ludwig et al. 1997) in succulent thicket (Kerley et al. 1999b; Lechmere-Oertel et al. 2005a), this change would be expected to cause a loss in functionality, particularly in areas adjacent to water. We hypothesize that this pattern can be interpreted in terms of a state-and-transition model and show that elephant have the ability to expand the grassland-state across the landscape, causing severe transformation. Finally, we argue that in fenced areas (created through physical or figurative barriers – Hayward & Kerley 2009) with abundant water supply, elephant piosphere effects are complex, which in the absence of long-term data and careful, scientific design of monitoring programmes limits our ability to predict and manage these impacts.

STUDY AREA

Addo Elephant National Park (33°31’S, 25°45’E) is located in the Eastern Cape Province, South Africa (Fig. 3.1). The park comprises several fenced sections with the majority of the elephant population confined to the Addo Main Camp section (AMC; 120 km² at the time of the study). AMC was originally fenced in 1954 (23.3 km²) to enclose the elephant of the region and incrementally expanded to accommodate growing numbers (from 22 individuals in 1954 to 384 in 2008; Kerley & Landman 2006). The area also supports a
diverse ungulate community (12 spp.), but elephant contribute the bulk (c. 80%) of herbivore biomass (South African National Parks Unpublished data).

The region is semi-arid with 260-530 mm rainfall annually, spread throughout the year, with small peaks in spring and autumn. Because no natural permanent surface water is available in AMC, a large number of artificial water points (pumped point sources) were established (from 6 in 1954 to a total of 12 in 2008; Fig. 3.1). The terrain comprises a series of low, undulating hills (60-350 m in height) in the Sundays River valley, where nutrient-rich soils give rise to succulent thicket habitats (Mucina & Rutherford 2006). Herbivory is
considered the key driver of thicket structure, with rainfall and fire playing relatively minor roles (Kerley et al. 1995). These thickets are typically evergreen, 2-4 m high, dense and characterized by a high diversity of growth forms (Mucina & Rutherford 2006). The tree succulent *Portulacaria afra* is locally dominant and occurs in a matrix of spinescent shrubs (e.g. *Azima tetracantha*, *Capparis sepiaria*, *Carissa bispinosa*, *Gymnosporia* spp., *Searsia* spp.) and low trees (e.g. *Euclea undulata*, *Schotia afra*, *Sideroxylon inerme*). Although grasses are usually sparse (Stuart-Hill & Aucamp 1993), couch grass *Cynodon dactylon* may be seasonally abundant where intensive utilization by elephant has removed the canopy shrubs.

**METHODS**

**Vegetation structure**

We measured the composition and structure (defined in terms of shrub volumes and densities) of the thicket shrub community along seven experimental plots located at increasing distances (100, 200, 300, 500, 1000, 1500 and 3000 m) from Hapoor water point in the area of AMC originally fenced in 1954 (Fig. 3.1). Hapoor represents one of only two water points that have maintained water availability for elephant since the initial fencing. Plots were permanently marked in 1977, when they were first surveyed, with further monitoring in 1981, 1989 and 2008 (providing temporal coverage of 31 years). Thus, the sampled plots experienced 23-54 years of elephant use over the experimental period, at a time when densities fluctuated between 1.0 and 4.1 elephant km\(^{-2}\). Since succulent thicket is an aseasonal habitat with an evergreen shrub community (Stuart-Hill & Aucamp 1993), we did not consider any seasonal variations in elephant effects.

Plots were 5 m wide, while plot length (17-45 m) scaled inversely with the abundance of the dominant shrub taxa. We estimated the volume (m\(^3\).m\(^{-2}\)) of all canopy shrubs (24 spp.: 5 succulents, 19 woody shrubs) encountered by measuring the maximum height and canopy diameters of individual plants. Because most shrubs are multi-stemmed re-sprouters, stems within 50 cm of each other at ground-level were considered to be of the same individual. Individuals were measured if at least half the rooted area occurred within the plot. We calculated shrub density as the number of individuals per unit area.
Ecological functioning

According to the landscape functionality framework of Ludwig et al. (1997), landscapes that capture resources (e.g. organic matter, soil material) are more functional than those where such resources are lost. In succulent thicket, resources are captured and retained beneath patches of canopy shrubs (forming raised organic-rich mounds - e.g. Kerley et al. 1999b), such that the loss of these patches causes a smoothing of the soil surface as resources, and hence functionality (Kerley et al. 1999b; Lechmere-Oertel et al. 2005a), is lost. Using these predictions, we estimated ecological functioning at increasing distances from water by measuring areas of run-on (i.e. convex soil surface) and run-off (i.e. concave soil surface; adapted from Ludwig et al. 1997) along three 50 m line-transects located at each marked experimental plot. Results are presented as the ratio between areas of run-on and run-off per plot.

To identify the likely mechanism of the predicted change in functionality, we hypothesized that this process will be associated with a change in the structure (or integrity) of the organic-rich mounds that occur beneath patches of canopy shrubs. Hence, we considered intact mounds to be those for which patch area was equal to, or exceeded mound area and thus where resources were conserved beneath patches. The reverse was true for exposed mounds; these occurred more frequently near water, reflecting areas vulnerable to erosion. Thus, at each marked experimental plot we measured the canopy and mound diameters of ten randomly selected shrub patches and estimated patch and mound area (m²), respectively. Ratios of patch and mound area were correlated with ratios of run-on and run-off per plot.

Intensity of use

Our approach assumed that elephant were the key drivers of vegetation structure and ecological functioning in AMC, and ignored the effects of other herbivores. Although this reflected our observations of the scale and magnitude of impacts on the shrub community (determined by the versatile and destructive foraging of elephant – e.g. Stuart-Hill 1992; Kerley & Landman 2006; Chapter 2), we validated this approach by estimating the relative intensity of use by herbivores at increasing distances from Hapoor water point. During the final survey we conducted standing-crop dung counts (Putman 1984) for all herbivores encountered at each experimental plot (area standardized to 250 m²). Because counts were
generally poorly distributed across plots for individual species, these were combined across species to estimate herbivore densities and for comparison with estimates of elephant density. Dung counts have been shown to provide reliable estimates of relative use between elephant and other herbivores (Barnes 2001; Young et al. 2005).

Data analysis


Non-metric Multidimensional Scaling (n-MDS) ordinations, based on Bray-Curtis resemblance matrices of shrub density data (Clarke 1993; Clarke & Gorley 2006), were used to visualize differences in community composition over the experimental period. Data were square-root transformed prior to analysis to reduce the influence of extremely dominant species, and the fit of the ordination assessed with a Stress value. Each point on a biplot represents the data from a single experimental plot. Ordination analyses were performed with Primer Version 6 (Clarke & Gorley 2006).

Using our conceptual understanding of the shape of the piosphere pattern and published examples (e.g. Graetz & Ludwig 1978; Thrash & Derry 1999) we followed Crawley (2007) in modelling trends in shrub volume and density using non-linear mixed-effects models (package nlme in R2.12.1; R Development Core Team 2010) based on logistic growth curves (Pinheiro & Bates 2000), with Sample Period (four levels: 1977-2008) as a grouping variable. These curves comprised three fixed parameters and were of the form

\[
y = \frac{\text{Asym}}{1 + e^{-\frac{(x - \text{Xmid})}{\text{Scale}}}}
\]

where Asym is the asymptote, Xmid is the curve inflection point and Scale is the magnitude of the dispersion of the function (i.e. the inverse of curve steepness). Because we had no a priori information on the random effects variance-covariance structure of the models, we initially associated random effects for each Sample Period with all the fixed parameters (i.e. Asym, Xmid and Scale). Where there were indications of model over-parameterization (Pinheiro & Bates 2000), model selection proceeded by systematically removing non-significant random effects and comparing models using Akaike’s information criterion (AIC) and standard likelihood-ratio tests (\(\alpha = 0.05\)). Superior models were indicated by a lower AIC value and
significant tests (Burnham & Anderson 2002). Diagnostic plots of observed and fitted values and residuals were inspected for deviations from model assumptions. No formal method exists for post-hoc comparisons in the nlme package. Therefore, once a final model was selected for a set of variables, we assessed the importance of Sample Period by iteratively manipulating level codes for this variable to create groups, and determining the corresponding $AIC$ for the modified model (with the same number of parameters as the original model). Modified models that decreased $AIC$ by at least two (relative to the original model; Burnham & Anderson 2002) were considered to improve the explanatory power.

Because shrub structure varied non-linearly with distance from water and we expected a clear relationship between ecological functioning and shrub structure, we modelled trends in functionality with a simple self-starting logistic growth curve.

**RESULTS**

**Intensity of use**

We recorded the dung of 10 mesoherbivore species at the experimental plots during 2008, but detected no relationship between dung densities for these species and distance from water ($R^2 = 0.03; F_{1,5} = 0.14; P = 0.726$). In contrast, dung densities for elephant, and thus intensity of utilization, declined exponentially ($R^2 = 0.96; F_{1,5} = 116.70; P < 0.001$; Dung density $= 0.07 \times e^{-0.01 \times \text{Distance to water}}$). This validated our approach and suggested that any piosphere effect observed was likely due to the effects of elephant.

**Vegetation structure**

The n-MDS ordination showed a trend of increased dissimilarity in shrub community composition over the experimental period, largely determined by the effects of elephant near water (100–300 m; Fig. 3.2). These changes could be described at two levels. First, an assessment of the cover of canopy shrubs and grasses (along 50 m line-transects) at each marked experimental plot showed that intensive utilization by elephant caused the replacement of the shrub community with a community of grasses (Fig. 3.3). This meant that during the final survey, 92.3% of the landscape at 100 m from water comprised grasses (specifically $C. dactylon$). Grass cover declined exponentially with distance from water ($R^2 = 0.84; F_{1,5} = 26.63; P = 0.004$; % Grass $= 1.02 \times e^{-0.001 \times \text{Distance to water}}$). Second, within the shrub community, individual species responded differently to elephant effects (Fig. 3.4). For
example, amongst the five canopy dominants for which we had sufficient data, *P. afra* appeared to be particularly vulnerable, showing a decline along the entire water gradient over the experimental period and disappearing from plots < 300 m from water by 1989. Following the disappearance of more vulnerable species, shrub communities near water were dominated by *C. sepiaria* and *A. tetracanta*; the former appeared to resist removal, while the latter may have benefitted from being utilised (Fig. 3.4).

Our mixed-effects models are based on only seven estimates of shrub volume or density at each of four years, which precluded the estimation of confidence intervals for individual parameter estimates. For this reason, although the results of our hypothesis tests are robust, care must be taken in over-interpreting the estimates of coefficients for individual years. Baring this in mind, our models showed a clear spatial pattern in shrub volume and density that is typical of piospheres (Fig. 3.5). For both response variables, model fit improved when model parameters were allowed to vary with Sample Period. Using this parameterization, *Asym* (i.e. the asymptote) and *Scale* (i.e. the inverse of curve steepness) varied significantly with time for shrub volume, while only *Asym* varied for density (Table 3.1). Contrary to our predictions, the displacement of asymptotes generally declined over the experimental period (volume: 59.6%; density: 6.0%) and were reached at distances between 2650 m (1977) and
Fig. 3.3 Contrasts in experimental plots located at 100 m (A), 200 m (B) and 300 m (C) from Hapoor water point between 1981 (left) and 2008 (right). Photo credits: M. Stalmans (1981), M. Landman (2008)

1070 m (2008) from water for volume and between 4000 m (1977) and 3760 m (2008) for density (Fig. 3.5; Table 3.1). Further modelling by grouping of Sample Periods revealed differences between all asymptotes for shrub volume (i.e. the best model had separate parameter estimates for each Sample Period), with estimates for the 1981-survey being the highest (Table 3.1). Asym estimates for density, however, appeared to stabilize post-1981. Increased curve steepness with time post-1981 (72.8%; Table 3.1), allied with decreased asymptotes and constant inflection points, implied a radial expansion of the area adjacent to water with severely reduced shrub volumes (Figs. 3.3 & 3.5). Estimates from the mixed-
Fig. 3.4 Trends in the density of the five dominant canopy species (A – *Portulacaria afra*, B – *Euclea undulata*, C – *Schotia afra*, D – *Azima tetracantha*, E – *Capparis sepiaria*) at increasing distances from water over the experimental period.
CHAPTER THREE Long-term variation in an elephant piosphere effect

Fig. 3.5 Best-fit mixed-effects logistic growth models of canopy shrub volume (solid lines; circles) and shrub density (dashed lines; crosses) as a function of distance from water.

Effects models showed that during 1989, volumes at plots between 100-300 m from water had declined by 33.0-17.8% (Table 3.2). However, during 2008, these reductions reached 90% across the same plots such that grass cover in this area ranged between 92.3-75.6%.

Ecological functioning

We detected a strong relationship between ecological functioning (expressed as the ratio between areas of run-on and run-off) and both shrub volume ($R^2 = 0.97; F_{1,5} = 157.30; P < 0.001$; Functionality = 0.83 * $e^{0.32 * \text{Shrub volume}}$) and shrub density ($R^2 = 0.82; F_{1,5} = 23.52; P = 0.005$; Functionality = 0.37 * $e^{3.56 * \text{Shrub density}}$). Hence, functionality increased rapidly with distance from water (Table 3.1; Appendix 3A) and reached an asymptote at 4890 m. Note, however, that this estimate extends beyond the sample transect and should be interpreted with caution. This process was correlated with an increase in the integrity of the organic-rich mounds that occur beneath patches of canopy shrubs ($R^2 = 0.74; F_{1,6} = 13.93; P = 0.014$; Functionality = 0.17 + (3.22 * Mound structure)). Only 2.5% of mounds near water were considered to be intact (i.e. patch area ≥ mound area; Table 3.1, Appendix 3B), and these were nearly 250% smaller than mounds recorded at 3000 m from water; 90.6% of mounds at the outer limit of sampling were intact.
**Table 3.1** Best-fit mixed-effects logistic growth model selection results and parameter estimates for canopy shrub volume, shrub density and ecological functioning. Coefficients vary by Sample Period where they differ significantly from population coefficients, while non-significant coefficients are represented only by the population value. Coefficients were considered significantly different \((P \leq 0.05)\) from zero.

<table>
<thead>
<tr>
<th>Best model parameters</th>
<th>Parameter estimates</th>
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<tr>
<td></td>
<td>Fixed effects</td>
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<tr>
<td>Shrub volume</td>
<td>Asym + Xmid + Scale</td>
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<tr>
<td>Run-on:Run-off area</td>
<td>Asym + Xmid + Scale</td>
</tr>
<tr>
<td>Proportion of intact mounds</td>
<td>Asym + Xmid + Scale</td>
</tr>
</tbody>
</table>

* Asym, Asymptote; Xmid, Curve inflection point; Scale, Inverse of curve steepness
* K, Number of model parameters; \(AIC\), Akaike information criterion; \(\Delta AIC_1\), \(AIC\) difference between the full model with random effects for each Sample Period associated with all fixed parameters and the best model with a reduced random effects structure; \(\Delta AIC_2\), \(AIC\) difference between a model with separate parameters for each Sample Period and a model with separate parameters for the selected period only.
* ** Sample Period different from all other periods combined.

**DISCUSSION**

Addo Elephant National Park has a long history (nearly 40 years) of demonstrating elephant effects on ecosystem patterns and processes, and currently provides the most comprehensive account of these effects in South Africa (reviewed in Kerley & Landman 2006). Nevertheless, despite the contribution these accounts have made toward the larger debate on managing elephant impacts (Kerley et al. 2008), the fact that impacts intensify in the vicinity of water (e.g. Mosugelo et al. 2002; Chamaillé-Jammes et al. 2007; Loarie et al. 2009) and the apparent vulnerability of succulent thicket to elephant (Kerley & Landman 2006), our study is the first to investigate these effects in relation to water in thicket. Furthermore, we provide the first explicit model of long-term variations in an elephant piosphere effect in a fenced system that may be used as a tool to monitor and manage the impact.
Table 3.2 Percentage change in canopy shrub volume and shrub density over the experimental period as predicted by mixed-effects logistic growth models (see Fig. 3.5; Table 3.1). The 1977-survey was used as the base case for all comparisons. Positive values show an increase with Sample Period, while negative values show a decline. Note that because \( X_{\text{mid}} \) and \( Scale \) coefficients for shrub density did not vary with Sample Period, percent change estimates do not vary with distance from water.

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<td>Shrub volume</td>
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<tr>
<td>100</td>
<td>34.5</td>
<td>-33.0</td>
<td>-99.2</td>
</tr>
<tr>
<td>200</td>
<td>24.8</td>
<td>-25.4</td>
<td>-97.1</td>
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<tr>
<td>300</td>
<td>16.6</td>
<td>-17.8</td>
<td>-89.3</td>
</tr>
<tr>
<td>500</td>
<td>5.7</td>
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<td>1000</td>
<td>1.8</td>
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<tr>
<td>1500</td>
<td>4.9</td>
<td>-5.1</td>
<td>-21.9</td>
</tr>
<tr>
<td>3000</td>
<td>6.0</td>
<td>-5.7</td>
<td>-22.7</td>
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<tr>
<td>Shrub density</td>
<td></td>
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<td>100-3000</td>
<td>-19.0</td>
<td>-24.6</td>
<td>-24.4</td>
</tr>
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At our study site, we observed a clear spatial pattern in elephant effects, i.e. shrub structure increased rapidly to an asymptote with distance from water, which is consistent with other piosphere patterns (e.g. Graetz & Ludwig 1978; Thrash 1998; Thrash & Derry 1999; Brits et al. 2002; Smith 2012). These results expand on the conclusions of Stuart-Hill (1992) and Kerley et al. (1999b) who argued that the top-down foraging of elephant maintains the structure and ecological functioning of succulent thicket. We show that in the vicinity of water, and consequently with intensive utilization, the thicket shrub community is vulnerable to transformation as shrub patches are opened up, canopy volume declines and species that are less tolerant of elephant effects (e.g. those that recruit or regenerate poorly or are vulnerable to pollarding or uprooting – O’Connor et al. 2007) are gradually removed. This has significant implications for ecological functioning as the organic-rich mounds that occur beneath patches of shrubs are increasingly exposed and trapped resources run-off. The endpoint is a highly transformed landscape adjacent to water, covered with a simple layer of ephemeral grasses and few of the structural elements that capture and utilize resources (Kerley et al. 1999b; Lechmere-Oertel et al. 2005a,b). Although our results are confounded by observations at a single water point (arrayed along a single axis), they are consistent with
the patterns of transformation at other water points in AMC (determined using Normalized Difference Vegetation Indices (NDVIs) – Smith 2012), and elsewhere in succulent thicket following intensive utilization by domestic browsers (e.g. Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995; Lechmere-Oertel et al. 2005b). Importantly, the latter studies show that a disturbance of the ecological processes in thicket, combined with generally slow regeneration dynamics, causes this trajectory of transformation to be virtually irreversible without active restoration. Thus, thicket landscapes with abundant water supply and elevated elephant numbers may be vulnerable to degradation (i.e. where ephemeral grasses dominate over woody shrubs, causing a decline in productivity and biodiversity – Stuart-Hill & Aucamp 1993; Kerley et al. 1995; Lechmere-Oertel et al. 2005b; Kerley & Landman 2006) as these patterns expand over time (Owen-Smith 1996; Gaylard et al. 2003).

Evidence from Hapoor water point support these predictions and show that shrub volume in particular has declined steadily at both the upper and lower limit of the piosphere pattern over the 31 year period of the survey; most striking is the roughly 300 m radial expansion of the grass-dominated habitats adjacent to water. Although Smith’s (2012) analysis (using NDVIs on Landsat TM imagery) was limited to areas within 1 km from water in AMC (which excluded the estimation of asymptotes), she confirmed the expansion of these grass-dominated habitats (NDVIs < 1) at other water points. Not surprisingly, the extent and rate of expansion varied between points, mostly in accordance with their management history, but probably also in relation to other landscape features and barriers (Hayward & Kerley 2009; Loarie et al. 2009). The latter implies that the observed patterns may also not be symmetric at each point, causing inconsistencies in the shape of the piosphere pattern. For water points with management histories comparable to that of Hapoor (Fig. 3.1), grass cover reached distances of roughly 450 m from water, expanding by ~300 m over a 16 year period.

Lechmere-Oertel et al. (2005b) argued that once the thicket system passes a threshold of self-restoration it loses resilience, thus tending toward an alternative state with reduced productivity (Stuart-Hill & Aucamp 1993). We predict that elephant have the ability to expand the grassland-state across the landscape, and that this pattern of transformation can be interpreted using a state-and-transition model (cf. Westoby et al. 1989). This suggests that attempts to use water availability as a tool to manage landscape heterogeneity in the presence of elephant (e.g. Pienaar et al. 1997; Gaylard et al. 2003; Owen-Smith et al. 2006) may be risky in succulent thicket that is vulnerable to such disturbances.

Elephant modify ecological patterns and processes at a range of scales (Kerley et al. 2008), and while the patterns are often clear, the mechanisms may not be (Chapter 2).
Although elephant piosphere effects are most apparent in the structure of woody communities, the scale of effects on associated biodiversity may be different from those observed for woody vegetation. Using modelled estimates from our final survey, we show that despite the clear relationship between shrub structure and ecological functioning in succulent thicket, the extent of elephant impacts at Hapoor water point varied between these features (displacement of asymptotes during 2008: shrub volume – ~1070 m; shrub density – ~3760 m; functionality – ~4890 m, but see cautionary note); we presume that this reflects differences in the sensitivity of these features to elephant. Given that water and elephants are unevenly distributed across the landscape (e.g. Chamaillé-Jammes et al. 2007), it is likely that our estimates will vary between water points. Thus, it will be critically important to develop a predictive understanding of the relationship between the structural and functional attributes (or pattern and process) of ecosystems with elephant, which by definition are key aspects of ecological heterogeneity (cf. Pickett et al. 1994). Failing this, attempts to use water availability as a tool to maintain landscape heterogeneity in the presence of elephant may fail in its objectives.

Although piosphere patterns generally expand with increased herbivore numbers and/or decreased rainfall, systems with multiple water points may show overlapping impacts, which reduce the extent of impact at each point (e.g. Graetz & Ludwig 1978; Owen-Smith 1996; Thrash & Derry 1999; Thrash 2000). During our 31 year study, we not only observed a decline in the thicket-dominated habitats adjacent to Hapoor, but also a significant decline in the displacement of asymptotes. Given that herbivory is the primary driver of thicket structure (as opposed to rainfall or fire, Stuart-Hill & Aucamp 1993; Kerley et al. 1995; Hayward & Zawadzka 2010) and that the elephant population (Kerley & Landman 2006) and water provisioning increased exponentially over the experimental period, we speculate that this decline reflects the overlap of impacts from neighbouring water points. Similarly, we presume that in the absence of a change in rainfall, the closing of an adjacent water point during the late-1970s (M. Landman Unpublished data) would have released utilization pressure at this time and increased shrub volume (from ~35% at 100 m to ~6% at 3000 m) during the 1981-survey. Importantly, the patterns of overlap varied for shrub volume and density, with the former showing a steady decline (but see above) over the experimental period (thus continued transformation), and the latter a stabilization post-1981. The stabilization in shrub density reflects the fact that the rootstocks of some species remain intact (thus, also maintaining the shape of the sigmoid curve) with intensive utilization, which suggests that these species might recover following a release in utilization pressure (e.g.
Kerley et al. 1995). The consequences of this for ecological functioning and ecosystem resilience are not clear. Although we had no information on elephant numbers at Hapoor water point for the study, it is likely that our piosphere effects co-varied with these changes; furthermore, these impacts will co-vary with rainfall and other confounding variables (e.g. fire) in more dynamic systems, using more dynamic ecological features. Thus, it will be critically important to include these variables and their interactions in models that describe piosphere patterns in order to develop a predictive understanding of the mechanisms that create and maintain these patterns. We further show that elephant piosphere effects vary both spatially and temporally between ecological features (i.e. community composition, shrub volumes and densities, shrub species). This suggests that a more integrated understanding of the effects of elephant on ecological heterogeneity may be required before water availability is used to manage elephant effects.

Piosphere effects are usually considered model systems that provide key insights into the effects of herbivores on ecosystems (e.g. Owen-Smith 1996; Adler & Hall 2005). Using multiple measures of biodiversity, we show that these effects are complex and that our ability to predict and manage such effects in the presence of elephant will be limited in the absence of long-term data. Instead we recommend an integrated multi-scaled approach to monitoring elephant effects in relation to water that incorporates both spatial and temporal variations and the structural and functional attributes of ecosystems. Furthermore, our findings clearly show the potentially adverse consequences of excessive water provisioning for succulent thicket communities (Walker et al. 1987; Owen-Smith 1996; Pickup et al. 1998; Grant et al. 2002; Gaylard et al. 2003). This suggests that the current exceptionally dense network of water points in AMC (i.e. 12 water points within 120 km²) compromises both biodiversity and conservation objectives (Kerley & Landman 2006; Kerley et al. 2008). Elsewhere (e.g. Kruger National Park), negative relationships between abundant water supply, biodiversity and ecological resilience (e.g. Walker et al. 1987; Owen-Smith 1996, James et al. 1999; Parker & Witkowski 1999; Grant et al. 2002) have resulted in a review of water provisioning policies, and the subsequent closing of water points (Owen-Smith 1996; Pienaar et al. 1997; Gaylard et al. 2003; Owen-Smith et al. 2006). Our results caution against the establishment of additional water points in recently included novel habitats, and we advocate a significant reduction in water provisioning in AMC, albeit with greater impacts at existing water points.
CHAPTER FOUR

Understanding the scale of elephant effects for conservation management: integrating plant community composition, community structure and species responses

INTRODUCTION

*Biological diversity* has gradually emerged as a central theme in the conservation management of southern Africa’s growing elephant populations (Whyte et al. 1999; Owen-Smith et al. 2006; Van Aarde et al. 2006). Specifically, management focus has shifted from manipulating population numbers to identifying and mitigating the extent and intensity of effects on biodiversity. This change brought with it the recognition that elephant influence a range of ecological patterns and processes at various spatial and temporal scales: from the composition and structure of plant and animal communities, to soil resources, litter production and nutrient dispersal (reviewed in Conybeare 2004, Skarpe et al. 2004, Kerley & Landman 2006, Kerley et al. 2008). The intensity and heterogeneity of the effects typically vary in relation to the availability of key resources, including surface water and the quantity and quality of food (Chamaillé-Jammes et al. 2007; Codron et al. 2011; Pretorius et al. 2011), and may be modified by other drivers of ecosystem change (e.g. rainfall variability, fire frequencies, and the influences of coexisting large herbivores – Trollope et al. 1998; Skarpe et al. 2004; Hayward & Zawadzka 2010). Thus, it is well recognised that elephant effects on vegetation structure and dynamics intensify in the vicinity of water, with consequences for ecological functioning and associated biodiversity (Owen-Smith 1996; Grant et al. 2002; Chamaillé-Jammes et al. 2007; Chapter 3). However, despite this general understanding of both the extent and intensity of the influences of elephant, these concepts are poorly integrated in empirical studies. For example, the conversion of tall woodlands to shrub coppice or treeless grasslands (Van de Vijver et al. 1999; Skarpe et al. 2004; Western 2007) presumably represents the upward transfer of accelerated impacts on plant species, providing insights into community responses (Folke et al. 2004; Carpenter et al. 2008). Identifying the distribution of elephant effects between elements of biodiversity may be particularly important, since the heterogeneity paradigm (implemented to monitor and manage the impacts - Biggs et al. 2008) emphasizes that ecosystems function across an integrated spatio-temporal hierarchy of patterns and processes (Wu & Loucks 1995; Pickett et al. 1997). Such an understanding may further provide insights into the issues around regime
Megaherbivores in succulent thicket: resource use and implications
PhD Thesis, Nelson Mandela Metropolitan University

CHAPTER FOUR

Elephant effects vary between elements of biodiversity

shifts (i.e. the extensive, often irreversible, long-term changes) in ecosystems, which are
difficult to predict and require indicators that provide advance warning (Folke et al. 2004;
Carpenter et al. 2008). This implies a more integrated understanding of both the rate and
trajectory of change between elements of biodiversity in relation to the resilience of the
system (Folke et al. 2004; Van Nes & Scheffer 2007).

In the succulent thickets of the Addo Elephant National Park, South Africa, nearly 40
years of research has demonstrated the consequences for biodiversity of maintaining high
levels (2-8 times recommended levels) of elephant utilization (reviewed in Kerley &
Landman 2006). In particular, the local extinction of many endemic plants has raised
conservation concerns (Lombard et al. 2001). The majority of this work followed a tradition
of using snap-shot natural experiments to measure the effects, contrasting elephant-occupied
areas with elephant exclosures. These contrasts are particularly dramatic for the canopy shrub
community (contributing the bulk of above-ground phytomass), and significant declines in
plant species richness, density and biomass have been recorded (Penzhorn et al. 1974; Barratt
& Hall-Martin 1991; Stuart-Hill 1992). However, apart from the apparent need for long-term
data, the approach of contrasting communities in the presence and absence of elephant has
limited our ability to predict the impacts (Kerley & Landman 2006). Nevertheless,
hypotheses regarding the long-term response of the canopy shrubs vary from persistence with
continued utilization (Stuart-Hill 1992; Kerley et al. 1995, 1999b) to consistent declines
(Gough & Kerley 2006; Chapter 3). Specifically, Stuart-Hill (1992) and Kerley et al. (1999b)
argued that the top-down foraging of elephant maintains the structure and ecological
functioning of thicket by protecting cover at ground-level. While the work of Barratt and
Hall-Martin (1991) contradicted these ideas in the short-term, they also speculated that such
an equilibrium might be possible after 20 years of utilization. Opposing these hypotheses is
empirical evidence of the vulnerability of succulent thicket to transformation as prolonged
utilization by domestic herbivores causes a gradual replacement of the canopy shrubs with
ephemeral grasses (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Lechmere-Oertel et al.
2005b). Instead of reaching an equilibrium, however, transformed thicket continues along this
trajectory of decline, owing to generally slow regeneration dynamics and the loss of key
ecological processes (Kerley et al. 1999b; Vlok et al. 2003; Lechmere-Oertel et al. 2005a;
Chapter 3). Consequently, Gough and Kerley (2006) predicted that similar patterns of
transformation might arise in the presence of elephant, and that thicket landscapes may be
vulnerable to degradation before any density-dependent population processes become
apparent. Thus, despite the importance of the canopy shrub community in ecological
functioning and resilience of succulent thicket and evidence of the impacts of elephant, no clear understanding has emerged regarding its long-term responses to elephant. Neither is it clear how the effects may be distributed within this community, providing limited insights into the broader community responses.

Using a unique experimental design, our study quantifies > 50 years of elephant effects on the canopy shrubs of the Addo Elephant National Park, contrasting the impacts between elements of the community; i.e. from community composition and structure (defined in terms of shrub volumes and densities), to the structure of individual canopy species. With this we demonstrate the importance of explicitly recognizing biodiversity and heterogeneity for the conservation management of elephant. Our study contributes toward recognizing the scale of elephant effects for monitoring, which is fundamental to preventing a mismatch at the management scale (Cumming et al. 2006; Lindenmayer & Likens 2009; Du Toit 2010; De Knegt et al. 2011).

STUDY AREA

Addo Elephant National Park (33°31’S, 25°45’E) is situated in the Eastern Cape, South Africa (Fig. 4.1). The park comprises several fenced sections with the majority of the elephant population confined to the Addo Main Camp section (AMC; 120 km² at the time of the study). AMC was originally fenced in 1954 (23.3 km²) to enclose the elephant of the region and incrementally expanded (Fig. 4.1) to support the steadily growing population (from 22 individuals in 1954 to 384 in 2008; Kerley & Landman 2006). Three sites (Exclosures; covering 4.3, 4.2 and 1.9 km²) that have excluded elephant for > 50 years, but are accessible to various large herbivores (e.g. kudu Tragelaphus strepsiceros, bushbuck Tragelaphus scriptus, common duiker Sylvicapra grimmia), were included for monitoring purposes.

The region is semi-arid with 260-530 mm rainfall annually, peaking in spring and autumn. In the absence of natural permanent surface water, water provision through pumped point sources increased significantly since the original fencing (from 6 in 1954 to a total of 12 in 2008; Chapter 3). The area comprises a series of low, undulating hills (60-350 m in height) in the Sundays River valley, where nutrient-rich soils give rise to succulent thicket habitats (Mucina & Rutherford 2006). These thickets are typically evergreen, 2-4 m high, dense and characterized by a high diversity of growth forms. The tree succulent Portulacaria afra is locally dominant and occurs in a matrix of spinescent shrubs (e.g. Azima tetracantha,
Fig. 4.1 Location and history of expansion of the Addo Main Camp section (study area), Addo Elephant National Park. Experimental plots were located in succulent thicket habitats at sites exposed to elephant since 1954 (Site 1), 1977 (Site 2) and 1984 (Site 3) and three Exclosures used as a control against which to measure elephant effects. Areas (covering 47.6 km²; 40% of AMC) included post-1984 were not surveyed.

*Capparis sepiaria, Carissa bispinosa, Searsia spp.* and low trees (*e.g.* *Euclea undulata*, *Schotia afr*, *Sideroxylon inerme*). Grasses may be seasonally abundant where intensive utilization by elephant has removed the canopy shrubs (Chapter 3).

**METHODS**

**Experimental design and sampling**

Much of the history of AMC reflects a response to managing the impacts of elephant (Kerley & Landman 2006). Thus, following Barratt and Hall-Martin (1991) and Lombard *et al.* (2001), we used the incremental expansion of AMC between 1954 and 2008 (Fig. 4.1) to
establish a gradient of utilization and thereby to quantify elephant effects on the canopy shrub community. The impacts were quantified at three levels: community composition (in terms of the relative abundances of the canopy species contributing to the community), community structure (defined in terms of shrub volume and density) and the structure (volume only) of individual canopy species. Our approach assumed that areas utilized for an extended period experienced relatively higher impacts, when compared to areas used for shorter periods; i.e. we (initially) assumed an even distribution of elephant (but modified by other drivers of foraging intensity – see later), and substituted space for time. Twenty-nine experimental plots were located at three sites (6-15 plots per site) exposed to elephant since 1954 (Site 1), 1977 (Site 2) and 1984 (Site 3), with an additional four plots located at the Exclosures (Fig. 4.1); the latter were used as a control against which to measure elephant effects (Lombard et al. 2001). Plots were permanently marked in 1977, when they were first surveyed, with further monitoring in 1981, 1989 and 2008 (providing temporal coverage of 31 years). This meant that during our final survey, sample sites represented 0, 24, 31 and 54 years of elephant utilization, respectively (Table 4.1). However, intensity of use also varied with each survey: for example, plots at Site 1 experienced between 23 and 54 years of utilization over the sample period (1977-2008), while impacts at Site 3 were initiated only following the 1981-survey (Table 4.1).

Table 4.1 Characteristics of sample sites incrementally exposed to elephant, and surveyed between 1977 and 2008.

<table>
<thead>
<tr>
<th></th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Exclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (km²)</td>
<td>23.3</td>
<td>14.4</td>
<td>33.5</td>
<td>10.4</td>
</tr>
<tr>
<td>Total time (yrs)</td>
<td>54</td>
<td>31</td>
<td>24</td>
<td>0</td>
</tr>
<tr>
<td>[variation with sample period*]</td>
<td>[23, 27, 35, 54]</td>
<td>[0, 4, 12, 31]</td>
<td>[0, 0, 5, 24]</td>
<td>[0]</td>
</tr>
<tr>
<td>Mean no. of elephant.km⁻²</td>
<td>2.4</td>
<td>1.5</td>
<td>1.2</td>
<td>0 [0]</td>
</tr>
<tr>
<td>[range]†</td>
<td>[0.9-4.0]</td>
<td>[1.8-3.2]</td>
<td>[1.8-3.2]</td>
<td>0 [0]</td>
</tr>
<tr>
<td>No. of permanent water points.km⁻²</td>
<td>0.26 : 0.13</td>
<td>0.07 : 0.14</td>
<td>0.03 : 0.09</td>
<td>0</td>
</tr>
</tbody>
</table>

* Includes a 10.6 km² area exposed to elephant since 1982. However, due to small sample sizes (n = 2), results for this site were combined with those for Site 3.
† Estimated as the mean over 54 years (1954-2008) using unpublished population numbers from K. Gough for every year. Note that because mean densities were standardized to 54 years, these are generally smaller than the range estimated according to the time each site was utilized by elephant.
Experimental plots were 5 m wide, while plot length (13-45 m) scaled inversely with the abundance of the dominant shrub taxa. We estimated the volume (m$^3$) of all canopy shrubs (34 spp.: 7 succulents, 27 woody shrubs) encountered by measuring the maximum height and canopy diameters of individual plants. Since most shrubs are multi-stemmed re-sprouters, stems within 50 cm of each other at ground-level were considered to be of the same individual. Individuals were measured if at least half the rooted area occurred within the plot. We calculated shrub density as the number of individuals per unit area.

Our approach assumed that herbivory by elephant was the primary determinant of vegetation structure in AMC, dominating the effects of other herbivores (e.g. kudu, bushbuck, common duiker) and other drivers of ecosystem change (e.g. fire and rainfall - Kerley et al. 1995; Hayward & Zawadzka 2010). Although this assumption should be treated with caution (Chapter 2), it reflected the fact that elephant comprise roughly 80% of large herbivore biomass in AMC (South African National Parks Unpublished data), and have been managed at densities that far exceed recommended levels for 50 years (Kerley & Landman 2006).

**Data analysis**

We described elephant effects for each site, recognizing that the intensity of utilization varied with sample period (Table 4.1). Data for the 1977, 1981 and 1989 surveys were available from Barratt and Hall-Martin (1991).

Non-metric Multidimensional Scaling (n-MDS) ordinations, based on Bray-Curtis resemblance matrices of shrub density data (Clarke 1993; Clarke & Gorley 2006), were used to visualize differences in community composition between sites. Six plots located ≤ 300 m from permanent water that showed extensive changes in shrub composition due to the effects of elephant (i.e. the near-complete replacement of the shrub community with grasses – Chapter 3) were excluded from the analyses because they dominated the ordinations across sites. Data were square-root transformed to reduce the influence of extremely dominant species, and the fit of each ordination was assessed with a Stress value; ordinations were corroborated with hierarchical agglomerative cluster analyses (Clarke 1993). Each point on a biplot represents the data from a single experimental plot. Analyses of Similarity (ANOSIM; 5000 Monte Carlo permutations) were used to test the null hypothesis of no difference in shrub composition between sample periods for each site. The $R$ statistic is centred on zero, with values close to zero representing low discrimination between groups; the global $R$
reflects the combined differences between groups. $R$ values were used as an index of the degree of change in shrub composition between groups. Multivariate analyses were performed with Primer Version 6 (Clarke & Gorley 2006).

We modelled trends in shrub volume and density (i.e. community structure) using linear mixed-effects models (package nlme in R2.12.1; R Development Core Team 2010) as described by Pinheiro and Bates (2000) and Zuur et al. (2007). Analyses were repeated for the volumes of five canopy dominants for which we had sufficient data: *P. afra*, *E. undulata*, *S. afra*, *A. tetracantha* and *C. sepiaria*. In these models we specified that the factors Sample period (0-31 years from 1977-2008), Site (four levels: 1-3 and Exclosure) and their interaction were fixed, and that Plots nested within Site were random. The random effects fulfilled the role of assigning repeated measures and accounted for spatial pseudoreplication. At a landscape scale, elephant foraging intensity may vary with proximity to water, topography and the availability and quality of food (Wall et al. 2006; Chamaillé-Jammes et al. 2007; Codron et al. 2011; Pretorius et al. 2011). However, because our experimental plots were generally located on even terrain with similar soils (a proxy for food quality - Pretorius et al. 2011), we expected surface water availability to be the primary determinant of elephant effects at this scale (Chapter 3). Thus, for each Sample period we determined the distance between each experimental plot and the nearest permanent water point (range: 0-4422 m; see Table 4.1 for trends in water provisioning at each site), and included this as a covariate (log-transformed to reduce the effects of extreme values) in our models. Plots located at sites that excluded elephant (i.e. the Exclosure, but also those with no elephant at the time of sampling) were assigned distances equalling 4500 m; i.e. slightly further than the most extreme observed distance to water, which we took to be the distance beyond which the impacts are most likely to be asymptotic (Chapter 3). Analyses started by modelling the response variable as a function of Sample period. Factors (fixed and random) were systematically added or removed and the best-model was selected using Akaike’s information criterion ($AIC$) and standard likelihood-ratio tests ($\alpha = 0.05$). Superior models were indicated by a lower $AIC$ value (Burnham & Anderson 2002). Random effects were fitted by restricted maximum likelihood and fixed effects by maximum likelihood. Data were examined for linearity prior to analyses, and diagnostic plots of observed and fitted values and residuals were inspected for deviations from the model assumptions. Where appropriate we extracted model estimates for each Site by controlling for Distance to water, using median distances.
RESULTS

Community composition

The n-MDS ordinations showed a clear change in shrub composition over the sample period for all elephant-occupied sites and the Exclosure (Fig. 4.2). However, inspection of ANOSIM $R$ values indicated that the magnitude and trajectory of these changes varied between sites (Table 4.2). With the exception of Site 2, the combined differences in shrub composition between 1977 and 2008 were comparable between sites (global $R = 0.34-0.39$), despite substantial variations in the intensity of utilization (Table 4.1). Importantly, these differences were also similar between sites with and without elephant, albeit likely that the trajectory of change varied. Using the 1977-survey as the base case for comparison, shrub communities at Site 1 (intensive utilization) and the Exclosure followed a trend of increasing dissimilarity with sample period (Table 4.2). For Site 1, these dissimilarities were statistically significant throughout, while only the 2008-survey was different for the Exclosure ($P = 0.029$). In contrast, shrub communities at Sites 2 and 3 initially showed increased dissimilarities associated with the introduction of elephant, but a degree of stabilization thereafter.

**Table 4.2 Analyses of Similarity (ANOSIM) results of the change in shrub composition between 1977 and 2008. The 1977-survey was used as the base case for comparison. $R$ values indicate the degree of change in composition between sample periods, with values approaching unity indicating a clear separation. The global $R$ reflects the combined differences between all surveys.**

<table>
<thead>
<tr>
<th>Site</th>
<th>Global test</th>
<th>Pairwise comparisons</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (since 1954)</td>
<td>0.34</td>
<td>&lt; 0.001</td>
<td>0.14</td>
</tr>
<tr>
<td>2 (since 1977)</td>
<td>0.26</td>
<td>0.001</td>
<td>-0.13</td>
</tr>
<tr>
<td>3 (since 1984)</td>
<td>0.39</td>
<td>&lt; 0.001</td>
<td>-0.06</td>
</tr>
<tr>
<td>Exclosure</td>
<td>0.36</td>
<td>0.003</td>
<td>-0.17</td>
</tr>
</tbody>
</table>

Community structure

Results from the mixed-effects models showed a clear linear relationship between shrub volume and Sample period (Fig. 4.3), and model fit improved when we included Site and Distance to water as factors (Table 4.3). Using this parameterization, shrub volume...
Fig. 4.2 Non-metric Multidimensional Scaling ordinations of the change in shrub composition between 1977 and 2008.

declined significantly with Sample period at all elephant-occupied sites (Fig. 4.3), but this effect varied among sites (and thus with the intensity of utilization; $F_{3,94} = 48.67, P < 0.001$). After controlling for Distance to water (coefficient = 0.51; SE = 0.08), model estimates indicated that volume declined weakly with Sample period ($P < 0.001$) at Sites 1 (14.6%; coefficient = -0.02, SE = 0.004) and 3 (16.0%; coefficient = -0.03, SE = 0.01), while decreasing strongly at Site 2 (42.5%; coefficient = -0.07, SE = 0.01). At the Exclosure, shrub volume nearly doubled (93.1% increase; coefficient = 0.17, SE = 0.02) over the same period (Fig. 4.3). Plots located near water (< 300 m) had severely reduced volumes ($F_{1,94} = 104.30; P < 0.001$), especially at Sites 1 and 2 that were exposed to elephant for the longest period of time.

Contrary to the best-model for shrub volume, model fit for shrub density was best (lowest AIC) when Distance to water was the only factor in the model; including Site, Sample period, or their interaction resulted in a deterioration in model fit (Table 4.3). Shrub densities
Fig. 4.3 Best-fit linear mixed-effects model of total shrub volume ($V; m^3.m^2$) as a function of Sample period (Sp; 0-31 years from 1977-2008) and Distance to water (Dw; m). See Table 4.1 for intensity of elephant use per site.

Table 4.3 Linear mixed-effects model selection results for total shrub volume and density.

<table>
<thead>
<tr>
<th>Candidate models</th>
<th>$K$</th>
<th>$AIC$</th>
<th>$A AIC$</th>
<th>$LL$</th>
<th>$-2LL$</th>
<th>$df$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub volume</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>38</td>
<td>508.08</td>
<td>-216.04</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>41</td>
<td>487.56</td>
<td>-20.52</td>
<td>202.78</td>
<td>26.52</td>
<td>3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sp + (Sp x S)</td>
<td>44</td>
<td>471.80</td>
<td>-15.76</td>
<td>191.90</td>
<td>21.76</td>
<td>3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sp + (Sp x S) + Dw</td>
<td>45</td>
<td>452.25</td>
<td>-19.55</td>
<td>181.13</td>
<td>21.55</td>
<td>1</td>
<td>&lt; 0.001**</td>
</tr>
<tr>
<td>Shrub density</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>36</td>
<td>16.66</td>
<td>27.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>39</td>
<td>19.04</td>
<td>2.37</td>
<td>29.48</td>
<td>3.63</td>
<td>3</td>
<td>0.305</td>
</tr>
<tr>
<td>Sp + (Sp x S)</td>
<td>42</td>
<td>16.63</td>
<td>-0.04</td>
<td>33.69</td>
<td>12.04</td>
<td>6</td>
<td>0.061</td>
</tr>
<tr>
<td>Sp + Dw</td>
<td>37</td>
<td>8.04</td>
<td>-8.62</td>
<td>32.98</td>
<td>10.62</td>
<td>1</td>
<td>1.000</td>
</tr>
<tr>
<td>Dw</td>
<td>36</td>
<td>6.04</td>
<td>-2.00</td>
<td>32.98</td>
<td>0.00</td>
<td>1</td>
<td>0.967**</td>
</tr>
</tbody>
</table>

Sp, Sample period; S, Site; Dw, Distance to water
$K$, Number of model parameters; $AIC$, Akaike information criterion; $A AIC$, $AIC$ difference relative to the previously selected simplest model; $LL$, Log-likelihood; $-2LL$, -$2(Log$-likelihood).

**, Best-model
declined strongly adjacent to water (coefficient = 0.06, SE = 0.01; $F_{1,98} = 18.00$, $P < 0.001$).

**Structure of the canopy species**

As expected, the effects of elephant on the structure of the canopy dominants varied between species. For most species, mixed-model fits improved when we included Sample period, Site and Distance to water as factors (Table 4.4). However, neither Site nor Distance to water was important in the best-model for *A. tetragona*, while Distance to water was also not important for *S. afra*. Where Distance to water featured as an important factor, shrub volume declined significantly near water for all species (Fig. 4.4).

**Table 4.4** Linear mixed-effects model selection results and best-model ANOVA tests for the volumes of individual canopy species.

<table>
<thead>
<tr>
<th>Canidate models</th>
<th>K</th>
<th>AIC</th>
<th>$\Delta AIC$</th>
<th>LL</th>
<th>-2LL</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Portulacaria afra</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>38</td>
<td>214.65</td>
<td>-69.32</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>41</td>
<td>209.15</td>
<td>-5.50</td>
<td>-63.57</td>
<td>11.50</td>
<td>3</td>
<td>0.009</td>
</tr>
<tr>
<td>Sp + S + (Sp x S)</td>
<td>44</td>
<td>202.99</td>
<td>-6.16</td>
<td>-57.49</td>
<td>12.16</td>
<td>3</td>
<td>0.007</td>
</tr>
<tr>
<td>Sp + S + (Sp x S) + Dw</td>
<td>45</td>
<td>185.43</td>
<td>-17.56</td>
<td>-47.72</td>
<td>19.56</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><strong>Euclea undulata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>38</td>
<td>238.58</td>
<td>-81.29</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>41</td>
<td>238.91</td>
<td>0.34</td>
<td>-778.46</td>
<td>5.66</td>
<td>3</td>
<td>0.129</td>
</tr>
<tr>
<td>Sp + S + (Sp x S)</td>
<td>44</td>
<td>235.54</td>
<td>-3.03</td>
<td>-73.77</td>
<td>15.03</td>
<td>6</td>
<td>0.020</td>
</tr>
<tr>
<td>Sp + S + (Sp x S) + Dw</td>
<td>45</td>
<td>231.72</td>
<td>-3.82</td>
<td>-70.86</td>
<td>5.82</td>
<td>1</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td><strong>Schotia afra</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>36</td>
<td>121.87</td>
<td>-24.94</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>39</td>
<td>106.35</td>
<td>-15.52</td>
<td>-14.18</td>
<td>21.52</td>
<td>3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sp + S + (Sp x S)</td>
<td>42</td>
<td>97.11</td>
<td>-9.24</td>
<td>-6.59</td>
<td>15.24</td>
<td>3</td>
<td>0.002 **</td>
</tr>
<tr>
<td>Sp + S + (Sp x S) + Dw</td>
<td>43</td>
<td>95.44</td>
<td>-1.68</td>
<td>-4.72</td>
<td>3.68</td>
<td>1</td>
<td>0.055</td>
</tr>
<tr>
<td><strong>Azima tetracanta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>38</td>
<td>7.49</td>
<td>34.26</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>41</td>
<td>10.94</td>
<td>3.45</td>
<td>35.53</td>
<td>2.55</td>
<td>3</td>
<td>0.467</td>
</tr>
<tr>
<td>Sp + S + (Sp x S)</td>
<td>44</td>
<td>11.34</td>
<td>3.85</td>
<td>38.33</td>
<td>8.15</td>
<td>6</td>
<td>0.228</td>
</tr>
<tr>
<td>Sp + S + (Sp x S) + Dw</td>
<td>45</td>
<td>8.11</td>
<td>0.63</td>
<td>40.94</td>
<td>13.37</td>
<td>7</td>
<td>0.064</td>
</tr>
<tr>
<td>Sp + Dw</td>
<td>39</td>
<td>6.59</td>
<td>-0.90</td>
<td>35.70</td>
<td>2.90</td>
<td>1</td>
<td>0.089</td>
</tr>
<tr>
<td><strong>Capparis sepriaria</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp</td>
<td>6</td>
<td>-100.36</td>
<td>56.18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp + S</td>
<td>9</td>
<td>-108.16</td>
<td>-7.79</td>
<td>63.08</td>
<td>13.79</td>
<td>3</td>
<td>0.003</td>
</tr>
<tr>
<td>Sp + S + (Sp x S)</td>
<td>12</td>
<td>-115.64</td>
<td>-7.48</td>
<td>69.82</td>
<td>13.48</td>
<td>3</td>
<td>0.004</td>
</tr>
<tr>
<td>Sp + S + (Sp x S) + Dw</td>
<td>13</td>
<td>-117.70</td>
<td>-7.06</td>
<td>71.85</td>
<td>4.06</td>
<td>1</td>
<td>0.044 **</td>
</tr>
</tbody>
</table>

Sp, Sample period; S, Site; Dw, Distance to water
K, Number of model parameters; AIC, Akaike information criterion; $\Delta AIC$, AIC difference relative to the previously selected simplest model; LL, Log-likelihood; -2LL, -2(Log-likelihood).

**, Best-model
After controlling for Distance to water, model estimates showed that *P. afra*, *E. undulata* and *C. sepiaria* volumes generally varied little with Sample period and Site (Fig. 4.4; Table 4.5): exceptions were Site 2 for *P. afra* (significant decline), Site 3 for *E. undulata* (significant increase) and the Exclosure for *C. sepiaria* (significant increase). Only *S. afra* declined significantly at all elephant-occupied sites over the survey period, albeit that this decline was significantly lower following intensive utilization at Site 1; we observed no change in the canopy volume of *S. afra* at the Exclosure (Table 4.5). Shrub volumes for *A. tetracantha* varied significantly with Sample period (Table 4.4), increasing by 163% (coefficient = 0.01; SE = 0.01) between 1977 and 2008.

**Fig. 4.4** Best-fit linear mixed-effects models of shrub volumes (V; m$^3$.m$^{-2}$) as a function of Sample period (Sp; 0-31 years from 1977-2008) and Distance to water (Dw; m) for individual canopy species. Surface plots for *Azima tetracantha* are not shown because best-models did not include Site or Distance to water; Distance to water was also not important in the best-fit model for *Schotia afra*. 

CHAPTER FOUR Elephant effects vary between elements of biodiversity
Table 4.5 Percentage change and significance levels of shrub volume over the sample period (31 years from 1977-2008) as predicted by linear mixed-effects models (see Fig. 4.4). Positive values show an increase with sample period, while negative values show a decline. Estimates were standardized using median Distance to water. Included in brackets are the coefficients ± SE.

<table>
<thead>
<tr>
<th>Canopy species</th>
<th>Percent change</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Exclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portulacaria afra</td>
<td></td>
<td>-4.0</td>
<td>-61.4</td>
<td>-6.3</td>
<td>55.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>[&lt;=-0.01 ± 0.01]</td>
<td>[&lt;=-0.03 ± 0.01]</td>
<td>[&lt;=-0.01 ± 0.01]</td>
<td>[0.26 ± 0.01]</td>
</tr>
<tr>
<td>Euclea undulata</td>
<td></td>
<td>-30.6</td>
<td>-39.7</td>
<td>65.5</td>
<td>34.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>[&lt;=-0.01 ± 0.01]</td>
<td>[&lt;=-0.02 ± 0.01]</td>
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<td>[0.02 ± 0.02]</td>
</tr>
<tr>
<td>Schotia afra</td>
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<td>-36.0</td>
<td>-64.3</td>
<td>-64.3</td>
<td>3.3</td>
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<tr>
<td></td>
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<td>[&lt;=-0.01 ± 0.01]</td>
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<td>[&lt;=0.01 ± 0.01]</td>
</tr>
<tr>
<td>Capparis sepiaria</td>
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<td>-16.1</td>
<td>37.9</td>
<td>152.0</td>
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<td>[&lt;=-0.01 ± &lt;0.01]</td>
<td>[0.01 ± &lt;0.01]</td>
<td>[0.02 ± 0.01]</td>
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</table>

ns, P > 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001
Letters a, b and c denote significant between-site effects.

DISCUSSION

Despite nearly 60 years of scientific research on the consequences of elephant for ecological systems (reviewed in Conybeare 2004, Skarpe et al. 2004, Kerley & Landman 2006, Kerley et al. 2008), our ability to predict the effects is limited by few long-term quantitative studies. Where these data exist (Barnes 1983; Trollope et al. 1998; Van de Vijver et al. 1999; Eckhardt et al. 2000), the focus is on savanna systems that respond strongly to other drivers of ecosystem change and confound our understanding of the role of elephant. In succulent thicket, elephant are the dominant herbivores and principal drivers of ecological patterns and processes (Stuart-Hill 1992; Kerley et al. 1995). Consequently, descriptions of the impacts in thicket are considered the most robust and comprehensive for South Africa, contributing significantly toward the larger management debate (Kerley & Landman 2006; Kerley et al. 2008). However, despite the importance of these accounts, only the work of Lombard et al. (2001) on the diversity of rare and endemic plants has played a role in developing a predictive understanding of the effects. Using data collected regularly over a 31 year period and an experimental design analogous to that of Lombard et al. (2001), our study expands on nearly 40 years of research in thicket (Penzhorn et al. 1974; Barratt & Hall-Martin 1991; Stuart-Hill 1992) to develop such an understanding for the canopy shrub community, a key functional guild (Kerley et al. 1999b; Lechmere-Oertel et al. 2005a; Chapter 3). With this we also expand on other elephant studies that cover a wide temporal...
range (from 6 to 60 years - Barnes 1983; Trollope et al. 1998; Van de Vijver et al. 1999), but are typically confounded by poor temporal replication (reducing the power for detecting trends; Lindenmayer & Likens 2009). Thus, we provide the first explicit models of the long-term effects of elephant on any plant community that may be used to monitor and manage the impacts.

While the conservation management of elephant is focused on identifying the consequences for biodiversity (Whyte et al. 1999; Owen-Smith et al. 2006; Van Aarde et al. 2006), the impacts should be understood in relation to the resilience of the system to prevent irreversible changes (Folke et al. 2004; Van Nes & Scheffer 2007). In succulent thicket, the canopy shrub community contributes the bulk of above-ground phytomass and shapes both the structural and functional complexity of the landscape. Thus, it is well recognised that this complexity declines following prolonged utilization by domestic herbivores, which causes the system to lose resilience as it tends toward a degraded grassland-state (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995, 1999b; Lechmere-Oertel et al. 2005a,b). Of significance is that the trajectory is considered near irreversible without active restoration (Vlok et al. 2003; Lechmere-Oertel et al. 2005b). Elephant, however, are thought to maintain the structure and ecological functioning of the canopy shrubs since their top-down foraging strategy promotes vegetative reproduction and resource trapping at ground-level (Stuart-Hill 1992; Kerley et al. 1995, 1999b). Herein lies the notion that elephant are the rightful conservators of succulent thicket (rather than domestic herbivores; Stuart-Hill 1991). While this is supported by evidence of their role in various ecologically important processes (Kerley & Landman 2006; Kerley et al. 2008), our results challenge these ideas following intensive utilization. Thus, we show that the canopy shrubs are vulnerable to being transformed as the accumulated influences of elephant reduce the structure and change community composition. The pattern of transformation is no different to that caused by domestic herbivores and is characterised by a gradual replacement of vulnerable species (e.g. those that recruit or regenerate poorly or are susceptible to uprooting - O’Connor et al. 2007) with a simple layer of ephemeral grasses and the loss of associated ecological functioning (Chapter 3). Contrary to predictions of an equilibrium (Barratt & Hall-Martin 1991) the decline continues even after 50 years of intensive use and despite the incremental expansion of the area to reduce the impacts. Thus, while the equilibrium hypothesis probably emerged as AMC was expanded and the intensity of the impacts declined (but only by spreading impacts to novel habitats - see for example Sites 2 and 3 during the 1989-survey in Table 4.2), we predict that the effects of elephant will eventually bring about landscape-level degradation (cf. Gough & Kerley...
2006) and a significant loss of biodiversity. The latter is supported by evidence for the local extinction of plants (Lombard et al. 2001) and reduced large herbivore abundances (specifically bushbuck, bushpig *Potamochoerus porcus* and Cape grysbok *Raphicerus melanotis* - Novellie et al. 1996; Castley & Knight 1997), which is occurring ahead of any density-dependent feedback that may limit elephant numbers (Gough & Kerley 2006; Chamaillé-Jammes et al. 2008). Although these results show the vulnerability of the canopy shrubs, it will be important to develop a greater understanding of the ecological thresholds in thicket. Chapter 3 predicted that such a threshold is exceeded near water where the impacts intensify, and that elephant have the ability to expand the alternative grassland-state across the landscape. Our results corroborate these ideas as the accelerated decline in shrub volume at Site 2 (and perhaps even the continued decline at Site 1) is likely a consequence of abundant water provisioning (Table 4.1), and the overlap of impacts between water points at the site (Owen-Smith 1996; Chamaillé-Jammes et al. 2007). Of significance is that shrub densities declined only in the vicinity of water where the generally persistent rootstocks were completely removed. This implies that some recovery of the canopy shrubs might be possible with a release in the intensity of utilization elsewhere (with unidentified implications for ecological functioning and resilience; Kerley et al. 1995), but that such a recovery is unlikely near water (Chapter 3). Thus, while our study may be confounded by spatial pseudoreplication and varying climatic conditions in the long-term (but see Kerley et al. 1995, Hayward & Zawadzka 2010), we show the consequences of maintaining high elephant densities (2-8 times recommended levels; Kerley & Landman 2006) and abundant water provisioning for succulent thicket. With this we reiterate concerns that the exceptionally dense network of water points in AMC compromises both biodiversity and conservation objectives as the utilization gradients that develop around water coalesce (Chapter 3). Moreover, our results suggest that attempts to use range expansion as a tool to reduce the impacts requires careful consideration (Van Aarde et al. 2006; Biggs et al. 2008). In particular, such management interventions may fail in their objectives if implemented without limiting population numbers and controlling local densities (e.g. by reducing surface water availability; Druce et al. 2008).

Predicting the impacts of elephant for management requires a detailed understanding of their spatial and temporal extent (Kerley et al. 2008; Du Toit 2010; De Knecht et al. 2011). This should be based on robust insights into the distribution of the effects between elements of biodiversity that typically differ in their vulnerability to elephant. Understanding these distributions may further contribute toward establishing appropriate indicators for
monitoring, particularly since monitoring programs often fail owing to poor planning and limited evidence for the utility (or strength) of the indicators (Lindenmayer & Likens 2009). However, with the exception of the work of Levick and Rogers (2008) on woody species and patch responses to large browsers, such relations are rarely established. Because we observed extensive changes to the thicket shrub community at all levels explored, we expected the influences on the canopy species to provide insight into community responses. Specifically, because these species dominate the diet (Paley & Kerley 1998; Chapter 2), we thought canopy volume would decline steadily as the intensity of utilization increased across sites.

Instead and with the exception of near-consistent declines around water (see also Chapter 3), the majority of the canopy dominants exhibited little change and resisted removal, whereas *A. tetracantha* might have benefitted from being utilised. Given the generally poor regeneration dynamics of most thicket plants (Vlok et al. 2003), this probably reflects the top-down foraging strategy of elephant that promotes vegetative reproduction at ground-level (Stuart-Hill 1992; O’Connor et al. 2007). These so-called hedging-effects are not novel (see for example effects on *Colophospermum mopane* – Smallie & O’Connor 2000; Styles & Skinner 2000; Kohi et al. 2011) and elephant are often thought to select previously hedged plants due to increased browse availability and quality; hence their dominance in the diet. Thus, while elephant determine the fate of many plant species (Kerley & Landman 2006; Kerley et al. 2008; Chapter 2), the vulnerability of these plants cannot necessarily be inferred from their relative abundance in the diet, unless they are also preferred foods. Moreover, such disparate responses between species and communities confound our understanding of the extent of the impacts, and imply that the canopy dominants might not be useful indicators of community change in succulent thicket. Elsewhere, large trees are iconic elements of savanna landscapes that play an important role in community structure and ecological functioning (e.g. Belsky 1994; Van de Vijver et al. 1999; Manning et al. 2006). As a consequence, they are considered obvious and suitable indicators for monitoring (e.g. Druce et al. 2009). However, these trees are also long-lived and slow-growing and may be manipulated by elephant in a variety of ways: from breaking branches and stems (pollarding), to toppling (where the roots may remain intact) and uprooting (Barnes 1983; Trollope et al. 1998; Van de Vijver et al. 1999; Eckhardt et al. 2000; O’Connor et al. 2007; Kerley et al. 2008). The ecological consequences of such effects differ considerably and determine the rate and trajectory of change, and therefore the utility (or strength) of trees as indicators. This suggests that predicting and monitoring the impacts requires a broader integrated understanding of the mechanisms.
driving the changes between elements of biodiversity, at various spatial and temporal scales (Kerley & Landman 2006; Kerley et al. 2008; Chapter 2).

Despite the shortcomings in our understanding, we detected two important species’ responses that require further exploring. First, *S. afra* appears to be particularly vulnerable to elephant, declining steadily even after 50 years of intensive use. Although this decline provides insight into community responses, such incremental changes are usually poor predictors of ecological thresholds (Folke et al. 2004; Carpenter et al. 2008), limiting the use of *S. afra* in monitoring. Second, the tree-succulent *P. afra* (commonly referred to as *spekboom*) is widely accepted to be particularly tolerant of the impacts (Barratt & Hall-Martin 1991; Stuart-Hill 1992), which we confirmed in our study. A notable exception, however, was the significant decline in canopy volume at Site 2 (61.4%), where the impacts accelerated possibly owing to abundant water provisioning. Given the vulnerability of succulent thicket to transformation (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995; Lechmere-Oertel et al. 2005b), we speculate that such novel responses should generate significant concerns in light of potential system shifts.

Finally, exclosure treatments are often considered appropriate controls (or baselines) against which to measure the impacts of elephant (Penzhorn et al. 1974; Barratt & Hall-Martin 1991; Stuart-Hill 1992; Levick & Rogers 2008). However, Cowling & Kerley (2002) questioned this assumption as they argued that plant communities might develop differently in the absence of elephant, experiencing so-called *megaherbivore-release* (Kerley & Landman 2006; Kerley et al. 2008). In succulent thicket for example, exclosure communities are probably regulated by bottom-up processes (as opposed to top-down processes in the presence of elephant), such as edaphic- and microclimatic-effects and competition for light (Stuart-Hill 1992). While it was beyond the scope of our study to test the efficacy of the exclosures in AMC, we detected a significant change in the thicket shrub community at these sites over the course of our experimental period. Importantly, the changes were often similar in magnitude to those caused by elephant, albeit in opposite directions. This illustrates the role of other drivers of community change and questions the use of exclosures in monitoring. By excluding such baselines the influences of elephant might be less dramatic: for example, models that describe and predict the impacts may vary significantly depending on the baseline (e.g. from exponential to linear), with obvious consequences for estimates of rates of change and vulnerability. Our findings have important implications for monitoring, and suggest that a predictive understanding of the influences of elephant requires a greater focus on demonstrating robust causal relationships (Kerley & Landman 2006; Kerley et al. 2008).
CHAPTER FIVE

Evidence for competition between African megaherbivores:
black rhinoceros diet shift in the presence of elephant

INTRODUCTION

Since Sinclair (1975) suggested that large mammalian herbivores are primarily food-limited (as opposed to predator-limited - see for example Sinclair et al. 2003, Fritz et al. 2011), the importance of competition and niche separation in structuring these species’ assemblages is widely recognised (Murray & Illius 1996; Putman 1996). In African large herbivore assemblages, megaherbivores (i.e. species weighing > 1000 kg as adults, comprising elephant *Loxodonta africana*, black rhinoceros *Diceros bicornis*, and others) typically dominate the biomass and utilise the greatest share of the available resources through their enhanced tolerance of lower-quality food (Owen-Smith 1988). Consequently, they are considered a separate trophic guild that play a key role in the abundance and structure of mesoherbivore communities (Fritz 1997; Fritz et al. 2002), and hence ecosystem functioning (*sensu* Duffy et al. 2007). These trophic interactions are particularly significant for elephant and are mediated mostly by powerful effects on vegetation structure and composition (reviewed in Kerley et al. 2008). For some mesoherbivores the impacts facilitate access to habitat and increase the availability and quality of food (Owen-Smith 1988; Makhabu et al. 2006; Valeix et al. 2011). As an example, the conversion of tall woodlands to shrub coppice improves access to nutrient-rich regrowth for browsers. However, where elephant are abundant they may be considered keystone competitors (*sensu* Bond 1993) that regulate resource utilisation in local communities, thus limiting large herbivore abundances (Fritz et al. 2002, 2011; Valeix et al. 2008). Nevertheless, despite the fact that megaherbivores (particularly elephant) dominate resources and structure the food niches of mesoherbivores, there exists little empirical evidence on how resources are shared within this trophic guild (e.g. Lamprey 1963; Jarman 1971; Leuthold 1978; Makhabu 2005; O’Kane et al. 2011a), and none for direct competition for food between megaherbivores. Understanding the role of these bottom-up controls is particularly important for this guild, which is relatively invulnerable to top-down processes (e.g. predation – except that imposed by man, disease; Owen-Smith 1988, Sinclair et al. 2003).
Because ecologically similar species are unable to coexist indefinitely on the same resources, interspecific competition is expected to promote the use of different resources (Schoener 1974, 1982; Pianka 1976). Amongst the megaherbivores, elephant and black rhinoceros coexist in diverse habitats (e.g. woodlands, grasslands, semi-deserts) and share similar foods owing to wide feeding tolerances for abundant items of varying structure (e.g. leaves, twigs, bark) and nutritional quality (Owen-Smith 1988). Nevertheless, elephant are mixed-feeders that utilise browse and green grass, depending on seasonal availability, while black rhinoceros are strict browsers that select mostly dwarf shrubs, succulents and forbs with their prehensile upper-lip (Owen-Smith 1988; Kerley et al. 2008). Thus, when seasonal resources are reduced (e.g. grasses and forbs during the dry season), the coexistence of these herbivores on woody browse is presumably facilitated by their enhanced tolerance of lower-quality food, provided that the quantity is not limiting. However, where elephant movements (seasonal and long-term dispersal) are constrained by fences, interspecific competition (exploitative and interference) may intensify as populations expand, effects on woody communities increase and browse availability declines. In these cases, competition is expected to be asymmetric in favour of elephant, owing to their larger size (elephant:rhinoceros body mass ratio: ♀ 3:1, ♂ 5:1), which confers an advantage in terms of the costs of agonistic interactions (Persson 1985; Berger & Cunningham 1998; Valeix et al. 2007). The competitive ability of elephant is further enhanced by their greater foraging capacity (e.g. felling trees to access branch tips or roots) and ability to achieve high rates of food intake (through simultaneous handling and chewing), across a wide vertical range (up to 8 m above-ground versus < 2 m for rhinoceros); these advantages reflect specialised foraging adaptations such as the mobile trunk (Owen-Smith 1988; Kerley et al. 2008).

Implicit in the theory that interspecific competition promotes the use of different resources (as opposed to complete exclusion), is the understanding that shifts in resource use may be correlated with the intensity of competition (Schoener 1974, 1982; Pianka 1976). In particular, demonstrating such shifts in response to the presence of a potential competitor is considered to be direct evidence of competition (Pianka 1976). In the succulent thickets of the Addo Elephant National Park, South Africa, elephant dominate large herbivore biomass and population densities have exceeded (2-8 fold) recommended levels for 50 years (Kerley & Landman 2006). As a consequence, elephant effects on the woody community are dramatic, and significant declines in species richness, density and biomass have been recorded (reviewed in Kerley & Landman 2006; Chapters 3 & 4). We expected these long-term impacts and high elephant densities to limit food availability for coexisting browsers,
thus increasing the potential for competition. Our study tested this for black rhinoceros by (1) describing the seasonal diet and dietary preferences of coexisting elephant and rhinoceros to determine how resources are shared within this guild, (2) assessing the degree of diet separation in relation to the seasonal availability of resources, and (3) contrasting the diet and preferences of rhinoceros in the presence and absence of elephant (using adjacent sites). We predicted that if competition is important in shaping the food niche of rhinoceros then (1) diet separation should increase towards the dry season (late autumn-winter) when seasonal resources are reduced and both diets converge on browse (Schoener 1982), and (2) through competitive release, rhinoceros should broaden their diet and shift their preferences (by including more preferred foods and/or excluding non-preferred items) in the absence of elephant (Schoener 1974; Pianka 1976). It is possible that the predicted change in diet may simply reflect differences in the availability of resources between sites (i.e. a site-effect). To account for this potential constraint, we further tested our results against the predictions of optimality theory in which (1) diet breadth is inversely correlated with the availability of resources (i.e. rhinoceros should maintain a restricted diet in the absence of elephant), and (2) preferences do not respond to a change in availability, unless selectivity changes (Pyke et al. 1977). Finally, we measured the nutritional costs of the predicted shift in resource use with faecal quality descriptors and discuss our results in terms of the potential consequences for coexisting megaherbivores in small, enclosed areas.

**STUDY AREA**

The study was conducted in adjacent fenced sections of the Addo Elephant National Park (33°31’S, 25°45’E), South Africa. At the time of the study (2001-2003), 11 black rhinoceros and nearly 400 elephant coexisted in the Addo Main Camp section (AMC; 120 km²), while seven rhinoceros were located c. 1.5 km north in a 7 km² area. No elephant were present at this site. The sites were generally similar except for the long-term (c. 50 years) browsing effects of elephant in AMC. Besides the megaherbivores, both sites supported a diverse mesobrowser community (5 spp.), dominated by kudu *Tragelaphus strepsiceros*. Rhinoceros in the Addo Elephant National Park are managed as a metapopulation with sub-populations elsewhere in the region.

The region is semi-arid with 260-530 mm rainfall annually, peaking in late-spring (November) and early-autumn (March). Nutrient-rich soils give rise to succulent thicket habitats (Mucina & Rutherford 2006), which covered c. 70-80 % of the study sites. These
thickets are typically evergreen, 2-4 m high, dense, thorny and dominated by the tree succulent *Portulacaria afra*. The remaining habitat at the sites comprised a mosaic of thicket, karoo and riverine types with grasslands derived from previous agricultural use. The vegetation is characterized by a high diversity of growth forms: drought-resistant succulents (e.g. *P. afra*), low trees (e.g. *Euclea undulata, Schotia afra, Sideroxylon inerme*) and spinescent woody shrubs (e.g. *Azima tetracantha, Capparis sepiaria, Carissa bispinosa, Gymnosporia* spp., *Searsia* spp.) contribute the bulk of plant biomass, while the understory hosts dwarf succulents, forbs, geophytes and perennial grasses. Couch grass *Cynodon dactylon* is seasonally abundant in grasslands and areas where intensive utilization by elephant has removed the canopy shrubs (Chapter 3).

**METHODS**

**Diet composition**

We determined the diet of elephant and rhinoceros by identifying plant epidermal fragments in faeces (Sparks & Malechek 1968). Reference slides of the epidermal tissues of > 350 potential food items at the sites were available for comparison. The technique is used extensively to contrast diets (e.g. Steinheim *et al.* 2005; Kerley *et al.* 2010) and its accuracies and biases are summarized in Holechek *et al.* (1982). Although faecal analysis may be biased toward less digestible food items in ruminants, these biases are likely to be reduced in megaherbivores with relatively poor digestion (Holechek *et al.* 1982; Owen-Smith 1988). Thus, we considered contrasts in fragment representation between herbivores and sites as valid indicators of dietary differences.

Fresh faecal samples were collected seasonally from November 2002-June 2003 (for elephant and rhinoceros in AMC) and August 2001-April 2002 (for rhinoceros, elephant absent). Four seasons were distinguished based on patterns of temperature, rainfall and frost: spring (September–November); summer (December-February); autumn (March-May); winter (June-August). Elephant faeces were collected opportunistically from family groups, while rhinoceros faeces were collected from latrines throughout the sites. Because the sites were located in close proximity (c. 1.5 km apart) and rainfall did not vary greatly between sample periods (i.e. between 387 and 321 mm during 2001/2 and 2002/3, respectively), we expected differences in rhinoceros diet to reflect a response to the effects of elephant, rather than sample period. Faeces were oven-dried and prepared following Chapter 2. We identified 100 epidermal fragments to species level per faecal sample and treated each sample as an
independent observation. In total, 41 elephant (10-11 samples per season) and 35 (elephant present; 8-9 samples per season) and 33 (elephant absent; 8-9 samples per season) rhinoceros faecal samples were analyzed. The diets were described as the frequency-of-occurrence of all the recorded plant species.

Food availability

Relative food availability was estimated by measuring plant canopy cover (e.g. Kerley et al. 2010; Chapter 2). Twenty 50 m line-transects were placed randomly and in proportion to the occurrence of habitat types at each site, during the wet (spring) and dry (late autumn-winter) season. Although most succulent thicket shrubs are evergreen, many grasses and forbs and some geophytes become dormant during the dry season (Stuart-Hill & Aucamp 1993), hence the need for the seasonal approach. We considered all food items encountered along transects as potentially available to elephant, but limited food availability for rhinoceros to items that occurred below their estimated maximum foraging height (175 cm; Wilson 2002).

Diet quality

We estimated rhinoceros diet quality between sites by measuring faecal nitrogen ($N_f$), phosphorous ($P_f$) and crude fibre ($NDF_f$) concentrations. Nitrogen and phosphorous availability is widely limiting to herbivore growth, reproduction and the maintenance of body condition (e.g. Grant et al. 1995; Wrench et al. 1997). We randomly selected 15 faecal samples from each site (across seasons) and measured $N_f$ using the Kjeldahl method (AOAC 1995), $P_f$ using inductively coupled plasma spectrometry, and $NDF_f$ according to the methods of Goering and Van Soest (1970). Sample analyses were conducted by the Grootfontein Agricultural Development Institute ($N_f$) and KwaZulu-Natal Department of Agriculture ($P_f$, $NDF_f$), South Africa. Concentrations are expressed as percent dry matter.

Data analysis

We generated accumulation curves (50 random iterations) of plant species recorded per faecal sample with which to assess the adequacy of sample sizes. Because none of the accumulation curves reached a stable plateau, the non-parametric Incidence-based Coverage Estimator (Foggo et al. 2003) was used to estimate total dietary richness. Differences
between observed and expected counts provided an estimate of the variation in dietary information at the upper limit of sampling effort.

Elephant and rhinoceros diets were contrasted seasonally using principal dietary items (PDI) and by grouping all plant species into broad growth form categories (i.e. grasses, woody shrubs, succulents, forbs, lianas, geophytes and epiphytes); we combined the seasonal data to contrast rhinoceros diets between sites. Our approach of using PDI was based on the observation that 64% (rhinoceros) and 74% (elephant) of the plant species utilized during the study contributed < 1% each to the diets, presumably as many are incidentally browsed.

Foods consumed in the greatest quantities (abundances; Petrides 1975) and which collectively contributed most of the variation in dietary information were considered PDI. These were identified by ranking plant species in decreasing order of abundance, plotting their cumulative contribution to the diet and scoring the slope of this curve relative to that at the origin (i.e. the contribution of the dominant item). PDI were considered to be those for which the slope of the cumulative curve was at least 10% of that at the origin: beyond this point, each plant species contributed relatively little to the diet. This is less subjective than the approach of Petrides (1975) in which an arbitrary cut-off based on the contribution of each species was used. We used non-metric Multidimensional Scaling (n-MDS) ordinations, based on Bray-Curtis resemblance matrices (Clarke 1993; Clarke & Gorley 2006), to visualise differences in the utilization of PDI across seasons and between sites. Each point on a biplot represents the data from one faecal sample. Data were square-root transformed to down-weight the influence of abundant items and the fit of each ordination was assessed with a Stress value; we corroborated ordinations with a Stress > 0.20 with hierarchical agglomerative cluster analyses (Clarke 1993). A non-parametric Analysis of Similarity (ANOSIM; 5000 Monte Carlo permutations) was used to test the null hypothesis of no difference in the utilization of PDI between groups. The $R$ statistic ranges between zero and one, representing low and high discrimination between groups, respectively. $R$ values were used as an index of the extent of dietary separation between elephant and rhinoceros for each season and trends (across seasons) were verified using conventional indices of resource overlap (e.g. Pianka 1973). Multivariate analyses were performed with Primer Version 6 (Clarke & Gorley 2006).

Differences between the consumption and relative availability of food items (i.e. preferences for plant species or groups) were assessed by calculating 95% confidence intervals for the mean utilization of each item (Neu et al. 1974). In principle, we considered food items to be preferred if utilization was greater than availability (i.e. subtracting percent
availability from percent utilization resulted in a positive value) and the lower confidence limit was greater than zero (where use = availability); negative values indicated avoidance. Preferences were calculated by combining the relative availability and utilization data across seasons.

ANOVA procedures (Tukeys’ test) were used to test differences in the use of growth forms across seasons and between sites. Where appropriate, percentage data were arcsine-transformed for normality and heteroscedasticity of variances.

RESULTS

Food availability

We recorded 145 plant species, comprising mainly woody shrubs (37%), forbs (18%) and succulents (17%) along transects and quantified their relative availability for elephant and rhinoceros; 60% of the recorded species were shared between sites. Although food availability is expected to decline to a minimum during the dry season (particularly, grasses, forbs and some geophytes), we detected no difference in the relative abundance of growth forms between seasons for elephant ($F_{6,266} = 0.66; P = 0.681$) or rhinoceros (with a narrower foraging height range; $F_{6,266} = 0.60, P = 0.728$) in AMC. Food availability for rhinoceros varied between sites ($F_{6,553} = 24.38; P < 0.001$), with grasses (18.5% vs. 42.7%) and woody shrubs (36.7% vs. 56.3%) being significantly more and less abundant in AMC, respectively.

Diet composition

In total, we identified 90 plant species in the diet of elephant and 92 (elephant present) and 87 (elephant absent) species in the diet of rhinoceros (Appendix 4A). These species accounted for c. 87-95% of the estimated richness at the upper limit of sampling effort, confirming that the sample sizes used here were adequate to describe and compare the diets.

Diet separation between coexisting elephant and rhinoceros

Only 18% (elephant) and 26% (rhinoceros) of the recorded plant species were utilised extensively, contributing 72-77% of the diets, and thus considered PDI (Appendix 4B). N-MDS ordinations showed a clear separation between elephant and rhinoceros in their use of PDI across seasons (Fig. 5.1), with a high degree of dissimilarity (53-63%), which was statistically significant ($P < 0.001$) in each instance. Diet separation increased from spring...
Fig. 5.1 Non-metric Multidimensional Scaling ordinations of principal dietary items identified in the diet of elephant (E) and black rhinoceros (R) in the Addo Main Camp section. ANOSIM (Analysis of Similarity) R values indicate the degree of diet separation across seasons; values approaching unity indicate clear separation.
Megaherbivores in succulent thicket: resource use and implications
PhD Thesis, Nelson Mandela Metropolitan University

CHAPTER FIVE Competition for food between African megaherbivores

(ANOSIM $R = 0.55$) through summer (ANOSIM $R = 0.78$) to autumn (ANOSIM $R = 0.81$), a trend that supports the predictions of competition theory. This corresponded with a decline in the number of shared PDI: from 16 shared in spring to only 6 in autumn, comprising 11 and 5 woody shrubs, respectively.

Woody shrubs were the most diverse group identified (elephant: 40 spp.; rhinoceros: 42 spp.) and formed equal proportions of the bulk of the diets in all seasons (Fig. 5.2). As expected, the diets diverged most noticeably with respect to growth forms that may only be available ephemerally, specifically grasses and forbs ($F_{18,476} = 3.88; P < 0.001$). Across seasons, rhinoceros utilised significantly more forbs, while elephant utilised more grasses during summer. Elephant also decreased their use of grasses and rhinoceros their use of forbs significantly from summer to winter (Fig. 5.2), possibly in response to a decline in the availability (or quality) of these groups. This provided circumstantial evidence that the pattern of increased diet separation coincided with a decline in food availability, and thus the avoidance of competition. Elephant compensated for the decline in grass utilisation by increasing their use of succulents (Fig. 5.2), particularly *P. afra* (summer: 4.2%; winter: 15.1%). With the exception of epiphytes and geophytes, we observed no differences between the consumption and relative availability of growth forms ($P > 0.05$; Fig. 5.3). Both herbivores preferred epiphytes ($P < 0.05$), while only rhinoceros avoided geophytes ($P < 0.05$).

Overall, approximately 69% (elephant) and 46% (rhinoceros) of the PDI were shared (11 spp.), comprising mostly woody shrubs (7 spp.), but also the dominant food item (*C. dactylon*) in both diets (Appendix 4B). Forbs were PDI only for rhinoceros, but of these, only *Chascanum cuneifolium* was never recorded in elephant diet (and thus utilised exclusively by rhinoceros). We observed similar preferences for shared PDI with only *C. bispinosa* preferred by rhinoceros ($P < 0.05$), but not elephant ($P > 0.05$; Appendix 4B).

**Diet shift in rhinoceros**

The n-MDS ordination showed a clear difference in rhinoceros diet between sites (60% dissimilarity; Fig. 5.4), which was statistically significant (ANOSIM $R = 0.69; P < 0.001$). In line with the predictions of competition theory, rhinoceros increased their diet breadth (estimated using PDI) by nearly 80% in the absence of elephant (paired $t$-test: $t_{(1)66} = 17.40, P < 0.001$; Appendix 4B). This was caused by an increase in the use of woody shrubs (11 spp.; 73%), succulents (3 spp.; 150%) and forbs (2 spp.; 50%), while lianas (4 spp.) were
Fig. 5.2 Seasonal diet, grouped into broad growth form categories (mean ± SD), of elephant (shaded bars) and black rhinoceros (clear bars) in the Addo Main Camp section.

The proportion of growth forms that contributed the bulk of the diets varied significantly between sites ($F_{6,462} = 38.78; P < 0.001$). In the absence of elephant, rhinoceros increased their use of woody shrubs (58.9% vs. 48.5%) and succulents (17.5% vs. 7.1%) and decreased their use of forbs (11.3% vs. 19.9%). Surprisingly, where elephant were present, grasses (mean: 20.8%; range: 8-63%) were particularly abundant (Fig. 5.2) and the diet was dominated (Appendix 4B) by the short mat-forming grass *C. dactylon* (mean: 13.7%; range: 5-35%). These abundances
Fig. 5.3 Normalized diet, grouped into broad growth form categories (mean ± 95% confidence interval), of elephant and black rhinoceros in the Addo Elephant National Park. Positive values with confidence intervals greater than zero indicate preference; negative values indicate avoidance.

were at least three times greater than those from the adjacent site (mean: 6.1%; range: 1-12%) without elephant. Although *C. dactylon* (5.2%) also featured as a PDI in the absence of elephant (Appendix 4B), the tree succulent *Euphorbia triangularis* (5.9%) and the spinescent woody shrub *A. tetracantha* (5.2%) were equally dominant. Despite the seasonal decrease in grass consumption shown by elephant in AMC (Fig. 5.2), presumably due to a decline in availability, rhinoceros maintained high levels of use (only different from elephant in summer; $F_{18,476} = 3.88, P < 0.001$) in all seasons (range: 17.6-30.5%). We thought that grass consumption may have been incidental and thus related to the utilisation of forbs and low-growing succulents. However, there was no correlation between the proportion of grass in the diet and that of these groups ($r_s = -0.26; n = 35; P = 0.138$), suggesting selection for grasses. Relative to availability, rhinoceros decreased their preferences for grasses between sites (Fig. 5.3), such that these were avoided foods ($P < 0.05$) where elephant were absent. Preferences for the remaining groups were similar between sites, with only geophytes showing a switch ($P < 0.05$) from avoided (elephant present) to preferred (elephant absent).
Twenty PDI were shared between sites, mostly woody shrubs (13 spp.; Appendix 4B). Few PDI were exclusively used at either site, despite these being present at both sites. We detected no difference in the preferences for PDI (Appendix 4B) shared between sites ($\chi^2 = 1.10; P = 0.577$) or with elephant ($\chi^2 = 1.50; P = 0.472$).

**Diet quality**

Despite the significant shift in rhinoceros diet between sites, $N_f$ (elephant present: mean $= 1.1\%$, SE $= 0.1\%$; elephant absent: mean $= 1.0\%$, SE $= 0.1\%$) and NDF$_f$ (elephant present: mean $= 91.2\%$, SE $= 1.3\%$; elephant absent: mean $= 90.3\%$, SE $= 1.0\%$) concentrations did not change ($N_f$: $t_{(2),28} = 1.11, P = 0.275$; NDF$_f$: $t_{(2),28} = 0.54, P = 0.593$). However, P$_f$ levels were significantly lower ($t_{(2),28} = -4.23; P < 0.001$) at sites where elephant were present (mean $= 0.14\%$, SE $= 0.01\%$), than at those where elephant were absent (mean $= 0.20\%$, SE $= 0.01\%$).

Because we detected no difference in $N_f$ or NDF$_f$ concentrations between sites, we hypothesised that grass utilisation played a positive role in the maintenance of constant diet quality. Results showed a significant positive relationship between the proportion of grass in...
the diet (varying from 1-47% between samples tested) and \( N_f \) levels \((R^2 = 0.24, F_{1,28} = 8.93, P = 0.006; N_f = 0.92 + (0.01 \times \% \text{ Grass}), \) but no relationship with \( \text{NDF}_f \) \((R^2 = 0.01; F_{1,28} = 0.13; P = 0.725) \) or \( P_f \) \((R^2 = 0.03; F_{1,28} = 0.71; P = 0.408) \). Note that because the proportion of grass and browse in the diet is inversely related, the above relationships are similarly related for browse.

**DISCUSSION**

Despite extensive evidence of the effects of elephant on food resources in the Addo Elephant National Park (Penzhorn *et al.* 1974; Stuart-Hill 1992; Chapters 3 & 4) and elsewhere (Owen-Smith 1988; Skarpe *et al.* 2004; Kerley *et al.* 2008), few studies have investigated the consequences of this for other large herbivores. Surprisingly, where this information exists, the emphasis has been on demonstrating that elephant facilitate herbivore access to habitat and increase the availability and quality of food (Owen-Smith 1988; Makhau *et al.* 2006; Valeix *et al.* 2011). This is despite clear evidence that elephant limit herbivore abundances across ecosystems through their ability to monopolise resources (Fritz *et al.* 2002, 2011; Valeix *et al.* 2008). Our study is the first to suggest direct competition for food with elephant, and by testing this for black rhinoceros we provide insights into the role of competition in structuring the megaherbivore guild.

Our results comprise two lines of evidence that support the predictions of competition theory (as opposed to optimality theory; Schoener 1974, 1982; Pianka 1976). First, we show a clear separation in diet between elephant and rhinoceros across seasons (i.e. avoiding competition), which increased towards the dry season as both diets converged on browse. Admittedly, this trend could also be interpreted as evidence of resource partitioning that enabled these megaherbivores to coexist (Schoener 1974). Thus, it may not necessarily indicate current competitive displacement, but rather some ghostly remnant of past competition (Connell 1980). We make no attempt to distinguish between the consequences of past and present interactions. However, our results also show that rhinoceros diet varied seasonally in the presence and absence of elephant (see below), suggesting that the trend of increased separation may be evidence of current displacement caused by elephant. The separation was characterised by the differential use of shared items (as opposed to the exclusive use of items), which we presume reflect the intensity of competition and the wide and tolerant feeding habits of megaherbivores (that limit the opportunities for exclusive use; Owen-Smith 1988). Thus, although we expected the diets to diverge strongly owing to the
near-exclusive utilization of grasses by elephant (and avoidance by rhinoceros; Owen-Smith 1988, Kerley et al. 2008), these were only more abundant in elephant diet during summer and were utilised extensively by rhinoceros (up to 63% of the diet in some individuals) throughout. We recorded similar patterns of abundant grass utilisation by rhinoceros in AMC prior to the present study, coinciding with our estimate of their diet where elephant were absent. That is, from August 2001 to April 2002 grass contributed c. 23.8% (SD = 11.5%) of the diet, and up to 47% in some individuals (M. Landman Unpublished data). The agreement between these findings lends support to the assumption that diet differences between sites are a response to the effects of elephant, rather than sample period. This is despite the fact that black rhinoceros are generally considered to be strict browsers, even in open grasslands: grass contributed < 5% of their foraging in 22 published accounts of the diet (e.g. Goddard 1970; Mukinya 1977; Owen-Smith 1988; Buk & Knight 2010), including the description by Hall-Martin et al. (1982) for a site in AMC without elephant. However, our interpretation of these results may be confounded as these studies used mostly direct observation or feeding-track techniques, which are vulnerable to underestimating the consumption of grasses (and forbs). Data from Parker et al. (2009), showing 15% grass utilisation, should also be treated with caution, as their faecal technique was unusually biased toward the selective retention of grasses. Nevertheless, the evidence of low grass consumption by black rhinoceros demonstrates the importance of our findings and the strength of our comparative approach.

Finally, when elephant reduced their intake of grasses during the dry season, the diets diverged, with rhinoceros utilising more forbs and sharing fewer of the dominant foods (mostly woody shrubs) with elephant. These results are broadly similar to the few studies that evaluated patterns of resource sharing between elephant and other large browsers in relation to changing food availability (e.g. Lamprey 1963; Jarman 1971; Leuthold 1978; Makhabu 2005; O’Kane et al. 2011a). However, in most cases, elephant maintained extensive diet separation by utilising different plant species and plant parts. Given the complex spatial and temporal interactions between large herbivores and their food resources, we can only presume that these studies were unable to detect competition with elephant because food availability was not limiting. Moreover, this reveals the merits of a dynamic approach (e.g. determining shifts in resource use in response to the presence of a competitor) to testing competitive interactions (Pianka 1976).

Our second line of evidence demonstrates that rhinoceros changed their selectivity in the absence of elephant by increasing their diet breadth and shifting their diet along the grass-browse continuum (elephant present: 20.8% grass, 79.2% browse; elephant absent: 6.1%
grass, 93.9% browse), and in relation to availability. In particular, rhinoceros switched their preferences for grasses such that these were avoided foods where there were no elephant. We expected the broader diet to include novel items that were either monopolised by elephant in AMC or had virtually disappeared from this site due the impacts of elephant (Penzhorn et al. 1974; Kerley & Landman 2006). Instead, we show that the increased breadth was characterised by a change in the abundances of shared items, such that a greater variety of foods comprised the bulk of the diet where elephant were absent. Thus, our study suggests the role of competition in shaping the food niche of rhinoceros: elephant partially excluded rhinoceros from browse resources and regulated their intake of the dominant foods. Although these results are confounded by a lack of replication across sites, they are broadly consistent with the diet shifts observed between other large herbivores in response to competition (e.g. shifts in diet separation between herbivores: Murray & Illius 1996, Putman 1996; shifts along the grass-browse continuum: Hulbert & Andersen 2001, Suryawanshi et al. 2010). It will be important to identify the mechanism (exploitative and/or interference) of the competitive interaction in this study, particularly as both reduced browse availability (Penzhorn et al. 1974; Stuart-Hill 1992; Chapters 3 & 4) and agonistic interactions between elephant and rhinoceros have been recorded for AMC (Kerley & Landman 2006). More recently, Tambling et al. (In press) further confirmed this interference behaviour by demonstrating that rhinoceros are the only large herbivores that change their activity patterns in the presence of elephant (as opposed to predators for the other herbivores) in AMC. It is possible that the observed shift in rhinoceros diet where elephant were absent could be a consequence of intraspecific competition. However, this seems unlikely as Hall-Martin et al. (1982) showed that rhinoceros in AMC were able to maintain their expected foraging realm (i.e. limited grass utilisation) despite extensive transformation of habitat at population densities c. 5 times that of the current study.

The reduced intake of preferred foods and change in diet along the grass-browse continuum has been shown to reduce diet quality in ungulates, with consequences for life-history traits (e.g. body mass and reproduction; Simard et al. 2008, Christianson et al. 2009). In our study, however, rhinoceros diet quality generally did not vary between sites, despite a significant shift in composition. Instead, the inclusion of grasses (particularly the highly nutritious *C. dactylon*) played an important role in maintaining constant N_f levels, while rhinoceros were seemingly able to tolerate the elevated fibre concentrations (fibre content of grass usually exceed that of browse - Van Soest 1994) through reduced retention times as hindgut fermenters (Foose 1982). The reduced P_f levels in AMC are consistent with results
for elephant at the same site (De Klerk 2009). While the causal mechanism of this decline remains unclear, we presume that it reflects either a site-effect and/or a consequence of the long-term browsing impacts of elephant (Kerley & Landman 2006). The implication of the latter is that a nutritional decrement to rhinoceros will likely arise through reduced phosphorous. Thus, apart from the greater proportion of grass in rhinoceros diet in the presence of elephant, it will be necessary to determine the dietary differences that have contributed toward these nutritional differences. It is important to recognise, however, that despite the ability of rhinoceros to maintain constant diet quality, their lack of specialised grazing adaptations (such as the trunk for elephant – Owen-Smith 1988; Kerley et al. 2008) may increase foraging costs, through reduced harvest- and handling-efficiencies of grasses (Foose 1982). In the short-term, we predict that the apparent increase in time spent foraging may be off-set by an enhanced tolerance for low quality food and by seasonally mobilising fat reserves (Owen-Smith 1988; Shrader et al. 2006). Although the long-term fitness consequences require exploring, these may be masked by the metapopulation management strategy of black rhinoceros in the Addo Elephant National Park.

In conclusion, our study suggests that competition for food between elephant and other browsers may intensify in fenced areas (created through physical or figurative barriers - Hayward & Kerley 2009) where populations expand and food availability declines. However, in larger open-systems, similar scenarios may arise within shared, preferred habitats. As an example, the conversion of tall riparian woodlands to open habitat along the Chobe River, Botswana, has caused a decline in the abundances of browsing bushbuck *Tragelaphus scriptus ornatus* (Skarpe et al. 2004). Although the mechanism of this decline remains unclear, it is likely that it partly (see Addy 1993 for the effects of reduced woody cover) reflects a decline in food availability. Our findings are important for three reasons. First, nearly 90% of South Africa’s elephant populations (but not numbers) are currently confined to small enclosed areas similar to AMC (Mketeni 2012). Second, in many cases, browse resources are expected to continue to decline as elephant populations expand in the absence of density-dependent population regulation (Gough & Kerley 2006; Chamaillé-Jammes et al. 2008; Kerley et al. 2008). Finally, because elephant also play a key role in facilitating access to resources for large herbivores (Owen-Smith 1988; Makhabu et al. 2006; Valeix et al. 2011), there likely exists a level of elephant utilization that maximises foraging opportunities, which need to be quantified and managed (Chapter 6).
CHAPTER SIX

Elephant effects on browse resources switches between increased and reduced availability: testing the case for black rhinoceros

INTRODUCTION

While the shared importance of facilitation and competition in structuring large herbivore communities is widely accepted (Bell 1971; Sinclair & Norton-Griffiths 1982; Murray & Illius 1996; Putman 1996), the relationship between these processes is little studied (Hobbs et al. 2006; Young et al. 2005; Odadi et al. 2011). In African large herbivore assemblages, elephant *Loxodonta africana* typically utilize the greatest share of the available resources and play a key role in the structure and functioning of these communities (Fritz et al. 2002, 2011). These trophic interactions are mediated mostly by effects on vegetation composition and structure (reviewed in Kerley et al. 2008), which probably intensify as elephant densities increase. For some herbivores the impacts facilitate access to habitat (Parker 1983; Valeix et al. 2011; see Pringle 2008 for effects on other vertebrates) and increase the availability and quality of food (e.g. Rutina et al. 2005; Makhabu et al. 2006; Kohi et al. 2011). As an example, the conversion of tall woodlands to shrub coppice improves access to nutrient-rich regrowth for browsers. However, where elephant are abundant, competition may intensify as the impacts reduce browse availability and alter habitats unfavourably (Owen-Smith 1988; Kerley et al. 2008; Chapter 5). In these cases, elephant limit browser abundances as woodlands are transformed to open habitat (Parker 1983; Addy 1993). However, despite the apparent dual role of elephant in shaping the food niches of large herbivores, their role in facilitating foraging opportunities has only been studied in isolation, while declining resource opportunities (a necessary requirement for competition - Tilman 1982) are rarely quantified (Young et al. 2005). Identifying the relative importance of elephant in these processes is significant given their status as keystone species (thus maintaining key processes), and the need to manage elephant effects on biodiversity by reducing competition (Owen-Smith 1988; Kerley & Landman 2006; Kerley et al. 2008).

In the succulent thickets of the Addo Elephant National Park, South Africa, elephant effects on the woody community are dramatic, such that significant declines in plant species richness, density and biomass have been recorded (reviewed in Kerley & Landman 2006). Consequently, recent evidence suggests that elephant and black rhinoceros *Diceros bicornis*
compete for browse resources, causing rhinoceros to shift their foraging along the browse-grass continuum and in relation to availability (Chapter 5). Opposing this competitive interaction is the hypothesis of Kerley et al. (1999a) that the formation of elephant pathways may facilitate access to habitat and food for herbivores in otherwise impenetrable thicket. However, it is also likely that the role of elephant in these processes may be linked, varying with the intensity of utilization (expressed as relative densities - e.g. Kerley et al. 2008; Chapter 3). We tested this by quantifying potential browsing opportunities for rhinoceros along a gradient of elephant utilization in the Addo Elephant National Park. With this approach we contrasted two alternative hypotheses with our null hypothesis of no change: 1) given the evidence for competition (Chapter 5), elephant consistently reduce browsing opportunities for rhinoceros, or 2) elephant initially facilitate access to browse through path formation, but these foraging opportunities decline (increasing the potential for competition) with intensive utilization. Since canopy shrub volume continues to decline with elephant utilization (Chapters 3 & 4), we did not test the unlikely scenario that browsing opportunities may increase towards an equilibrium. We expected elephant to influence both the availability and structure of browse (e.g. Rutina et al. 2005; Kohi et al. 2011), affecting potential harvest rates and consequently foraging effort (Spalinger & Hobbs 1992). Thus, we quantified potential browsing opportunities using browse biomass, between-bite distances and bite mass, for potential between- and within-bite harvest rates. Because herbivory by elephant is considered the key determinant of thicket structure (as opposed to rainfall or fire - Kerley et al. 1995; Hayward & Zawadzka 2010), we discuss our results in terms of the role of elephant in driving herbivore foraging opportunities.

STUDY AREA

Addo Elephant National Park (33°31’S, 25°45’E) is situated in the Eastern Cape, South Africa (Fig. 6.1). The park comprises several fenced sections with the majority of the elephant population confined to the Addo Main Camp section (AMC; 120 km² at the time of the study). AMC was originally fenced in 1954 (23.3 km²) to enclose the elephant of the region and incrementally expanded (Fig. 6.1) to accommodate the steadily growing population (from 22 individuals in 1954 to nearly 400 in 2003; Kerley & Landman 2006). Three sites (Exclosures; covering 4.3, 4.2 and 1.9 km²) that have excluded elephant for > 50 years, but are accessible to other large herbivores (e.g. kudu Tragelaphus strepsiceros,
Fig. 6.1 Location and history of expansion of the Addo Main Camp section (study area), Addo Elephant National Park. Experimental transects were placed in succulent thicket habitats at five sites incrementally exposed to elephant since 1954, and three Exclosures used as a control against which to measure elephant effects. Areas included post-1994 (covering 16.5 km²; 13.9% of AMC) were not surveyed.

bushbuck *Tragelaphus scriptus*, common duiker *Sylvicapra grimmia*), were established for monitoring purposes. While only 11 black rhinoceros occurred in AMC during the study, the area previously supported > 40 individuals (Emslie 2007).

The region is semi-arid with 260-530 mm rainfall annually. In the absence of natural permanent surface water, various pumped water points maintain water availability year round (Chapter 3). The area comprises a series of low, undulating hills (60-350 m in height) in the Sundays River valley where nutrient-rich soils give rise to succulent thicket habitats (covering c. 70% of the area). These thickets are typically evergreen, 2-4 m high, dense and characterized by a high diversity of growth forms (Mucina & Rutherford 2006). The tree
succulent *Portulacaria afra* is locally dominant and occurs in a matrix of spinescent shrubs (e.g. *Azima tetracantha*, *Capparis sepiaria*, *Carissa bispinosa*, *Searsia* spp.) and low trees (e.g. *Euclea undulata*, *Schotia afra*, *Sideroxylon inerme*). Couch grass *Cynodon dactylon* is seasonally abundant in areas where intensive utilization by elephant has removed the canopy shrubs (Chapter 3).

**METHODS**

**Experimental design**

We used the incremental expansion of AMC between 1954 and 2003 (Fig. 6.1) to establish a gradient of elephant utilization and quantify potential browsing opportunities for rhinoceros. Thus, following Barratt and Hall-Martin (1991) and Lombard *et al.* (2001), our approach assumed that areas utilized for an extended period experienced relatively higher impacts, due to higher mean elephant densities, when compared to areas utilized for shorter periods; i.e. we (initially) assumed an even distribution of elephant and substituted space for time. We estimated elephant density for each site as the mean over 49 years, using population numbers from Gough and Kerley (2006) for every year. Forty-three, 30 m line-transects were located at five sites (6-13 transects per site) exposed to elephant, representing mean densities between 0.4 and 2.3 elephant.km$^{-2}$ (Table 6.1). We also placed 12 transects at the Exclosures (Fig. 6.1) and used these as a control against which to measure elephant effects (Lombard *et al.* 2001).

**Table 6.1** Characteristics of sample sites incrementally exposed to elephant in the Addo Main Camp section.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area (km$^2$)</th>
<th>Total time (yrs) utilised by elephant</th>
<th>Mean no. of elephant.km$^{-2}$ [range]$^{†}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>23.3</td>
<td>49</td>
<td>2.3 [0.9–4.0]</td>
</tr>
<tr>
<td>2</td>
<td>14.4</td>
<td>26</td>
<td>1.3 [1.8–3.2]</td>
</tr>
<tr>
<td>3</td>
<td>10.6</td>
<td>21</td>
<td>1.1 [1.8–3.2]</td>
</tr>
<tr>
<td>4</td>
<td>22.9</td>
<td>19</td>
<td>1.0 [1.8–3.2]</td>
</tr>
<tr>
<td>5</td>
<td>31.0</td>
<td>8</td>
<td>0.4 [2.3–3.2]</td>
</tr>
<tr>
<td>Exclosure</td>
<td>10.4</td>
<td>0</td>
<td>0 [0]</td>
</tr>
</tbody>
</table>

$^{†}$ Estimated as the mean over 49 years (1954-2003) using population numbers from Gough and Kerley (2006) for every year. Note that because mean densities were standardized to 49 years, these are generally smaller than the range estimated according to the time each site was utilized by elephant.
Because surface water availability is a key limiting resource for elephant, their impacts intensify in the vicinity of water (Chamiallé-Jammes et al. 2007; Chapters 3 & 4). In succulent thicket this results in the near complete replacement of the thicket shrub community with grasses (Chapter 3), and therefore the near loss of browsing opportunities. Thus, to contextualize our gradient of elephant utilization and quantify the upper-limit of impacts on potential browsing opportunities for rhinoceros, we also surveyed eight transects placed within 300 m of Hapoor water point. Hapoor is located in the area of AMC originally fenced in 1954 (Site 1), and is one of only two water points that have maintained water availability for elephant since the initial fencing. All other experimental transects were located > 1000 m from permanent water (i.e. the distance at which elephant effects tend toward an asymptote in thicket – Chapter 3) to reduce the effect of water. Since our experimental transects were generally placed on even terrain with similar soils (a proxy for food quality - Kohi et al. 2011; Pretorius et al. 2011), we expected surface water availability to be the primary determinant of elephant effects at this scale.

Our approach assumed that elephant were the principle drivers of vegetation structure (and hence browsing opportunities), dominating the effects of other herbivores (e.g. kudu, bushbuck, common duiker). While this assumption should be treated with caution (Chapter 2), it reflected the fact that elephant dominate large herbivore biomass in AMC (South African National Parks Unpublished data) and have been managed at densities that far exceed (2-8 fold) recommended levels for 50 years (Kerley & Landman 2006). We recognize that the effects of rhinoceros on vegetation structure may be comparable to that of elephant (e.g. O’Kane et al. 2011b), but presumed that these were off-set in AMC through differences in population density.

**Potential browsing opportunities**

Since we were interested in browsing opportunities for rhinoceros specifically, we sampled at a scale that matched their foraging behaviour. Thus, we used available information on black rhinoceros bite sizes (quantified as the stem diameter - in millimetres - at point of browsing) and foraging heights (maximum: 175 cm) in succulent thicket (Wilson 2002) to define our sample units (i.e. bites) and sampling range. Along each transect, we sampled rhinoceros browsing opportunities by clipping and collecting all potential bites within the estimated foraging height range that intersected the line. All canopy shrubs (27 spp.: 5 succulents, 22 woody shrubs) encountered along transects were sampled and we used
species-specific mean bite sizes where possible (Wilson 2002). Collected material was oven-dried to constant mass. Since succulent thicket is an aseasonal habitat with an evergreen shrub community (Stuart-Hill & Aucamp 1993), we ignored seasonal variations in browse availability. Our technique was broadly similar to the bite volume technique developed and used by Emslie (1999) for rhinoceros.

We quantified potential browsing opportunities in terms of browse biomass (g dry mass m\(^{-1}\)) and between-bite harvest rates, and hence foraging effort. For browse biomass, we used available data on black rhinoceros food preferences in succulent thicket (quantified where elephant were absent; Chapter 5) to differentiate between preferred and non-preferred items; preferred items are typically utilized more frequently when alternative foods are available on an equal basis (Johnson 1980). Bite mass was investigated by randomly selecting 10 bites per site for each of the five canopy dominants with adequate data, i.e. *P. afra*, *E. undulata*, *S. afra*, *A. tetracantha* and *C. sepiaria*; these species are important food items for rhinoceros in succulent thicket, contributing a portion of the bulk of the diet (Chapter 5). Data for Hapoor water point were excluded from these analyses because most canopy shrubs were characteristically severely reduced (or completely removed) following intensive utilization by elephant (Chapters 3 & 4).

**Correlates of potential browsing opportunities**

To identify the likely correlates of the change in potential browsing opportunities, we used the hypothesis of Kerley et al. (1999a) to predict that this will be associated with the formation and spread of elephant pathways. That is, path formation (reflecting the movement and foraging effects of the entire population) may initially facilitate access to browse in otherwise impenetrable thicket, but with continued utilization these paths gradually replace the canopy shrubs (*sensu* Chapter 3), causing the loss of browsing opportunities. Thus, at each experimental transect we counted (for no. pathways m\(^{-1}\)) and measured the width (for path area m\(^{-1}\)) of each elephant path that intersected the line. In addition, because the top-down foraging of elephant reduces canopy height in thicket (Barratt & Hall-Martin 1991; Stuart-Hill 1992), presumably with implications for herbivore foraging height, we also recorded these heights at 50 cm intervals along each transect (calculated as the mean of 61 points per transect).
Data analysis

We modelled trends in browse biomass and potential harvest rates using ordinary least-squares regressions. Using our conceptual understanding of the effect of elephant on thicket structure, and hence potential browsing opportunities, we tested three candidate models: a null hypothesis (no effect, intercept only), \( y = \beta_0 \); linear model (constant decline), \( y = \beta_0 - \beta_1 x \); quadratic model (browsing opportunities reach a maximum at intermediate elephant densities, but decline toward the extremes), \( y = \beta_0 + \beta_1 x + \beta_2 x^2 \). In these models, \( y \) = potential browsing opportunity, \( x \) = intensity of utilization expressed as mean elephant density (Table 6.1), and \( \beta \) are constants. We evaluated model fit by testing for a significant contribution (\( \alpha = 0.05 \)) of the quadratic term to the linear model on the basis of an \( F \)-test (Crawley 2007). Because we had no information on realized elephant numbers (hence mean densities) at Hapoor water point, we excluded the data for this site from the regressions; these data are presented as the mean ± SD.

We further used multiple regression analysis to assess whether the number or area of elephant pathways or canopy height was associated with potential browsing opportunities for rhinoceros (using total browse biomass as the response variable). Model selection proceeded by systematically removing non-significant terms (i.e. terms with the smallest non-significant partial \( F \)-statistic) from the full-model, comprising all explanatory variables and their interactions. Because multiple regression analysis is sensitive to co-linearity between the explanatory variables (Wetherill et al. 1986), we used hierarchical partitioning procedures (package hier.part in R2.14.0; R Development Core Team 2011) to confirm model fit and evaluate the relative independent contribution of each explanatory variable to the minimal adequate model (Mac Nally 2000). In all instances, diagnostic plots of observed and fitted values and residuals were inspected for deviations from model assumptions.

RESULTS

Potential browsing opportunities

Nearly two-thirds of the canopy shrub species that we recorded at our sites are important food items for black rhinoceros in succulent thicket (Chapter 5), comprising both dominant and preferred foods. We detected no change in the incidence of these species between sites (total: mean = 18 spp., \( R^2 = 0.27 \), \( F_{1,5} = 1.50 \), \( P = 0.289 \); preferred: mean = 12 spp., \( R^2 = 0.05 \), \( F_{1,5} = 0.23 \), \( P = 0.656 \)), but recorded noticeably fewer species at Hapoor water point (total: 6 spp.; preferred: 4 spp.). Thus, with the exception of Hapoor, we
concluded that the predicted change in potential browsing opportunities was likely associated with a change in species abundance, rather than richness.

For all regression models of browse biomass and between-bite distances, model fit improved significantly when we added a quadratic term to the linear model (total biomass: $SS_{\text{linear-quadratic}} = 3718.70, P < 0.001$; preferred biomass: $SS_{\text{linear-quadratic}} = 3048.80, P < 0.001$; between-bite distances: $SS_{\text{linear-quadratic}} = 1.19, P < 0.001$). Browse biomass (total and preferred) and potential between-bite harvest rates initially increased with the intensity of utilization, reaching a maximum at the equivalent impact of roughly 1.6 elephant km$^{-2}$ (Fig. 6.2; Table 6.2). At the maximum, modelled estimates of total and preferred biomass were on average 223% and 254% higher, respectively, than that recorded in the absence of elephant (Exclosures), while potential between-bite harvest rates were 75% higher (i.e. on average, distances between bites decreased from 0.84 m to 0.21 m toward the maximum). With continued utilization, however, browsing opportunities declined and presumably followed a trend toward the minimum recorded near water (Fig. 6.2). Here, browse biomass was 17 (total) and 43 (preferred) times lower than the estimated maximum, while between-bite distances reached 2.6 m.

Table 6.2 Regression model equations and ANOVA tests of the relationship between browse biomass and within- and between-bite potential harvest rates and the intensity of elephant utilization.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Preferred model equation</th>
<th>$R^2$</th>
<th>$F$</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Browse biomass (g dry mass.m$^{-1}$)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total biomass</td>
<td>$y = 14.76 + 42.07x - 13.46x^2$</td>
<td>0.54</td>
<td>30.42</td>
<td>2, 52</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Preferred biomass</td>
<td>$y = 10.81 + 36.58x - 12.19x^2$</td>
<td>0.45</td>
<td>21.19</td>
<td>2, 52</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><strong>Potential harvest rate</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bite distance (m)</td>
<td>$y = 0.84 - 0.78x + 0.24x^2$</td>
<td>0.70</td>
<td>60.01</td>
<td>2, 52</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Bite mass (g dry mass)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portulacaria afra</td>
<td>Log ($y$) = 1.42 - 0.12x</td>
<td>0.07</td>
<td>4.68</td>
<td>1, 59</td>
<td>0.035</td>
</tr>
<tr>
<td>Euclea undulata</td>
<td>$y = 13.84$</td>
<td>0.02</td>
<td>1.19</td>
<td>1, 59</td>
<td>0.281</td>
</tr>
<tr>
<td>Schotia afra</td>
<td>Log ($y$) = 0.93 - 0.18x</td>
<td>0.20</td>
<td>14.05</td>
<td>1, 59</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Azima tetracantha</td>
<td>$y = 8.10$</td>
<td>0.04</td>
<td>2.34</td>
<td>1, 59</td>
<td>0.132</td>
</tr>
<tr>
<td>Capparis sepiaria</td>
<td>Log ($y$) = 0.70</td>
<td>0.06</td>
<td>2.14</td>
<td>1, 59</td>
<td>0.149</td>
</tr>
</tbody>
</table>

$y$, Potential browsing opportunity; $x$, Mean elephant density (Table 6.1)
CHAPTER SIX Elephant effects and black rhinoceros browsing opportunities

Fig. 6.2 Relationship between potential browsing opportunities for rhinoceros, expressed as browse biomass and between-bite distances, and the intensity of elephant utilization. Solid and dotted lines show total and preferred biomass, respectively; dashed lines show bite distances. Data for Hapoor water point are presented as the mean ± SD.

Generally, bite mass for the canopy dominants varied little with mean elephant density (Table 6.2). For *P. afra* and *S. afra*, however, bite mass (log transformed) declined linearly such that potential within-bite harvest rates were 89% (*P. afra*) and 159% (*S. afra*) lower at their minimum than harvest rates at the Exclosures.

**Correlates of potential browsing opportunities**

As expected, the number ($R^2 = 0.41; F_{1,54} = 36.84; P < 0.001$) and area ($R^2 = 0.33; F_{1,54} = 26.49; P < 0.001$) of elephant pathways increased with the intensity of utilization, eventually replacing the canopy shrubs near water (Fig. 6.3). Canopy height declined steadily along the same gradient ($R^2 = 0.33; F_{1,54} = 25.66; P < 0.001$).

Results from the multiple regression analysis showed that 40% ($F_{2,52} = 17.26; P < 0.001$) of the change in total browse biomass could be explained by elephant path area (coefficient = 26.47; SE = 9.87) and canopy height (coefficient = -11.97; SE = 3.78). Hierarchical partitioning confirmed our model selection and determined that for the best-
Fig. 6.3 Structural features of the thicket shrub community that respond to the effects of elephant, and likely correlate with potential browsing opportunities for rhinoceros. Solid, dotted and dashed lines show canopy height and the area and number of elephant pathways, respectively.

model, canopy height contributed more of the variation (54.1%) in browse biomass.

DISCUSSION

While the keystone role of elephant in shaping large herbivore communities is widely accepted (e.g. Owen-Smith 1988; Fritz et al. 2002, 2011; Kerley et al. 2008), the scale at which this manifests is not understood. By describing a unimodal relationship between potential browsing opportunities for black rhinoceros and elephant effects, our study provides insights into the dual role of elephant influencing herbivore foraging. This may be particularly significant as elephant typically regulate resource utilization in local communities, with consequences for herbivore dynamics and ecosystem functioning (Fritz et al. 2002, 2011). That is, at high densities elephant monopolize resources and limit herbivore abundances through competition, while at low densities these herbivores are unable to compensate fully; we presume the latter partly reflects a loss of the role of elephant in
facilitation. Thus, we expand on the studies that demonstrated increased browsing opportunities due to elephant (e.g. Rutina et al. 2005; Makhabu et al. 2006; Kohi et al. 2011) and those that inferred reduced availability as herbivore numbers declined (e.g. Fritz et al. 2002), by suggesting that the role of elephant in these processes scales with the intensity of their effects. Our study is matched only by that of Young et al. (2005) showing increased and reduced grass cover (the former mediated by interactions with cattle) in the presence of elephant, with consequences for zebra Equus burchelli abundances.

At our study site, more than 50% (and up to 70%) of the variance in potential browsing opportunities could be explained by the intensity of elephant utilization (expressed as mean densities). Elephant effects on preferred browse for rhinoceros appeared to be more complex (i.e. only 45% of the variance explained), which probably reflects the interplay of their food preferences (Chapter 5) and the differential responses of the canopy shrub species to the impacts (Kerley & Landman 2006; O'Connor et al. 2007; Kerley et al. 2008; Chapter 4). Nevertheless, our results partly supports the hypothesis of Kerley et al. (1999a) that elephant initially facilitate access to browse as pathways are formed through impenetrable thicket. This coincides with a decrease in the distances between bites, which we predict may increase potential harvest rates (through reduced search times) and reduce foraging effort (Spalinger & Hobbs 1992). These patterns are broadly similar to the patterns of browse facilitation described by Makhabu et al. (2006) using individual trees in Combretum-Capparis shrublands; i.e. trees with high accumulated elephant impacts had a greater number of twigs available for re-browsing, than trees with no or low impacts. The consequence of this was an increase in the abundance of browsing impala Aepyceros melampus (Rutina et al. 2005) and kudu (Makhabu et al. 2006). With continued elephant utilization, however, we show that browse biomass gradually declines and between-bite distances increase (thus reducing potential harvest rates and increasing foraging effort) as the pathways expand and coalesce and canopy height declines. At the end-point near water, the canopy shrubs are virtually completely replaced with paths (cf. Chapter 3), causing the near loss of browsing opportunities. We thought that the predicted decline in between-bite harvest rates at higher elephant densities could be off-set by rhinoceros potentially taking larger bites that would require less handling time and may be chewed more efficiently (Spalinger & Hobbs 1992). For example, moose Alces alces select larger bites as tree and stem densities decline and the distances between food patches increase (Shipley & Spalinger 1995; Shipley et al. 1998). Instead, we show that available bite sizes for the five canopy dominants either did not vary with mean elephant density, or were significantly lower at higher densities. This suggests that
rhinoceros may have limited opportunity to compensate for potentially reduced harvest rates at high levels of impact, causing a further increase in foraging effort. Although our predictions follow the functional response relationships of other browsers (e.g. Trudell & White 1981; Wickstrom et al. 1984; Spalinger et al. 1988), it will be important to explore how rhinoceros foraging responds, particularly as their selection of browse may be influenced by factors other than food availability (e.g. landscape topography, habitat heterogeneity, etc.; Lent & Fike 2003; Buk 2004; Morgan et al. 2009).

Our model of the change in potential browsing opportunities reflects the accumulated effects of elephant over time; i.e. the effects accumulate until the relationship switches from increased to reduced availability. The decline in browse availability is closely associated with habitat transformation in succulent thicket, as ephemeral grasses gradually replace the canopy shrubs removed by elephant (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995; Chapters 3 & 4). Importantly, this transformation brings about a loss of resources (e.g. organic matter, soil material) and ecological functioning that is nearly irreversible without active restoration (Vlok et al. 2003; Lechmere-Oertel et al. 2005a,b; Chapter 3).

Consequently, transformed thicket is usually considered less productive, leading to reduced herbivore fitness (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Milne & Kerley 2009). This suggests that browsing opportunities might not recover following intensive utilization by elephant, such that our model may be dominated by declining availability and an increased potential for competition (sensu Pringle et al. 2007, Odadi et al. 2011). We speculate that this implies a loss of the keystone role of elephant for rhinoceros foraging in succulent thicket. Elsewhere, however, the relative importance of elephant for herbivore foraging may be more dynamic on the basis of the seasonal availability of resources. In savanna habitats, for example, we expect elephant effects on browse availability to decline during the wet season when grasses dominate the diet, while the reverse may be true during the dry season when the diet is characterised by browse (Owen-Smith 1988; Kerley et al. 2008). Thus, analogous to the interactions within grazing herbivore assemblages (Arsenault & Owen-Smith 2002; Odadi et al. 2011), facilitative effects may dominate during the growing season, while competition between elephant and coexisting browsers may be more apparent during the dormant season. However, these ideas require further exploring by contrasting seasonal effects and by establishing the mechanisms through which these processes are expressed (e.g. Young et al. 2005; Odadi et al. 2011). Specifically, resource facilitation and competition may manifest through interactions between food availability and quality. For example, Hobbs et al. (2006) show that competition between elk *Cervus elaphus canadensis* and cattle arise as elk
densities increase and grass biomass declines; these grazing effects cause an increase in the nitrogen content and digestibility of the available food, which enhance cattle diet quality. We predict that changes in food quality brought about by the effects of elephant (Holdo 2003; Kohi et al. 2011) may modify our model of changing browse availability along a gradient of elephant utilization. Thus, the hypothesis of Musgrave and Compton (1997) that increased feeding damage by insects is a consequence of declining plant phenolics in AMC, provides circumstantial evidence that browse quality varied with elephant effects in our study. This suggests that quantifying the role of elephant in herbivore foraging requires a broader integrated approach that incorporates both food availability and quality.

While our study is limited by a lack of replication across sites and assumes an even distribution of elephant (but modified locally in relation to the availability of surface water) to estimate the intensity of their effects, we provide insights into the relative importance of elephant for rhinoceros foraging in succulent thicket. Thus, it is important to recognize that elephant densities in AMC have consistently exceeded recommended levels (Kerley & Landman 2006) and our estimated threshold (i.e. the equivalent impact of roughly 1.6 elephant.km$^{-2}$) for declining browse availability. On the basis of our model this implies that managing elephant at these densities may compromise the foraging-, and conservation opportunities of rhinoceros through increased competition. This is supported by evidence that elephant and rhinoceros compete for browse resources in AMC, causing rhinoceros to change their foraging strategies (Chapter 5) and activity patterns (Tambling et al. In press). We predict that the threshold between increased and reduced browsing opportunities will vary between herbivores, and in relation to species-specific food preferences. For rhinoceros, the threshold is similar for total and preferred browse, but it is unlikely that this will be the case among more selective foragers. This highlights the need to quantify the importance of elephant in the foraging of other large herbivores, before our model may be used as a tool in management. Instead, we demonstrate the role of elephant for rhinoceros foraging, linked to a potential loss of this role at higher densities, which should be recognized and managed.
CHAPTER SEVEN

General discussion

The aim of this study was to contribute toward our understanding of the resource use, impacts and interactions of megaherbivores (specifically elephant *Loxodonta africana* and black rhinoceros *Diceros bicornis*) in the succulent thickets of the Eastern Cape, South Africa. While megaherbivores dominate the biomass in this system (and most others across southern Africa), elephant are by far the most abundant and utilise the greatest share of the available resources. Consequently, I focused mostly on the role of elephant as their effects were expected to off-set that of rhinoceros through high population densities. This was further facilitated by nearly 60 years of scientific research on elephant resource use and impacts, of which the work in thicket is considered the most robust and comprehensive; in contrast, there exists scarily little information on these issues for rhinoceros anywhere. Despite this extensive database, however, much of the available information is of a descriptive nature. Thus, more broadly this study contributes toward developing a predictive understanding of the impacts of elephant, which informs the larger management debate. In this way I provide novel insights into three key issues, tested using a series of discreet studies in the succulent thickets of the Addo Elephant National Park (AENP): first, a mechanistic understanding of the influences of elephant (Chapters 2 & 4); second, predictive insights into elephant impacts on plant communities (Chapters 3 & 4); finally, an understanding of the knock-on-effects of the impacts for coexisting large herbivores (Chapters 5 & 6). The latter was tested specifically for black rhinoceros, which had the dual purpose of investigating the interactions between megaherbivores.

Developing a mechanistic understanding of elephant effects

Although elephant are considered keystone species (Owen-Smith 1988; Fritz *et al.* 2002, 2011; Kerley *et al.* 2008), the mechanisms of their influences on ecological systems are mostly inferred. For effects on plant communities, in particular, herbivory is often assumed the primary cause of declines in species richness, density and biomass (e.g. Laws 1970; Penzhorn *et al.* 1974; Moolman & Cowling 1994; Lombard *et al.* 2001). However, despite their broad diets (Chapter 2) and robust feeding style (Kerley *et al.* 2008) elephant impacts are not limited to what they eat. In fact, Paley (1997) estimated that more than half of their
daily food requirements are discarded during feeding. Thus, I contribute toward developing a mechanistic understanding of the effects by describing the diet of elephant and testing the assumption that the decline among Important Plants (i.e. the regionally rare and endemic small succulent shrubs and geophytes; Moolman & Cowling 1994; Lombard et al. 2001) is a consequence of herbivory (Chapter 2). I show that only about 18% of the species previously thought vulnerable to elephant herbivory, occur in the diet. Thus, for at least 82% of the Important Plants it is not clear whether the decline is due to elephant, and if so, by which mechanism (e.g. trampling, knock-on-effects, etc.). Identifying alternative mechanisms is particularly challenging given that many of the impacts have not been quantified and may have a range of knock-on effects (Chapter 6); the latter being particularly understudied. The accurate prediction of the impacts should therefore be based on establishing robust cause-and-effect relationships. In the absence of this, conservation management interventions (which by virtue of involving elephant are costly and attract significant public attention, and even litigation) may fail in their objectives. This is supported by evidence that the culling of elephant in the Kruger National Park did not prevent the loss of tall trees (Owen-Smith et al. 2006). The reasons are not clear, but some suggest that this tree mortality reflects an aging population that recruited during a period of low elephant densities (i.e. so-called megaherbivore release; e.g. Owen-Smith et al. 2006). Similarly, reducing elephant numbers per se may be a costly intervention if trees are pushed over during the strength training of elephant bulls; i.e. a potentially short-term effect caused by specific individuals (Midgley et al. 2005). This emphasizes the need, and supports the views of others (e.g. Sutherland et al. 2004; Valeix et al. 2008), that it is a priority to develop a predictive understanding of the mechanisms of elephant impact on biodiversity and ecosystem functioning.

**Predicting elephant impacts on plant communities**

Despite nearly 60 years of scientific research on the consequences of elephant for ecological systems (reviewed in Owen-Smith 1988, Conybeare 2004, Skarpe et al. 2004, Kerley & Landman 2006, Kerley et al. 2008), our ability to predict the effects is limited by few long-term quantitative studies. Where these data exist (Barnes 1983; Trollope et al. 1998; Van de Vijver et al. 1999; Eckhardt et al. 2000), the focus is on savanna systems that respond strongly to other drivers of ecosystem change (e.g. rainfall variability, fire frequencies, and the influences of coexisting large herbivores – Trollope et al. 1998; Skarpe et al. 2004; Hayward & Zawadzka 2010) and confound our understanding of the role of elephant. In
succulent thicket, elephant are the dominant herbivores and principal drivers of ecological patterns and processes (Stuart-Hill 1992; Kerley et al. 1995). Consequently, descriptions of the impacts in thicket are considered the most robust and comprehensive for South Africa, contributing significantly toward the larger management debate (Kerley & Landman 2006; Kerley et al. 2008). Particularly the work of Lombard et al. (2001) has raised considerable conservation concern as they demonstrated the local extinction of many rare and endemic plants. However, despite the importance of these accounts (reviewed in Kerley & Landman 2006), the majority measured the impacts by contrasting elephant-occupied areas with elephant exclosures. This further limits our ability to develop predictive insights (Kerley & Landman 2006), causing vastly contrasting hypotheses regarding the long-term response of thicket to elephant (Barratt & Hall-Martin 1991; Stuart-Hill 1992; Kerley et al. 1995, 1999b; Gough & Kerley 2006). Evaluating this may prove particularly important for the canopy shrub community that shapes both the structural and functional complexity of the landscape, and therefore the resilience of the system (Kerley et al. 1999b; Lechmere-Oertel et al. 2005a). Thus, using data collected regularly over a 31 year period and a unique experimental design (Barratt & Hall-Martin 1991; Lombard et al. 2001), I quantified more than 50 years of elephant effects on the canopy shrubs of the AENP (Chapter 4). Moreover, I tested spatial and temporal variations in the effects near water, where the impacts are expected to intensify (Chapter 3). Understanding such variations is critical, as water availability is increasingly used as a tool to manipulate elephant distributions in an attempt to maintain landscape heterogeneity (Pienaar et al. 1997; Gaylard et al. 2003; Owen-Smith et al. 2006).

Surprisingly, there exists no information for any system with elephant on which to base these management interventions (Owen-Smith et al. 2006). Thus, I expand on nearly 40 years of research in thicket (Penzhorn et al. 1974; Barratt & Hall-Martin 1991; Stuart-Hill 1992), and expand on other elephant studies that cover a wide temporal range (Barnes 1983; Trollope et al. 1998; Van de Vijver et al. 1999; Eckhardt et al. 2000), but are typically confounded by poor temporal replication. This part of the study provides the first explicit models of the long-term effects of elephant on any plant community that may be used to predict, monitor and manage the impacts.

Contrary to previous indications that the top-down foraging of elephant maintains the thicket shrub community (Stuart-Hill 1992; Kerley et al. 1995, 1999b), I confirm its vulnerability to transformation as the accumulated influences of elephant reduce community composition and structure (Chapters 3 & 4). The pattern of transformation is characterised by a gradual replacement of vulnerable species (e.g. those that recruit or regenerate poorly or are
susceptible to pollarding or uprooting - O’Connor et al. 2007) with a simple layer of ephemeral grasses and the loss of ecological functioning. Given that the decline continues even after 50 years of intensive use and that the trajectory of transformation is near-irreversible without active restoration (Vlok et al. 2003; Lechmere-Oertel et al. 2005b), I predict that the impacts will eventually bring about landscape-level degradation (i.e. where ephemeral grasses dominate over woody shrubs; cf. Gough & Kerley 2006) and a significant loss of biodiversity. In this way, the long-term influences of elephant are no different to those observed for domestic herbivores in thicket (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Kerley et al. 1995, 1999b; Lechmere-Oertel et al. 2005a,b). The potential for degradation accelerates near water and in areas with abundant water provisioning, as the impacts between water points expand and coalesce. Of significance is that shrub densities decline only in the vicinity of water where the generally persistent rootstocks are completely removed. This implies that the canopy shrubs might recover with a release in the intensity of utilization elsewhere (for example by expanding habitat, reducing population numbers and controlling local densities – Chapter 4), but that such a recovery is unlikely near water. The interaction between elephant and thicket might also be more dynamic during periods of increased rainfall, but this is probably off-set in the Addo Main Camp section by maintaining high densities (Hayward & Zawadzka 2010). Certainly, in more dynamic systems these interactions are more dynamic (e.g. Dublin et al. 1990), emphasising the need for long-term, predictive insights. Lechmere-Oertel et al. (2005b) argued that once the thicket system passes a threshold of self-restoration it loses resilience, tending toward an alternative state with reduced productivity (Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Milne & Kerley 2009). I predict that such a threshold is exceeded in the vicinity of water, that elephant have the ability to expand the alternative grassland-state across the landscape, and that this pattern of transformation can be interpreted using a state-and-transition model (cf. Westoby et al. 1989). These results show the consequences of maintaining high elephant densities (2–8 times recommended levels; Kerley & Landman 2006) and abundant water provisioning for succulent thicket.

Predicting the effects of elephant requires a detailed understanding of their spatial and temporal extent (Kerley et al. 2008). This should be based on robust insights into the distribution of the impacts between elements of biodiversity that typically differ in their vulnerability to elephant; the latter implying different rates and trajectories of change. However, with the exception of the work of Levick & Rogers (2008) on woody species and patch responses to large browsers, such relations are generally not established. This is
surprising given the recognition that ecological systems function across an integrated spatio-temporal hierarchy of patterns and processes (Wu & Loucks 1995; Pickett et al. 1994, 1997), and the change toward using the heterogeneity paradigm to monitor and manage elephant impacts (Biggs et al. 2008). Results from the present study show an uneven distribution of effects between all elements of biodiversity explored: from community composition and structure, to the structure of individual canopy species and ecological functioning (Chapters 3 & 4), to the availability of potential browse resources for black rhinoceros (Chapter 6). Importantly, these elements show different rates and trajectories of change with an increase in the intensity of utilization. That is, community composition and structure and associated ecological functioning decline, while the canopy species show varying responses. Although the trend in potential browse availability for rhinoceros excludes the long-term perspective of the other elements, it shows a unimodal response curve. The inconsistencies in these patterns are probably not limited to thicket, and I use the impacts of elephant on large trees in savanna systems to illustrate this. This example has the added advantage of demonstrating the importance of identifying the mechanisms of the influences of elephant (Chapter 2) as this determines the ecological consequences of the impacts, and therefore the rate and trajectory of change. While these findings confound our interpretation of the extent of the impacts, it demonstrates the importance of explicitly recognizing biodiversity and heterogeneity for the conservation management of elephant. Certainly, using more dynamic elements and including other confounding variables (e.g. fire, rainfall variability) will complicate this understanding even further. Thus, in addition to having long-term data to develop predictive insights, it will be critically important to establish the relations between the structural and functional attributes of ecosystems (or patterns and processes) at various spatial and temporal scales, and including a clear understanding of the mechanisms driving the changes (Chapter 2).

The contribution this study has made toward developing a predictive understanding of the influences of elephant was largely achieved through the visionary insights of Barratt & Hall-Martín (1991) during the late-1970s – from here the establishment of the long-term monitoring plots. Added to this is the approach of using the incremental expansion of the Addo Main Camp section to establish a gradient of elephant utilization, assuming that areas utilised for an extended period experienced relatively higher impacts, when compared to areas used for shorter periods (Lombard et al. 2001; Chapters 4 & 6). This approach has the advantage of estimating the intensity of use in terms of time of utilization (Chapter 4) and mean densities (using known elephant numbers; Gough & Kerley 2006; Chapter 6), but may be confounded by assuming an even distribution of elephant. Despite these opportunities, the
interpretations presented in this study emerge from a single study site (the Addo Main Camp section), dominated by a single vegetation type and characterised by a history of unusually high elephant densities - a phenomenon that spans much of the research on elephant in succulent thicket (Cowling & Kerley 2002; Kerley & Landman 2006). Thus, while the results of the hypothesis tests are robust, care must be taken when extrapolating these findings.

Finally, exclosure treatments are often considered appropriate controls (or baselines) against which to measure the impacts of elephant and other herbivores (Penzhorn et al. 1974; Barratt & Hall-Martin 1991; Stuart-Hill 1992; Levick & Rogers 2008). However, while their use clearly limits our ability to predict the effects, it is also argued that plant communities develop differently in the absence of megaherbivores (experiencing megaherbivore-release), which questions the suitability of exclosures as controls (Cowling & Kerley 2002; Kerley & Landman 2006; Kerley et al. 2008). In line with these predictions, I detected a significant change in the canopy shrub communities of the exclosures of the AENP over time, which was often similar in extent to that caused by elephant. Although this result is confounded by small sample sizes, it demonstrates the role of other drivers of community change (e.g. edaphic- and microclimatic effects, competition for light; Stuart-Hill 1992). This would suggest that using exclosures in monitoring sets a philosophical trap. In particular, by excluding such baselines the influences of elephant might be less dramatic: for example, models that describe and predict the impacts may vary significantly depending on the baseline (e.g. from exponential to linear), with obvious consequences for estimates of rates of change and vulnerability. These findings have important implications for monitoring and support earlier suggestions (Chapters 2, 3 & 4) that a predictive understanding of the influences of elephant requires a greater focus on developing robust causal relationships (Kerley & Landman 2006; Kerley et al. 2008).

Understanding the interactions between elephant and black rhinoceros

Few studies have investigated the consequences of the impacts of elephant for other large herbivores (Kerley et al. 2008). Surprisingly, where this information exists, the emphasis has been on demonstrating that elephant facilitate herbivore access to habitat and increase the availability and quality of food (Owen-Smith 1988; Makhabu et al. 2006; Valeix et al. 2011). This is despite clear evidence that elephant limit herbivore abundances across ecosystems through their ability to monopolise resources (Fritz et al. 2002, 2011; Valeix et al. 2008). Nevertheless, I expected the long-term impacts and high elephant densities of the
AENP to limit food availability for coexisting browsers, thus increasing the potential for competition. I tested this for black rhinoceros by assessing the degree of diet separation between these megaherbivores in relation to the seasonal availability of resources, and contrasting the diet and preferences of rhinoceros in the presence and absence of elephant using adjacent sites (Chapter 5). Notwithstanding the limitations of a lack of replication across sites, results support the predictions of competition theory as I show (1) a clear seasonal separation in resource use between these megaherbivores that increase as resource availability declines, and (2) rhinoceros change their selectivity in the absence of elephant by expanding and shifting their diet along the grass-browse continuum, and in relation to availability (Schoener 1974, 1982; Pianka 1976). Although black rhinoceros are generally considered strict browsers (e.g. Goddard 1970; Mukinya 1977; Hall-Martin et al. 1982; Owen-Smith 1988), the most significant shift in diet occurred as they increased their preferences for grasses in the presence of elephant. I predict that the lack of specialised grazing adaptations (such as the trunk for elephant – Owen-Smith 1988; Kerley et al. 2008) may increase foraging costs in rhinoceros, through reduced harvest- and handling-efficiencies of grasses (Foose 1982). In the short-term, this may be off-set by an enhanced tolerance for low quality food and by seasonally mobilising fat reserves (Owen-Smith 1988; Shrader et al. 2006). While the long-term fitness consequences require exploring, these may be masked by the metapopulation management strategy of black rhinoceros in the AENP. These results suggest that managing elephant at high densities compromises the foraging opportunities of coexisting browsers in small fenced areas (created through physical or figurative barriers - Hayward & Kerley 2009) and overlapping preferred habitats where the impacts intensify. This study is the first to suggest direct competition for food with elephant, and by testing this for black rhinoceros I provide insight into the role of competition in structuring the megaherbivore guild.

Despite the above evidence for competition, however, Kerley et al. (1999a) hypothesised that the formation of elephant pathways may facilitate access to habitat and food for herbivores in otherwise impenetrable thicket. Thus, it is likely that the role of elephant in these processes may be linked and that this varies with the intensity of utilization (Chapter 6). I tested this by quantifying potential browsing opportunities for rhinoceros along a gradient of elephant utilization (Chapter 4) in the Addo Main Camp section. I show that browse biomass and potential between-bite harvest rates initially increase with the intensity of elephant utilization as pathways are formed through impenetrable thicket. At the maximum, modelled estimates of total and preferred biomass are on average 223% and 254%
higher, respectively, than that recorded in the absence of elephant (Exclosures); potential between-bite harvest rates are 75% higher. However, with continued elephant utilization, browse biomass declines and between-bite distances increase as the pathways expand and coalesce and canopy height declines. This model of the change in potential browsing opportunities for rhinoceros reflects the accumulated effects of elephant over time; i.e. the effects accumulate until the relationship switches from increased to reduced availability. In succulent thicket the decline in browse availability is closely associated with habitat transformation (Chapters 3 & 4), which is virtually irreversible following the loss of ecologically important processes (Vlok et al. 2003; Lechmere-Oertel et al. 2005b). I speculate that this implies a loss of the keystone role of elephant for rhinoceros foraging in thicket. It will be important, however, to explore how rhinoceros foraging responds, particularly as their selection of browse may be influenced by factors other than food availability (e.g. landscape topography, habitat heterogeneity, etc.; Lent & Fike 2003; Buk 2004; Morgan et al. 2009). Elsewhere, the relative importance of elephant for herbivore foraging may be more dynamic on the basis of the seasonal availability of resources. For example, in savanna habitats elephant effects on browse availability is expected to decline during the wet season when grasses dominate the diet, while the reverse may be true during the dry season when the diet is characterised by browse (Owen-Smith 1988; Kerley et al. 2008). Thus, analogous to the interactions within grazing herbivore assemblages (Arsenault & Owen-Smith 2002; Odadi et al. 2011), facilitative effects may dominate during the growing season, while competition between elephant and coexisting browsers may be more apparent during the dormant season. However, these ideas require further exploring by contrasting seasonal effects and by establishing the mechanisms through which these processes are expressed (e.g. Young et al. 2005; Odadi et al. 2011). Nevertheless, this provides novel insights into the relative importance of elephant for rhinoceros foraging in succulent thicket.

Emerging management lessons

The issues around elephant management are complex and heavily value-laden (Biggs et al. 2008) and should therefore be approached with considerable caution where uncertainties exist. Scientific uncertainties arise mostly because the consequences of maintaining high elephant densities for extended periods remain unknown (Owen-Smith et al. 2006; Biggs et al. 2008; Kerley et al. 2008). Through the precautionary principle (Cooney 2004) these
uncertainties may be dealt with either by keeping elephant numbers low in the hope that this prevents the loss of biodiversity, or by allowing densities to increase until the levels of utilization that reduce diversity have been established (Owen-Smith et al. 2006). The decision will largely be driven by society through the values attached to elephant and biodiversity in general. However, the present study and the information reviewed in Kerley & Landman (2006) clearly indicate the consequences of maintaining high elephant densities for succulent thicket. For the AENP this is ahead of any evidence for density-dependent population regulation (Gough & Kerley 2006). Thus, in the absence of a clearer understanding of the ecological thresholds in thicket, this suggests that limiting elephant numbers should be a priority and a precautionary measure. While the efficacy of the management tools available to manage the impacts are rarely established (Van Aarde et al. 2006; Van Aarde & Jackson 2007), the research questions addressed in this study highlight some important management lessons for elephant in thicket and in small fenced areas in general. These include:

- Elephant piosphere effects are complex and our ability to predict and manage these effects will be limited in the absence of long-term data (Chapter 3). Instead, an integrated multi-scaled approach to monitoring the effects in relation to water is required that incorporates both spatial and temporal variations and the structural and functional attributes of ecosystems. Attempts to use water availability as a tool to manage landscape heterogeneity in the presence of elephant may be risky in succulent thicket that is vulnerable to such disturbances. For the Addo Main Camp section, in particular, the exceptionally dense network of water points compromises both biodiversity and conservation objectives as the utilization gradients that develop around water coalesce (Chapter 3). These results caution against the establishment of additional water points in recently included novel habitats, and suggest that reduced water provisioning in the area should be a management priority.

- The incremental expansion of the Addo Main Camp section, to support the steadily growing population and reduce the effects on biodiversity, did not achieve this goal and caused accelerated effects in novel habitats. This suggests that attempts to use range expansion as a tool to reduce the impacts requires careful consideration (Van Aarde et al. 2006; Biggs et al. 2008). In particular, such management interventions may fail in their objectives if implemented without limiting population numbers and controlling local densities (e.g. by reducing surface water availability; Druce et al. 2008).
• Developing a predictive understanding of the spatial and temporal variations of elephant impacts between elements of biodiversity and the mechanisms driving these changes are key to their management. This implies that the effective conservation management of elephant can only be achieved through the careful, scientific design of monitoring programmes.

Opportunities for future research

As is the case with most scientific studies, more questions were raised during the course of this study than can be answered. Based on the insights developed, the following are important outstanding research opportunities that may contribute toward understanding the interactions between these megaherbivores and their resources:

• The role of rhinoceros as a driver of ecological patterns and processes in succulent thicket (and elsewhere) remains severely understudied. In fact, apart from the work presented in this thesis, there exist only a handful of published records of their diet and even fewer of the influences on plants. Thus, there exists a need to develop predictive insights into rhinoceros resource use and preferences and determine their effects on plant communities, particularly as the latter may be similar in extent to that of elephant.

• For elephant, our interpretation of their use of resources in thicket is focused in the Addo Main Camp section of the AENP, at a time where some vulnerable plant taxa had been removed. It is likely, however, that elephant diet and preferences vary spatially (between thicket types) and temporally (seasonally and annually) in relation to the availability of resources. Evaluating the role of herbivory as a threat to plant diversity requires a broader understanding of these variations. This information may prove useful for elephant in novel habitats, with abundant vulnerable taxa and accelerated impacts (Chapter 4).

• Developing a predictive understanding of the influences of elephant on plant communities and associated biological diversity in succulent thicket and elsewhere requires a greater focus on (i) establishing robust causal relationships between elephant and the impacts, (ii) determining the spatial and temporal extent of the effects between elements of biodiversity, and (iii) evaluating potential knock-on-effects. Overall a rigorous research programme that incorporates the natural history of elephant is required that tests hypotheses on the interactions between the impacts, elephant
densities and ecological patterns and processes. This should be developed across the Eastern Cape where the reintroduction of elephant into various private reserves presents a potential series of replicated experiments. Specific research foci for thicket may include the following:

- The mechanisms of elephant impact responsible for the decline and/or loss of Important Plants cannot be inferred from available information. It would be useful to monitor the fate and mechanisms of change for a large sample of these plants (for example by observing marked individuals) in relation to the landscape features that constrain the impacts (e.g. landscape topography, surface water availability).

- Other drivers of ecosystem change (e.g. rainfall variability and the influences of coexisting large herbivores) confound our interpretations of the role of elephant. These variables and their interactions should be included in models that describe the impacts, particularly as the role of climate will increase over time. Recent fluctuations in rainfall in the region of the AENP appear to have brought about a recovery of the thicket shrub community in the presence of elephant (M. Landman Personal observation). It may be possible to evaluate this using the long-term monitoring plots of Chapters 3 & 4. This would further contribute toward our understanding of the recovery potential of thicket (providing insights into its resilience), which is otherwise considered near impossible without active restoration.

- Elephant movements and impacts are constrained by various biotic and abiotic factors, of which I only tested the influences of surface water availability (Chapter 3). Factors that require further exploring include landscape topography and the availability and quality of food.

- In light of extensive evidence for the consequences of elephant for biological diversity, there exists an urgent need to establish the ecological thresholds in thicket, and the indicators that may prove useful in monitoring. This should be based on a robust understanding of the distribution of the effects between elements of biodiversity (incorporating both patterns and processes) at various spatial and temporal scales. While it is clear that the canopy dominants investigated in Chapter 4 may not provide such monitoring insights, the
significant decline of the tree-succulent *Portulacaria afra* at sites with abundant water provisioning requires further exploring.

- The knock-on-effects of elephant, particularly for large herbivores, remains understudied, presumably because the mechanisms are unclear. The long-standing pattern of declining bushbuck *Tragelaphus scriptus*, bushpig *Potamochoerus porcus* and Cape grysbok *Raphicerus melanotis* numbers in the presence of elephant in the AENP requires testing by investigating the influences of reduced food and unfavourable habitat modification. Furthermore, it will be important to test the potential dual role of elephant in the foraging of these browsers (Chapter 6) to determine the level of elephant utilization that contribute positively toward these opportunities in thicket.

- Despite their dominance and the importance of elephant and black rhinoceros as drivers of ecological patterns and processes in succulent thicket and elsewhere, the interactions between these megaherbivores are poorly studied. For elephant and rhinoceros in thicket it will be useful to identify the mechanism (exploitative and/or interference) of the competitive interaction described in Chapter 5, particularly as both reduced browse availability and agonistic interactions have been recorded for the Addo Main Camp section. Finally, it will be necessary to explore how rhinoceros foraging might respond to the model of browsing opportunities described in Chapter 6 to determine the realised role of elephant in rhinoceros foraging and conservation.
REFERENCES


References


*References*


The issues around elephant management are complex and heavily value laden (Biggs et al. 2008) and should therefore be based on robust science and approached with considerable caution where uncertainties exist. We, therefore, welcome the opportunity to expand on the debate around the drivers of the decline among Important Plants in the Addo Elephant National Park (Landman et al. 2008), following Midgley’s (2009) contribution. We are, however, not supportive of his conclusion that elephants should be damned without evidence of their causative involvement in the decline of Important Plants, but rather reiterate the need to understand the mechanisms of this decline.

In developing his conclusion, Midgley (2009) offers some arguments that apparently bring into question the results presented. He firstly questions the applicability of microhistological faecal analysis for diet description, offering an opinion as to the disproportionate retention of grass material over other plant species. This technique has been extensively validated (e.g. Hansen et al. 1973; Todd & Hansen 1973; Johnson & Wofford 1983), although admittedly not for hindgut fermenters, such as elephant. Given their relatively poor digestion compared with ruminants, it is however reasonable to expect that elephants would suffer fewer such biases than the ruminants on which these validations are based. Furthermore, it is revealing that some of the species which Midgley (2009) suggest should not be well represented (species with ‘swollen stems or with succulent leaves’ – represented in this study by members of the Asphodelaceae, Crassulaceae, Euphorbiaceae, Portulacaceae and Viscaceae families) are actually very well represented in the estimated diet (contributing roughly 15%). The implication that grasses would be overrepresented is also not supported by the data that show relatively little grass (in relation to what is available) in the diet (roughly 34%). Finally, Landman et al. (2008) point out that the results of these analyses concur well with the diet described by direct observation. Based on the above, we are not convinced that these diet data should be discarded.

Midgley (2009) then correctly points out that elephant impacts are not limited to what they eat. This is supported by research in the Addo Elephant National Park. For example, Paley (1997) estimated that more than half of the equivalent of elephant daily food requirements was discarded during the feeding process, while Lessing (2007) showed that
elephants discarded roughly 25% of harvested forage material (Kerley et al. 2008). However, this discarded material is typically from large plants on which elephant feed robustly. We suspect that this would not be the case with the small plants typical of the Important Plants. This does however not change the conclusion regarding the role of elephant herbivory.

We agree with Midgley’s (2009) next point regarding the response of plants to elephant herbivory, and this has been pointed out elsewhere (Kerley et al. 2008). He makes an excellent point in suggesting that plant responses, plant growth rates and the total biomass killed by elephant needs to be determined. It should also, however, be recognized that although they are the dominant herbivores in terms of biomass (e.g. Stuart-Hill 1992), elephants are not the only herbivores in the Addo Elephant National Park. Is it, therefore, valid to blame only the elephants for the decline in Important Plants, or focus exclusively on elephants in measuring impacts? Kerley et al. (1999a) suggested that the role of tortoises (which prefer to feed on Important Plants) in the decline of Important Plants needs to be tested. Such interesting and valid avenues of research will be ignored if we presuppose that elephants are the only drivers of this process.

Midgley (2009) further suggests that the food availability assessments could not demonstrate selectivity due to the inclusion of the Nyathi section (separated by a road and railway line from the main elephant area) in the analyses. This interpretation is not correct, as food availability was not assessed in Nyathi. We are also not aware of any data showing that there are fewer Important Plants in Nyathi compared with the main elephant area. The most recent vegetation map (Mucina & Rutherford 2006) shows that nearly 50% of the area of Nyathi comprise thicket types that occur in the main elephant area. Our data therefore support the concept of selective feeding by elephant.

We are in full agreement of his next point as we make it ourselves in interpreting our findings: one of the possibilities for the paucity of Important Plants may be because they have already declined. Midgley (2009) suggests that this would be to the point where ‘such plants will not be available to be selected as food anymore’. But, why then do we see an ongoing decline as shown by Lombard et al. (2001)? If Important Plants are too rare for elephants to bother with, should the abundance of these species not stabilize at some low level of abundance? Alternatively, some other process (which we are ignoring in our focus on elephants) is coming into play. It is, furthermore, not clear why Midgley (2009) also concludes that knowledge of elephant diet will be of little value in identifying possible impacts in other areas.
To return to Midgley’s (2009) conclusion that ‘elephants should be seen as major drivers in the decline of Important Plants in the Addo Elephant National Park, we advise caution before implementing management interventions. One of the lessons we should have learnt from the culling of elephants in the Kruger National Park was that this did not necessarily achieve the intended management objectives. So, killing large numbers of elephants did not prevent the loss of tall trees (Owen-Smith et al. 2006). The reasons for this are not clear, but there are suggestions that tree mortality may reflect an aging population that recruited during a period of low elephant numbers about a century ago (e.g. Owen-Smith et al. 2006). Alternatively, trees may be pushed over by bull elephants in a process to develop their strength (Midgley et al. 2005). This latter interpretation is a classic example of a mechanism that is apparently not only of scientific interest, but also has profound value from a conservation management perspective – killing a few elephant bulls will not necessarily relieve the pressure on the trees.

In conclusion, we reemphasize the need, and support the views of others (e.g. Sutherland et al. 2004; Valeix et al. 2008) that it is a priority to develop a predictive understanding of the mechanisms of elephant impact on biodiversity and ecosystem functioning. In the absence of a predictive understanding, conservation management interventions (which by virtue of involving elephants will be costly and attract significant public attention, and even litigation) may fail in their objectives. It is only by demonstrating appropriate cause-and-effect relationships between elephants and ecosystem change that we will have confidence in the assumption that elephants are responsible for the observed changes.
Appendix 2 Percentage contribution of plant species to the diet of elephant in the Addo Elephant National Park. + indicates significantly preferred and - significantly avoided.

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<th>Plant species</th>
<th>% Diet</th>
<th>Family</th>
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Appendices: 111
Appendix 3 Best-fit mixed-effects logistic growth models of (A) the ratio between areas of run-on and run-off, and (B) the proportion of intact mounds, as a function of distance from water.
Appendix 4A Mean accumulation curves (50 random iterations) of plant species recorded per faecal sample for elephant and black rhinoceros.
Appendix 4B Percent contribution (mean ± SD) and preferences of principal dietary items identified in the diet of elephant and black rhinoceros in the Addo Elephant National Park. Symbols + or – show significant preference or avoidance, respectively; dashes indicate that the item was not recorded in the diet; n-PDI, non-principal dietary item.

<table>
<thead>
<tr>
<th>Family</th>
<th>Principal dietary item</th>
<th>Elephant</th>
<th>Rhinoceros (Elephant present)</th>
<th>Rhinoceros (Elephant absent)</th>
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<tr>
<td>Poaceae</td>
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<td>2.9 ± 3.3 +</td>
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<tr>
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<td>n-PDI</td>
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<tr>
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<td>1.7 ± 1.9 +</td>
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<td><strong>Woody shrubs</strong></td>
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<td>n-PDI</td>
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<td>4.0 ± 3.3 +</td>
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Number of principal dietary items: 16, 24, 43