ELEPHANT IMPACTS ON BIODIVERSITY

STATUS OF BIODIVERSITY RESEARCH IN THE KNP

RINA GRANT, ANDREW DEACON, CHRIS MARGULES, LIZ POON

Introduction

A major theme of the current KNP Management Plan is biodiversity. The biodiversity objective includes a major 'ecosystem objective', which in turn is broken down into atmospheric ecosystem, aquatic ecosystem, terrestrial ecosystem and the impact of alien species objectives. Research and management objectives need a description of biodiversity as it is and as a benchmark against which to measure the success or failure of research and management programs. This success or failure is tested against this biodiversity benchmark with a monitoring program.

It is unlikely that a compilation of any existing field records of species locations will be sufficient for this purpose. Only a few small places in the world with a long history of field studies can lay claim to comprehensive and adequate data bases of species locations and even those are really only adequate for some components of the biota at some scales. Field records are often collected in an opportunistic manner, due to time and financial constraints. The species recorded are therefore the ones of interest to the collector and the places they are recorded from are the places where those species of interest are most likely to be found. Accordingly, extensive and often detailed collections of field records in museums and herbaria, and in natural resource management agencies, cannot be used to represent geographical coverage or biota coverage. The best way to acquire a representative picture of the biodiversity is to conduct a systematic ecological field survey.

An ecological survey is the start of the science-application chain as it applies to the problem of protecting biodiversity. This chain, from basic science to management runs from field survey (or, traditionally, field observations) and the various theoretical underpinnings used to design the survey, through data analysis and theoretical conclusions, to recommendations on management options and critical evaluation of their success or failure. The chances of success are enhanced if this whole chain is pursued systematically and in such a way that accumulated experience is used to modify any part of the chain as this becomes necessary or useful.

This report focuses on the start of the chain, the survey design. A sound design directly addresses the question of where, in the landscape, to make field collections of species' records so that these collections are a representative sample of what is actually there. Such a design requires (i) a conceptual framework based on ecological theory; (ii) design principles for locating field sample sites based explicitly on the conceptual framework; (iii) a determination of which measurements to make at the chosen field sites to facilitate data analysis in addition to records of the target species; and (iv) appropriate analytical methods for predicting wider distribution patterns from the point samples that field records represent. Once the survey is complete, an ongoing monitoring program can then be designed based on a sub-set of field sample sites nested within the survey sites. This brief introduction and the discussion below relies heavily on Margules & Austin (1994) and Haila & Margules (1996).

The idea is to obtain an accurate sample of species' distribution patterns so that the wider geographic ranges can be predicted accurately from this sample. Monitoring can then be used to detect range expansion or contraction. Records of the presence or absence of species could be used for this purpose. For different management purposes it will be necessary to get an indication of abundance patterns and changes in vegetation structure for example.

While environmental variables are good predictors of species distribution patterns, ecological and evolutionary history play important roles. In ecological time, past management practices, fire frequency and intensity and herbivory, for example, mediate the responses of species to underlying environmental variables. Perhaps these disturbances have a greater impact on abundance and structure than species composition, but no doubt they can help determine distribution patterns. Similarly, species with relict distributions or vicariant species occupying similar but geographically isolated niches might be detected with geographic replication of samples within environmental stratifications, but may not be modeled adequately for predictive purposes. Plant species in the hyper-diverse Fynbos (Cowling 1992) and south western Western Australia may be cases in point.

The conceptual framework

Field records are often the only data available for distribution maps, the limitations and spatial bias inherent to collections of field records of species is exemplified in Fig. 1, a map of reptiles and frogs in KNP (Zambatis & MacFadyen 2002).

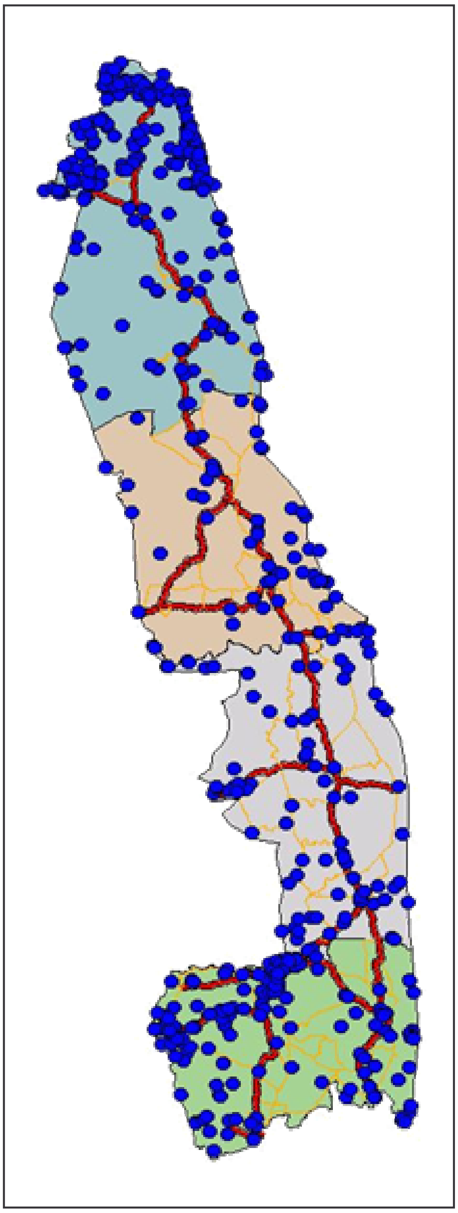

Fig. 1. Existing field records of frogs and reptiles within KNP (Zambatis & MacFadyen 2002).

Plant ecologists use the continuum concept (Gleason 1926) to explain observed species distribution patterns. This concept holds that each species has a unique distribution within the environment determined by its genetic make-up and physiological requirements, which is constrained by competitive interactions with other species. Herbivory and fire are other obvious constraints. This is closely related to the niche concept used by animal ecologists (Whittaker et al 1973; Austin 1985) and similar continuum patterns have been observed for animals (e.g. Rotenberry & Wiens 1980; Wessels et al 1998).

This is an appropriate conceptual framework for ecological survey design because it links species distribution patterns to variation in the environment.

KNP survey design

Survey will accurately sample the true distribution patterns of the species recorded. Therefore, a network of sites, that would accurately represent species distribution in an area, need to be identified to cover all possible habitats. Although the initial aim of the project was to design a network of sites for comparable future species surveys for the area north of the Olifant river, there was interest from the KNP researchers to extend the project to design such a network of survey points for the entire KNP.

The suggested survey design protocol for KNP consist of the following steps:

Stratify KNP using variables that reflect the major environmental gradients within the park.

Geology and rainfall are well known predictors of species distribution patterns in KNP at the Park-wide scale. The rainfall surface was divided into six classes differing by 100mm each. This was then intersected with 15 geological types (Bristow & Venter 1986). Potentially this overlay could give rise to 90 combinations of rainfall and rock type, but in fact only 46 of these combinations occur in KNP.

Some of these combinations were represented by very few 1x1' grid cells (see Figure 2 below). There were 10 combinations with fewer than 15 grid cells and in all 10 cases these were the result of different rainfall classes on the same geology. The actual rainfall for each grid cell in these rare combinations was examined by a team of KNP experts. These combinations were either merged with the nearest rainfall class on the same geology, or were kept separate if the team felt it represented an unique ecosystem. Six of the 10 were merged, leaving four small combinations.

Determine the number of field sites needed to sample each ED adequately.

A field site consists of a number of transects, determined by the number of terrain units present at each site.

A total of 205 sites were selected using these criteria. Each site consists, in turn, of a number of terrain units to be determined at the site. If, on average, there are 5 terrain units per site, there would be a grand total of 1,025 quadrats to be surveyed in the entire KNP as a minimum set.

Field measurement.

Field surveys will consist of two aspects:

- A Habitat component survey that will act as surrogate for species presence/absence and soil- associated processes and available habitats. (The predicted results form these surveys are presented as tables and maps in the map appendix)

- A species survey, that will record presence/absence of a specific species, and will be used as ground-truthing for the habitat / surrogate survey.
    - This will be achieved by encouraging visiting scientists to collect specimens on the selected sample sites.

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EVALUATION OF THE SMALL VERTEBRATE HABITAT REQUIREMENTS WHICH CAN BE INFLUENCED BY ELEPHANT

ANDREW DEACON

An evaluation of all the faunal habitats in the KNP were done in order to establish the main habitat categories that reflect the minimum requirements of the vertebrate species. By implication these species will be lost when the specific habitat is lost, or gained when the habitat expands.

It should be noted that this is not a consideration of the optimal habitat, but rather the minimum habitat required to support the animal. The reason for this approach is that if the optimal habitat is lost due to some changes in the environment, the animal will still be able to survive in the remaining supportive habitat. For example: trees with cavities are very good habitat for rock monitors; should these trees disappear, this reptile will persist by inhabiting rocky outcrops, which will then be the minimum habitat required.

Table 1. The minimum breeding habitat required by the 35 frog species that occur in the KNP:

Frog species in the KNP	35	35	
Non-vegetative sites Aquatic	2	33	94.2%
Amphibious	31		
Vegetative sites Low to Short tree (2-10m)	2	2	5.7%

Table 2. The minimum sheltering habitat required by the 117 reptile species that occur in the KNP:

Reptile species in the KNP	117	117	
Non-vegetative sites Aquatic	7		
Ground (burrowing, terrestrial or termite mounds)	72	102	87.1%
Outcrops	23		
Vegetative sites Tall shrubs (1-2m)	3		
Low to Short tree (2-10m)	5	14	11.9%
Tall to High tree (10-20m+)	6		
Other Dead tree	1	1	0.8%

Table 3. The minimum nesting habitat required by the 468 birds species frequenting the KNP:

Bird species in the KNP	468	468	
Birds not breeding in the KNP:			
Migrants – not nesting in KNP	50	54	11.7%
Birds not resident – not nesting in KNP	4		
Birds breeding in the KNP – nesting sites:		413	88.3%
Non-vegetative sites Cliffs and bedrock	18		
On the ground	65	102	21.7%
Tunnel in soil or banks	19		
Non-woody vegetative sites Reedbeds	20		
Clumps of vegetation (shrubs, brushwood)	15	67	14.3%
Dense grass	32		

Woody vegetative sites* Tall shrubs (1-2m)	18	28	5.9%
Low tree (2-5m)	10		
Short tree (5-10m)	47	187	40.0%
Tall tree (10-20m)	116		
High tree (>20m)	24		
Total woody plants	*215*	*215*	*45.9%*
Other Trees in water	11	14	2.9%
Dead trees (logs)	3		

*Size classes according to Edwards (1983).

Table 4. The minimum sheltering habitat required by the 148 mammal species that occur in the KNP:

Mammal species in the KNP	148	148	
Non-vegetative sites Aquatic	4	115	77.7%
Ground (terrestrial, burrowing)	88		
Rocky outcrops	8		
Caves	15		
Vegetative sites Low to Short tree (2-10m)	9	23	15.5%
Tall to High tree (10-20m+)	14		
Other Sheltering habitat not known (mainly certain bats)	10	10	6.7%

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Table 5. P ercentage of vertebrate species in KNP that will be affected by a significant change in the specific habitat.

<table>
<tr><th></th><th>**Bird species</th><th>**Reptile habitats</th><th>**Frog habitats</th><th>**Small mammals</th><th>Invertebrates *</th></tr>
<tr><td>No of species in KNP</td><td>468</td><td>117</td><td></td><td>9.5 %</td><td rowspan="2">10.3 %</td></tr>
<tr><td>Tall trees 10 –20 m</td><td>30 %</td><td>5.1 %</td><td></td><td rowspan="2">6.1 %</td></tr>
<tr><td>Trees 5 – 10m</td><td>10 %</td><td></td><td></td><td></td></tr>
<tr><td>Trees & shrubs 2 – 5 m</td><td>2 %</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Shrubs 1 – 2 m</td><td>4 %</td><td>5.1 %</td><td>5.7 %</td><td></td><td></td></tr>
<tr><td>Grassland</td><td>7 %</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Open area</td><td>14 %</td><td>61.5 %</td><td></td><td>59.5 %</td><td></td></tr>
<tr><td>Logs & stumps</td><td>0.06%</td><td>0.9 %</td><td></td><td></td><td></td></tr>
<tr><td>Riverine vegetation</td><td>6.6 %</td><td>6 %</td><td>5.7 %</td><td>2.7 %</td><td>44.9 %</td></tr>
<tr><td>Dung</td><td></td><td></td><td></td><td></td><td>41 %</td></tr>
</table>

** Study done Makalali Private Game Reserve see Govender N in the Biodiversity chapter.*

*** From literature survey of species habitat requirements in the KNP see Deacon A in the Biodiversity chapter*

Table 6 Tree species specially favoured by elephant

Elephant density/km^2	Favoured species disappears with utilization	Favoured species tolerant to utilization	Species that disappear with intense utilization	Species targeted when elephant move into a new area
Sclerocarya birrea		x	x	x
Euphorbia ingens	x			
Cussonia paniculata	x			
Schotia brachypetala		x		
Pappea capensis		x	x	
Acacia caffra			x	
Euclea crispa			x	
Faidhervia albida			x	x
Acacia xanthophloea		x		
Aloe martlotthi	x			
Elephantorrhiza burkei	x			
Adansonia digitata		x	x	
Colophospermum mopane		x		
Grewia bicolor		x		x
Grewia flavescens		x		x
Grewia monticola		x		x
Hyphaene coeriacea		x		x
Ficus sycomorus		x	x	
Portulacaria affra		x		

ASSESSING THE ELEPHANT INFLUENCE ON THE STRUCTURE OF AFRICAN UNGULATE COMMUNITIES USING LONG TERM AND SEMI-EXPERIMENTAL DATA.

MARION VALEIX HERVE FRITZ. SIMON CHAMAILLE-JAMMES. MATHIEU BOURGAREL. FELIX MURINDAGOMO.

Abstract

The role of interspecific competition in structuring large herbivore communities is often considered central but is difficult to demonstrate without experiment, and experiments are very difficult to carry out on large ungulate communities. Here, we investigate the existence of competition using long-term census data. The elephant population in Hwange National Park, Zimbabwe, was culled and maintained stable up to 1986, and has tripled since then. Animal population trends were available since 1967 through water pan censuses. This situation provided a quasi-experimental context ideal to test hypotheses about interspecific competition drawn from a previous comparative study at a regional level. We tested the hypothesis that because of an asymmetrical competition for browse in the dry season, an increase in elephant numbers should: i)- be correlated to a decrease in mesobrowsers and mesomixed-feeders, ii)- should not affect mesograzers and iii)- should not affect another megaherbivore. Eight out of the twelve mesoherbivores studied confirm our predictions. The four browsers studied have decreased since 1986 when elephants started to increase. Four out of the eight grazers studied seem unaffected by elephant increase whereas the four others differ from what we had predicted, *i.e.* decreased after 1986. The giraffe, another megaherbivore, seemed unaffected by elephant increase. The results only partly corroborate the hypothesis suggested in previous studies. As some of the grazers declining were dependent on surface water and/or riparian habitat, and that the two largest mesobrowsers and mesomixed-feeders were also water-dependent, it could be that competition for water was in fact a leading factor. We then discuss the possibility of a diversity of mechanisms, including indirect effects of habitat through predation, and the necessity to investigate habitat modification and water competition. This study suggested that some mesoherbivores could suffer competition from elephants but given the importance of this issue, and as other studies challenge this hypothesis, it is necessary to further investigate alternative explanations such as the impact of climatic episodes.

Keywords: mesobrowsers-mesograzers. interspecific competition. Megaherbivores. population trends. water pan census.

Some notes on the impacts that elephants (*Loxodonta africana*) have on Southern Ground Hornbills (*Bucorvus leadbeateri*)

K. Morrison and A. Kemp

Southern Ground Hornbills (*Bucorvus leadbeateri)* are classified as Vulnerable according to the Eskom Red Data Book of Birds on South Africa, Lesotho and Swaziland (Barnes 2000). This is due to the species having experienced a 50% decline in range and more than a 10% decline in numbers over the past three decades. However, the results of a recent Population and Habitat Viability Assessment workshop suggest that the species may actually be Endangered (Daly *et al.* in press.).

Southern Ground Hornbills require a mosaic of habitat types for foraging and nesting, including savanna, grasslands and woodland areas (Kemp 1995).

Nest sites

Southern Ground Hornbills nest in cavities with a median internal diameter of 40 cm either in trees (96%) or in cliff faces (4%) (Kemp & Begg 1996; Knight 1990). In a study of nesting trees in the Kruger National Park, 96% of all Southern Ground Hornbill nests were found in 12 tree species, with five of these tree species housing 80% of the nest sites: *Combretum imberbe, Ficus sycomorus, Diospyros mespiliformis, Sclerocarya birrea* and *Adansonia digitata* (Kemp & Begg 1995). Nest sites were found in both live and dead trees, with a mean nest height of 4.6 m.

Southern Ground Hornbills are absent from regions lacking tall trees, and there is strong evidence to suggest that nesting sites are a significant factor limiting breeding success (Kemp & Begg 1996). In the Kruger National Park, Kemp & Begg (1996) found that the estimated mean annual cavity loss was 7.7%, although the rate of cavity formation was not determined. Elephants, fire, wind, floods and lightening are all likely to play a role in the loss and formation of nesting sites (Henley & Henley 2005; Kemp & Begg 1996). Henley & Henley (2005 *in press.)* suggested that the majority of mature woody tree species felled by elephants in the Associated Private Nature Reserves were not tree species used predominantly by Southern Ground Hornbills for nesting. However, *Sclerocarya birrea* is one of the top five tree species felled by elephants in the south eastern basalt zones in the Kruger National Park. Although the felling of a tree will result in the loss of nest site, the extent of this loss requires further investigation. The potential of nest cavity formation as a result of the feeding activities of elephants, however, needs further investigation, as does the potential increase in vulnerability of trees to fire following bark puncturing and stripping by elephants.

Impact of elephants on Southern Ground Hornbill foraging

In drier seasons, when wildlife is more concentrated around watering points, Southern Ground Hornbills have been observed foraging on dung beetles as they moved between the middens, of particularly elephants and rhino over a concentrated area (Kemp 2005 *pers comm*).

Implication for management / decision making

Elephants do have an impact on the nesting sites and foraging habits, in the drier seasons, of Southern Ground Hornbills. These impacts can be both beneficial and detrimental. Research is required to fully understand the nature and extent of this relationship.

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BRIEF ON THE IMPACT OF ELEPHANT OVER-POPULATION ON TREE-NESTING VULTURES AND OTHER RAPTORS IN NATIONAL, PROVINCIAL AND PRIVATE PARKS AND RESERVES

ANDRÉ BOTHA,

The continuous escalation of elephant populations in southern Africa, especially those in fenced National, Provincial and Private Parks and Reserves has had various impacts on the habitats and species that share those areas with these mega-mammals. The Birds of Prey Working Group of the Endangered Wildlife Trust is particularly concerned with the impact of elephant populations on tree-nesting vultures and raptors in such areas and believe that, should such elephant populations not be sustainably managed, these families of birds could be severely affected due to the destruction of suitable nesting sites.

The following tree-nesting vulture and raptor species are listed in the *Red Data Book of Birds of South Africa, Lesotho and Swaziland (2000)* and are believed to be affected by the abovementioned threat:

- **Vulnerable**
  Hooded Vulture
  African Whitebacked Vulture
  Lappetfaced Vulture
  Whiteheaded Vulture
  Tawny Eagle
  Martial Eagle
  Southern Banded Snake Eagle
  Bateleur
  Pel’s Fishing Owl
- **Near-threatened**
  Secretarybird
  Bat Hawk
  Ayre’s Eagle
  Crowned Eagle

Management implications

Although limited quantitative data is currently available in this regard, reports on negative impacts on such species have already been received in the last year from provincial reserves in Limpopo and KwaZulu-Natal as well as conservation areas further afield in Swaziland, Botswana and Namibia. In fact, observations in Swaziland suggest that species such as African Whitebacked- and Lappetfaced Vultures prefer to avoid nesting in areas with high densities of elephants. The Birds of Prey Working Group, together with partners such as BirdLife South Africa, is currently attempting to gather more information in this regard and would be happy to share such information once it has been collated and analysed.

We would therefore like to urge decision-makers to take this aspect into consideration when making decisions about the future management of elephant populations in conservation areas.

The effect of elephant habitat alteration on ground dwelling invertebrate diversity

Navashni Govender

Introduction

Balancing increasing elephant numbers with biodiversity conservation in reserves has become a concern for many protected area managers. Elephants are considered important agents of disturbance creating heterogeneity and thus contributing to the maintenance of biodiversity. However elephants also damage vegetation through their destructive feeding habits, and this has led to pressure to reduce elephant populations in many reserves. Quantitative data on the impact of elephants on invertebrates, the main component of biodiversity at the species level, are lacking. The aim of this study was to assess the effect that habitat alteration by elephants has on the diversity of selected ground-dwelling invertebrates (ants, centipedes, millipedes, spiders, scorpions and termites) through the provision of logs and dung as a potential refuge niche for these invertebrate communities.

Methodology

An index of elephant impact on vegetation, quantity of refugia (logs and dung) produced and invertebrate diversity associated with the refugia were determined. Invertebrate diversity was sampled at experimental sites were refugia (logs and dung) were added and at sites where refugia was removed.

Results

Invertebrate abundance, species richness and diversity were always higher under refugia than the control plots that lacked refugia.

Future research

This research was conducted at the microhabitat scale (addition and exclusion of logs and dung), which may be considered a relatively small scale within the broader landscape. Therefore in order to drawn conclusion about the general patterns, future research should investigate these relationships and association patterns over a much larger spatial gradient.

Conclusions

The results of this study illustrated the importance of refugia (logs and dung) produced by elephants for ground-dwelling invertebrate species in the savanna environment. The extent of the influence of the refugia varied both spatially and temporally and this should be considered in future monitoring. Conservation organisations now have as their primary goal the conservation of biodiversity and not just single species preservation, and that elephants are not more important than any other component, but do acknowledge that they are important and major ecosystem drivers. However, the effects of elephant management on biodiversity as a whole, or even on smaller, less charismatic species, have rarely been comprehensively assessed. There is clearly a need for information on the effects of elephant on all aspects of diversity, or at the very least on the effects of elephants at the species, population and community levels for a broader range of taxa. While further research on a broader range of organisms is necessary, elephant impact on at least some aspects of biodiversity, through the process of facilitation of refugia can be considered to be positive.

Appendix

The invertebrate groups, families and species unique to each of the treatments,(sites with no refugia (control) and sites with refugia (logs and dung)) that was sampled during the experimental trial at Makalali Private Game Reserve. No termite or ant species was unique to the refugia substrate or control.

Substrate	Taxa	Family	*Genus*	Species
Control	Spider	Corinnidae		sp1
Control	Spider	Gnaphosidae		sp5
Control	Spider	Lycosidae		sp3
Dung	Spider	AGELENIDAE		sp2
Dung	Spider	Ctenidae	*Ctenus*	sp
Dung	Spider	Gnaphosidae		sp4
Dung	Spider	Sparassidae	*Olios*	sp
Dung	Spider	Lycosidae		sp1
Dung	Spider	Lycosidae		sp2
Dung	Spider	Lycosidae		sp7
ung	Millipede	Odontopygidae	*Spinotarsus*	sp2
Dung	Spider	Salticidae		sp2
Dung	Spider	Salticidae		sp5
Dung	Centipede	Scolpendridae	*Cormocephalus*	*anceps segnis*
Dung	Centipede	Scolpendridae	*Scolopendra*	*morsitans*
Dung	Millipede	Spirostreptidae	*Triaenostreptus*	sp
Dung	Spider	Theridiidae	*Zeonina*	sp
Dung	Spider	Thomisidae	*Runcinia*	*flavida*
Log	Spider	Agelenidae		sp1
Log	Spider	Araneidae	*Argiope*	sp1
Log	Spider	Miturgidae	*Cheiracanthium*	*furculatum*
Log	Spider	Miturgidae	*Cheiracanthium*	sp
Log	Spider	Gnaphosidae		sp3
Log	Millipede	Harpagophoridae	*Zinophora*	*diplodonta*
Log	Millipede	Harpagophoridae	*Zinophora*	sp
Log	Spider	Oxyopidae	*Hamataliwa*	sp
Log	Spider	Palpimanidae	*Iheringia*	*biplagiata*
Log	Spider	Philodromidae	*Tibellus*	*minor*
Log	Spider	Salticidae		sp4
Log	Spider	Salticidae		sp8
Log	Spider	Salticidae		sp9
Log	Spider	Thomisidae	*Heriaeus*	*crassispinus*
Log	Spider	Thomisidae	*Heriaeus*	*transvaalicus*

Gardeners of the gods?: the role of elephants in the Eastern Cape Subtropical Thickets

GRAHAM I. H. KERLEY & MARIETJIE LANDMAN

Introduction

Elephants *Loxodonta africana* have frequently been hypothesized to play a key role in ecological processes in the Subtropical Thickets of the Eastern Cape (Midgley 1991, Stuart-Hill 1992, Kerley *et al*. 2005). However, our understanding of elephant functioning is influenced by a number of critical constraints on this understanding that reflect the history of elephant exploitation, conservation, research and management in the Eastern Cape. These constraints are set out in no particular order of importance.

Elephants were historically recorded at high densities in the Eastern Cape, particularly in the thicket vegetation east of the Gamtoos River (Skead 1987, Boshoff *et al*. 2002). Soon after Europeans settled in the Cape these elephant herds attracted large numbers of hunter/explorers who exploited the elephants for their ivory. This resulted in a rapid eradication of the elephants from over 90 % of the landscape (Skead 1987) before any real details of their ecology could be formally documented.

The Eastern Cape is the interface between summer and winter rainfall systems, which together with geologically and topographically complex landscapes results in a complex interdigitation of a number of biomes, with all seven of South Africa's biomes being represented in the province. This complexity has masked our understanding of elephant ecology in the region, as it is difficult to explain how they used the landscapes when landscapes may constitute patches of potentially suitable or unsuitable habitat at a scale of hectares. At a broad level, Boshoff *et al*. (2002) hypothesised that elephants occurred at high densities on the coastal lowlands and along the river valleys where there would have been abundant forage and water. The interfluves would have been used relatively ephemerally by elephants, given the low frequency of surface water in these areas. Boshoff *et al*. (2002) also hypothesized that elephant movements between valley systems would have taken place on the coastal lowlands or against the escarpment. A more recent reconstruction of elephant distribution and densities within the area of the Subtropical Thicket Ecosystem Planning project (see also Boshoff *et al.* 2002 Addo) has suggested that elephant distribution and abundance varied considerably between the different vegetation types (Kerley *et al*. Unpubl). This would undoubtedly have influenced the relative impact of elephants across these landscapes, but information on how this varied is not available.

By the end of the 19^{th} Century, the once vast population of elephants in the Eastern Cape had been reduced to a single herd in the Addo bush. At this time this herd, estimated at about 140 individuals, was the largest of the four remaining herds (others being Knysna, Kruger and Thembe) in South Africa (Whitehouse 2001). This population was further reduced to about 16 animals in 1919 through an active eradication attempt (Hoffman 1993). Ongoing attrition with humans reduced the population to only 12 animals in 1931 when the Addo Elephant National Park (AENP) was established (Whitehouse 2002). Another animal was killed before these elephants were herded into the then unfenced AENP. Mortalities of the unfenced population remained high, so that when the AENP was finally fenced in 1954 the population was just 22 animals (Whitehouse 2002). Subsequent to fencing, the Addo population has grown significantly, and now numbers over 420 individuals.

Although elephants have been reintroduced into a number of private nature reserves (Shamwari, Kwandwe, Amakhala, Bayete, Lalibela) these populations have been poorly studied beyond records of introduction (see population accounts in Kerley *et al*. 2002). Thus there are no studies in the peer-reviewed literature on the role of these other elephant populations in thicket vegetation. A consequence of this is that our understanding of the role of elephants in the Eastern Cape thickets is limited to studies on a single population in a few vegetation types (i.e. the Addo population). Given that a total of 112 vegetation types have been described for Subtropical Thicket (Vlok *et al*. 2003), this suggests that we should use considerable caution when extrapolating these findings across Subtropical Thicket. In many cases, the available studies on the Addo elephants represent classic pseudoreplication (e.g. Kerley *et al.* 1999b), requiring further caution when interpreting these findings.

Since the AENP population was fenced in 1954, elephant densities (1.6 – 4.1 elephant/km^2) have consistently been above the recommended carrying capacity. Two estimates of carrying capacity have been published in the peer-reviewed literature. Penzhorn *et al.* (1974) recommended that elephant densities should not exceed 0.4 elephant/km^2 in the AENP, based on an extrapolation of elephant densities in other areas of Africa with similar rainfall. More recently, Boshoff *et al.* (2002), using a forage production approach with modelled potential herbivore communities, estimated ecological carrying capacities of between 0.25 and 0.52 elephant/km^2 for the AENP. Thus even the lowest density since fencing the AENP has been about three times greater than published estimates of carrying capacity. Interpreting findings regarding the impacts of elephant on thicket vegetation based on work in the AENP should therefore be done with caution in view of the fact that these elephant densities “are exceptionally and unusually high” (Cowling & Kerley 2002).

Much of the research on elephant impacts in the AENP has adopted an approach of comparing elephant occupied areas with a suite of sites within the AENP that have been protected from elephant browsing since the population was fenced in 1954 (the so-called botanical reserves). This approach assumes that the botanical reserves represent a “control treatment” which can be used as a baseline to assess the impacts of elephant on thicket vegetation (Cowling & Kerley 2002). However, this assumption may not be realistic, as the fact that these areas have been protected from megaherbivore (elephant and black rhinoceros) browsing indicates that they may be subjected to “megaherbivore release”, in which plant and animal communities may develop differently in the absence of megaherbivores (cf. Stuart-Hill 1992, Kerley *et al*. 2005).

A further assumption on which research in the AENP is generally based is that the changes observed within the elephant enclosure can be attributed to the impacts of the elephant (c.f. Penzhorn *et al*. 1974, Stuart-Hill 1992). Stuart-Hill (1992) justified this assumption on the grounds that elephants comprised 78 % of the large mammal herbivore biomass in the AENP at the time of his study. However, the presence of a range of other herbivores, frequently at high densities, does call this assumption into question (Cowling & Kerley 2002). Furthermore, the elephant impacts may have knock-on effects. Thus, Kerley *et al*. (1999a) postulated that path creation by elephants may facilitate access to geophyte and small succulent plants for tortoises in otherwise impenetrable thicket.

Any interpretation of the impacts of elephants in Subtropical Thicket, as reviewed here, has to be done in the light of the above points.

Roles

If we aim to understand the impacts of elephant, it is critical that the connections between elephants and the putative impacts are clearly understood and demonstrated. For example, for over 30 years the observation that *Aloe* sp. were disappearing in the elephant enclosure was assumed to be a response to elephant herbivory (Penzhorn *et al.* 1974), despite the fact that *Aloe* sp. are generally recognised to be unpalatable (Shearing 1994). It was only in 2004 that Davis

(2004) showed that elephant actually consumed aloes, although it is still not clear why they are so vulnerable to elephant impacts.

The mechanisms of elephant impacts vary considerably, as a variety of ecological processes are influenced by elephant. Thus, Boshoff *et al.* (2001) showed that elephant played a role in 11 of 19 broad ecological processes that they identified as being important in thicket. This contrasted with a smaller species such as blue duiker *Philantomba monticola* which only contributed to five such processes (Boshoff *et al*. 2001).

Elephants are mixed feeders, consuming a range of plants and plant parts from grasses, through to browse and bark, and including fruit and bulbs. The large body size of elephant and their robust feeding style allow them to be very broad in their dietary use, and to date a total of 146 plant species (representing 51 families) have been recorded in their diet (Archibald 1955, Paley & Kerley 1998, Landman in prep., Davis 2004 - Appendix). This is nearly five times more species than that consumed by their coexisting ruminant browsers (e.g. kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus*, etc), and is only approached (at 120 species – Landman Unpubl.) by the other non-ruminant megaherbivore in the thicket, the black rhinoceros *Diceros bicornis* (Kerley *et al*. 2005). It can therefore comfortably be stated that elephant feeding will influence the fate of more plant species than any other mammalian herbivore species in the Eastern Cape thickets.

Interestingly, despite their dietary breadth, elephants are relatively poor seed dispersers, dispersing only 21 plant species through endozoochory, and in this regard are nearly matched by black rhinoceros (20 species) and eland *Taurotragus oryx* (20 species – Mendelson 1999). The volume of their forage intake (and hence faecal output) allows them to disperse large numbers of these seeds (Sigwela 2004). The mechanism for this relatively poor seed dispersal is not clear, but may reflect a non-selective feeding behaviour in terms of plant phenology.

Impacts

Soil resources

Kerley *et al*. (1999b) measured micro-topography and soil nutrients inside the AENP elephant enclosure and compared this to data for the botanical reserve, using the approach of Landscape Functional Analysis, along 50 m transects. They showed an apparent decline in the proportion of the landscape that represented run-on zones (i.e. where resources such as water, litter, soil and nutrients are trapped during overland flow) while the proportion of run-off zones (i.e. where these resources are lost) increased under elephant herbivory. The consequences of this were a decline in soil nutrients. Unfortunately, given the lack of replication in this study, it is not possible to demonstrate that these effects were really significant or due to the impacts of elephants. However it was suggested that elephant impacts were less deleterious than those of goats. These studies need to be repeated and replicated in order to assess whether elephants do lead to dysfunctional landscapes, and at what level of elephant impact this occurs.

Litter production

One of the consequences of their feeding style is that elephant tend to discard large amounts of plant material that they have plucked from a plant without ingesting it all. This is particularly apparent when elephant are feeding on woody shrubs, where a large branch may be broken off the plant and some of the foliage ingested before being discarded. Paley (1997) estimated the amount of material being discarded within the AENP (27 000 kg/day) and calculated that it comprised 67 % of the then estimated daily food requirements of the elephants. This discarded material enters the litter pool, and is typically much coarser than the normal litter inputs, and differs also in terms of nutrients. It may therefore be hypothesized that elephant discarded feeding material significantly alters the size, nutrient levels and dynamics of the litter pool in thicket vegetation.

Landscape patches

Kerley *et al*. (1995) hypothesized that thicket vegetation was adapted to small-scale disturbance patches such as those brought about by elephant feeding and trampling, but the role of elephants in patch formation has rarely been assessed. Although elephant have been observed creating open patches where they excavate soils to practise geophagy in Addo or where they trample the vegetation around small ephemeral water bodies (pers. obs), this has not been quantified.

Landman (in prep.) used the variations in elephant occupation in different portions of the AENP elephant enclosure as the enclosure was expanded, as well as population count data, to assess the accumulated impact of elephant presence (expressed as "mean elephant/yr") on the extent of open habitat patches (as opposed to dense thicket). She showed a significant increase in the proportion of the landscape that was path or open habitat with increasing elephant presence. The number of paths initially increases with increasing elephant occupation (Figure 1), but in the extreme situation decline as the paths coalesce to form larger open patches. These changes had significant consequences for browse availability (see later), but have not been further investigated. It may be hypothesized that this path formation may have profound knock on effects by virtue of changes in micro-climate that are associated with the change in vegetation density. Thus, Henley (2001) showed that air and soil temperatures of such open habitat becoming much more extreme than in intact thicket. This change in microclimate has varied but as yet unknown implications for processes ranging from soil litter processes (c.f. Lechmere-Oertel 2003) to plant and animal physiology and to seedling germination and survival.

Impacts on plants

The impact of elephant on the Subtropical Thicket of the AENP was first recognised by Penzhorn *et al*. (1974). At the time of their study 67 elephants were confined to a 2270 ha enclosure, and it was assumed that any difference in vegetation between the inside and outside of the enclosure was due to the influence of elephants. Penzhorn *et al*. (1974) used 10 paired quadrats (2 m x 10 m) located along the Armstrong fence to assess total species richness and biomass of plants contributing more than 1 kg/quadrat. Total plant biomass was significantly reduced within the enclosure, with mean biomass/quadrat only 45 % of that outside. The mean mass/quadrat of *Portulacaria afra, Schotia afra, Azima tetracantha* and *Euclea undulata* were less than half of the mass outside, while that of *Capparis sepiaria* increased by 50 % in the elephant enclosure. Although species richness did not differ significantly between treatments, at least two species, a tree aloe, *Aloe africana*, and the epiphyte, *Viscum rotundifolium*, was absent from the enclosure.

Following the observations by Penzhorn *et al*. (1974), the elephant enclosure was enlarged by *c*. 5000 ha on three occasions from 1977 to 1984 to reduce the impact of elephant on the vegetation. During 1977, Barratt & Hall-Martin (1991) located 38 belt-transects (13 m – 30 m long) in the Park and compared height, crown diameters and elephant damage (as a function of canopy volume) of plants in the elephant enclosure and botanical reserves. An additional seven transects were placed at regular intervals away from a permanent water point inside the enclosure and all transects were sampled during 1977, 1981 and 1989. Owing to the enlargement of the elephant enclosure, elephant densities decreased from 3.8 (1977) to 2.0 elephants/km^2 (1989) during this period. This study therefore included elephant density and time since exposure to elephants as descriptive variables (Cowling & Kerley 2002). Results indicated a significant reduction in canopy height and volume inside the elephant enclosure during 1977, while in the absence of elephants (botanical reserve) canopy volume increased. Newly incorporated areas showed a decrease in canopy height and volume, tending towards the 1977 values of the original elephant enclosure. Barratt & Hall-Martin (1991) hypothesised that 'areas exposed to 20 years of elephant utilisation appeared to reach a loose equilibrium between plant biomass loss due to elephant browsing and total biomass regeneration'. Cowling & Kerley (2002) however pointed out that it would be difficult to justify this statement as elephant density, and therefore browsing intensity, fluctuated over this period. The percentage of plants newly damaged by elephants was found to be species dependent, with *P. afra* showing significantly more damage in 1989, followed by *S. afra*, *E. undulata*, *A. tetracantha* and *C. sepiaria*. Barratt & Hall-Martin (1991) confirmed the disappearance of *A. africana* from the elephant enclosure (Penzhorn *et al*. 1974) and indicated a significant decrease in species richness in elephant exposed areas when compared to botanical reserve sites. During 1977, canopy volume of sites within 300 m of permanent water was found to be significantly less (2.5 times) than sites further than 1 km.

The disappearance of *V. rotundifolium* from the elephant enclosure, observed by Penzhorn *et al*. (1974), prompted an investigation into the size and frequency of the common mistletoes (*Moquinella rubra, V. rotundifolium, V. crassulae, V. obscurum*) and their associated host plants inside and outside the enclosure. Midgley & Joubert (1991) showed that despite the high incidence of host plants in the elephant enclosure all mistletoes were virtually locally extinct, while the frequency of mistletoes outside the enclosure ranged from 7 % (*V. rotundifolium* on *Acacia karroo*) to 77 % (*V. rotundifolium* on *Maytenus heterophylla*). Due to their high nutritional status, mistletoes are thought to be selected by browsing herbivores and may therefore be useful indicators of browsing intensity.

Stuart-Hill (1992) expanded the debate on the impact of elephant on the structure and composition of Succulent Thicket, and contrasted the effect of elephants and goats on the shrub component. Using a snap-shot natural experiment (Diamond 1986), he identified three browsing treatments in and around the AENP (predominantly elephant or goat browsing and neither elephant nor goat browsing in botanical reserves), and compared the frequency, percentage canopy cover and density of 23 shrub species in seven circular quadrats at each treatment. Stuart-Hill (1992) further contrasted the architecture (triangular with base on the ground, umbrella shaped or box shaped) of shrub species between treatments, placing particular emphasis on *P. afra.* Results suggested that elephants and goats had a noticeable effect on the density and cover of trees and shrubs, with goat browsing being considerably more detrimental than elephant browsing. Relative to botanical reserves, elephant browsing significantly increased (with the exception of *P. afra*) the density of the woody component, while significantly decreasing woody canopy cover. Although elephant browsing did not reduce woody species richness, it limited the variation in floristic composition to only a few species (*P. afra, C. sepiaria, E. undulata, S. afra*) and caused a significant decrease in the frequency of *Euphorbia mauritanica* (82 %). *Rhigozum obovatum* and *Crassula ovata* showed a relative decrease greater than 50 % in response to elephant browsing, but this was non-significant. Elephants further reduced the proportion of box-shaped *P. afra* plants, thereby increasing the proportion of triangular and umbrella-shapes. Plants protected from elephant browsing had well developed 'skirts' of rooted branches, with only 8 % having none. Elephants increased the proportion of 'full skirts' relative to the control, but this was non-significant. Stuart-Hill (1992) concluded that Succulent Thicket is adapted to the 'top-down' browsing by elephant, which maintains thicket in a relatively optimum state by protecting canopy cover at ground level. In contrast, the 'bottom-up' browsing by goats produce umbrella-shaped shrubs that are vulnerable to mortality and less likely to reproduce vegetatively.

Moolman & Cowling (1994) focused on the endemic-rich geophyte and low succulent flora (especially Liliaceae, succulent Asclepiadaceae, Crassulaceae, Euphorbiaceae and Mesembryanthemaceae), which from a conservation perspective, is the most important component of thicket. Adopting the approach used by Stuart-Hill (1992), they contrasted the impact of elephant and goat browsing relative to control sites on the cover and richness of the endemic-rich component. At five sites, quadrats (100 m x 25 m) were located within each of the treatments and the cover and identity of all geophytes and low succulents noted in 20 1m^2 plots randomly located in three microsites (open, under *P. afra* shrubs, under *E. undulata* shrubs). Because thicket is thought to be adapted to the 'top-down' browsing by elephants, which protects shrub microsites, but not the 'bottom-up' browsing by goats, which destroys shrub microsites (Stuart-Hill 1992), Moolman & Cowling (1994) hypothesised that elephants will have less impact on the endemic-rich flora than goats. Furthermore, the mosaic of open and dense thicket associated with elephant browsed thicket was expected to result in a more diverse endemic-rich flora than would be found in either control or goat browsed sites. Due to their large bite sizes elephants were further thought to be less likely to select low succulents and geophytes. Results indicated that 63 % of the 19 endemics identified were recorded in elephant browsed sites. Generally, species richness, density and cover was lower in elephant browsed than control sites, with nearly all species occurring in open sites (across all treatments), most under *E. undulata* shrubs but less than half under *P. afra* shrubs. The cover of the Crassulaceae was however higher in the *E. undulata* microsite of elephant browsed treatments, possibly due to their palatability and ability to reproduce vegetatively (hence resilience to elephant browsing). Moolman & Cowling (1994) suggested that elephant densities need to be reduced in order to reduce the impact they have on the structure of the geophyte and low succulent shrub component of Succulent Thicket.

More recently, Lombard *et al*. (2001) used an iterative reserve-selection procedure to identify a system of botanical reserves in the AENP that would conserve the components of the flora (mostly low succulents and geophytes) with high conservation value (Albany Centre Endemics, Red Data Book taxa, or taxa very rare within the Park, referred to as 'special species') and that are particularly vulnerable to elephant browsing (Moolman & Cowling 1994). They divided the AENP into 16 selection units, based on the length of time of exposure to elephant browsing, and sampled each unit for the presence and frequency of 75 special species (Johnson *et al*. 1999), and two indicator species of elephant browsing intensity (*V. rotundifolium*, *V. crassulae* (Midgley & Joubert 1991). Browsing history had a strong impact on species richness and abundance. Species richness for Spekboomveld units declined exponentially with length of exposure to elephant browsing, halving approximately every 7 years of exposure. Similarly, Bontveld units exposed to 13 years of browsing showed a 7-fold decrease in species richness when compared to unbrowsed Bontveld units. Across all units, species abundance decreased with increasing length of exposure to elephant browsing, with most species recorded only at low densities after 20 years of browsing and more than half of the flora confined to small populations after 42 years of browsing. Lombard *et al*. (2001) concluded that elephants, at current stocking densities, had a negative impact on plant species diversity, with the endemic and threatened component of Succulent Thicket being most vulnerable. They recommended a system of botanical reserves, in addition to those already proclaimed, in order to conserve this floristic component.

References to the impact of elephants on Succulent Thicket have focussed primarily on herbivory, with other mechanisms being largely ignored. Many inferences to the diet of elephant in thicket have been through indirect means (e.g. Penzhorn *et al*. 1974, Barratt & Hall-Martin 1991), assuming that differences between the elephant enclosure and control sites is due to elephant herbivory, and therefore these plants should necessarily be consumed by elephants. Landman & Kerley (in prep) however suggests that not all the impacts of elephants on the vegetation should be attributed to elephant herbivory as plants previously thought to disappear due to herbivory (e.g. Moolman & Cowling 1994, Johnson *et al*. 1999, Lombard *et al*. 2001) do not occur in the diet of elephants.

Insects

Musgrave & Compton (1997) measured phytophagous insect feeding damage on plants representing five species inside the AENP elephant enclosure and compared this to data for the botanical reserves. They demonstrated a significant increase in abundance of feeding damage in the presence of elephants, which they attributed to an increase in the nutritional quality of browsed plants through a decline in secondary chemical compounds such as tannins brought about by browsing. This hypothesis has however yet to be tested, nor has it been shown which insect species were involved in this feeding process, and what their population responses were.

Vertebrates

The impacts of elephants on other herbivores have not been directly investigated, besides the work by Landman (in prep) on black rhinoceros foraging opportunities (see below).

Kerley *et al*. (1999a) hypothesized that elephant may increase habitat availability for tortoises through their creation of open habitat patches and paths. This is based on Mason's (1997) demonstration that leopard tortoises *Geochelone pardalis* and angulate tortoises *Chersina angulata* both preferred thicket margins and avoided dense thicket. While it is clear that tortoise densities are relatively high in the AENP, this hypothesis has yet to be tested. The suggestion by Kerley *et al.* (1999a) that some of the changes in the plant community attributed to elephant damage (declines in geophytes and small succulent shrubs), may in fact be caused by increased tortoise access indicates that this interaction needs to be investigated urgently if we are to understand the mechanisms of the impacts of elephants.

Sigwela (1999) compared the diet of kudu in the elephant enclosure to that of kudu in the botanical reserves, assuming that kudu did not routinely move through the elephant proof fence. He showed that there was no apparent effect of elephant on the diet of kudu. This is surprising, given the extensive changes that occur in the vegetation in these sites and the fact that kudu diet (28 species) includes many of the plant species recorded as being impacted by elephant (Sigwela 1999), and elephant consume all the plant species recorded in the diet of kudu. This suggests that dietary items are not limiting to either kudu or elephant at the present densities of vegetation and browsers at these sites.

There has been a decline in the numbers of Cape grysbok *Raphiceros melanotis* and bushbuck in the AENP elephant enclosure over the last decade (M.H. Knight, J.G. Castley, SANParks, pers.com.). This is postulated to be a response to changes in habitat structure brought about by elephant. However, it is not known whether populations outside the elephant enclosure have remain unchanged over this period, or whether putative changes in habitat structure are the consequences of elephant impacts (reasonably likely given the observations recorded above) or some other process such as global climate change.

Black rhinoceros browse availability

The reduction of vegetation cover and density by elephants, as a result of path formation, results in a change in potential browse availability for black rhinoceros (Landman in prep.). The increase in elephant paths, associated with increases in elephant densities, initially facilitates access to browse by black rhinoceros, but the subsequent dominance of the landscape by these paths results in a loss of foraging opportunities (Figure 2). The over-utilisation of thicket vegetation by elephant compromises the potential of this vegetation type to contribute towards black rhinoceros foraging, and hence conservation opportunities. There exists potential conflict between the management and conservation of these two megaherbivore species, which needs to be recognised and managed.

Ecological cascades

Given the abundance, generalist feeding behaviour and diversity of impacts of elephant, it can be expected that elephant can have a number of cascading effects on their ecosystems. Surprisingly in the light of the history of concerns about elephant impacts in the AENP, little attention has been paid to this phenomenon. Kerley *et al*. (1999a) hypothesized that one such example could be that elephants improved access for tortoises which then increased browsing pressure on the low growing succulent and geophyte flora. In contrast, however, the often repeated statement that the endangered flightless dung beetle *Circellium bacchus* is dependent on the presence of megaherbivores, chiefly elephants, for its persistence is patently nonsense. There are thriving populations of this species in the Gamtoos River valley and sections of the Sundays River valley which have not had elephants for more than 100 years and 50 years, respectively. This is longer than the pupation period of even the most recalcitrant beetle larvae, indicating their ability to utilize non-megaherbivore dung.

Understanding the cascading effects brought about by elephant will be critical to really understanding the consequences of having or not having elephants on these landscapes, but probably the real challenge will be to develop an understanding of what different densities of elephants may have on these complex ecosystems

Conclusions

Accumulating evidence indicates that biodiversity is altered within the elephant enclosure of AENP, but it is not clear that this is exclusively due to elephants, or if so, if this is an "elephant effect" *per se* or an effect due to too many elephants. Future research needs to focus more clearly on the effects of elephant density *per se* rather than on the simple presence or absence of elephants. In this respect, Landman (in prep.) has made a significant advance with her use of relative measures of elephant stocking over time. The recent establishment of a number of elephant populations in the Eeastern Cape provides new opportunities to get to grips with this question. Furthermore, we need to move beyond describing changes ascribed to the presence of elephants to focusing on the mechanisms of elephant impacts on biodiversity. Such demonstrated cause and effect relationships will allow us to move beyond assuming that these observed impacts are directly attributable to elephant. It is also obvious that we need to understand the impacts of elephants in other Eastern Cape ecosystems, as elephants have recently been introduced into Karoo landscapes where there is no evidence that populations were resident in the past (Boshoff *et al*. 2002).

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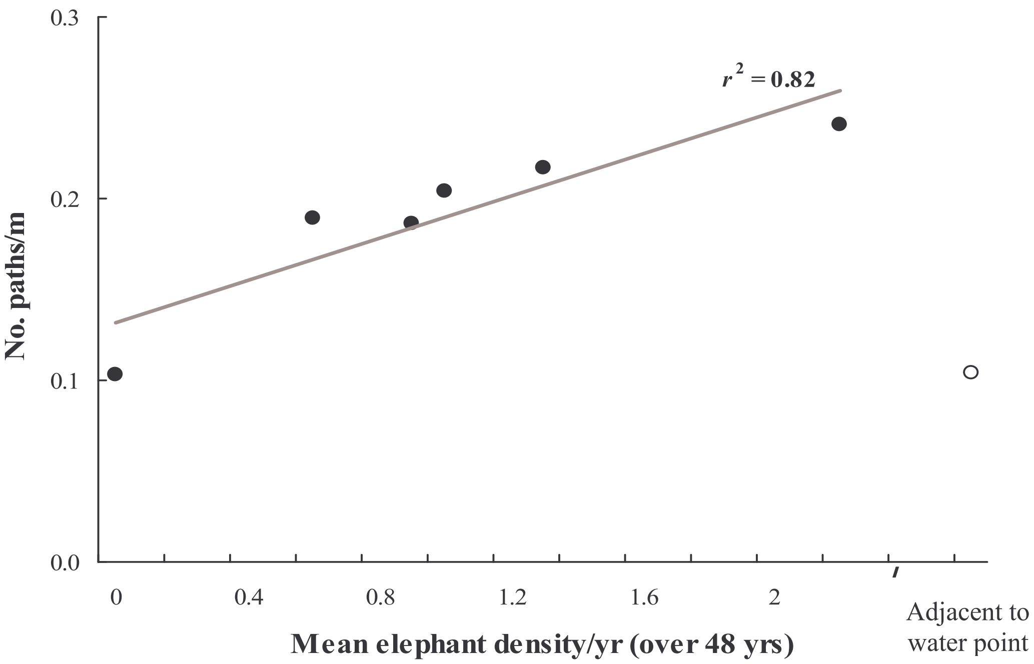
Appendix: Percentage contribution of plant species, including taxonomic and physiognomic categories, to the diet of elephant in the Subtropical Thicket of the Addo Elephant National Park. Data from Archibald (1955) only indicate present (*) and major plant species (**) identified in the diet. Plant nomenclature follows Arnold and De Wet (1993).

Family	Plant species	Archibald (1955)	Paley & Kerley (1998)	Landman (in prep)	Davis (2004)
Woody shrubs					
Anacardiaceae	*Rhus crenata*			1.15	0.28
Anacardiaceae	*Rhus glauca*			0.02	
Anacardiaceae	*Rhus incisa*				0.08
Anacardiaceae	*Rhus longispina*		0.53	2.93	2.16
Anacardiaceae	*Rhus pterota*		4.41	1.93	0.69
Anacardiaceae	*Rhus refracta*			0.05	0.17
Anacardiaceae	*Rhus sp.*				0.40
Apocynaceae	*Carissa haematocarpa*		0.35	6.10	0.36
Araliaceae	*Cussonia spicata*				7.29
Asparagaceae	*Asparagus africanus*	*		0.15	0.71
Asparagaceae	*Asparagus crassicladus*			0.98	0.17
Asparagaceae	*Asparagus densiflorus*			0.51	0.10
Asparagaceae	*Asparagus racemosus*		1.76	0.44	0.04
Asparagaceae	*Asparagus striatus*	*	0.18	0.95	0.27
Asparagaceae	*Asparagus suaveolens*		0.18	0.17	0.43
Asparagaceae	*Asparagus subulatus*			1.71	0.67
Asparagaceae	*Asparagus sp.*		0.26		0.77
Asteraceae	*Brachylaena ilicifolia*		0.62		
Bignoniaceae	*Rhigozum obovatum*			0.07	0.02
Boraginaceae	*Ehretia rigida*			0.51	0.94
Capparaceae	*Boscia oleoides*			0.27	0.06
Capparaceae	*Cadaba aphylla*		0.09	0.49	0.06
Capparaceae	*Capparis sepiaria*		0.26	2.85	0.66
Capparaceae	*Maerua cafra*			1.17	
Celastraceae	*Cassine aethiopica*		0.97	0.10	0.02
Celastraceae	*Gymnosporia capitata*		0.97	1.95	0.21
Celastraceae	*Gymnosporia polyacantha*	**	0.26	2.95	2.09
Celastraceae	*Gymnosporia undata*	**			
Celastraceae	*Maytenus heterophylla*		0.26	1.05	0.39
Celastraceae	*Putterlickia pyracantha*		0.62	2.51	0.02
Ebenaceae	*Diospyros dichrophylla*			0.12	
Ebenaceae	*Diospyros sp.*				0.29
Ebenaceae	*Euclea undulata*	*	4.76	1.27	0.43
Euphorbiaceae	*Clutia affinis*			0.24	0.08
Euphorbiaceae	*Jatropha capensis*			0.73	
Fabaceae	*Acacia karroo*		1.50	0.12	0.04
Fabaceae	*Prosopis glandulosa*				0.04
Fabaceae	*Schotia afra*	**	1.94	3.39	3.93
Fabaceae	*Schotia latifolia*				0.05
Fabaceae	*Sesbania punicea*				0.15
Flacourtiaceae	*Dovyalis caffra*		0.18	0.02	0.02
Flacourtiaceae	*Dovyalis rhamnoides*		0.44		
Flacourtiaceae	*Scolopia zeyheri*		0.09		
Loganiaceae	*Buddleja saligna*		0.09		
Meliaceae	*Nymania capensis*				0.12
Oleaceae	*Olea europaea*			0.32	0.02
Plumbaginaceae	*Plumbago auriculata*		1.23	0.54	0.40
Ptaeroxylaceae	*Ptaeroxylon obliquum*		0.09	1.34	2.78
Rhamnaceae	*Scutia myrtina*		0.26	0.29	
Salvadoraceae	*Azima tetracantha*		2.82	4.41	15.37
Sapindaceae	*Pappea capensis*		0.35	0.24	0.04
Sapotaceae	*Sideroxylon inerme*		0.26	0.51	0.02
Solanaceae	*Lycium cinereum*		0.44		
Solanaceae	*Lycium ferocissimum*		0.79	0.02	0.08
Solanaceae	*Lycium oxycarpum*		0.09		
Solanaceae	*Lycium schizocalyx*		0.18		
Solanaceae	*Lycium sp.*		2.29		
Tiliaceae	*Grewia occidentalis*				0.04
Tiliaceae	*Grewia robusta*		0.26	2.27	0.11

Family	Plant species	Archibald (1955)	Paley & Kerley (1998)	Landman (in prep)	Davis (2004)
Succulents					
Asclepiadaceae	*Sarcostemma viminale*		0.44	0.22	
Asphodelaceae	*Aloe africana*			0.10	
Asphodelaceae	*Aloe ferox*				0.58
Asphodelaceae	*Aloe pluridens*				0.33
Asphodelaceae	*Aloe striata*			0.02	
Cactaceae	*Opuntia ficus-indica*				1.98
Crassulaceae	*Adromischus sphenophyllus*			0.02	0.06
Crassulaceae	*Crassula muscosa*			0.02	0.02
Crassulaceae	*Crassula ovata*	*	0.09	0.10	0.04
Crassulaceae	*Crassula perforata*			0.80	2.16
Crassulaceae	*Crassula spathulata*			0.12	0.09
Crassulaceae	*Crassula subaphylla*				0.04
Crassulaceae	*Crassula tetragona*			0.05	0.05
Euphorbiaceae	*Euphorbia caterviflora*				0.30
Euphorbiaceae	*Euphorbia inermis*				0.02
Euphorbiaceae	*Euphorbia ledienii*				0.04
Euphorbiaceae	*Euphorbia mauritanica*		0.62	0.41	0.23
Euphorbiaceae	*Euphorbia rhombifolia*				0.02
Euphorbiaceae	*Euphorbia tetragona*				0.02
Euphorbiaceae	*Euphorbia triangularis*			0.12	
Mesembryanthemaceae	*Mesembryanthemum aitonis*		0.09		
Mesembryanthemaceae	*Platythyra haeckeliana*		5.56		
Mesembryanthemaceae	*Trichodiadema bulbosum*				0.77
Mesembryanthemaceae	*Unidentified sp.*		1.06		0.40
Portulacaceae	*Portulacaria afra*	**	7.85	9.34	1.84
Zygophyllaceae	*Zygophyllum morgsana*		0.71	0.02	
Grasses					
Poaceae	*Aristida diffusa*			0.02	0.08
Poaceae	*Cenchrus ciliaris*				0.02
Poaceae	*Cymbopogon plurinodis*			0.34	
Poaceae	*Cynodon dactylon*	**	31.04	19.56	10.68
Poaceae	*Enneapogon scoparius*			0.17	
Poaceae	*Eragrostis curvula*		0.18	2.59	2.90
Poaceae	*Eragrostis obtusa*			3.15	
Poaceae	*Eustachys paspaloides*			0.10	
Poaceae	*Fingerhuthia africana*			0.61	0.13
Poaceae	*Panicum deustum*		4.32	4.46	7.95
Poaceae	*Panicum maximum*	**	1.50	0.90	0.04
Poaceae	*Pennisetum clandestinum*			1.90	1.16
Poaceae	*Sporobolus fimbriatus*				2.48
Poaceae	*Stipa dregeana*		0.18	0.24	0.25
Poaceae	*Themeda triandra*			0.05	0.54
Lianas					
Asclepiadaceae	*Cynanchum obtusifolium*		0.18		
Asclepiadaceae	*Cynanchum sp.*			0.02	
Asparagaceae	*Myrsiphyllum volubile*			0.05	
Asteraceae	*Senecio macroglossus*			0.07	2.02
Cucurbitaceae	*Cucumis africanus*				0.06
Cucurbitaceae	*Kedrostis nana*			0.66	0.04
Geraniaceae	*Pelargonium peltatum*		0.09	0.22	0.06
Loranthaceae	*Moquinella rubra*			0.02	
Luzuriagaceae	*Behnia reticulata*			0.02	0.04
Ranunculaceae	*Clematis brachiata*				0.04
Vitaceae	*Rhoicissus digitata*	*	0.18	0.71	4.49

Family	Plant species	Archibald (1955)	Paley & Kerley (1998)	Landman (2003)	Davis (2004)
Forbs					
Acanthaceae	*Blepharis capensis*			0.17	0.13
Acanthaceae	*Hypoestes aristata*		0.62	0.17	
Acanthaceae	*Hypoestes forskaolii*			0.39	
Acanthaceae	*Isoglossa ciliata*		0.88		
Aizoaceae	*Aizoon glinoides*		1.15		
Aizoaceae	*Aizoon rigidum*		0.09	0.51	2.45
Aizoaceae	*Galenia pubescens*		1.85		
Asteraceae	*Cineraria lobata*		0.09		
Asteraceae	*Cuspidia cernua*		2.38	0.90	0.02
Asteraceae	*Osteospermum calendulaceum*		1.06		
Asteraceae	*Pentzia globosa*		0.26		
Asteraceae	*Senecio chrysocoma*			0.02	0.26
Asteraceae	*Senecio linifolius*		0.18		0.17
Brassicaceae	*Lepidium desertorum*		0.09		
Chenopodiaceae	*Atriplex semibaccata*		0.53		
Chenopodiaceae	*Chenopodium albium*		3.09		
Chenopodiaceae	*Salsola kali*				0.12
Commelinaceae	*Commelina benghalensis*			0.17	
Euphorbiaceae	*Phyllanthus verrucosus*			0.02	0.13
Fabaceae	*Indigofera sp.*				0.23
Lamiaceae	*Leucas capensis*			0.05	0.04
Lamiaceae	*Salvia scabra*				0.04
Malvaceae	*Abutilon sonneratianum*			0.27	
Rubiaceae	*Galium spurium*		0.18		
Scrophulariaceae	*Aptosimum procumbens*			0.02	
Scrophulariaceae	*Phyllopodium cuneifolium*				0.09
Sterculiaceae	*Hermannia althaeoides*		0.26		
Verbenaceae	*Plexipus cuneifolius*				0.04
Geophytes					
Asphodelaceae	*Bulbine sp.*			1.39	0.12
Commelinaceae	*Cyanotis speciosa*		2.12		
Dracaenaceae	*Sansevieria aethiopica*		0.18		
Dracaenaceae	*Sansevieria hyacinthoides*	**	0.18	0.71	0.08
Epiphytes					
Viscaceae	*Viscum sp.*			0.63	6.91


0.3
0.2
0.1
0.0
No. paths/m
$r^2 = 0.82$
0
0.4
0.8
1.2
1.6
2
Adjacent to water point
Mean elephant density/yr (over 48 yrs)

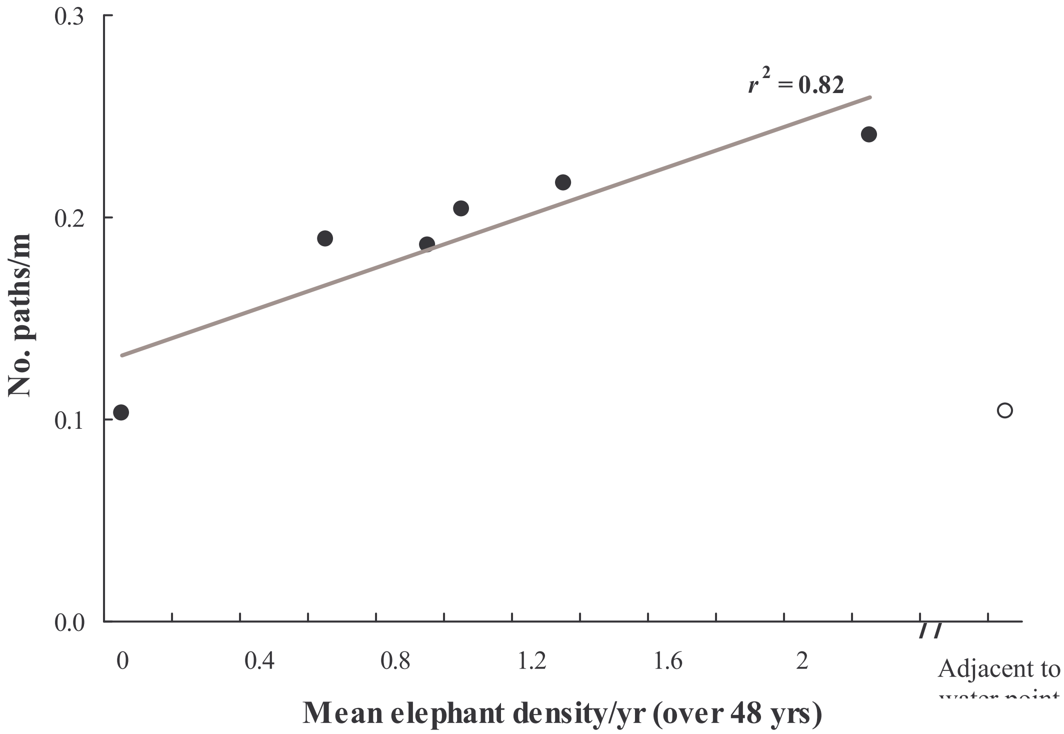


Figure 1: The relationship between path density and the accumulated mean elephant density within the Addo Elephant National Park. (Landman in prep.)

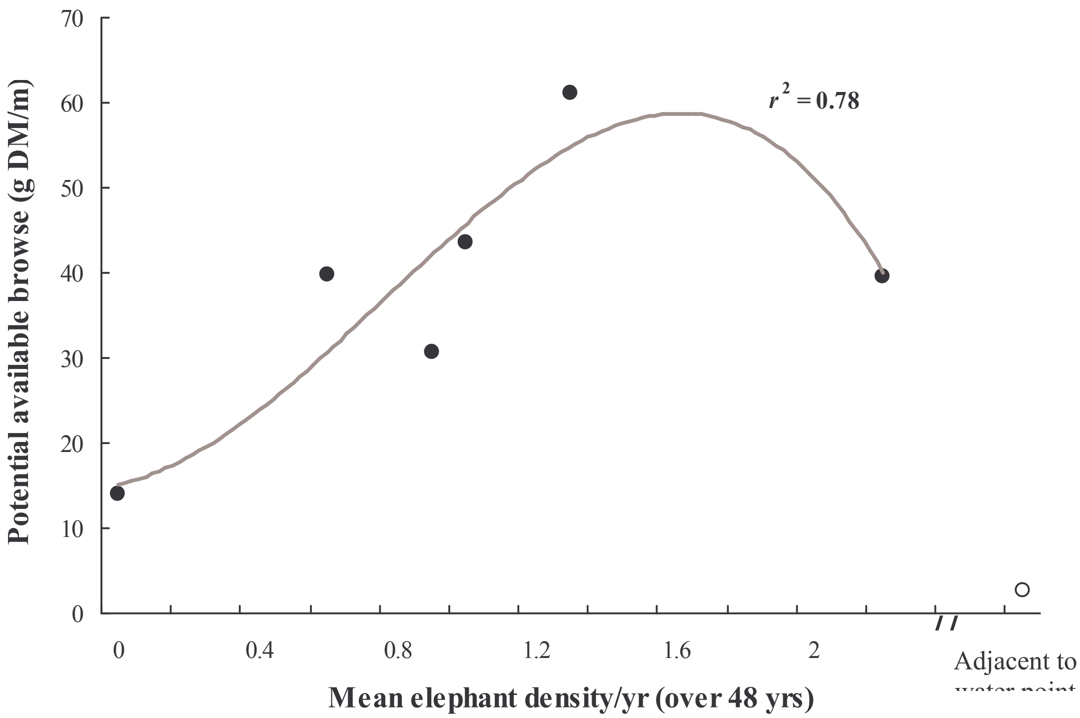


Figure 2: Accumulated impact of elephant presence on potential available browse (g DM/m) for black rhinoceros in Subtropical Thicket (Landman in prep).

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PLANTS UTILISED BY ELEPHANT

G. ZAMBATIS

Biological Reference Collection

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Acacia ataxacantha	Flame thorn	Favoured species (Steyn, A. & Stalmans, M. 2001) Browsed (Williamson, B.R. 1975)	Along streams and rivers	
Acacia burkei	Black monkey-thorn	Browsed (Van Wyk, P. 1984) Uprooted, snapped stems / trunks, debarked (Hiscocks, K. 1999)	Western side of KNP - granites and low lying areas	Slow grower (Van Wyk, P. 1984)
Acacia caffra	Common hook-thorn	Favoured species (Steyn, A. & Stalmans, M. 2001)	Pretorius Kop area – rare	Fairly fast grower (Van Wyk, P. 1984)
Acacia davyi	Corky-bark thorn	Highly utilised (Steyn, A. & Stalmans, M. 2001)	Highest peaks of the Malelane mountains	
Acacia gerrardii subsp. *gerrardii* var. *gerrardii*	Red thorn	Browsed (Van Wyk, P. & Fairall, N.1969) Debarked (Roux, J. *pers. comm*. 2005)	Widely spread in KNP but more abundant in low lying areas	Fairly fast grower (Van Wyk, P. 1984)
Acacia grandicornuta	Horned thorn	Debarked (Hiscocks, K. 1999)	Brackish flats in south of KNP along Sabie river	Fairly fast grower (Van Wyk, P. 1984)
Acacia nigrescens	Knob thorn	Browsed (Van Wyk, P. 1984; Williamson, B.R. 1975) Frequently uprooted (Baxter, P.W.J. 2003) Ring barked, uprooted, debarked (Engelbrecht, A.H. 1979) Debarked (Hiscocks, K. 1999; Roux, J. *pers. comm*. 2005) Leaves and pods (Venter, F. & J. 1996)	Throughout the KNP, abundant on basaltic soils	Slow grower (Van Wyk, P. 1984)
Acacia nilotica var. *kraussiana*	Scented pod-thorn	Browsed (Van Wyk, P. & Fairall, N.1969)	Throughout the KNP on low-lying	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Debarked (Hiscocks, K. 1999) Utilised (Steyn, A. & Stalmans, M. 2001)	brackish areas along streams and rivers	
Acacia polyacantha subsp. *campylacantha*	White-stem thorn	Browsed (Van Wyk, P. 1984)	Very rare in KNP - north-west of Punda Maria camp, near Shingwedzi and north of the Luvuvhu river	Fast grower (Van Wyk, P. 1984)
Acacia robusta subsp. *clavigera*	Robust thorn	Leaves occasionally browsed (Van Wyk, P. 1984) Debarked (Hiscocks, K., 1999) Browsed (Williamson, B.R. 1975)	Throughout KNP on banks of rivers and streams	Fast grower (Van Wyk, P. 1984)
Acacia senegal var. *rostrata*	Three-hook thorn	Browsed (Van Wyk, P. & Fairall, N. 1969) Debarked (Hiscocks, K. 1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Acacia sieberiana	Paperbark thorn	Browsed (Williamson, B.R. 1975)	Pretorius Kop area, Crocodile Bridge area and near Nhlanguleni picnic spot	Fast grower (Schmidt, E. *et al.* 2002)
Acacia tortilis subsp. *heteracantha*	Umbrella thorn	Browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Nel, P.J. 1988) Debarked (Hiscocks, K. 1999) Bark, leaves & pods utilised (Venter, F. & J. 1996)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Acacia welwitschii subsp. *delagoensis*	Delagoa thorn	Browsed (Van Wyk, P. 1984; Van Wyk, P. & Fairall, N. 1969)	South of Olifants river where basalts and granites meet, also Lower Sabie area and Nhlanguleni area	Slow grower (Van Wyk, P. 1984)
Acacia xanthophloea	Fever tree	Considerable damage (Biologiese Afdeling, Jaarverslag, 1959) Extensively damaged (Van Wyk, P. 1984) Browsed (Van Wyk, P. & Fairall, N. 1969; Nel, P.J. 1988) Debarking (Botha, J. 2002) Branches and leaves utilised (Venter, F. & J. 1996)	Eastern half of the KNP (basalt) along streams and rivers	Fast growing (Van Wyk, P. 1984)
Adansonia digitata	Baobab	Fruit, stem, leaves utilised (Van Wyk, P. 1984)	Northern area of KNP	Fast grower (Davies, L. *pers. comm.*

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Preferentially utilise (Baxter, P.W.J. 2003) Debarking (Nel, P.J. 1988; Whyte, I.J. 1996) Browsed (Williamson, B.R. 1975) Stems (Venter, F. & J. 1996)		2005)
Afzelia quanzensis	Pod-mahogany	Browsed (Van Wyk, P. 1984)	Punda Maria, N'wambiya, Lebombo mountains, near Orpen gate	Slow grower (Van Wyk, P. 1984)
Albizia adianthifolia var. *adianthifolia*	Flat-crown Albizia	Browsed (Van Wyk, P. 1984)	North-west of Punda Maria in forest communities near springs	Fast grower (Van Wyk, P. 1984)
Albizia brevifolia	Mountain false-thorn	Browsed (Van Wyk, P. 1984)	Rocky situations north of Olifants river and in dense stands on Nwamuriwa hill and Pafuri area	Slow grower (Van Wyk, P. 1984)
Albizia forbesii	Broad-pod false-thorn	Heavily browsed (Van Wyk, P. 1984)	Rare, granitic soils, often along rivers and streams	Slow grower (Van Wyk, P. 1984)
Albizia harveyi	Common false-thorn	Heavily browsed (Pooley, E. 1994; Van Wyk, P. & Fairall, N. 1969) Debarked (Hiscocks, K.1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Albizia petersiana subsp. *evansii*	Many-stemmed false-thorn	Browsed (Van Wyk, P. & Fairall, N. 1969) Debarked (Roux, J. *pers. comm.* 2005)	Abundant along the Karoo sediments	Slow grower (Van Wyk, P. 1984)
Albizia tangayicensis subsp. tanganyicensis	Paperbark false-thorn	Severely damage (Van Wyk, P. 1984) Leaves & young branches (Venter, F. & J. 1996)	Only against the slope of the ridges in Punda Maria	Fairly fast grower (Van Wyk, P. 1984)
Albizia versicolor	Large-leaved false-thorn	Browsed (Van Wyk, P. 1984) Leaves and shoots utilised (Venter, F. & J. 1996)	Granitic soils in Pretorius Kop area and sandveld area of Punda Maria	Fast grower (Van Wyk, P. 1984)
Aloe marlothii subsp. *marlothii*	Mountain aloe	Severe damage (Biologiese Afdeling, Jaarverslag 1959) Preferred species (Steyn, A. & Stalmans, M. 2001)	Mainly in southern areas of the KNP and in rocky situations	Slow grower (Davies, L. *pers. comm.* 2005)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Utilised except in inaccessible areas (Sowry, R. *pers. comm.* 2005)		
Androstachys johnsonii	Lebombo ironwood	Browsed (Van Wyk, P. 1984)	Lebombo range, Punda Maria and Pafuri	Slow grower (Van Wyk, P. 1984)
Anthocleista grandiflora	Forest fever tree	Leaves & branches (Van Wyk, P. 1984; Venter, F. & J. 1996) Browsed (Schmidt, E. *et al.* 2002)	Sabie river and Tshipudza in Punda Maria area	Fast grower (Van Wyk, P. 1984)
Antidesma venosum	Tassel berry	Leaves and young shoots (Venter, F. & J. 1996)	Deep sandy soils of Pretorius Kop and Punda Maria areas	Fast growing (Venter, F. & J. 1996)
Atalaya alata	Lebombo krantz ash	Probably utilised (Van Wyk, P. 1984)	Rare in KNP –Occurs on the Lebombo mountains in ravines	Slow grower (Van Wyk, P. 1984)
Balanites maughamii	Green thorn	Browsed (Van Wyk, P. 1984)	Throughout KNP on sandy and granitic soils	Slow grower (Van Wyk, P. 1984)
Baphia massaiensis	Sand camwood	Well utilised (Williamson, B.R. 1975)	N'wambiya sandveld	Slow grower (Davies, L. *pers. comm.* 2005)
Berchemia discolor	Brown ivory	Fruit and leaves browsed (Van Wyk, P. 1984) Branches broken (Hiscocks, K. 1999) Leaves & young branches utilised (Venter, F. & J. 1996)	Throughout KNP but rare, limited to granite, rhyolite, sandy soils and termite mounds	Slow grower (Van Wyk, P. 1984)
Bolusanthus speciosus	Tree Wistaria	Sporadically damaged (Van Wyk, P. 1984) Browsed (Van Wyk, P. & Fairall, N. 1969)	Throughout the KNP	Fairly fast grower (Van Wyk, P. 1984)
Boscia albitrunca	Shepherd's tree	Browsed (Williamson, B.R. 1975)	Throughout KNP, generally rare, but abundant in Pafuri area	Slow grower (Van Wyk, P. 1984)
Boscia angustifolia	Rough-leaved shepherd's tree	Browsed (Williamson, B.R. 1975)	Northern area of the KNP on sandstone ridges between Punda Maria and Pafuri	
Brachylaena huillensis	Lowveld silver oak	Branches and leaves browsed (Van Wyk, P. 1984)	Punda Maria, N'wambiya sandveld and northern part of the Lebombo mountains	Extremely slow grower (Van Wyk, P. 1984)
Burkea africana	Wild seringa	Utilised (Van Wyk, P. 1984) Browsed (Williamson, B.R. 1975)	Sandveld around Punda Maria	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Cassia abbreviata subsp. *beareana*	Long-tail Cassia	Browsed (Van Wyk, P. & Fairall, N. 1969; Venter, F. & J. 1996) Branches broken (Hiscocks, K.1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Cleistanthus schlechteri var. *schlechteri*	False tamboti	Favoured by elephants (Van Wyk, P. 1984; Pooley, E.1994) Utilised (Nel, P.J. 1988)	N'wambiya sandveld and Pafuri	Slow grower (Van Wyk, P. 1984)
Colophospermum mopane	Mopane	High on diet (Van Wyk, P.1984) Pushed over & browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Nel, P.J. 1988) Shrubs more utilised (Swart, H.B. 1995) Leaves and twigs preferred (Williamson, B.R. 1975; Venter, F. & J. 1996)	Abundant in the KNP north of the Olifants river, west of Timbavati river	Slow grower (Van Wyk, P. 1984)
Combretum apiculatum subsp. *apiculatum*	Red bushwillow	Pushed over & browsed (Van Wyk, P. & Fairall, N. 1969) Uprooted frequently (Baxter, P.W.J. 2003) Uprooted (Hiscocks, K. 1999) Selectively damaged close to water (Brits,J. 1999; Thrash *et al.* 1991) Debarked (Roux, J. *pers. comm*. 2005) Well utilised (Williamson, B.R. 1975) Browsed (Venter, F. & J. 1996)	Abundant in KNP on granitic and rhyolite soils	Slow grower (Van Wyk, P. 1984)
Combretum celastroides	Trailing bushwillow	Browsed (Williamson, B.R. 1975)	N'wambiya sandveld, alluvial soils next to Luvuvhu river, Dzundwini in the Punda Maria area	
Combretum collinum subsp. *gazense*	Rhodesian bushwillow	Browsed (Van Wyk, P. 1984; Van Wyk, P. & Fairall, N. 1969)	Pretorius Kop and Punda Maria	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Browsed (Williamson, B.R. 1975)		
Combretum erythrophyllum	River bushwillow	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996)	Sabie and Luvuvhu rivers	Fast grower (Van Wyk, P. 1984)
Combretum hereroense	Russet bushwillow	Leaves browsed (Van Wyk, P. 1984; Van Wyk, P. & Fairall, N. 1969; Venter, F. & J. 1996) Branches utilised (Hiscocks, K. 1999) Debarked (Roux, J. *pers. comm.* 2005) Well utilized (Williamson, B.R. 1975)	Throughout KNP, along rivers and streams and brackish flats	Slow grower (Van Wyk, P. 1984)
Combretum imberbe	Leadwood	Browsed & pushed over (Van Wyk, P. & Fairall, N. 1969) Branches broken, preferred species (Hiscocks, K.1999) Debarked (Roux, J. *pers. comm.* 2005) Well utilised (Williamson, B.R. 1975) Browsed (Venter, F. & J. 1996)	Throughout the KNP but mostly low lying areas	Very slow grower (Van Wyk, P. 1984)
Combretum mossambicense	Knobbly climbing bushwillow	Browsed (Williamson, B.R. 1975)	Throughout the KNP but more common in the northern areas	
Combretum zeyheri	Large-fruited bushwillow	Uprooted frequently (Baxter, P.W.J. 2003) Branches broken (Hiscocks, K.1999) Debarked (Roux, J. *pers. comm.* 2005). Well utilised and roots favoured (Williamson, B.R. 1975)	Throughout the KNP except brackish flats	Slow grower (Van Wyk, P. 1984)
Commiphora africana var. *africana*	Hairy corkwood	Uprooted (Van Wyk, P. & Fairall, N. 1969) Roots browsed (Zambatis, N. *pers. comm.* 2005)	Throughout the KNP	
Commiphora edulis subsp. *edulis*	Rough-leaved corkwood	Browsed (Van Wyk, P. 1984)	Extreme northern area of the KNP	Fast grower (Van Wyk, P. 1984)

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SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Commiphora glandulosa	Tall common corkwood	Moderately utilised (Nel, P.J. 1988)	Widely distributed on both basalt and rhyolite, abundant in the Pafuri area	Fast grower (Van Wyk, P. 1984)
Commiphora mollis	Velvet corkwood	Browsed (Van Wyk, P. & Fairall, N. 1969) Moderately utilised (Nel, P.J. 1988)	Throughout the park	Fairly fast grower (Van Wyk, P. 1984)
Commiphora pyracanthoides	Firethorn corkwood	Browsed (Williamson, B.R. 1975)	Throughout the KNP but abundant in Mopane veld in rocky situations	
Commiphora schimperi	Glossy-leaved corkwood	Roots, bark and leaves eaten (Pooley, E. 1994)	Fairly rare. Granitic soil south of Sabie River and in the vicinty of Satara and Punda Maria	Slow grower (Van Wyk, P. 1984)
Commiphora viminea	Zebra-bark corkwood	Moderately utilised (Nel, P.J. 1988)	North and north-east of Punda Maria on basaltic soils	Fast grower (Schmidt, E. *et al.* 2002.)
Cordia grandicalyx	Round-leaved saucer-berry	Browsed (Van Wyk, P. 1984)	Sandveld north of Shingwedzi river	Fast grower (Van Wyk, P. 1984)
Cordia sinensis	Grey-leaved saucer-berry	Browsed (Van Wyk, P. & Fairall, N.1969)	Associated with termitaria and along streams	
Crossopteryx febrifuga	Sand-crown berry	Browsed (Van Wyk, P. 1984; Williamson, B.R. 1975)	Sandveld areas in the Punda Maria & Pafuri areas	Slow grower (Van Wyk, P. 1984)
Croton gratissimus var. *gratissimus*	Lavender fever tree	Browsed (Van Wyk, P. 1984; Williamson, B.R. 1975)	Throughout KNP	Fast grower (Pooley, E. 1994)
Croton megalobotrys	Large fever berry	Tree extensively utilised (Van Wyk, P. 1984) Heavily browsed (Van Wyk, P. & Fairall, N. 1969)	Only on alluvial soils	Fast grower (Van Wyk, P. 1984)
Croton pseudopulchellus	Small lavender croton	Browsed (Williamson, B.R. 1975)	Northern sandveld of KNP	
Cussonia spicata	Common cabbage tree	Browsed. (Zambatis, G. *pers. comm.* 2005; Venter, F. & J. 1996). Highly utilised (Steyn, A. & Stalmans, M. 2001)	Relatively rare in the KNP, found on hills and ridges	Fast grower (Van Wyk, P. 1984)
Dalbergia armata	Thorny rope.	Favoured (Steyn, A. & Stalmans, M. 2001)	Thickets in the Pretorius Kop and Punda Maria area	

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Dalbergia melanoxylon	Zebra wood	Roots are eaten (Van Wyk, P. 1984) Severely damaged (Van Wyk, P. & Fairall, N. 1969) Roots, Underground parts (Van Wyk, P. & Fairall, N. 1969) Branches broken, preferred species (Hiscocks, K.1999) Browsed (Williamson, B.R. 1975)	Throughout KNP	Slow grower (Van Wyk, P. 1984)
Dichrostachys cinerea	Sickle bush	Heavily browsed (Van Wyk, P. & Fairall, N. 1969) Branches broken (Hiscocks, K. 1999) Browsed (Williamson, B.R. 1975)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Diospyros lycioides	Bluebus	Browsed (Williamson, B.R. 1975)	Rare in KNP, occurs mostly in Pretorius Kop area	Relatively fast grower (Venter, F. & J. 1996)
Diospyros mespiliformis	Jackal berry	Branches broken (Hiscocks, K. 1999) Debarked (Roux, J. *pers. comm*. 2005) Browsed (Williamson, B.R. 1975; Venter, F. & J. 1996)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Diplorhynchus condylocarpon	Horn-pod tree	Browsed (Schmidt, E. et al. 2002; Williamson, B.R. 1975) Heavily Browsed (Van Wyk, P. & Fairall, N. 1969) Browsed (Williamson, B.R. 1975)	Sandveld around Punda Maria	Medium fast grower (Van Wyk, P. 1984)
Dombeya rotundifolia var. *rotundifolia*	Common wild pear	Utilised (Steyn, A. & Stalmans, M. 2001) Heavily browsed (Venter, F. & J. 1996)	Granitic, rhyolite and sandy soils. Pretorius Kop, Malelane, Punda Maria areas and on the Lebombo Mountains	Fast grower (Van Wyk, P. 1984)
Erythrina latissima	Broad-leaved coral-tree	Browsed (Zambatis, G. *pers. comm*. 2005; Venter, F. & J. 1996) Bark utilised (Pooley, E.1994)	Koppies and ridges around Malelane and Pretorius Kop	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Erythrina lysistemon	Sacred coral-tree	Browsed and debarked. (Pooley, E. 1994; Venter, F. & J. 1996)	Koppies in the south of the KNP and sandstone ridges in Punda Maria area	Fairly fast growing. (Van Wyk, P. 1984)
Euclea divinorum	Magic guarri	Branches utilised (Hiscocks, K. 1999) Debarked (Roux, J. *pers. comm*. 2005) Browsed (Williamson, B.R. 1975)	Throughout the KNP, often on brackish flats	Slow grower (Van Wyk, P. 1984)
Faidherbia albida	Ana-tree	Preferentially utilised (Baxter, P.W.J. 2003) Browsed (Venter, F. & J. 1996)	River beds and banks	Fast grower (Van Wyk, P. 1984)
Ficus abutilifolia	Large-leaved rock fig	Heavily utilised (Nel, P.J. 1988)	Throughout the KNP on koppies and mountains	Slow grower (Van Wyk, P. 1984)
Ficus capreifolia	Sandpaper fig	Browsed (Schmidt, E. et al. 2002)	Along watercourses and permanent rivers throughout the KNP	Fairly fast grower (Davies, L. *pers. comm.* 2005)
Ficus ingens var. *ingens*	Red-leaved rock fig	Browsed (Van Wyk, P. 1984) Heavily utilised (Nel, P.J. 1988)	Throughout the KNP on koppies and mountains	Fairly fast grower (Van Wyk, P. 1984)
Ficus sansibarica subsp. *sansibarica*	Knobbly fig	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996)	Mainly sandy areas around Punda Maria	Fairly fast grower. (Van Wyk, P. 1984)
Ficus sur	Broom cluster fig	Leaves occasionally eaten (Venter, F. & J. 1996)	Rare, confined to rivers and streams	Fast growing (Venter, F. & J. 1996)
Ficus sycomorus subsp. *sycomorus*	Sycamore fig	Browsed (Zambatis, G. *pers. comm*. 2005; Venter, F. & J. 1996) Heavily utilised (Nel, P.J. 1988)	Throughout the Park along rivers and streams, also deep sandy soils on ridges	Fast grower (Van Wyk, P. 1984)
Ficus tettensis	Small-leaved rock fig	Heavily utilised (Nel, P.J. 1988)	Koppies, mountains north of Olifants river. Rare	Slow grower (Van Wyk, P. 1984)
Flueggea virosa subsp. *virosa*	White-berry bush	Browsed (Williamson, B.R. 1975)	Throughout KNP	
Galpinia transvaalica	Transvaal privet	Browsed (Van Wyk, P. 1984; Pooley, E. 1994; Venter, F. & J. 1996)	Widespread but rare	Slow grower (Van Wyk, P. 1984)
Garcinia livingstonei	African mangosteen	Roots and bark utilised (Venter, F. & J. 1996)	Throughout KNP on riverbanks	Slow grower (Venter, F. & J. 1996)
Gardenia volkensii subsp. *volkensii*	Transvaal gardenia	Browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Hiscocks, K. 1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Fruits (Venter, F. & J. 1996)		
Grewia bicolor var. *bicolor*	White-leaved raisin	Severely browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Hiscocks, K. 1999)	Widespread in the KNP	Slow grower (Davies, L. *pers. comm.* 2005)
Grewia flava	Velvet raisin	Severely browsed (Van Wyk, P. & Fairall, N. 1969)	Mopane communities in the north	Fairly slow grower (Venter, F. & J. 1996)
Grewia flavescens	Sandpaper raisin	Severely browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Hiscocks, K. 1999) Browsed (Williamson, B.R. 1975)	Widespread in the KNP	Fairly fast grower (Davies, L. *pers. comm.* 2005)
Grewia hexamita	Giant raisin	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996) Severely browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Hiscocks, K. 1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Grewia microthyrsa	Lebombo raisin	Severely browsed (Van Wyk, P. & Fairall, N., 1968)	Northern areas of the KNP, sandveld areas of Punda Maria and N'wambiya sandveld	
Grewia monticola	Silver raisin	Severely browsed (Van Wyk, P. & Fairall, N. 1969) Utilised (Hiscocks, K. 1999) Browsed (Williamson, B.R. 1975)	Widespread in the KNP, usually on sandy soils and in stony areas	Slow grower (Van Wyk, P. 1984)
Grewia retinervis	False rough-leafed raisin	Browsed (Williamson, B.R. 1975)	N'wambiya sandveld	
Guibourtia conjugata	Small copalwood	Utilised (Van Wyk, P. 1984)	Sandveld around Punda Maria	Slow grower (Van Wyk, P. 1984)
Gymnosporia glaucophylla	Blue spikethorn	Branches broken (Hiscocks, K. 1999)	South of the Olifants river	
Gymnosporia senegalensis	Red spikethorn	Browsed (Van Wyk, P. & Fairall, N. 1969)	Throughout the KNP. Along rivers and dry river beds	
Hyphaene coriacea	Lala palm	Utilise fruit (Pooley, E.1994)	Basaltic soils, along streams and rivers	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
		Heavily browsed (Van Wyk, P. & Fairall, N. 1969) Pushed over (Nel, P.J. 1988)		
Hyphaene petersiana	Northern Lala palm	Fruit, new shoots (Stevenson-Hamilton, J. 1937) Browsed (Williamson, B.R. 1975)	Alluvial areas in Mopane veld	Slow grower (Van Wyk, P. 1984)
Kigelia africana	Sausage tree	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996)	Throughout the KNP – Riverine	Fast grower (Van Wyk, P. 1984)
Kirkia acuminata	White seringa	Pushed over (Nel, P.J. 1988)	Lebombo mountains, koppies and Pafuri area	Fast grower (Van Wyk, P. 1984)
Kirkia wilmsii	Mountain seringa	Elephants relish trees (Van Wyk, P. 1984)	Mainly Malelane mountains in Berg-en-Dal area. A few on the western boundary west of Olifants river	
Lannea schweinfurthii var. *stuhlmannii*	False marula	Heavily browsed (Van Wyk, P. & Fairall, N. 1969) Debarked (Hiscocks, K. 1999) Debarked (Roux, J. *pers. comm.* 2005) Bark, twigs and roots utilised (Venter, F. & J. 1996)	Throughout the KNP	Fairly fast grower (Van Wyk, P. 1984)
Maerua angolensis	Bushveld Bead-bean	Browsed (Venter, F. & J. 1996)	Very rare in KNP, usually in rocky areas and termitaria	800mm per year (Venter, F. & J. 1996)
Maerua parvifolia	Dwarf bush-cherry	Browsed (Williamson, B.R. 1975)	Throughout KNP, often on termitaria	
Manilkara mochisia	Lowveld milkberry	Debarked, preferred species (Hiscocks, K. 1999)	Widespread in the KNP but not on basaltic plains in eastern half	Slow grower (Van Wyk, P. 1984)
Markhamia zanzibarica	Maroon bell-bean tree	Browsed (Van Wyk, P. 1984; Schmidt, E. et al. 2002.)	Sandveld areas around Punda Maria and koppies in Pretorius Kop area	Slow grower (Van Wyk, P. 1984)
Mimusops zeyheri	Transvaal red-milkwood	Browsed (Venter, F. & J. 1996)	Relatively rare, mainly limited to dense ravines and riverine bush	Medium to fast grower (Venter, F. & J. 1996)
Mundulea sericea	Cork bush	Heavily browsed (Van Wyk, P. & Fairall, N. 1969;) Browsed (Williamson, B.R. 1975; Venter, F. & J. 1996))	Mostly in deep sandy areas of Punda Maria and Pretorius Kop	Fast grower (Pooley, E. 1994)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Nuxia oppositifolia	Water elder	Browsed (Van Wyk, P. 1984)	Riverine	Slow grower (Van Wyk, P. 1984)
Olax dissitiflora	Small sour plum	Browsed (Van Wyk, P. 1984; Nel, P.J. 1988)	Scare but throughout KNP	Slow grower (Van Wyk, P. 1984)
Ormocarpum trichocarpum	Caterpillar-pod bush	Browsed (Van Wyk, P. & Fairall, N. 1969) Branches broken (Hiscocks, K. 1999)	Widespread in KNP, low lying brackish soils	Fast grower (Davies, L. pers comm. 2005)
Ozoroa paniculosa var. *paniculosa*	Common resin tree	Browsed (Van Wyk, P. 1984)	Limited to northern sandveld regions	Moderately fast grower (Van Wyk, P. 1984)
Ozoroa sphaerocarpa	Currant resin tree	Browsed (Van Wyk, P. & Fairall, N. 1969)	Limited to the granitic soils in the southern area of the KNP – Pretorius Kop / Malelane area	Relatively fast grower (Van Wyk, P. 1984)
Pappea capensis	Jacket plum	Browsed (Van Wyk, P. & Fairall, N. 1969; Venter, F. & J. 1996) Utilised (Hiscocks, K. 1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Parinari curatellifolia	Mobola plum	Leaves and fruit utilised (Venter, F. & J. 1996)	Well drained, sandy soils of Punda Maria and Pretorius Kop areas	Slow grower (Van Wyk, P. 1984)
Pavetta edentula	Gland-leaf tree	Browsed (Van Wyk, P. 1984)	Southern areas of the KNP	Slow grower (Van Wyk, P. 1984)
Pavetta schumanniana	Poison bride's bush	Browsed (Van Wyk, P. & Fairall, N. 1969)	Pretorius Kop / Malelane area and Shangoni / Punda Maria area in deep sandy soils	
Peltophorum africanum	African-wattle	Debarked (Roux, J. *pers. comm.* 2005) Browsed (Williamson, B.R. 1975) Leaves and twigs eaten (Venter, F. & J. 1996)	Throughout the KNP	Fast grower (Van Wyk, P. 1984)
Piliostigma thonningii	Camels foot	Browsed (Van Wyk, P. 1984; Williamson, B.R. 1975; Venter, F. & J. 1996)	Sandy soils, Pretorius Kop and Punda Maria	Slow grower (Van Wyk, P. 1984)
Philenoptera violacea	Apple-leaf	Browsed (Van Wyk, P. 1984; Van Wyk, P. & Fairall, N. 1969) Branches broken (Hiscocks, K. 1999) Browsed (Williamson, B.R. 1975)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Phoenix reclinata	Wild date palm	Foliage and stems utilised (Van Wyk, P. 1984) Browsed (Venter, F. & J. 1996)	Throughout the KNP on river banks and in beds	Slow grower (Van Wyk, P. 1984)
Portulacaria afra	Porkbush	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996)	Mountainous areas of KNP- Malelane, Lebombo mountains south of the Olifants river and Punda Maria	Slow grower (Van Wyk, P. 1984)
Pseudolachnostyylis maprouneifolia var. *maprouneifolia*	Kudu berry	Leaves and fruit utilised (Van Wyk, P. 1984) Heavily browsed (Van Wyk, P. & Fairall, N. 1969) Browsed (Williamson, B.R. 1975)	Stony soils mostly on the Lebombo range, north of Olifants river and also in koppies and ridges in the Punda Maria area	Slow grower. (Van Wyk, P. 1984)
Pteleopsis myrtifolia	Myrtle bushwillow	Browsed (Van Wyk, P. 1984)	Punda Maria area and N'wambiya	Slow grower (Van Wyk, P. 1984)
Pterocarpus angolensis	Transvaal teak	Browsed and pushed over (Van Wyk, P. 1984) Debarked (Zambatis, N. *pers. comm.* 2005) Heavily browsed (Van Wyk, P. & Fairall, N. 1969) Browsed & ring barked (Williamson, B.R. 1975) Browsed (Venter, F. & J. 1996)	Deep sandy soils in Pretoriuskop area, between Skukuza and Crocodile Bridge, between Skukuza and Orpen and the Punda Maria area	Slow grower (Van Wyk, P. 1984)
Pterocarpus lucens subsp. *atunesii*	Thorny teak	Browsed (Van Wyk, P. 1984; Williamson, B.R. 1975)	N'wambiya sandveld	Slow grower (Davies, L. *pers. comm.* 2005)
Pterocarpus rotundifolius subsp. *rotundifolius*	Round-leaved teak	Browsed (Van Wyk, P. 1984; Venter, F. & J. 1996) Debarked (Hiscocks, K. 1999)	Throughout the KNP	Slow grower (Van Wyk, P. 1984)
Rhus gueinzii	Thorny Karee	Browsed (Van Wyk, P. & Fairall, N. 1969)	Throughout the KNP	Fast grower (Pooley, E. 1994)
Rhigozum zambesiacum	Mopane Pomegranate	Browsed (Van Wyk, P. & Fairall, N. 1969)	Widespread in the KNP, especially in the brackish flats near rivers and stream and on basaltic soils	Fast grower (Davies, L. *pers. comm.* 2005)
Salvadora australis	Transvaal mustard tree	Browsed (Van Wyk, P. 1984)	Eastern side of KNP, abundant along the Shingwedzi river and at Pafuri	Very slow grower (Van Wyk, P. 1984)
Schotia brachypetala	Weeping boer-bean	Debarked (Hiscocks, K. 1999; Roux, J. *pers. comm.* 2005)	Throughout the KNP, abundant in the south and occurs on termitaria and banks of rivers and streams	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Sclerocarya birrea subsp. *caffra*	Marula	Bark stripped, fruit, leaves (Van Wyk, P. 1984) Browsed (Van Wyk, P. & Fairall, N. 1969; Venter, F. & J. 1996) Preferentially utilised (Baxter, P.W.J. 2003) Pushed over, broken at trunk, branches broken, debarked (Coetzee,B.J. *et al*. 1979) Heavily utilised at times (Nel, P.J., 1988) Debarked (Hiscocks, K. 1999; Roux,J. *pers. comm*. 2005) Fruit (Stevenson-Hamilton, J. 1941) Elephant impact main cause of mortality amongst marula trees (Jacobs, O.S. 2001) Stem breakage killed trees 2 - 8m (main stem breakage) (Jacobs, O.S. 2001) 8-14m bark damage (Jacobs, O.S. 2001) More than half the marula trees sampled in the KNP are suffering elephant damage with elephants being the main cause of 7% mortality. (Jacobs, O.S. 2001) Tree structure is altered resulting in coppicing (Jacobs, O.S. 2001) Damage to shorter trees (2-5m) higher than damage to taller trees (5-14m) (Jacobs & Biggs 2002)	Throughout KNP	Fast grower (Van Wyk, P. 1984)
Sesamothamnus lugardii	Transvaal sesame bush	Browsed & uprooted (Van Wyk, P. 1984)	Rare in KNP (Only two localities) - south of the Olifants river and the sandveld north-east of Punda Maria	Slow Grower (Van Wyk, P. 1984)
Spirostachys africana	Tamboti	Browse fresh leaves (Pooley, E. 1994; Venter, F. & J. 1996)	Throughout KNP, especially on the brackish flats in the south	Slow grower (Van Wyk, P. 1984)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Stadmannia oppositifolia subsp. *rhodesica*	Silky plum	Browsed (Van Wyk, P. 1984)	Sandstone ridges east/north-east of Punda Maria and in the vicinity of Olifants camp	Slow grower (Van Wyk, P. 1984)
Steganotaenia araliacea var. *araliacea*	Carrot tree	Utilise leaves and bark (Van Wyk, P. 1984)	Rare. Hills and ridges in Malelane & Pretorius Kop area, Olifants, Letaba and Punda Maria area	Fast grower (Van Wyk, P. 1984)
Sterculia rogersii	Common star-chestnut	Browsed (Van Wyk, P. & Fairall, N. 1969) Break branches and uproot (Kelly, H.L.P. 2000) Utilised (Nel, P.J. 1988)	Throughout KNP but is rare in all areas except Pafuri region	Slow grower (Van Wyk, P. 1984)
Strychnos madagascariensis	Spineless monkey-orange	Browsed (Pooley, E. 1994) Heavily utilised (Van Wyk, P. & Fairall, N. 1969)	Throughout KNP, more abundant in the Pretorius Kop area	Slow grower (Van Wyk, P. 1984)
Strychnos spinosa	Green monkey orange	Fruit (Pooley, E. 1994) Browsed (Williamson, B.R. 1975)	Riverbanks, sandy and stony areas, fairly rare in KNP	Slow grower (Van Wyk, P. 1984)
Terminalia phanerophlebia	Lebombo cluster-leaf	Browsed (Van Wyk, P. 1984)	Malelane mountains, koppies near Pretorius Kop and the Lebombos	Slow grower (Van Wyk, P. 1984)
Terminalia prunioides	Thorny cluster-leaf	Browsed (Van Wyk, P. & Fairall, N. 1969; Williamson, B.R. 1975)	Throughout KNP	Slow grower (Van Wyk, P. 1984)
Terminalia sericea	Silver cluster-leaf	Uprooted frequently (Baxter, P.W.J. 2003) Utilised (Nel, P.J. 1988) Debarked (Roux, J. *pers. comm.* 2005) Browsed (Williamson, B.R. 1975)	Deep, sandy soils on the western half of the KNP, sandstone areas of Punda Maria, Pumbe sandveld and Pretorius Kop	Slow grower (Van Wyk, P. 1984)
Vangueria infausta	Wild Medlar	Leaves and young branches utilised (Venter, F. & J. 1996)	Throughout the KNP on stony and sandy soils	Slow grower (Venter, F. & J. 1996)
Vepris reflexa	Bushveld white ironwood	Browsed (Van Wyk, P. 1984)	Throughout the KNP on koppies and ridges (nowhere common)	Slow grower (Van Wyk, P. 1984)
Vitex patula	Sand fingerleaf	Browsed (Schmidt, E. *et al.* 2002)	Punda Maria on sandy soils	

WOODY TAXA				
SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Warburgia salutaris	Pepper-bark tree	Utilised (Botha, J. *et al.* 2004)	Sandstone ridges north-west of Punda Maria	Fast grower (Van Wyk, P. 1984)
Xeroderris stuhlmannii	Wing bean	Fruit and leaves utilised (Venter, F. & J. 1996)	N'wambiya sandveld, near Dzundwini hill and sandveld between the Limpopo & Luvuvhu rivers	Slow grower (Van Wyk, P. 1984)
Ximenia americana var. *americana*	Blue sourplum	Browsed (Williamson, B.R. 1975)	Throughout the KNP in dry rocky areas	
Xylia torreana	Sand ash	Occasionally utilised (Van Wyk, P.1984)	N'wambiya sandveld and sandveld north-west of Punda Maria	Slow grower (Van Wyk, P. 1984)
Ziziphus mucronata subsp. *mucronata*	Buffalo-thorn	Branches broken (Hiscocks, K. 1999) Debarked (Roux, J. *pers. comm.* 2005) Browsed (Williamson, B.R. 1975)	Widespread in KNP	Fast grower (Van Wyk, P. 1984)
Ziziphus rivularis	False buffalo-thorn	Sporadically utilised (Van Wyk, P. 1984)	Lebombo mountains between Crocodile Bridge and Sabie river and Mphongolo river	Fast grower (Van Wyk, P. 1984)
HERBACEOUS TAXA				
Brachiaria nigropedata	Spotted signal grass	Grazed (Williamson, B.R. 1975)	Sandy well drained soils, mostly found in the Punda Maria and Pretorius Kop area	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Citrullus lanatus	Bitter Mellon	Well utilised (Williamson, B.R. 1975)	Pretorius Kop area	Annual creeper
Cynodon dactylon	Couch grass	Grazed (Williamson, B.R. 1975)	More common in the southern KNP & in overgrazed trampled areas	Perennial grass (Gibbs Russell, G.E. *et al.* 1991)
Dactyloctenium aegyptium	Crowfoot	(Williamson, B.R. 1975)	Throughout the KNP in disturbed areas near water	Annual grass (Gibbs Russell, G.E. *et al.* 1991)
Dactyloctenium giganteum	Giant crowfoot	Main grass species in stomach (Williamson, B.R. 1975)	Throughout the KNP in disturbed areas on river banks or near water	Robust Annual (Gibbs Russell, G.E. *et al.* 1991)
Digitaria eriantha	Common finger grass	Grazed (Williamson, B.R. 1975)	Throughout the KNP in a wide range of habitats	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Eragrostis rigidior	Curly leaf	Grazed (Williamson, B.R. 1975)	Sandy loam, disturbed areas throughout the KNP	Perennial (Gibbs Russell, G.E. *et al.* 1991)

WOODY TAXA

SPECIES	COMMON NAME	UTILIZATION	HABITATS & DISTRIBUTION IN KNP	GROWTH RATE
Heliotropium zeylanicum		Grazing (Zambatis, N. *pers. comm.* 2005)	Northern area of the KNP in alluvial soil and sandy river banks	Perennial herb (Retief, E. & Herman, P.P.J., 1997)
Heteropogon contortus	Tanglehead	Grazed (Williamson, B.R. 1975)	Hillsides and rocky areas on well-drained soils throughout the KNP	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Hyparrhenia filipendula	Fine thatching grass	Grazed (Williamson, B.R. 1975)	Southern & northern areas of the KNP with a high annual rainfall – Pretorius Kop, Stols Nek and Punda Maria	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Hyperthelia dissoluta	Yellow thatching grass	Grazed (Williamson, B.R. 1975)	Roadsides and disturbed places - Pretorius Kop and Punda Maria	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Ischaemum afrum	Turf grass	Grazed (Williamson, B.R. 1975)	Throughout the KNP usually near water in black turf soils	Perennial (Gibbs Russell, G.E. *et al.* 1991)
Ledebouria revoluta	Common ledebouria	Browsed (Williamson, B.R. 1975)	Pretorius Kop area	Bulbous
Melinis repens	Natal red top	Grazed (Williamson, B.R. 1975)	Although mainly in the south it occurs throughout the KNP in disturbed areas	Annual or perennial (Gibbs Russell, G.E. *et al*. 1991)
Panicum maximum	Guinea grass	Grazed (Williamson, B.R. 1975)	Throughout the KNP in shady places and along river banks	Usually perennial (Gibbs Russell, G.E. *et al*. 1991)
Siphonochilus aethiopicus	Wild ginger	Uprooted (Crouch, N.R. *et al.* 2000)	Rare in KNP –Pretorius Kop area	Bulbous plant
Tylosema fassoglensis	Creeping Bauhinia	Entire plant utilised (Williamson, B.R. 1975)	Throughout the KNP in rocky situations - Lebombo mountains, clay & sandy soils and rocky situations	Robust, creeping, shrublet with tuber
Urochloa trichopus		Grazed (Williamson, B.R. 1975)	In Pafuri area, usually on sandy soils, floodplains and riverbanks	Annual (Gibbs Russell, G.E. *et al.* 1991)
Vigna unguiculata	Wild cow pea	Browsed (Williamson, B.R. 1975)	Throughout the KNP, usually on sandy soils, disturbed areas, and next to streams	Trailing herb with tuber

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SUMMARY AND CONCLUSIONS: THE IMPACTS OF ELEPHANTS ON BIODIVERSITY

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Do elephants impact on biodiversity? The written submissions featured here and workshop discussions all support the conclusion that elephants do indeed influence the biodiversity of the ecosystems in which they are present, to a greater or lesser extent. These conclusions are also a reflection of the plethora of scientific studies published elsewhere that have addressed this issue. These impacts may vary from declines in population abundance of specific species (and sometimes this may lead to extirpation) to landscape level effects, and include some interesting knock-on effects as exemplified by the decline in resources for birds that require tall trees or trees with hollows for nesting in. Available examples of biodiversity affected by elephants cover most of the broadest definition of biodiversity from populations to landscapes, and also extend to ecosystem services. There do however appear to have been no studies undertaken on the impacts of elephants on the genetics of species as yet.

Evidence for the impacts of elephants has been presented in a somewhat eclectic mix of largely autecological studies. Most of the rationale for these studies are not clearly established within a larger framework addressing the so-called elephant problem, but really seem to reflect the interests of the scientists involved. Thus our understanding of elephant impacts does not really reflect any cohesive effort to address the issue.

Within South Africa, the most cohesive approach to understanding elephant impacts on biodiversity appears to have developed in the Eastern Cape, largely through the serendipitous availability of a series of elephant exclosures associated with a confined population of elephant, and as a consequence of studies tending to be built on each other, rather than happening independently. This did not, however, happen through any formal programme. A major recent breakthrough here is the development of a quantitative elephant impact measure in terms of accumulated elephant density by Landman (in prep.). This is an attempt to focus on the effects of different elephant densities, and again the incremental expansion of the Addo elephant enclosure provides a serendipitous experimental design that does not appear to be available elsewhere.

A pause for reflection will identify another interesting pattern in the findings presented here or discussed at the workshop: no studies reported an absence of elephant impacts on biodiversity. This conclusion has to be treated with deep caution however, as this is more likely to reflect the biases against reporting non-significant (in a statistical sense) findings, rather than a true absence of impacts. This identifies the need to ensure that such findings are included into future syntheses of the problem.

So what can we conclude regarding the impacts of elephants on biodiversity?

The information presented here on impacts of elephant clearly shows that there are a diversity of such effects and that we have clear evidence of a smoking gun – elephants do undoubtedly affect biodiversity. This apparently deep insight has actually long been known and the frustration here revolves around an old question (how do elephants affect biodiversity?) being readdressed, together with its corollary of “if and how these impacts should be managed”. Unfortunately, we can not answer this yet as we do not have the full answer to the first question: we actually have limited understanding as to **how** elephants affect biodiversity.

A bit of reflection leads to the realization that asking how elephants affect biodiversity is analogous to asking about the length of a piece of string – with two important distinctions.

Firstly, the string question is one dimensional (length) whereas the elephant question has a multitude of dimensions if properly asked. Thus the answer to the elephant question depends on which aspect of biodiversity is being considered, the productivity of the ecosystem in question (with obvious sub-dimensions of the role of soil fertility, rainfall, temperatures and plant growth forms in determining productivity), the time frames of impacts and most importantly the number/density/residency of the elephants that are impacting the system. The question is further compounded by possibly synergistic or antagonistic influences of co-existing herbivores or people on these elephant impacts.

The second distinction between the string and elephant impacts questions is that the string question is fundamentally trivial (unless the string of interest is supposed to be holding your trousers up), as string can always be cut or joined to suite the demand (including your sagging clothing) – hence its rhetorical nature. In contrast, the elephant impacts question is central to the persistence of biodiversity, the sustainability of the tourism industry and the debate about animal rights. We can not afford the luxury of allowing this question to be seen as rhetorical, and need to recognise that there is a very real risk of this.

The frustrating part about the question regarding elephant impacts is that it has been so poorly addressed. The question first emerged as the "elephant problem" in East Africa in the 1960s (Parker 1983). Locally, it popped up again in the Kruger National Park (KNP) in 1967, as elephant populations grew to apparently unsustainable levels. There was a similar emergence of this question in the Eastern Cape Thickets of the Addo Elephant National Park (AENP) due to a relatively small population being restricted to a small area.

Despite the clear understanding that there is an "elephant problem" in South Africa and the culls or modest park expansions that were applied in the KNP and AENP, respectively, there has been no real demonstrated commitment to actually understanding the impacts of elephant on biodiversity. One consequence is that the increasingly unpopular KNP cull had to be suspended in 1994 when it could not be justified in terms of "hard" scientific evidence. The fact that this did not lead to a massive research programme to truly address the issue was a glaring error of judgement on behalf of the South African government, conservation authorities and interested scientists.

As a consequence, a decade of opportunity has slipped by while the KNP elephant population increased, social and political support for culling declined and ecosystems bore the brunt of the increasing elephant population. The impacts of elephants on biodiversity and how to manage them can no longer be swept under the carpet, but one has to pause to mourn the unused opportunities of the last 40 years, and particularly the last ten years. It is no comfort to note that Parker (1983) in writing of the Tsavo elephant crisis of the 1960s wrote "Scientific contribution to resolving the issue was hampered by lack of data".

So what can now be done to address the elephant problem? Despite the lack of a strong unequivocal understanding of the full nature of the impacts of elephants, there is sufficient evidence that doing nothing will place important ecosystems (and the tourism industry) at risk. There is a school of thought that a better understanding of the problem is needed before an appropriate intervention can be designed. The problem with this approach is that it is open ended (when will we know enough?) and suffers from the same logical flaw that Ehrlich (1991) identified in terms of whether we know enough about global biodiversity (i.e. how many species are there?) to initiate conservation efforts. Ehrlich (1991) likened this to demanding a stock take of a burning library building before efforts could be made to save the books.

Another suggested approach appears to be the euphemistically termed local density reduction linked with adaptive management. While this may be intrinsically attractive to those with an inclination to manage ecosystems (as opposed to doing nothing or merely observing them), there are enough questions about the application of this approach and the analysis and utility of any findings that may emerge, to suggest some caution.

What is clearly needed is a partnership and common ground approach between scientists and managers (facilitated by funders) to undertake truly elegant research (that may include experimental interventions) based on elegant, well phrased questions – how many elephants, for what period will have what influence on what aspect of biodiversity in a system of specified productivity and with specified biodiversity management goals? When should agencies simply phrase this question in terms of elephant numbers and when should they use other approaches (such as impacts and desired levels of heterogeneity)? The focus on the elephant question can also not afford the luxury of ignoring other emerging complications such as global change.

Another lesson that also needs to be learnt from the past experience with regards to the elephant problem is that any research programme will have to be of a significant duration. With an animal that lives for up to 65 years and a generation time of well over a decade, short term studies will not provide the sorts of answers that are needed. Again, the lesson of Tsavo needs to be remembered. After the catastrophic die-off of elephants in the 1960s, there was a brief burst of scientific research that only lasted to the mid 1970s. The problem however persists.

South Africa is in a unique position with regards to dealing with elephant impacts in a number of ways. Firstly, in having to face the elephant problem at a number of locations and scales, reflecting the very large number of isolated elephant populations now existing across South Africa. Of these the Kruger population and problem is possibly the largest, but a number of private owners of elephants are also anxiously looking for guidance on what to do with burgeoning elephant populations in small privately owned reserves. This variety of elephant populations is actually an advantage as they provide the basis to develop generalisations regarding elephant impacts across a number of sites. In addition, South Africa is relatively well resourced in terms of scientific expertise and capacity, and should be able to tackle the research problem appropriately. Finally, South Africa is relatively well off in terms of its ability to fund this sort of research, and hence may be able to make a leading contribution to resolving what is in essence an African problem, while safeguarding its tourism revenues.

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