# Granivores as ecosystem regulators of woody plant increasers in semi-arid Savannas of the Lowveld, South Africa

**Leif Michael Petersen**

A Thesis submitted in partial fulfilment of the
requirements for the degree of Magister Scientiae
in the Faculty of Natural Sciences,
University of the Western Cape, South Africa

November 2006

# Granivores as ecosystem regulators of woody plant increasers in semi-arid Savannas of the Lowveld, South Africa

**Leif Michael Petersen**

## Keywords

- Savanna
- Granivores
- Regulators
- Increasers
- Megaherbivores
- Southern African Wildlife College
- Kempiana
- Welverdiend
- Grass biomass
- Bush encroachment

# Abstract

## Granivores as ecosystem regulators of woody plant increasers in semi-arid Savannas of the Lowveld, South Africa

**Leif Petersen**

*MSc Thesis, Biodiversity and Conservation Biology Department; University of the Western Cape*

In recent years, a global trend of increasing woody vegetation densities in semi-arid savanna habitats has been recorded, commonly described in South Africa as ‘bush encroachment’. The shrubs and trees that do this (Increasers) have wrought significant economic and ecological impacts upon carrying capacities of large areas of savannas. This occurs as suitable grazing areas are incrementally engulfed in shrubs and trees establishing new equilibria, from open savannas (essentially grasslands with scattered trees) into closed woodlands (treelands with scattered grasses). In many places such increasers have reached proportions where economically viable livestock properties can no longer be grazed (Child 1995).

Factors such as megaherbivore overabundance, overgrazing, atmospheric $CO_2$ enrichment and incorrect fire management regimes are commonly blamed for change in woody vegetation densities in South African savannas. Additional to these factors, small mammals have been pinpointed as ecosystem regulators in semi-arid Australia (Noble 1997) and USA (Weltzin *et al*. 1997). In both cases, small mammal species were largely eradicated & increases in woody vegetation densities subsequently occurred. Granivorous small mammals are abundant in South African semi-arid savannas and have high dietary nutritive demands which would encourage them to consume energy rich tree and shrub seeds. Similar to the work of Noble (1997) and Weltzin *et al*. (1997) this study is an investigation into the role of small mammal granivores in South African savannas as potential ‘regulators’ of increasers in the ecosystem.

Research was conducted in a semi-arid Lowveld savanna across three management areas; 1: A large herbivore exclosure (the Southern African Wildlife College - SAWC); 2: A ‘natural’ area managed as a conservation zone with a wide variety of indigenous South African wildlife (Kempiana) and; 3: A communally managed grazing area utilised by domestic cattle and goats (Welverdiend).

Grass biomass was measured for each study site using a disk pasture meter (Bransby & Tainton 1977). Highest levels of grass biomass (effectively small mammal understorey cover) were found at the SAWC megaherbivore exclosure (5,744 tonnes/ha), followed by Kempiana (3,360 tonnes/ha) and Welverdiend (466 tonnes/ha).

Within the three management areas 4,300 live trapping nights were conducted between August and December 2000 to find resident small mammals. In total 106 unique small mammals were captured of which 70% were from the SAWC, 21% trapped in Kempiana and 9% were from Welverdiend. In all, 11 spp of small mammals were captured. All were represented at the SAWC, eight from Kempiana and three from Welverdiend. Both abundance and diversity of small mammals appeared related to site habitat structure and grass biomass.

In a follow-up experiment 21 individuals of the three most commonly captured small mammals of the area (*Tatera leucogaster*, *Aethomys namaquensis* and *Aethomys chrysophilus*) were captured and caged for 24 hour periods where a cafeteria containing seeds and seedlings of common increasers in the region (*Terminalia sericea*, *Acacia nilotica*, *Acacia exuvialis* and *Dichrostachys cinerea*) was accessible at all times. After 24 hours the small mammal was evacuated from the cage and analysis of seed/seedling consumption took place. Altogether 45% of seeds offered to captive small mammals were either partially or totally chewed after a 24 hour period. In the same period 72% of seedlings offered were predated by the captive rodents.

Grass biomass and trapping studies showed that small mammal abundance and diversity showed a direct positive correlation to grass biomass understorey and habitat quality. The second part of the experiment revealed a relatively consistent and active effort on behalf of the captive rodents to target both increaser seeds and seedlings.

This thesis demonstrates a link between grass biomass, small mammal abundance and diversity, and their potential increaser seed/seedling predatory activities in the semi-arid Lowveld Savannas of South Africa.

# Declaration

I declare that this report "Granivores as ecosystem regulators of woody plant increasers in semi-arid Savannas of the Lowveld, South Africa" is my own work, that is has not been submitted for any degree of examination in any other University, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Leif Michael Petersen
November 2006

# Acknowledgements

The six years spanning this study has been a remarkable period in my personal and professional life. Since the commencement of my research and completion of this document the advice, influence and persistence of many people was invaluable. Those that stand out at this point include:

- My supervisor; Dr Eugene Moll – for encouraging my escapades to South Africa, supervising my research, patiently waiting for me to get my act together and then for his constructive advice throughout the process and development of this study

- My study colleagues and field assistants from the Southern African Wildlife College; Isaac Gregory, Marion Atyeo, Jamie Goodwin and Adam Eyles

- The SAWC, its lecturers and staff of 2000 who were my introduction to the African continent and allowed me to stay, use the facilities and cause havoc with Adam Pires

- Advisors and supporters; Prof. George Bredenkamp for accommodating me in Pretoria (2000) on my initial research foray. Ms Lyn Pullen for tolerating me while all the ideas were being randomly generated. Prof. Tim Dunne of the University of Cape Town for his advice on statistics in relation to my results

- My wife Sally for her encouragement and support, and to my family whom have been patiently waiting in Australia for my backpacking holiday to finish.

# Table of Contents

# Index of Figures

# Index of Tables

# Appendices

Appendix 1: Field data sheets and rodent capture data/field notes

Appendix 2: Related reports from the Southern African Wildlife College that have contributed to/stemmed from this study (Gregory 2000, Fourie 2003 & Atyeo 2004)

# Prologue

In this thesis, much information and contextual data regarding southern African savannas has been drawn from Bothma (2004). Whilst this is a secondary reference Bothma is a widespread and oft referred industry source, which aptly summarises general savanna data applicable for this study. Where further investigation or scientific analysis is warranted, primary references and additional studies have been sourced.

From a managerial perspective, the central Lowveld of South Africa is a semi-arid region in South Africa. Strictly speaking Acocks (1953) and Booysen and Tainton (1984) refer to the area as an Arid Savanna zone within the Savanna Biome. Unless I have referred to these Authors, my managerial perspective shall prevail in this document.

Referencing has been compiled using the guidelines for the South African Journal of Botany.

# 1. Literature review

## *Savannas - 'grasslands with scattered trees'*

### Introduction

In Africa the savanna biome is an extensive landscape covering up to 66% of the landmass (Mucina *et al.* 2005). Savannas are characterised by a well-defined grassy component with a distinct upper layer of scattered or dense shrubs and/or trees. Climatically savannas occur in tropical and sub-tropical summer rainfall areas with high summer temperatures; and their distribution is constrained by lack of sufficient rainfall, fire and grazing pressure (Bothma 2004). The density, height and growth form characteristics of both woody and grassy components vary considerably within the biome. In southern Africa two distinct savanna types are recognised - arid eutrophic savannas and moist dystrophic savannas (Booysen & Tainton 1984), which are alternately described as sweet and mixed veld (Acocks 1953).

The relative biological stability of savannas as landscapes through evolutionary time has given rise to a unique and charismatic assemblage of wildlife, and a high faunal diversity (Skinner & Smithers 1990, Thomson 1992). In addition to supporting such diversity, there is widespread evidence that savannas have supported human populations at subsistence levels throughout the continent for millennia (Child 1995). This association has in turn meant that savannas have been subject to intense, recurrent human disturbances such as fire, cropping and selective removal of resources. These disturbances have increased from the 19th century to present through exponential human population increase, increasing areas of commercial agriculture, and more recently management of savannas for game animal farming and tourism (McNaughton 1992).

### Types

Savannas can be classified ecologically or by management regimes. Each is described separately for reasons of clarity.

### *Ecological*

South African savannas are subdivided into four structural floristic groupings (as described by Acocks (1953) & Bothma (2004):

- Fine leaved savannas dominated by *Acacia* spp. Found mostly on clay soils and on the sands of the arid Kalahari region
- Broad-leafed savannas dominated by *Combretum* spp. and occurring on sandy loam soils. Commonly described as mixed bushveld
- A mountain or sour bushveld type of savanna dominated by broad leaved *Burkea* and *Terminalia* species
- Mopane veld dominated by *Colophospermum mopane* and *Terminalia* spp.

Whilst assemblages of plants and the composition of ecosystems vary between savannas, all give a similar overall appearance and impression to the observer. Common to all savannas is a more-or-less continuous ground (or understorey) cover of perennial grasses where woody plants seldom form a closed canopy. The grass cover within these systems is the key to maintaining productivity; good soil water relations and soil stability (Smit *et al*. 1999).

In general regional savannas with their associated climatic conditions and vegetation have the ability to support a multitude of animal species.

### *Management*

From a management perspective, savannas are divided broadly into three categories,

- Sweet veld
- Sour veld; and
- Mixed veld

**Sweet veld** occurs in lower lying, semi-arid areas that receive 200-500 mm of rainfall per year, and are associated with clayey soils with a high alkaline content.

Dominant trees are *Acacia* spp. Grazing plants are palatable both throughout the year and across their entire lifecycle, making sweet veld a commercially attractive landscape.

**Sour veld** occurs in high-lying montane regions with rainfall of >650 mm per year. Soils are generally well drained, sandy with a low base content. Trees are increasingly broad leaved and dominated by *Combretum* spp. Edible species tend to lose their palatability at maturity; and due to translocation of nutrients from growing points and leaves to the roots at the end of the growing season, are only palatable for grazing animals for 6-8 months of the year.

**Mixed veld** tends to occur in the transitional zone between sweet and sour veld, and is suitable for grazing for between 6-10 months of the year.

Despite distinguishing between these three management categories, savanna vegetation types are generally contiguous within each landscape; displaying spatial variation aligned to gradual shifts in climate and soil type. South African savanna types are generally constrained by rainfall and soil type (Bothma 2004). Figure 1-1 shows the extent of the Savanna Biome in South Africa.

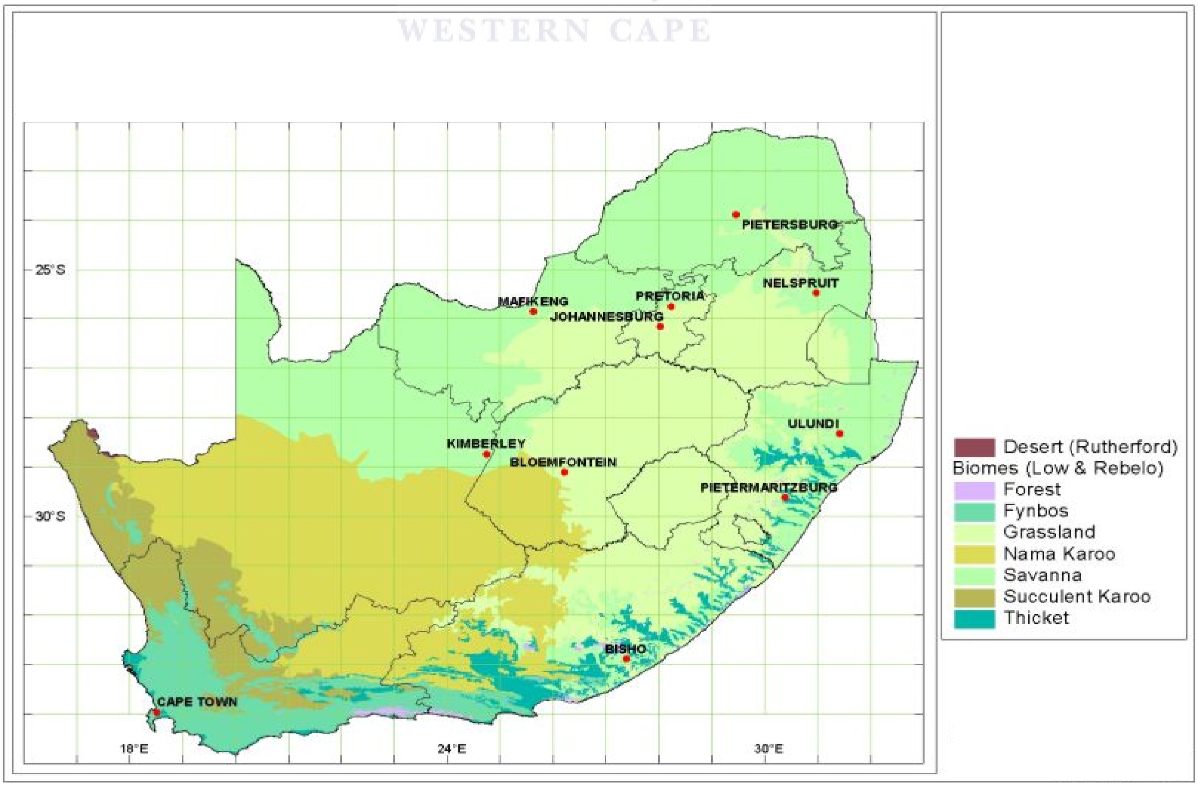

**Figure 1-1:** Biomes of South Africa (Low & Rebelo 1996).

## Savanna processes and disturbance

Studies of savanna ecosystems throughout southern Africa and the world demonstrate that savannas are complex and strongly interlinked ecosystems (e.g.: Jeltsch *et al*. 1998, Noble 1997, Dean *et al*. 1999). In general, the natural balance between shrubs, trees and grasses (the theoretical Clements "Climax State") is seldom attained. High levels of spatial and temporal variability, small-scale heterogeneity, disturbance and factors for tree-grass co-existence create a complex landscape where primary productivity varies drastically in both space and time (McNaughton 1991, Jeltsch *et al*. 1998). This heterogeneity may be due to the number of species, habitat types, and disturbance related activities. For example:

1. Different sized trees provide unequal benefits to animal populations in arid savannas (Dean *et al.* 1999)

2. Various tree and grass alliances and densities create unique resource combinations for ecosystem processes (e.g.: Walter 1979)

3. Large-scale changes can be wrought by particular events such as a fire, drought, etc. Whilst small-scale changes are continuously brought about by animals such as elephant and other megafauna who, in their day-to-day functioning, seek to modify the ecosystem towards their own purposes

In effect a savanna is an ecosystem comprised of innumerable small patches of heterogeneity (Jeltsch *et al.* 1998), each of which has a unique set of conditions, resources and availabilities. Disturbances are relatively common, leading to this small patch landscape being in a state of continual flux.

Such landscape dynamism, in addition to highly localised complexities, creates a managerially difficult landscape. Human management of these ecosystems is commonly limited to use of fire and the management of herbivory (Teague & Smit 1992, Bothma 2004). Human understanding of these habitats remains limited, as intervention in such habitats creates numerous and varying impacts. However, it is known that savanna dynamics are such that disturbance is seen as an essential force for the functioning and management of the ecosystem (Trollope 1981, Jeltsch *et al.* 1998, Bothma 2004).

### *Vegetation Dynamics*

Succession in savannas is multidirectional, occurring over different time scales and consisting of multiple stable points in the same locality (Walter 1979, Bothma 2004). Walter (1979) highlights that climatic savannas (such as those of the Lowveld region) are comprised of antagonistic grass and shrub species, which through various allelopathic and resource partitioning actions, actively attempt to exclude each other from the landscape. Walter (1979) highlights that in savannas receiving <400mm per annum the fibrous root system of grasses limits the amount of water available for trees that have more coarse roots that extend deeper into the soil. Therefore, in such landscapes the grassy component attains dominance. Where tree species are able to link crowns together to form a closed canopy, dominance is shifted to woody plants as conditions on the ground become more shaded and limit grass growth.

### *Patch dynamics*

Unique localised nutritive resource availability and resource conditions determines the assemblages of associated plant species. Where conditions are similar, alliances and associations between plant species of savannas become prominent (Walter 1979, Jeltsch *et al.* 1998). Such alliances can be recognised throughout savannas; e.g.: in arid savannas of the Kalahari where *Acacia erioloba* and *A. haematoxylon*, the only two large tree species, were thought to be responsible for the structure of plant and animal communities and determine pattern and patch dynamics (Jeltsch *et al.* 1996). Similarly, patterned *Sclerocarya birrea* subsp. *caffra* alliances on granite ridges are commonplace in the savannas of Limpopo Province; as is Mopane veld, dominated by *Colosphermum mopane* trees. Such localized areas of dominance foster similar alliances as outlined by Jeltsch *et al.* (1998) in arid savannas. These alliances generate differing habitat conditions throughout the landscape and cause spatial heterogeneity, which in turn favours or excludes various associated fauna and flora species.

Such ecological differences, intermediate disturbances from fire, animals etc. and overall landscape patchiness complicate the management of savanna systems (Pickett & White 1985). Areas of vegetation heterogeneity, alongside seasonal rainfall change affect faunal inhabitants of the savanna landscape. For example, on a local scale *Sclerocarya* ridgetops are a well-utilized habitat by megaherbivores such as the elephant *Loxodonta africana* (Petersen & Moll *unpublished* 2000), who roam through the landscape in search of such preferential habitats, particularly when the trees are in fruit.

In addition to the inherent patchiness of the landscape, it is apparent that even within sites of similar vegetation alliances there are factors that impact on species diversity on a micro level. For example, in arid savannas Jeltsch *et al.* (1998) found that large and small trees do not play identical roles in maintaining biodiversity and that large individual trees are disproportionately important in providing shade, shelter and resting places. Furthermore the subcanopy soils beneath leguminous *Acacia* spp. trees are nutrient enriched; supporting other localized species (Jeltsch *et al.* 1998, Bothma 2004). Different local combinations of plants and conditions in turn attract different fauna and disturbances, bringing about short to medium terms changes on a localized patchy scale – the theory of intermediate disturbance (Pickett & White 1985).

In summary even biologically similar savanna habitats contain subtle differences in nutritive availability, vegetative composition, and associated faunal inhabitants. Such heterogeneity within, between and across vegetative alliances is a key feature of southern African savannas.

### *Fire*

Fire serves as a selection mechanism in savanna ecosystems by creating diversity in both time and space (Hugo 2004) with numerous potential ecological impacts related to frequency, intensity and seasonality. Fire in savannas is a keystone process and global commonality in semi-arid landscapes (Bond & Keeley 2005). For example, prior to European settlement Australian semi-arid savannas were maintained by frequent bushfires that killed the majority of shrub seedlings germinating after fuel generating rains (Noble 1997). Additionally Weltzin *et al.* (1997) identifies fire as a significant historical force in Mesquite (*Prosopis* spp.) landscapes of semi-arid Texas, USA.

As a testament to the ability to cope with fire, some 90% of southern African savanna plants are pyrophytic (Bothma 2004). It is considered by Bond & Keeley

(2005), that savanna landscapes of southern Africa will deteriorate if not defoliated regularly; be it through grazing or fire. Naturally caused fires would generally take place in spring or autumn where electrical storms and low moisture content of vegetation would create conditions conducive to fire events (Werger 1974).

Fire intervals influence vegetative composition in savannas. For example, too frequent fire decreases the grass canopy leading to increasing woody plant densities (Trollope 1982). Similarly fire exclusion reduces productivity of palatable grass species and results in increases in woody vegetation densities and fuel load (Bothma 2004). Jacobs & Biggs (2001) agrees and showed that changes in woody vegetation in response to fire did not involve a decrease in species diversity but rather a change in vegetation structure and morphology.

Fires bring about vegetation change by changing intensity, frequency (Jacobs & Biggs 2001), duration and fire height (Trollope 1982). Fire intensity, a measure of energy released in fires, varies with fuel moisture content, wind, and slope conditions (Jacobs & Biggs 2001). Fire intensity generally increases when frequency is low, leading to ‘hotter’ fires causing greater damage to shrub and tree layers. Topkill, the killing of upper tree and shrub components, forces woody plants to coppice from the stem base, thereby increasing cover of woody material (Trollope 1982).

Faunal populations are also impacted by fire, both immediately and with declining effect over time as vegetation recovery takes place. The first two years after an area has been burnt may be regarded as a dynamic stage, with a number of changes in mammal species richness and composition taking place due to local faunal transition, colonisation and extinction (Rowe-Rowe & Lowry 1982).

Anthropogenically, fire is a complicating factor for landscape management in southern Africa, especially in savannas with inherent patchiness and uneven spread of microhabitats and biodiversity (Bond & Keeley 2005).

### ***Faunal impacts***

In ‘natural’ southern African savannas megaherbivores such as elephant are considerable engineers of the landscape. These large, highly adaptable herd animals consume between 150-300 kg of plant material per day; both browsing and grazing material. Studies in Hwange National Park, Zimbabwe, showed that 87 browse species, 42 grass species and 36 herb species were consumed by local elephant herds over a study period of a few weeks (Williamson 1975). Other significant consumers of savanna plants and potential shapers of this landscape include:

1. Giraffes (*Giraffa camelopardalis*) have been demonstrated to modify ecosystems, mostly through the suppression and reduction of woody plants

2. Hippopotamus (*Hippopotamus amphibius*) graze up to 50 kg of short grass material per day (1,500 kg per month)

3. Black rhino (*Diceros bicornis*) that browse up to 45 kilograms of vegetation per day (1,350 kg per month)

4. Buffalo (*Syncerus caffer*) will graze up to 15 kg of grasses per day (potentially 450 kg of grass per month)

(Modified from Bothma 2004, & Young *et al.* 2005)

Importantly, where megaherbivore populations exceed their food supply and their movements are restricted, they can devastate habitats. In a Zimbabwean Miombo woodland the destruction of feeding trees by elephants, subsequent fires and then revisits by elephants showed a 45% reduction in tree biomass over a five year period (1972 – 1976) (Guy 1981). Additionally, overgrazing and significant habitat damage from commercial cattle farming is a common problem in savanna and grassland habitats worldwide (Bransby & Tainton 1977).

In addition to consumption of vegetation, megaherbivores create pathways and selectively modify savannas by both removing vegetation and transporting seeds of trees to new sites through the process of consumption and defecation. Localized deposition of tree seeds in herbivore dung have been indicated as a probable landscape forming factor in arid savannas by Jeltsch *et al.* (1998). This is corroborated by Williams *et al.* (2000) in New Zealand where introduced Australian possums (*Trichosurus vulpecula*) passed many seeds of various plant species – some 6 - 83% are passed intact. Up to 78% of these seeds germinated successfully.

Personal observation of fully intact seeds of *S. birrea* in elephant dung also shows evidence of the potential for dispersal (corroborated by Whyte *pers comm.* 2000). Many savanna plants have invested significant evolutionary effort into their growth and reproduction in order to encourage the use of such dispersers.

### *Balancing seed loss and dispersal*

In terms of plant reproduction, relationships between flora and fauna are complex and dynamic, balanced between mutualist and antagonist species (Walker *et al.* 1981). In many cases trees and shrubs are reliant on herbivores to disperse seeds, enabling better survival opportunities for offspring. Elephant dispersal of *Sclerocarya* seeds through consumption, digestion and defecation is a typical example of successful utilisation by a plant of an animal in southern African savannas (Whyte *pers comm*. 2000). This process, one of mutual benefit to both the elephant (who gains some nutritional benefit from *Sclerocarya* leaves, branches and fruits) and plant species (that gain free transportation of seed into new habitats), typifies the balance for the plant between tolerating damage and consumption by herbivores, yet gaining distribution into other habitats. Whilst falling short of a conventional mutualistic relationship (for example elephant chewing and digestion may destroy the *Sclerocarya* seed and the damage to the parent tree can be considerable) there are inherent reasons for both species to increase the population of *Sclerocarya* – species survival and broader distribution for the *Sclerocarya*, and creating increased food sources for elephants. Miller (1996) details a similar process for indehiscent savanna acacias that commonly depend on ungulates for successful dispersal. Without ungulate dispersers seed pods fall directly under the parent tree canopy, and few, if any reach sites suitable for seed germination. Despite heavy seed mortality many that are consumed are deposited elsewhere in the veld, and should conditions be appropriate, seedlings sprout from dung in open, unshaded habitats after heavy rain (Miller 1996).

The various stratgies used by plants to encourage dispersal of seeds throughout a habitat are discussed in Table 1-1.

Table 1-1. Plant dispersal mechanisms commonly seen in South Africa

| Dispersal mechanism | Description | Plant species | Life-form | Location |
|---|---|---|---|---|
| Endozoochory | Fruit and gut | *Sclerocarya* spp. | tree | Lowveld, South Africa |
| | Seed and gut | *Acacia karroo* | tree | Karoo, South Africa |
| | | *Acacia exuvialis* | tree | Lowveld, South Africa |
| Epizoochory | Lodgement in fur/hair | *Heteropogon contortus* | grass | Lowveld, South Africa |
| | | *Sporobolis* spp. | grass | South Africa |
| Wind | | Combretum apiculatum | tree | Lowveld, South Africa |
| | | Terminalia sericea | tree | Lowveld, South Africa |

(Table adapted from Ridley 1930, Acocks 1953, Raven *et al.* 1986)

Such dispersal is not restricted to large and medium sized mammals, underground seed caches built by seed-collecting rodents may also act as a determinant of the distribution of trees in savannas (Jeltsch *et al.* 1998). Van der Wal *et al.* (2005) discusses the effects of rodents on seed predation as part of a two phase dispersal strategy by plants, whereby plant seeds are consumed by birds, passed in faeces, collected by rodents *Tamias amoenus* (yellow pine chipmunks) and *Peromyscus maniculatus* (deer mice) and cached, whereupon some seeds would germinate. Seed gathering by these rodents generally removed seeds from exposed, low quality sites (bird faeces on the ground surface) to a soil environment that may help maintain seed viability and promote successful seedling establishment. These animals would carry seeds up to a distance of 12 m and bury them in caches approximately 7.5 mm below the soil surface, and ensuring a high quality dispersal service.

Significantly for the plant, the period between seed dispersal and seedling establishment is an extremely vulnerable stage (Noble & Slayter *in* Gill (ed.)1981). Plants that rely on faunal dispersal of seeds must try to limit seed losses through chewing and digestion by herbivores so they may pass intact into new potential habitats. Strategies to limit seed loss include:

- Hardseededness – making seeds impervious to external forces. Such seeds only germinate after scarification through fire or external effect. *Acacia* species throughout southern Africa and Australia display this trait, exemplified by *A. exuvialis* growing in the central Lowveld

- High levels of toxins or alkaloids that inhibit seed predation by encouraging avoidance. Immature *Sclerocarya* fruits are not only bitter tasting prior to ripeness but are also green and therefore less obvious as a food item

- Encapsulating seeds in protective shells, pods or jackets. *Dichrostachys cinerea* encapsulates all seeds in a protective pod. Such a pod may protect individual seeds from predation.

- Releasing many seeds of little nutritive reward for consumers (although this can be to the detriment of seedling survival). *Acacia nilotica* in Kenya can produce more than 30,000 seeds in a single season (Tybirk 1989), similarly *D. cinerea* produces large seed volumes presumably to increase potential for germinants. See Plate 1-1

(Above points adapted from Raven *et al.* 1986)

**Plate 1-1:** *Dicrostachys cinerea* bearing abundant seed pods and seeds, Kempiana property, June 2006.

In summary, the relationships between flora and fauna are complex and dynamic, with many plants reliant on megaherbivores for successful seed distribution. However the costs of this reliance to the plant can be considerable, with significant seed and foliage loss a likely consequence. Protective measures to promote seed survival are commonplace, but can be to the detriment of seed distribution and germination.

## Disturbance and ecosystem health

Savannas are highly disturbance-influenced habitats. Forces of patch dynamics influenced by abiotic and biotic factors create disturbance conditions that prevent climax ecosystem establishment, maintaining a multidirectional, multiple stable point effect. This is best described by Bothma (2004) as the “State and Transition Model”, which describes changes such as the structure or species composition of semi-arid ecosystems that are driven by disturbance factors or stochastic rainfall events. It is important to note that such disturbance will have minimum and maximum thresholds for positive ecological impact, for exclusion or increase in fire frequency and could create conditions aversive to successful biological function. Likewise, whilst elephant browsing creates habitat space and translocates seeds and nutrients, there lies a point of critical activity where this effect becomes negative for the biodiversity of the area, i.e.: vegetation destruction outweighs habitat clearing benefits (e.g.: Guy 1981). Indeed where ecosystems have been disturbed or degraded to a point where formerly dominant organisms were eliminated or debilitated, they have demonstrated a causal connection between losses in biodiversity and declines in ecosystem function (Avenant 2000).

In protected areas, where biodiversity preservation is a major stated goal, practical implementation and management of disturbance regimes can be difficult. Anthropologically, the line between beneficial and negative disturbance is a difficult concept for ecosystem management.

## Management of savanna ecosystems

As we have seen, the complexities and patchiness in savanna landscapes are considerable. Anthropologic attempts at controlling and managing such ecosystems through agriculture (managing fire events, introduction of commercially important grazers such as cattle) and nature conservation (limiting fire events and manipulating herbivory) have, despite best intentions, frequently created economically and ecologically unpredicted habitat circumstances. In a landscape of co-dominant trees and grasses, in which science does not understand the mechanisms of this co-existence (Jeltsch *et al.* 1998) correct management of such areas has become the subject of much debate (e.g.: Trollope 1981, Thomson 1992, Child 1995, Noble 1997).

As the scientific body adds to the level of knowledge, management practice tends towards more ecologically inclined. Monitoring of tree and shrub populations, grazing sward, large mammal populations, fire frequency and occurrence, erosion and management activity have all created a broader perspective for managers of savanna landscapes from which to make decisions. Whilst it is recognised through science that savanna ecology is a disturbance led process, minimum and maximum levels, and timing, of disturbances are seldom agreed. Management encompassing best practice for savanna flora and fauna remains an extremely complex matter, requiring broad in-depth understanding of landscape dynamics over a period far longer than the average managerial career.

### ***Summary:***

From review of the literature, the following summary can be made:

- Savannas are highly complex, dynamic and competitive landscapes
- The high level of dynamism is reflected in the tree-grass competition, which is further complicated by fire and the activities of grazing and browsing mammals
- Plant animal interactions are extremely important, complicated and little understood
- Management of these heterogeneic and disturbance-driven landscapes is difficult

## *Increasing Woody Plant Densities 'treelands with scattered grass'*

### What is this phenomenon?

Numerous anecdotal and scientific studies in Australia (Bazzaz & McConnaughay 1992, Noble 1997), the USA (Weltzin *et al.* 1997), and southern Africa (Bredenkamp 1986, van Vegten 1984, Child 1995, Hudak 1999, Smit *et al.* 1999) point to incremental vegetation change throughout savanna and semi-arid ecosystems whereby certain woody plant species increase their densities to the point where other vegetation (such as grasses and forbs) are actively excluded from landscapes.

In southern Africa this phenomena is recognised by scientists and land managers and commonly labelled as 'bush encroachment', characterized by increasing predominance and densities of 'increaser' indigenous plant species. Such species gradually replace palatable grass species in a slow densification process to the detriment of grazing potential (Trollope 1981, Hudak 1999). Increaser species are those recognised as gaining in proportional representation within landscapes over time (in this case local shrubs and trees), which generally occurs at the expense of 'decreaser' species (grasses), which are reduced in population by a compensatory proportion (Child 1995). Increaser species landscape change and subsequent bush encroachment have wrought significant economic and ecological impacts upon carrying capacities as large areas of savannas are engulfed in woody vegetation. Importantly, such encroachment has reached proportions where many previously economically viable livestock properties can no longer be grazed (Child 1995). Bush encroachment is widespread on land managed by all South African socio-economic groups for agriculture (Hudak 1999) and conservation management (Pieterson *pers comm.* 2000).

Historically little has been known about the ecology of bush encroacher species in southern Africa and what the 'normal' densities of the different encroacher species were (Bredenkamp 1986). From the general literature (e.g.: Bredenkamp 1986, Child 1995, Bothma 2004), consultation with land managers (Pieterson *pers comm*. 2000) and my personal experience, the Mimosaceae and Combretaceae tree families are known to display this tendency. In addition to the lack of clarity on specific encroaching species, I have found no definite criteria that exists for the quantification of encroachment. Bredenkamp (1986) postulates that a species may probably obtain an undesirable high density under habitat conditions most favourable for its specific ecological requirements, especially when competition is reduced. Such density changes drive habitat change and eventually influence thresholds in the landscape into new equilibria.

Significantly once woody vegetation has taken hold through this process, the interval in which the area can return to ‘normal’ has been estimated to be some 1000 years under natural processes (Thomson 1992, Child 1995). This would entail that established scrub must live out its life span, which can be considerable, and assuming that soils have not been extensively modified and animal and fire pressure are reduced, grass species can return.

Despite poor clarity on this potentially serious managerial issue, it is apparent that bush thickening is becoming more widespread. In my experience practicing land management professionals in savanna regions of southern Africa often refer to the problem of gradually increasing woody vegetation densities, with such densification a catalyst for ‘follow-on’ conservation and management issues.

## Causal factors

Although vaguely understood, the phenomenon of increasers and encroachment appears to be site management and disturbance related (Bredenkamp 1986). Difficulties arise in quantifying disturbance as southern African savannas are already naturally disturbance-influenced landscapes (Bothma 2004). Overgrazing of grass species has been identified by many (e.g.: Britton & Sneva 1981, Van Vegten 1984) as the leading cause of increased woody plant density in many regions of southern Africa. The role of fire as a determinant of woody plant density has also been given considerable attention (e.g.: Trollope 1981, Thomson 1992, Child 1995, Bond & Keeley 2005).

In general, such increaser-dominated systems have been directly or indirectly influenced by human activity. Teague & Smit (1992) describe influences leading to encroachment as Primary and Secondary, with primary including climate or soil, and secondary including the impact of fire and herbivores. Secondary influences are often enhanced or constrained by primary influences, which are directly impacted through management practices. Much of the blame for bush encroachment has been associated with secondary effects of overgrazing, poor stock management, altered fire regimes, fencing and artificial watering points.

### Overgrazing

Grazing mammals may affect their habitat by selective feeding on particular plant species and plant parts, and by disturbing the substrate in which these plants are rooted. When these activities are concentrated (such as overgrazing in specific plant communities) they can result in the restructuring of ecosystems. Trollope (1981) & Smit *et al.* (1999) highlight that reduced perennial grass cover frequently leads to bush encroachment, which has been shown to reduce the carrying capacity of stock such as cattle by up to two-thirds on dry rangeland. In short, overgrazing through inappropriate grazing seasons or excessive stocking rates presents the following effects:

- Removal of vegetation through consumption and trampling
- Reduction of litter through compaction and loss of biomass
- Destruction of biological soil crusts that protect the soil from erosion

Should overgrazing continue unabated, the physical properties of soils may be changed, altering vegetation composition (i.e.: encouraging increaser species), reducing ecological and economic productivity. Overgrazing upsets the competitive balance between grass and tree components of savannas. The grass cover within these systems is the key to maintaining productivity; good soil water relations and soil stability (Child 1995). Impoverishment of this grass cover from overgrazing by wild or domestic animals causes transpiration to decrease, allowing more water to remain in the soil to the benefit of woody plants (Walter 1979). Species such as *Acacia* consequently develop luxuriantly, increasing levels of shade over grassy layers, and producing many fruits and seeds which are dispersed in areas where grass cover and competition is reduced, thus favoring the tree and shrub species (Walter 1979).

The logical process of overgrazing leading to woody vegetation density increases has been outlined by Smit *et al.* (1999):

1. Grasses are initially suppressed by cattle or other grazing animals during brief periods of overgrazing
2. A greater proportion of tree species initially receive the opportunity to germinate under more favourable conditions
3. Grass cover remains sufficient to support fires of adequate intensity to burn the vegetation
4. Woody species coppice after the fire, and there is vigorous ground level growth
5. Further overgrazing reduces the grass layer more, to a point where fire can no longer control the growth of woody plants
6. Ground level coppices form an impenetrable thicket, thus excluding all browsers and grazers

Incidences of overgrazing have increased with the rise in agricultural production in South Africa and a predominance of domestic farm animals. In general these domestic farm animals (cows and goats in the study area) are grazers, with indigenous cattle such as the Nguni (*Anon* 2000) and goats becoming folivorous when grazing is scarce (Noble 1997). Where these goats and cattle are mixed each will actively compete with the other for whatever herbage is available. A typical scenario is one of grazing cattle until the landscape deteriorates beyond the current carrying capacity, then replacing cattle with smaller economic units such as goats who can more efficiently consume remaining elements of the vegetation. As could be expected in semi-arid regions, in times of poor rainfall and high stock numbers, overgrazing is the net result. Similarly, selective overgrazing from continual short term grazing episodes by cattle which occasionally return and consume only the most palatable vegetation during each visit will also drive vegetation change as certain desired species are selected for continuously, thinning the population of the more palatable grazing plants (Savory 1978).

### *Altered grazing/browsing patterns and human induced change*

In landscapes where the composition of indigenous mammals has been altered through the introduction of increased or exotic animal species, consumption patterns have been changed interfering with the balance of vegetation. The rise of commercial agriculture and associated rapid global human population growth has meant that domestic cattle and sheep (*Ovus aries*) have become some of the most dominant grazing herbivores in semi-arid regions of Australia, the USA and southern Africa. This change has increased the balance of bulk roughage feeders compared to indigenous animals with more varied feeding strategies. In areas of southern Africa the introduction of cattle as the most predominant grazing species has changed the fodder grass vegetation into often impenetrable woody thickets predominately consisting of *Dichrostachys* and *Acacia* spp. within a few decades (van Vegten 1984).

Human-induced habitat changes have altered the composition and overall biomass of the indigenous fauna, with management regimes favouring one or two palatable grass species for grazing stock over a variety of vegetation favoured by mixed feeders of a natural system (de Jager *pers comm*. 2006). Human created artificial water points associated with economically important animals have led to an overall increase in herbivore biomass and increased the pressure placed on grazed vegetation (Child 1995). In both commercial agriculture and game ranching/conservation land uses, where water was a limiting factor and then provided, most species increased, at least temporarily, and movement patterns changed. Artificial water points and associated altered animal movement patterns created significant habitat change around waterholes (as witnessed by myself in Kruger National Park since 2000). This modification of the vegetation affects different species differently, with some increasing as conditions became more favourable to their needs, while others decline or eventually disappear altogether (Noble 1997). Managerially, placement of water points has been primarily dictated by an animal-centric view, with only secondary considerations given to the impacts of such activities on habitats and plant communities.

Overgrazing and mismanagement of fire have frequently led to the loss of sensitive grazers like the roan antelope and sable in many significant protected areas of southern Africa (Smit *et al.* 1999). Conversely, browsing species such as Kudu have benefited from this vegetation change, which have increased in numbers due to extensive bush encroachment. Having once achieved an advantage these species grow in number and hold the vegetation at a level favourable to themselves, thus maintaining a new habitat balance. This phenomenon is well known for the European rabbit which benefits from a closely cropped sward and is able to increase in numbers to a level at which the rabbits keep the grass short to their own advantage (Child 1995, Smit *et al.* 1999).

Habitat-related altered herbivore abundances and species composition combined with economic favouritism of certain animal species have created a situation whereby natural indigenous browsing and grazing of many landscapes no longer takes place. Over time new patterns of disturbance, perpetuated by modified and increased grazing animal populations, drive ecosystem change.

## Climate change

It is commonly reported that global climate change and altered weather patterns have the potential to impact on habitats throughout the world. The release of large quantities of carbon dioxide, methane, and other pollutants is expected to alter global temperatures and change seasonal precipitation patterns through modifications of global atmospheric and oceanic circulation (Flannery 2005). The biomes most at variance with climate potential are $C_4$ grasslands and savannas, especially in more humid regions including the wetter regions of Africa (Bond & Keeley 2005). Southern African savannas are climatically controlled landscapes, especially in regard to rainfall (Higgens *et al*. 2000). Any increase in rainfall events and quantity may interfere with grass and shrub co-dominance, as the once restrictive factor of limited water availability becomes less of a constraint to growth. At similar latitudes throughout the world, where annual rainfall is higher (e.g.: coastal areas of Mozambique, Australia and Brazil) woodlands and forests are predominant landscapes. Equally, where the rainfall is less, grasslands predominate (inland South Africa and Brazil). By increasing rainfall in climatically controlled semi-arid savannas, encouragement of tree growth will drive successionary processes further as higher density woodlands are developed. Indeed, when profiling bush encroaching species, Bredenkamp (1986) noted that increases in density of woody plants in bushveld vegetation could be the result of higher rainfall. Any rise in rainfall averages may well stimulate increaser tree growth within savannas. It stands to reason that conversely, should average rainfall decrease, then grass species would be encouraged over and above development of shrubs and trees.

Flannery (2005) and other climate change studies note that climate change will generate additional weather 'extremes' than historically experienced. Extremes in savannas may include increased periodic storms and summer rainfall events, longer winter droughts of increased intensity, and hotter/colder extremes in summer and winter. Whilst cooler winter extremes will allow more frost events to occur, hotter summers may create intense or more frequent fires. In terms of increaser vegetation, an increase in frost events would detrimentally affect grass layers more than shrubs and trees. Winter frosts tend to impact understorey vegetation due to temperature inversion cooling the ground level significantly more than upper vegetation layers (de Jager *pers comm.* 2006). These newfound climatic extremes may in turn 'burn off' grass species disproportionately more than trees and shrubs. As grass species die off, more opportunity is created for tree species to establish.

Conversely, hotter fires in summer will favour woody plants over grasses due to significant fire adaptive traits and deeper root systems to escape radiated heating effects (Trollope 1982). Climate change typified by increased rainfall, local weather extremes and coupled with further disturbance events such as fire could potentially drive significant alterations within semi-arid habitats.

### Atmospheric $CO_2$ enrichment

Closely linked to human created climatic alteration, atmospheric $CO_2$ enrichment, created from the burning of fossil fuels, industrial processes and wholesale land clearing must be considered in vegetation change. Empirical records provide incontestable evidence of global changes including the rising concentration of $CO_2$ in the earth's atmosphere (Bazzaz & McConnaughay 1992, Mousseau & Saugier 1992, Rogers *et al.* 1994, Hewitson *pers comm.* 2006). Plant growth is commonly stimulated by the elevation of $CO_2$. However such altered conditions generally benefit $C_3$ plants (trees, shrubs and sedges) over and above $C_4$ species (tropical grasses). Genetically $C_3$ plants have improved photosynthetic pathways and abilities to uptake atmospheric $CO_2$ and assimilate it into plant structures than $C_4$ plants. As such it is generally accepted that $C_3$ species in competitive assemblages have improved competitive ability relative to $C_4$ species as a result of atmospheric $CO_2$ enrichment (Mousseau & Saugier 1992, Rogers *et al*. 1994). In savannas the woody plants such as trees and shrubs are generally $C_3$ species, whilst tropical grasses comprise the majority of $C_4$ individuals. As $CO_2$ levels rise, woody plants are gaining a competitive advantage over neighbouring grasses, creating further opportunities for increaser growth.

### *Altered fire regimes*

The role of fire as a determinant of woody plant density in savannas has been given much attention in the global literature with conservation and scientific texts showing that altered fire regimes in savannas are considered to be a direct cause of woody plant encroachment (Gill *et al*. 1981, Trollope 1982, Archer 1995, Noble 1997). Overall, savannas are considered to be the most frequently burnt ecosystems in the world, burning several times in a decade and some burning twice or more per year (Bond & Keeley 2005). These authors now regard fire as a 'global herbivore', although fire differs from herbivory in that it regularly consumes dead and living material and, with no protein needed for its growth, has broad "dietary" preferences.

At a landscape level the fire 'herbivore' brings about wholesale vegetation change in savannas. Such changes are directly influenced by a number of factors:

- **Fuel consumption**. Savanna landscapes are sources of a wide variety of fuels, influenced by various plant turpinoids, oils etc. that enhance the flammability of the vegetation. High flammability and fuel accumulation (e.g.: higher populations of increasers) may mean hotter, more intense fires

- **Fire location.** Depending on fuel accumulation, fires burn and spread at different intervals within the landscape. Fires burning treescapes burn at higher intensity, burning at higher levels in the stratum such as the canopy, whereas grassland fires are limited to the ground layer, including moribund plant material and soil organic matter

- **Fire intensity**. The energy released by a fire relates to the source of the fuel, weather conditions and seasonal impacts (i.e.: dry season fires vs wet season fires)

- **Fire severity**. Linked to ecosystem impact in terms of species loss, and damage to reproductive capacity

- **Fire frequency**. The number of times an area burns gives the overall fire frequency. High numbers of fires, specifically those that are anthropogenically created can be cause for ecological damage (i.e.: the fire return period)

- **Season**. Season of burning brings about different intensity fires, creating different impacts. Anthropogenic fires often burn outside 'natural' fire seasons, exasperating ecological effects.

(Adapted from Bond & Keeley 2005)

On a practical level, fires bring out a myriad of resultant effects that can be difficult to predict. Intense fires (such as those that occur after years of fire exclusion and additional fuel accumulation) have the potential to kill the grass sward whilst stimulating some woody plant seeds to germinate. Many notable increaser tree and shrub species, such as those in the Mimosaceae Family (including *Acacia* and *Dichrostachys*), require fire scarification of seeds for effective germination. Increased fire regimes may also encourage such trees to predominate over and above species without these traits. Any additional fires in the landscape would then occur to the detriment of the grass layer and the benefit of such woody shrubs (Noble 1997). In an altered environment with many increaser shrubs subsequent fires would burn at higher temperatures, favouring more woody vegetative growth over that of grasses; creating a 'positive feedback' effect as compounding fires encourage more trees and shrubs to germinate. Increaser encroached savannas, therefore, support hotter fires, which positively select for flammability (Bond & Keeley 2005); actively excluding grass species to the benefit of woody plants.

Alternately, cool fires burning when combustible material is in small amounts will thoroughly burn the grass layer, leaving much of the tree layer undamaged, and as such can also favour increaser woody species (Thomson 1992). Once trees and shrubs are above a critical height and diameter they are able to tolerate fire effects, survive and reproduce better than other species.

Such effects make fire management of ecosystems an unpredictable science. It is, therefore, reasonable to conclude that despite best intentions land managers may end up inadvertently creating beneficial conditions for increaser species when management burns are used in savannas. To date, the most effective fire management concept for savannas has been described by (Higgens *et al.* 2000) as a patch burning methodology, rethinking many other historical techniques. This, and many alternative fire management strategies are currently in use by managers, of which the long term consequences are little known. Fire, in combination with altered grazing/browsing regimes, overgrazing and other effects, is a significant complicating factor in the management of savanna ecosystems.

## Compounded effects on management

As we have seen, each individual causal factor (overgrazing, altered grazing/browsing patterns, climate change, $CO_2$ atmospheric enrichment, and altered fire regimes) yields impacts of a significant propensity to change landscapes in their own right. These impacts increase in intensity by compounding with one another to drive ecosystem change. In South Africa the high intensity of landscape usage, from commercial to communal agriculture through to game ranching and conservation areas, may well play a role in exacerbating rates of increaser thickening and habitat change. This can be best categorised into two effects:

1. Restricting conservation benefit, and
2. Economic cost for land managers.

### *Restricting conservation benefit of protected areas*

Habitat change at the detriment of some species and in favour of others will alter any grazing/browsing balances in the landscape. Such alterations allow new wildlife dominances to take place, potentially to the detriment of biodiversity. Increased tree strata alliances such as those created by encroaching *Acacia* spp. will actively restrict other vegetation growth and modify soils to better suit more *Acacia* through nitrogen fixation. The knock-on effects of this change mean reduced grass cover due to competition for limited available resources, increased browsing and reduced grazing benefits for wildlife leading to an emigration of grazers. In addition hotter fires will take place due to an increase in woody fuels to the detriment of floral and faunal species diversity.

### *Economic impact*

The economic implications of bush encroachment are enormous, not only as far as actual combat against encroachment is concerned (Scott 1967, Bredenkamp 1986) but especially concerning commercial production of meat and game animals (Child 1995). Increased woody plant densities require a high level of human, mechanical or chemical input to rectify the imbalances created; at great financial cost. Various management programmes are being conducted on clearing increasers or bush encroachers in South Africa, and current costs of clearing moderately tree choked landscapes with machinery, labour and pesticides average around R10,000 per hectare (Groenhof *pers comm*. 2006). In terms of lost production, increasing woody plant densities have left previously economically viable commercial livestock and game properties in a state where the carrying capacity has been significantly reduced or no longer able to be grazed (Bredenkamp 1986, Child 1995, Bothma 2004).

## Historical solutions to woody plant encroachment

### *Management of woody plants*

In terms of managing or removing increasers, any bush clearing or thinning that takes place in encroached areas would have to be economically justifiable in terms of costs to production and ecologically beneficial to local wildlife (Child 1995). Contemporary aids to woody plant control include;

- Use of fire to burn out wooded thickets, re-applied numerous times to attempt to clear newly germinated tree species

- Use of browsers such as goats concentrated in restrictive pens to consume vegetation

- Mechanical clearing and soil disturbance through use of heavy machinery such as bulldozers, tractors and chainsaws

- Hand clearing with large numbers of peoples and saws, pangas etc.

- The use of chemical herbicides to kill woody plant species or treat the soil.

Remembering the dynamic state of savannas, there are some practical difficulties associated with attaining a desired tree density, especially as appropriate densities are often not exactly known and ideal species mix not understood or absolute (Walker *et al*. 1981, Smit *et al*. 1999). Any such activity requires considerable management input and broad-based habitat understanding to implement efficiently, notwithstanding financial resources to do so.

### Making use of natural system dynamics

A largely hypothetical approach to controlling bush encroachment is that of using the natural functioning of savanna systems to stimulate the development of open savanna. This theory is based on the surmise that trees and their nearest neighbours are determined by the level of competition for resources (Child 1995). Allelopathic tendencies displayed by tree species to limit the growth of neighbours can bring about a limited controlling effect (Smit *et al*. 1999). A managed process of low density thinning, combined with the removal of heavy grazing impact, may lead to a suppression of the growth of other woody species in the area over the longer term.

### Summary

- Although bush encroachment studies and their economic impacts are poorly recorded in southern Africa, increases in woody plant densities are commonly recognised by land managers
- Land management is constrained by a lack of knowledge of the dynamism of savanna landscapes over longer periods of time (especially in relation to the average career of a land manager)
- Bush encroachment is commonly considered to be caused by
    - Altered grazing and browsing patterns (e.g.: introduction of domestic stock)
    - Climate change
    - $CO_2$ enrichment
    - Altered fire regimes
- The incidence of bush encroachment leads to altered ecological function in landscapes as new tree-grass balances are created, bringing about considerable potential and actual economic costs
- Resolution of bush encroachment is managerially problematic

## *Small mammals of the savannas*

Like their larger counterparts, small mammals are important contributors to the biodiversity of woodland savanna ecosystems in sub-Saharan Africa (Linzey & Kesner 1997). Such animals are important ecosystem components as consumers, dispersers of seed, burrowers and prey for carnivores and raptors (Avenant 2000).

In this study, small mammals are considered to be all those less than three kilograms in weight, or standing less than 0.5 m tall. This group includes a diverse range of herbivores, carnivores and scavengers.

In general changes in small mammal habitats are associated with changes in small mammal diversity, and ecological disturbance in these habitats is associated with decreases in small mammal richness (Rowe-Rowe & Lowry 1982). Due to specific food and habitat cover requirements, small mammals are likely to be adversely impacted by overuse of habitats from both domestic and wild megaherbivores.

Small mammal community structure and species richness have been related to biotic and abiotic variables such as habitat structure and complexity, area, productivity, predation, trampling and grazing, surrounding landscape, and the distance between areas of similar habitats (Avenant 2000). Presumably due to the practical difficulties of study, lack of knowledge and the megaherbivore focus of conventional wildlife managers, small mammals are generally ignored in the management of nature reserves in South Africa.

In this study, my research focuses on the largest group of small mammals, the Rodentia, and in particular the granivores (seed eaters).

### The granivores

In terms of mammals, granivores are best represented in southern African savannas by members of the Order Rodentia. This Order comprises three sub-Orders:

- **Sciuromorpha** - squirrels, marmots and prairie dogs
- **Myomorpha** - rats, mice and voles

- **Histricomorpha** - porcupines, capybara and agouti.

Within these suborders there are various families; Bathyergidae (Molerats), Hystricidae (Porcupines), Pedetidae (Springhares), Gliridae (Dormice), Sciuridae (Squirrels), Thryonomyidae (Canerats), Petromuridae (Dassie Rat), and Muridae (Rats and Mice) (Skinner & Smithers 1990). In addition to the rodents other common savanna granivorous mammals are found in Order Lagomorpha; represented by hares and rabbits (not studied in this research).

**Rodentia**

Globally there are more than 1,700 rodent species Skinner & Smithers (1990) which represents 40% of all mammal species (Hickman 1993). In Africa there are 83 distinct species (Skinner & Smithers 1990).

Rodents are a widely radiated class of mammals whose name is derived from the Latin verb ‘rodere’, to gnaw (Skinner & Smithers 1990). They vary considerably in size, appearance and habitats, and have prodigious powers of reproduction. The members of this Order are highly adaptable and are found in all habitats on earth outside the Antarctic (Hickman 1993).

Rodents are commonly found in all southern African habitats; becoming arid and semi-arid area specialists. Sciuridae occur throughout Africa, in all habitat types receiving between 100 – 750 mm rainfall per annum. They are not commonly found at the driest end of this range. The Muridae are an extremely widespread family throughout southern Africa, with representatives across the region. Histricomorpha have a lone representative in southern Africa, the porcupine (*Hystrix africae-australis*) which has a very wide distribution range from semi-arid to mesic habitats (Skinner & Smithers 1990).

All rodent species are characterised by a pair of continuously growing, ever-sharpened incisor teeth situated on the anterior part of the upper and lower jaws. The canine teeth are absent, leaving a large gap (the diastema) to allow indigestible chewed items to fall free of the mouth. All rodents have well developed jaw muscles and rotary chewing action to best masticate their food; allowing individuals to consume tough seeds and pods as food. Chewing action in rodents is of significant strength with a few millimetres of tooth surface eroded every week, stimulating further tooth growth (Young 1981) and continuous further chewing action. In many rodents the hind legs are longer than the forelegs, which are used for handling of food. In some this tendency is carried to the extent of producing a hopping, bipedal gait. Rodents generally have acute eyesight and hearing, especially those with an arboreal habit. Rodents are polyestrous and able to breed throughout the year, producing numerous young at a time, cared for in a nest (Young 1981).

### Fluctuations in numbers

A classic characteristic of rodent populations is highly fluctuating seasonal population growth and collapse (Young 1981). The phenomenon of booming populations is usually recorded as a ‘plague’, although such events are now known to occur in regular cyclical fluctuations extending over many years (Young 1981, Chesson *et al.* 2004). It is considered unlikely that a regular stability of population levels occurs, with large fluctuations occurring in 3 – 10 year intervals, often following a resource ‘pulse’ (Chesson *et al.* 2004). Such an event would be caused by increased solar radiation, potentially in a good rainfall year with improved local vegetation growth to the benefit of small mammal diets and therefore reproductive ability. Population numbers would also depend on the particular balances set up within the animal communities – interactions between plants, herbivores, carnivores and parasites in conjunction with plant growth. When rodent numbers peak the animals show unusual behaviour patterns including migration, entering a pathological state and becoming cold and torpid with a low blood sugar content (Linzey & Kezner 1997). The pressure of competition and lack of food reduces overall numbers of individuals relatively quickly. Due to short life cycles and ability for rapid breeding this population phenomenon is most noticeable in small mammals (Chesson *et al.* 2004).

### Habitat requirements for rodents

Like all other living organisms, rodents require ample food, shelter and suitable habitat for general survival with specific niches upon which they depend. These are determined by:

- Food and moisture availability
- Suitable cover and plant densities

- Suitable habitat materials from which to build nests and line burrows etc.

The act of foraging for food is a major determinant of the home range size of rodent species (Monadjem & Perrin 1998), i.e.: when food sources are ample home ranges will shrink, and when food sources scarce home ranges will grow.

**Vegetative cover, structure and rodent densities**

Significantly for this study is that small mammals depend on structurally rich vegetation as shelter (Smit *et al*. 2001), where high vegetation density allows for relatively safe foraging activity over long periods. Low cover may restrict foraging time, and create significant gaps for predator species access. Rodents display a strong predator avoidance strategy, avoiding heavily grazed habitats (Smit *et al.* 2001) and conducting reduced activities on clear, well moonlit nights when predator activity (such as owl movements) is highest (Bowers & Dooley 1993). Vegetative cover in rodent habitats is important to provide shelter and protection from visually oriented predators such as birds of prey (Rowe-Rowe & Lowry 1982).

Non-arboreal rodents, and to a lesser extent all rodents, are reliant on protective cover provided from lower vegetative strata in the landscape; such as the grass canopy. Where this grass cover is reduced in biomass (for example through grazing or fire) suitable protective cover will be lost, and rodent species will either avoid such areas in preference for others of higher quality - or face greater potential of predation.

Jooste & Palmer (1981) postulated a specific qualitative relationship between rodent population density and vegetative cover; proposing that a threshold level of cover is necessary for population increase. Studies conducted by Perrin & Johnson (1999) showed the striped mouse (*Rhabdomys pumilio*) was absent in areas with <5 cm of grass understorey cover. This was previously demonstrated by Bond *et al.* (1980) where the abundance of *Rhabdomys* correlated significantly with grass biomass cover. It was postulated in both studies that the risk of predation prevented the mice from entering the areas of low vegetative cover.

Grazing by megaherbivores could be a significant modifier of the grass layer, with combined effects of vegetation consumption and trampling reducing the overall biomass of material and creating a modified vegetation structure. This has been shown by Smit *et al.* (2001) in eastern USA where exclusion of grazing by megaherbivore grazers in formerly heavily grazed habitats had a significant effect on abundance of small rodent communities. Inside exclosures higher densities of wood mice (*Apodemus sylvaticus*) and field voles (*Microtus agrestis*) were recorded. The seed predation intensity of beechnuts and acorns by small rodents was significantly higher in ungrazed situations, particularly in habitats that were excluded from grazing. So linked is this rodent-habitat alliance that Avenant (2000) proposes that conservators should manage ecosystems by monitoring the correlation between small mammals and grass cover as an informative tool.

## Role in the ecosystem – seed consumers and habitat regulators

### Seed consumers

In general, small mammals must spend a large proportion of their time foraging to meet the demands of high energy requirements due to small body mass to area ratios and to maintain body temperature (Knight & Knight-Eloff 1986).

As herbivores, small mammals would have a high self interest in consuming plant materials with the highest energy return – such as seeds and fruits. Such targeted consumption could have potential knock-on effects for the survival of seeds and seedlings in the field.

Logically granivores would commonly consume highly abundant seeds in savanna ecosystems. Those of the Order Rodentia are well known as consumers of herbivorous matter, especially seeds and seedlings; although records of actual diets for most species in southern Africa are considerably vague. Despite this, there is a growing recognition of the significant ecological role of small mammals within habitats.

### Habitat regulation

At present it is known that within semi-arid North American grasslands pocket gophers (*Geomys bursarius*) alter micro-topography and local soil nutrients creating tiny patches of higher productivity. These patches attract other herbivores, both insects and mammals, which further alter the nutrient status and plant composition (Manson *et al.* 2001). Rodents such as the Cape Gerbil (*Tatera capensis*) are known for *Protea* spp. pollinating services in the Clanwilliam Mountains in South Africa's West Coast region (Turner *pers comm*. 2006). Seed and seedling predation by small mammals such as *Tatera* is considered to be the primary factor limiting the recruitment of serotinous Proteaceae throughout the Cape Floristic Kingdom (Bond & Breytenbach 1985). Similarly, predation studies by Hulme (1994), showed that various rodent species in the United Kingdom consumed 100% of the tissue of plant seedlings encountered.

Small mammals with a granivorous habit also play a potential role in seed dispersal. Williams *et al.* (2000) in a study of small mammals as potential seed dispersers in New Zealand investigated the ability of digestion of various small mammals to destroy seeds. It was noted that small rodents (discussed in the following text box) generally destroyed all of the seeds eaten thus acting as seed predators. However, introduced possums (*Trichosurus vulpecula*) passed many seeds of various plant species tested of which between 6 - 83% were intact. In addition the time required for possums to pass 50% of all seeds averaged 3.7 days, allowing ample time for significant dispersal by the mammal to take place. Between 3 - 78% of these post-digested seeds germinated successfully. Likewise in arid grassy dunes of the Kalahari, seeds from 50 antelope and 10 rodent faecal pellets were collected by Dean & Milton (1991). The antelope pellets contained 154 intact *Hypertelis salsaloides* seeds, although nothing but finely mascerated plant matter and insect fragments were found in the rodent pellets.

As potentially significant seed and seedling predators, rodents could play an important role in habitat regulation in savannas. At this point it is important to distinguish between the acts of seed consumption and seed predation, as either can bring about drastically different results for plant seeds.

## Consumption vs Predation

In terms of food, the word predator is defined by the Oxford Dictionary (1983) as “a predatory animal, preying upon others”, where prey is “an animal that is hunted or killed by another for food” and “to have a harmful influence on”. In comparison, the term “Consume” means “1. To use up; 2. To eat or drink up, especially in large quantities”.

Implicit in a predator-prey relationship is a harmful effect to the prey (ie: being killed and eaten), which is generally an unavoidable consequence of such interactions. Although a popular English dictionary uses an animal-centric definition, predation of plants is also commonplace, as long as the ‘victim’ plant or seed is rendered inert by its predator herbivore. Conversely, by definition consumption does not necessarily preclude the death of a plant or seed, merely its eating. In nature there are numerous examples where consuming an organism does not necessarily mean its death, for example cattle primarily consume grass, but the parent plant will survive and grow more shoots in time. In this study the differentiation between such predation and consumption is a crucial one, as habitat conditions in savanna ecosystems are dependent on it.

Large mammal consumption of seeds (e.g.: the elephant and *Sclerocarya* fruit example), despite some seed loss through chewing or digestion would, as discussed earlier, create opportunity for seeds surviving the digestive process to spread and germinate throughout the landscape. The high ecological effort made by plants to encase seeds in accessory fruits to reward the consumer is a technique of maximising seed distribution potential. As per the above definitions, in the case of megaherbivore species, it appears commonplace that consumption does not equal predation of seeds, as many will pass via the digestive system intact - able to later sprout in a new habitat to the favour of the plant.

From reviewing references and field studies, consumption of seeds by Rodentia appears to be detrimental for plant species; taking on characteristics of a predatory relationship. Presumably seeds that pass through the digestion process whole have a significantly higher germination potential than those that are significantly chewed, unless such chewing was a significant cause of seed scarification (i.e.: for *Acacia* spp).

Through the thorough and intensive chewing action of rodents in mastication of food using sharpened chisel-like teeth, only very small seeds would escape comprehensive chewing and be consumed, digested and passed whole. Rodent consumption of seeds could therefore act as an effective predatory action. This theory is demonstrated in Williams *et al.* (2000) who noted that viable seeds of small-seeded (<1 mg) species passed through ship rats (*Rattus norwegicus*), although all larger seeds (>1mg) were destroyed by the chewing and digestive process. In the case of many larger tree seeds with substantial food reservoirs required to commence initial sprouting, where rodent chewing occurs such consumption of seeds would become a predatory action. “Smaller herbivores destroy more seeds than medium sized ones and larger herbivores would cause the least destruction” (Miller 1995).

Conversely, Sciuridae (squirrels) generally create numerous seed caches throughout home ranges to store seeds from local plants for access at a later time. As the process of seed eating is delayed through this action, there is a greater likelihood of seed ‘escape’ from predation. Occasionally seeds are dislodged from caches into suitable germinating habitats or caches are abandoned (due to death of the rodent, memory loss of cache location etc.) and conditions are such that seeds are able to germinate.

Rodents therefore provide both beneficial and negative effects for seeds within a landscape. Non-hoarding rodents (namely the Muridae, Hystricidae) would be generally detrimental to seed survival and germination acting as seed predators, and those of the Sciuridae with hoarding instincts can be both detrimental and beneficial to seed survival, depending on level of hoarding and immediate predation.

## Small mammal landscape regulation

We have seen that small mammal seed and seedling predation is a common activity in nature and that it can lead to potentially significant habitat impacts. However, whether seed consumers have a significant effect on plant establishment has been a significant little-understood question in plant population biology (Maron & Simms 1997). The considerable difference between seed consumers (a great many herbivorous mammals) and seed predators (in this case rodents) leads to the question: are such small mammal seed predators effective landscape regulators? Historic and contemporary studies of faunal savanna landscape management have focused on megaherbivore grazing, browsing and modification (e.g.: elephants destroying trees) and anthropogenic management of landscapes (fires, grazing management) and consequent changes (e.g.: Thomson 1992, Child 1995, Damm 2002, Bothma 2004).

Numerous international studies have demonstrated conclusively that small mammals play a significant role in regulating ecosystems. In California Maron & Simms (1997) noted rodent activity in dune ecosystems, and found where rodent granivory was greatest (65% and 86% of bush lupine shrub *Lupinus arboreus* seeds were removed from plots by rodents over two seasons), there is a sparse seed bank (6.6 seeds $m^2$), and granivory significantly reduced seedling emergence (in the same period 18% and 19.4% fewer seedlings emerged from rodent exposed versus protected plots).

Studies in New Mexico, USA by Weltzin *et al.* (1997), concluded that tree-shrub encroachment has coincided with the eradication of the once widespread native herbivore, the black tailed prairie dog (*Cynomys ludovicianus*). At the beginning of the twentieth century biologists estimate that "perhaps 5 billion prairie dogs occupied millions of acres of short and mixed grass prairie" (Long 1998). Eradication by farmers and government, regarding them as pests, has now reduced these animals down to 2% of their former range (Long 1998). Since this eradication, mesquite (*Prosopis glandulosa*) has slowly been attaining dominance in grasslands throughout the region (Weltzin *et al.* 1997). Field research indicated the prominent role of *Cynomys* in seed and pod removal of *Prosopis*; significantly 3-99 times greater within prairie dog colonies than without. In addition, prairie dogs and associated herbivores girdled and destroyed 100% of *Prosopis* seedlings within 2 days of planting, and even 1 yr old seedling survival was reduced by 50% within prairie dog colonies. Despite this, on-colony seedling reserves were substantial (950 plants per ha), indicating that prairie dogs supressed rather than eradicated *Prosopis* from colony sites. Findings of the study showed that removal of *Cynomys* led to rapid development of *Prosopis* stands, as the dietary habits of these animals effectively suppressed *Prosopis* development.

Curtin *et. al* (2000) in a near desert/grassland ecotone of the Chihuahuan desert, Mexico, also noted that where rodents such as *Dipodomys* sp. (Kangaroo rats) were removed by exclosures, the proportion of woody vegetation cover increased by more than three times.

In heavily bush encroached semi-arid Australia, study of historical photographs and mammal records (from +/- 100 years ago) supports the idea that a combination of light grazing by native herbivores such as kangaroos (*Macropus* spp.), episodic fire, and browsing of regenerating shrubs by medium sized marsupials such as bettongs (*Bettongia* spp.) produced the mosaics of open and closed plant communities as noted by early settlers. This has been demonstrated where exclosures on Rottnest Island (Western Australia) prevented the resident small marsupial quokka (*Setonix branchyuras*), (now extinct on the mainland continent) from killing tree seedlings regenerating after a fire (Noble 1997).

Each of these studies highlights the potential role played by small mammals in regulating woody vegetation seed and seedling survival in semi-arid landscapes. In many cases this knowledge has only been gained after removal or eradication of small mammal species from habitats pre-empting significant landscape change through colonisation by woody thickets. Internationally small mammal species are now being recognised as partly responsible for maintaining savanna communities through preventing establishment and dominance of woody plant species, and for preventing the transition of grassland and savanna areas into woodlands (e.g.: Noble 1997, Weltzin *et al.* 1997).

The widespread and abundant populations of small mammal granivores in southern African savannas, coupled with issues of bush encroachment leads to the central question of this study:

“What is the role (if any) of granivores in the regulation of woody increaser tree and shrub species in southern African savanna ecosystems?”

## 2. Aim of study – Granivores and ecosystem regulation

Historic increases in woody plant density in savannas and grasslands have been documented worldwide (Archer 1995). This phenomenon is of considerable environmental and socio-economic concern, impacting on woody plant and tree density, habitat conservation, nutrient cycling, soil erosion (Weltzin *et al.* 1997), and subsistence and commercial agricultural production.

To date research in Africa has concentrated on the effects of large herbivores (such as cattle and wild ungulates) on agricultural production in relation to increasing woody plant densities in savanna regions (Scholes 1986, Child 1995).

This study tests the hypothesis that indigenous small mammals may act as 'ecosystem regulators' in the southern African savanna biome. Two complementary experiments were conducted to aid in qualifying this statement:

**EXPERIMENT ONE – Determination of small mammal abundance and diversity across differing land uses:**

Live trapping of small mammals to identify species and assess species abundance in the homogenous plant communities of three land use types:

1: a "natural" landscape
2: a megaherbivore exclosure
3: communal agricultural land.

All study areas are on or adjacent to the Kempiana property, Timbavati Game Reserve, central Lowveld, South Africa.

**Brief**

Throughout areas of healthy southern African grassland and savannas, a wide variety of rodent species are known to occur, including *Tatera leucogaster* (bushveld gerbil), *Saccostomus campestris* (pouched mouse), *Aethomys chrisophilus* (red veld rat) and *Aethomys namaquensis* (Namaqualand rock mouse) (De Graaf 1981, Skinner & Smithers 1990, Mushasha 1998).

Trapping across the three different land-use types with varying grass biomass cover was conducted to test whether small mammal activity is dependent on habitat (a cover requirement) as is postulated by Smit *et al*. (2001).

Results from this exercise should infer small mammal habitat preferences, the effects of megaherbivores (if any), and anthropologic management on small mammal numbers through habitat modification and herbivory.

### EXPERIMENT TWO: Seed and seedling predation by resident small mammals

**Brief:**

The three most common small mammal species of Kempiana (as determined by Experiment One) were all considered in the literature to be granivorous, consuming seeds and seedlings of a variety of plant species as a large proportion of their diet (De Graaf 1981, Skinner & Smithers 1990, Mushasha 1998). Twenty three of these individuals were each confined to a cage for a 24-hour period with a cafeteria containing seeds and seedlings of various local woody increaser species. Predation of the various seeds and seedlings was recorded as evidence of seed and seedling predatory activity.

In addition to the above experiments, other complementary investigations in relation to small mammal abundance, diversity and diets in the local area were conducted under my supervision. These are later described in text boxes to aid in clarifying my findings

# 3. Region of study

## *The central Lowveld, South Africa*

The study area is located in the Limpopo Province of South Africa, centring on three distinct land-use types in and around the Kempiana property, part of the Timbavati Game Reserve and managed as a contractual area of Kruger National Park.

The central Lowveld is situated in the north-eastern part of South Africa in Limpopo Province and measures some 2.58 million hectares (Newenham 2000). The region is bounded to the north by the Selati, and to the south by the Sabie Rivers. The west sections of the Lowveld are densely populated with numerous urban and scattered agricultural smallholdings and the east is represented by the Kruger National Park. The region is characterised by a west to east gradient in topography, climate and former political boundaries, which have resulted in several distinct land use zones (Shackleton 2000). Three distinct and common land uses of the region (communal agriculture, conservation area and megaherbivore exclusion zones) were researched in this study.

### Study area

The study area abuts the Kruger National Park and is situated between 24°29' S and and 31°16' E (Pieterson 1998). This area is classified by Acocks (1953) as Arid Lowveld, considered by Booysen and Tainton (1984) to be part of the Arid Savanna Biome, and is mapped as Granite Lowveld by Mucina *et al*. (2005). These savannas occupy the base rich soils of the hotter, drier lowland valleys (Lowveld) of South Africa. All field research for this study took place in what is described as *Acacia* dominated sweetveld, a habitat that supports a year round assemblage of fauna that moves freely between the Kruger National Park (KNP - 10km east of the research areas) and the Kempiana property. A map of the area of study is shown in Figure 3-0-1.

Figure 3-0-1. Local region and study areas – central Lowveld South Africa (Original map Honeyguide CC 2005)

### *Climate*

The research area has a wide range of climatic extremes experienced throughout the year. Average temperatures recorded for this environment range from 8-23$^0$C in winter through to 18-30$^0$C in summer, with temperature extremes known to have reached – 4$^0$C and 40$^0$C (Newenham 2000).

Booysen and Tainton (1984) classify Arid Savannas as those where the rainfall is restricted to 5 - 6 months of the year and ranging between 250-650 mm/yr. The research area has a definite wet season during the summer months with most rainfall occurring between September and May; with little to no rain in the cooler months. Rainfall data collected from the two closest stations in Hoedspruit (approximately 65 km north-west) and the Satara camp (48 km north-east of the Orpen gate) in the KNP report an average rainfall of approximately 568 mm per annum (based on a 40 year average between 1956 – 1997). At Satara, maximum rainfall was 940 mm in 1963, with a minimum of 300 mm in both 1962 and 1978. Over the past 70 years of rainfall records it has been noted that definite wet and dry cycles occur, each lasting some eight to twelve years that alternate with each other - this results in periods of drought and/or flooding. This study took place after a period of greater than average rainfall, occurring after a 1:50 year rainfall episode that caused widespread flooding throughout the north and north-eastern parts of South Africa and southern Mozambique.

**Note:** While the habitat is defined in the literature as an arid savanna, the region itself is recognised by landscape managers as a semi-arid zone in terms of production and management (Pieterson *pers comm.* 2000). For this reason I refer to the area as a semi-arid savanna in this study.

### *Geology*

The Lowveld area is underlain by Basement rocks of the Bandelierkop Complex, typified by potassic granites and grandiorite (Shackleton 2000). The soil type in Kempiana is typical of the area and surrounds, and is dominated by a shallow sandy lithosol on underlying granite; with a more heavy clay soil on gabbros. The majority of the soils derived from both sets of parent material are shallow, seldom reaching beyond 1.2m in depth (Pieterson 1998). Localised ridges are common, formed on underlying granite and supporting *Sclerocarya* communities.

Topographically, the terrain is flat to undulating throughout the research area.

### *Vegetation*

Arid savannas are physiognomically diverse and include open sparse grassland with scattered shrubs and short trees, through to dense thickets (Booysen & Tainton 1984). Spinescent nano- and microphyllic shrubs and trees, in particular of *Acacia* spp. dominate the woody component of these savannas. Common tree species are members of the Combretaceae (*Terminalia serecia*, *Combretum collinum*, *C. hereroense*, *C. zeyheri*, and *C. apiculatum*), and Mimosaceae (*Acacia nilotica*, *A. gerrardii*, *A. nigrescens*, and *Dichrostachys cinerea*), although the widely heterogenous landscape means that dominance varies considerably from area to area.

Both *T. sericea* and *D. cinerea* are common in the area, tending towards being encroachers in some areas. Ridges formed on underlying granites commonly contain *Sclerocarya* as dominant individual trees in some areas, particularly in Welverdiend communal lands where *Sclerocarya* groves are commonplace. The vegetation is described by Pieterson (1998) as tall open woodland dominated by *Sclerocarya birrea* and falls into the Gertenbach (1983) classification as mixed *Cormbretum/Terminalia sericea* woodland and thornveld.

Xerophytic tussock grasses grow commonly throughout the study area, specifically, *Panicum maximum* and *Sporobolus* spp. Other common grass species, growing within a mosaic of patches and conditions include: *Themeda triandra, Digitaria eriantha*, *Pogonathria squarosa, Eragrostis curvula, E. gummiflua*, *Bothriochloa insculpta*, *Hyparrhenia* sp., *Heteropogon contortus*, *Aristida bipinarta*, and *Cynodon dactylon*.

### *Fire*

Fires are a regular feature of the Lowveld environment, with fire intensity and duration influenced/determined by dry winters and frost conditions (Booysen & Tainton 1984). The herbaceous layer is more inflammable than the deciduous woody layer, and dense woody vegetation with a low herbaceous biomass is less prone to a fire than mixed grass-woody vegetation. Fires in South African savannas are mostly surface fires, occasionally becoming crown fires in extreme conditions of weather or fuel load (Walker 1981, Booysen & Tainton 1984).

Where fire management regimes have been in place the Lowveld savannas have historically been burnt on a three to five year rotation (Pieterson *pers comm*. 2000). Controlled burns are deemed necessary at such intervals to stimulate species germination and growth. Fires are generally induced anthropogenically (conservation, agricultural management or accidental) or by lightning, although the former is by far the most common causal factor. Fires chiefly occur in late autumn, winter and/or spring, when the grasses are moribund and fuel loads are high (Booysen & Tainton 1984). Due to the dynamics of competing grassy and tree layers, the biomass of grassy and woody layers are generally inversely in proportion with each other; directly affecting fuel loads, fire spread and intensity.

## *Study areas*

This study focuses on different land use types within the Kempiana area that have been subjected to different management regimes and considered to provide insight to potential management related issues.

Considering the divergent land uses and resultant site impacts, efforts were made to reduce heterogeneity between study areas and sample sites in terms of vegetation and habitat type. In order to compare sites of historic similarity and exclude potential error in sampling, all study sites for this research were based on *Sclerocarya* dominated ridges; as such plant assemblages formed similar communities throughout the landscape. The study areas include:

**Kempiana –** a 14,000 ha. area subjected to grazing by indigenous herbivores and a 'natural' fire regime (generally a three to five year rotation). Considered a 'natural' location and managed for conservation land use. The area is contiguous with Kruger National Park

For this study four 90 x 40m sample sites were established within the Kempiana property. Kempiana is part of the privately owned Timbavati Nature Reserve, which in turn is contractually managed by Kruger National Park - undergoing identical policy and management as the adjacent protected area.

Kempiana is typical of open woodland of the region and is the habitat for major South African mammal species common in the region. Major biotic and abiotic influences in Kempiana include:

**Meso- and megaherbivores:** All sample sites were in areas contiguous with Kempiana property. Various large grazing, browsing and mixed feeders occur throughout Kempiana and common species are Elephant (*Loxodonta africana)*, Blue wildebeest (*Connochaetes taurinus)*, Burchell's Zebra (*Equis burchelli*), Giraffe (G*iraffa camelopardalis)*, Buffalo (*Syncerus caffer*) and Impala (*Aepyceros melampus)*. A wide range of mesoherbivores inhabit the area including common duiker (*Sylvicapria grimmia*), and scrub hare (*Lepis saxatilis*). These animals have varied feeding heights and diets, consuming plants across the full range of habitats.

**Grazing pressure:** Indigenous herbivore stocking rates vary between reserves in the Lowveld, and Parsons *et al.* (1997) reported a mean for three local reserves as 0.33 Large Stock Units (LSU) per hectare.

**Fire:** Both management and lightning fires occur. Management fires are set in early winter, and lightning fires generally occur during late spring or opportunistically in relatively dry times of year. Sections of Kempiana are burnt on 3 – 5 year cycles. The 2000 study area was previously burnt in 1997 and 1998.

**Human modification:** Kempiana is typical of nature areas of the Lowveld in that gravel roads have been established throughout the landscape. In addition there is a permanent waterhole on a nearby section; approximately 2 km from the area of study. It is possible that both these developments could have had some impact on megaherbivore activity; roads possibly decreasing animal densities due to greater disturbance and vehicle traffic, and the waterhole potentially increasing densities of animals during dry seasons by them congregating around limited perennially available water. Hippopotamus (*Hippopotamus amphibius*) have become resident on site since the construction of the waterhole, with the resident population fluctuating between a single individual and three animals during the study. Orpen Road, a major thoroughfare connecting KNP with the town of Hoedspruit (65 km west), demarcates the fenceline and southern boundary of Kempiana.

Other than infrastructural development in the vicinity no deliberate human modification of the study sites has taken place in Kempiana. No watering, enrichment planting or active removal of plant or animal species has occurred (other than very occasional problem animal control or poaching by neighbourhood villagers). All study sites were located away from human activity and movements, although within 500 m from gravel roadways for ease of access.

Non-conservation land use boundaries (such as the Welverdiend communal lands) of the Timbavati are perimeter fenced, with the remainder of open boundaries into Kempiana and Kruger National Park.

**Other management impacts:** Limited harvesting of resources takes place within the reserve, occasional firewood (dead and naturally felled material) and thatch grasses (*Hyparrhienia* sp.) for roof construction and building are taken by local people (Pieterson *pers comm*. 2000).

**Southern African Wildlife College** (SAWC) – a 33 ha. fenced large herbivore exclosure, fully enclosed within the Kempiana property. The College area is subject to a managed fire regime, with controlled burns taking place on an annual basis to limit fuel load build up created in part by lack of large herbivore grazing over the site

Three 90 x 40m sample sites were established on typical *Sclerocarya* ridgetops on the SAWC campus. Prior to the establishment of the 33 ha campus site in 1997 the area was managed as part of the Kempiana property by KNP. Despite the exclusion of large mammals the site appears unimpacted to the naked eye, similar in all regards to the surrounding Kempiana but for the more dense vegetation cover.

The SAWC Campus and study sites are managed under the following treatments:

**Meso- and megaherbivores:** All sample sites within the SAWC were in areas of extremely limited megaherbivore activity. Since the college site was fenced the only meso-mammal within the confines of the area has been a single common duiker *Silvicapra grimmia* (Family Antilopinae; sub-family: Cephalophinae). *S. grimmia* is a selective browser consuming leaves, flowers and fruit (Skinner & Smithers 1990). Feeding height of *S. grimmia* was considered to be generally higher than the area of interest for this study, although it is possible (unlikely) some incidental impacts of the duiker may have occurred on the sites through trampling of grass or disturbance of small mammals. Some scrub hares *Lepus saxatilis* (Family Leporidae) graze on local grass species, with a preference for green grasses (Skinner & Smithers 1990) that would influence hare movements as preferred food availabilities change.

**Grazing pressure:** Overall grazing pressure on the SAWC grounds is minimal. The impact of the common duiker was considered negligible, as the LSU value of a duiker is 0.09, inferring that more than 10.5 individuals would equate to the equivalent consumption impacts of one 18 month old steer (Bothma 2004). Assuming the undeveloped portion of the SAWC is 20 ha, this equates to an LSU quotient of 0.0045 for the site.

**Fire:** Management of fuel loads is conducted as part of the SAWC Campus fuel reduction management plan conducted essentially to prevent accidental fires impacted on the thatched infrastructure. As such controlled fires are carried out during the early winter season. In areas adjacent to the College buildings, fire management takes place every year as a risk mitigation measure for building and infrastructure. The three Campus sample sites had been burnt on a yearly basis.

**Human modification:** Since the fencing of the Campus, the SAWC has been developed as a formal training institution. The College has a human presence of +/- 100 individuals per day, although their activities are restricted to developed parts of the site such as paved walkways, classrooms and accommodation. More than two-thirds of the SAWC is undeveloped and in a relatively natural state, with minimal human disturbance. For the undeveloped sections of the site, other than exclusion of large herbivores and for some areas, increased fire regime, no deliberate human modification of the sites had taken place since enclosure. This includes no watering, enrichment planting or removal of plant species. Some areas within the SAWC have been mowed, although these were not adjacent or within areas of study. Additionally research took place away from internal site roads and the perimeter fence, which may influence small mammals movements.

**Other management impacts:** For the purposes of this study, the SAWC Campus serves as a more intensively managed natural setting similar in all regards to Kempiana, except for the absence of large herbivores.

**Welverdiend –** the surrounds of the village and local community of Welverdiend, a local communally utilised landscape that is used as a rangeland for cattle and goats and is contiguous to the Kempiana study area.

Two 90 x 40 m sample sites were established within *Sclerocarya* dominated plots in communal grazing lands surrounding the local community and village of Welverdiend (population +/- 10,000 people). Due to limited resources and potential for human interference with the Welverdiend experiment only two sample sites were selected in the area.

Welverdiend consists of scattered smallholdings (minimum size 10 x 10m) and rural people reliant on agriculture or money sent from family members working off-site. According to Shackleton (2000), the current population density of the area is 146 persons/km$^2$, although in Welverdiend this is highly concentrated within a village area, with greatly reducing density concentrically outwards from the village centre. Approximately 60-70% of the potentially economically active population of Welverdiend are not employed in the formal economy. Reliance on natural resources to sustain livelihoods is high and most harvest several different kinds of resources from the communal lands, including, fruits, thatch grass, fuelwood, mushrooms, reeds and construction wood (Twine *et*. *al*. 2000). The village surrounds are used as a grazing common, with large tracts of subsistence grazing in the immediate locality to the township. Closer to homes, nearly all households cultivate small areas around the homestead during the rainy season, and 30-40% of households also cultivate demarcated arable fields on the periphery of the village or further afield. The remaining land is zoned as communal grazing area (Shackleton 2000). Fuelwood is the primary energy source of between 94 and 100% of households – even for those supplied with electricity (Twine *et al.* 2000). The communal grazing lands surrounding Welverdiend have had some degree of exploitation for at least several decades resulting in a clear alteration of plant community physiognomy (Shackleton 2000).

**Meso- and megaherbivores:** The communal lands are generally devoid of permanent populations of indigenous large grazing and browsing mammal species typical of Kempiana. Occasional intruder individuals from adjacent protected areas occur (e.g.: predators chasing potential prey items from Kempiana into the area, or fence transgressing elephants), but none were seen during the study. Meso- and megaherbivores are represented by domestic cattle and goats that range across the landscape daily. Approximately one-third of households possess cattle (Shackleton 2000). Despite such landscape alterations, it is likely that common duiker (*Sylvicarpa grimmea*), hares (*Lepus saxatilis*) and some other scattered mammals are resident.

**Grazing pressure:** Grazing commonage in the area is typically heavily stocked by cattle and goats, supporting livestock at levels of up to four times the recommended stocking rate for the area (Shackleton 1993). After daylight livestock grazing and foraging in communal lands, stock are herded into protective kraals within Welverdiend villiage at night to prevent theft and predation by lions. Daily herding and kraaling practice significantly affects herbivory, regularly concentrating impacts - increasingly so in areas immediately surrounding kraal areas. Such activity tends to concentrate herbivory around the village, with such effects decreasing with increasing distance from human settlement. Communal land stocking rates are close to ecological carrying capacity at 0.88 +/- 0.09 LSU per ha (Parsons *et al.* 1997). It is important to note that livestock impacts go beyond that of plant consumption, since trampling and nutrient redistribution also take place. Well-developed patches of erosion towards rivers and roadways are apparent.

Visibly the Welverdiend landscape consists of a montage of low-cropped grasses, interspersed with thickets of young shrubs clustered tightly around the stems of larger trees in woody thickets such as *Sclerocarya birrea* and *Dichrostachys cinerea*, amongst which herds of cattle and goats forage.

**Fire:** There is no known formal fire management regime on the communal lands. However fires do occur, but only at times when sufficient fuel loads build up. In general communal areas are burnt (accidentally or deliberately) whenever there is sufficient fuel. Although fires burn frequently in these areas, fire intensities are generally low because of the high grazing pressure (Shackleton 2000).

**Human modification:** Communal areas of the region have had high and increasing densities of people since the 1960s and have thus been exposed to increased domestic stock herbivory for a long period of time (Shackleton 1993). Other than the management of grazing, human activity in the area is based around subsistence economic extraction of natural resources and landscape modification. This includes harvesting of firewood and building materials, road building and expanding human populations, all the effects of which are intensified in areas closer to human settlements.

Roads, both formally constructed and makeshift shortcutting tracks are prominent throughout the landscape, particularly adjacent to human settlement. Well-compacted cattle walking tracks are conspicuous around kraals and waterholes with water being provided artificially through a series of boreholes and earth-walled dams. No additional vegetation had been planted on the site.

Both sample sites were in areas approximately 3km from the Welverdiend village settlement and utilised as communal grazing lands, frequented by cattle and goats.

# 4. Materials and methods

To best determine small mammal abundance and diversity across the study areas, similar trapping activities were conducted in each sample site. Once general small mammal diversity and abundance became known, the seed/seedling predation experiment was conducted on the grounds of the SAWC utilising the most abundant small mammal species.

## Selection of research plots

In all three study areas (Kempiana, SAWC and Welverdiend) sample sites were subjectively placed in *Sclerocarya* groves using the phytosociological methodology of Mueller-Dombois & Ellenberg (1974). For experimental homogeneity all sites shared *Sclerocarya* as the dominant tree, with sub-dominant *Acacia* spp. patches. Individual relevés were selected on the following basis:

- Each sample site shared locally common trees, shrubs and grass species representative of the plant community

- The habitat, soil and topography was as uniform as possible within the area

- Plant cover was as homogenous as possible.

After sample site selection all taxa were identified and recorded on field data sheets (see Appendix 1), with recordings of dominance used for comparison, and eventual selection for small mammal trapping. Species within plots were assigned life form classes (e.g.: tree, shrub, grass, etc). Plot size was determined using Whittaker's Gradient analysis (Mueller-Dombois & Ellenberg 1974), measuring environmental variance outwards from the centre of the *Sclerocarya* grove. Each study area varied between 1250 – 2500 m$^2$ in size, depending on the limit of environmental variance noted through gradient analysis (Mueller-Dombois & Ellenberg 1974).

In total, four research plots were selected in Kempiana (Sites A, B, C & D), three in the SAWC (Sites E, F & G) and two in Welverdiend (Sites H & I). The differing number of sample sites in each study area reflected the limited resources available for the study (in particular vehicles, labour, time, and limited available habitat at the SAWC). In addition the Welverdiend component of the experiment required full-time guarding of traps from incursions by local people, which limited sampling time on that study area.

### Small mammal trapping

All sites within the study areas were located at least 500 m apart to achieve sampling independence. Animals were trapped in Sherman and Elliot (Elliot Scientific Company, Victoria; Australia) live traps, allowing for identification, marking and release of individuals upon visitation. Trapping grids were set in a

10 x 5 configuration (50 traps per night), although Welverdiend sites G and H consisted of a trapping grid in a 10 x 10 configuration (100 traps per night) – increased to account for logistical difficulties for operating in that area. Traps in all grids were placed approximately 5 m apart. Traps were baited with a mixture of rolled oats and peanut butter, as commonly used in small mammal trapping exercises by Rowe-Rowe & Lowry (1982), Jeltsh *et al.* (1998) and suggested by Pieterson (*pers comm*. 2000). Traps were set and baited early in the evening, and then checked the following morning. Traps were left closed during the day as the key small, herbivorous mammals are considered by Skinner & Smithers (1990) to be predominately nocturnal and crepuscular. In addition, daytime trapping presented potentially high stress levels and dehydration exposure for trapped subjects. All animals captured were identified, tagged by fur clipping and released. Traps in which the bait had been consumed overnight were rebaited. Traps found closed but which contained no animal were counted as a fail. When 95% of animals caught each night over three consecutive trapping nights were recaptured, it was considered that the small mammal population had been accurately measured at that site and trapping was discontinued (Breytenbach *pers comm*. 2000). Figure 4.1 shows the trapping layout for the small mammal trapping experiment across the different study areas

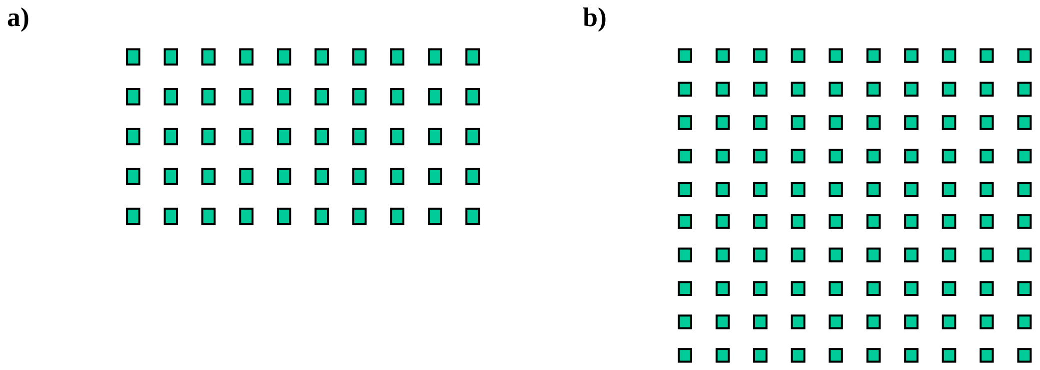

Figure 4.1: **Schematic diagram showing the configuration of trapping grids for A) Kempiana and SAWC study areas (50 traps @ 5x5m grids)** and B) Welverdiend study area (100 traps @ 5x5m grids), central Lowveld region, South Africa.

Trapping was conducted throughout each site in each of the study areas. Table 4-1 outlines dates, location, and trapping nights per site.

**Table 4-1:** Dates, locations, sites, trap quantities, trapping nights and total trapping figures for small mammal trapping, Kempiana, SAWC and Welverdiend locations

| Date | Study area | Site | Number of Traps | Number of nights | Total | Trap nights |
|---|---|---|---|---|---|---|
| 1/9/00 – 5/9/00 | Kempiana | A | 50 | 4 | 200 | **1,450** |
| 15/9/00 – 20/9/00 | | B | 50 | 6 | 300 | |
| 26/9/00 – 5/10/00 | | C | 50 | 10 | 500 | |
| 28/10/00 – 5/11/00 | | D | 50 | 9 | 450 | |
| 20/8/00 – 31/8/00 | SAWC | E | 50 | 11 | 550 | **1,850** |
| 6/9/00 – 14/9/00 | | F | 50 | 9 | 450 | |
| 6/10/00 – 22/10/00 | | G | 50 | 17 | 850 | |
| 21/9/00 – 25/9/00 | Welverdiend | H | 100 | 5 | 500 | **1,000** |
| 23/10/00 – 27/10/00 | | I | 100 | 5 | 500 | |
| All sites | | | | **76 nights** | | **4,300** |

### *Measure of grass biomass*

Average grass biomass was measured using a Disc Pasture Meter (Bransby & Tainton 1977). This instrument quantifies the amount of grass material trapped under the sliding disc of the hand-operated device. One hundred readings were recommended as an adequate sample size for calculating grass biomass in each management regime (Pieterson *pers comm.* 2000). Grass biomass was measured in October 2000 in all sample sites in the three study areas.

### *Seed and seedling predation*

#### Seed collection and propagation

Seeds of common increaser species in the area were collected and some were propagated in a plant nursery. Increaser species were chosen from observation and in discussion with various scientists and land managers (including Moll, Balfour, Child, Breytenbach & Pieterson *pers comm.* 2000). Additional review of the literature for common tree and shrub species in the Kempiana area (Coates-Palgrave 1977, Venter & Venter 1996, SAPPI 1999) lead me to select the tree and shrub species outlined in Table 4.2.

**Table 4-2-2:** Selected 'increaser' species in the Kempiana region of the central Lowveld, South Africa

| ***Name*** | **Common name** | **Family** |
|---|---|---|
| *Dicrostachys cinerea* subsp. *africana* | Sickle bush | Fabaceae |
| *Acacia nilotica* subsp. *Kraussiana* | Scented thorn | Fabaceae |
| *Acacia exuvialis* | Flaky thorn | Fabaceae |
| *Terminalia sericea* | Silver cluster leaf | Combretaceae |

Seeds typical of the tree or shrub species were extracted from freshly picked, sun dried fruits and hand sorted to separate those of highest quality in terms of size, level of damage (insect, scale, etc.). All collected and inspected seeds were considered to be viable samples for germination. A selection of these seeds were kept for the predation experiment with the remainder used for propagation. For propagation, each was treated for germination as appropriate for the species. All seeds are fire tolerant and required some level of scarification (using sulphuric acid) before germination was possible (Tietema 1992).

Once scarified, species were mixed in mapped seedling trays containing a mixture of 30 seeds. It was envisaged that seedlings would be offered in conjunction with unscarified, naturally occurring seeds to selected and caged locally occurring small mammal species.

### Small mammal trapping and seed/seedling predation

In a separate trapping exercise on the SAWC grounds 23 of the most abundant local rodents were live-captured using Sherman traps. The number and diversity of small mammals used in this experiment are outlines in Table 4.3.

**Table 4-2-3:** Trapped small mammal species used in seed/seedling predation experiment

| Species | Number |
|---|---|
| *Tatera leucogaster* | 6 |
| *Aethomys chrysophilus* | 8 |
| *Aethomys namaquensis* | 9 |
| **Total** | **23 individuals** |

Each of these captures were utilised in the predation experiment and kept for periods of 24 hours. Enclosures (measuring 1 x 1 m) were filled with grass, leaves and other local habitat material, and rodent subjects offered a 'batch' of seeds and seedlings (similar to Mushasha 1998). Seeds and seedlings of increaser species were offered in pre-set amounts, and upon evacuation of the small mammal subject from the cage assessed for chewing damage from the inhabitant. All seeds and seedlings were offered to small mammals in the form of a seed/seedling cafeteria whereby small mammals could choose between the various offerings. As no surface water was generally available on site, none was provided within the enclosure for the duration of stay. As in nature it was assumed that small mammals gain much of their water requirements through consumption of vegetative structures (Skinner & Smithers 1990).

Seeds and seedlings of commonly occurring increaser shrub and tree species were offered within the cafeteria, whereby one sample of each species' seed or seed pod(s) were grouped together where possible; each located in the cafeteria separated by wooden partitions. In an attempt to increase the variability of offerings, and to prevent the rodent finding a cache of preferred species the rodent was faced with a mixed range of seeds and seedlings within each partition. Table 4-2-4 shows the tree and shrub species included and quantity of seeds and seedlings offered to each captive small mammal over a 24-hour period. Seed quantity offered was determined by a ‘best guess’ based on amounts found within clusters or pods within the habitat. One seedling was offered per captive mammal, an amount determined by germination success at that time.

**Table 4-2-4:** Various locally occurring increaser seed and seedling species with quantities offered to the 23 captive small mammals over separate 24 hour captivity periods

| Species | Seed quantity | Seedling quantity |
|---|---|---|
| *Dicrostachys cinerea* | 2 seed pods (entire = +/- 5 seeds per pod) | 1 seedling |
| *Terminalia sericea* | 5 winged seeds (entire) | 1 seedling |
| *Acacia exuvialis* | 5 seeds (dehisced) | 1 seedling |
| *Acacia nilotica* | 1 seed pod (entire = +/- 5 seeds) | 1 seedling |

Seed and seedling damage was quantified after each 24-hour period when the small mammals were released. Seeds and seedlings were considered predated or destroyed if the damage caused by small mammal chewing was considered great enough to prevent the eventual successful growth of the plant; initially considered to be a level of 50% or more being chewed. Subsequent discussions with Mr Trevor Pezet, a seed technologist at Enza-Zaden (formerly Yates Seeds in Australia) revealed that in his opinion, should a seed be partially eaten by a rodent, insect, etc. either the cotyledon or the embryo would be damaged – and the loss of either would severely compromise germination ability of the seed. Should chewing scarification occur with minimal damage to the embryo, such a breach of the seed wall would potentially allow pathogens or other predators into the seed. In this case immediate rain in combination with fortuitous location with soil and sunlight would be essential for seedling survival. He believed that for each day that passes where this does not happen creates an increased chance of failure over time. For species such as *Dichrostachys* and *A. exuvialis* who shed their seeds in the seasonally dry winter, such survival after chewing would be extremely unlikely. For this study all seeds recorded as chewed have thus been recorded as predated as survival under such conditions is considered to be less than 1% and decreasing over time (Pezet *pers comm*. 2006)

Predation in seedlings invariably meant the chewing and loss of the cotyledons, which in all cases ended seedling survival (*personal observation* 2000).

### *Concurrent experiments*

In addition to the field research reported on above, a number of alternative research programmes took place at the SAWC over the same and later periods. The unpublished results from these studies have been used to support my own observations and give a more complete picture of the diversity, diets and seasonal abundance of local small mammals. These included:

- Gregory I (2000) How habitats in differing land use types relate to suitable hunting grounds for the Barn Owl (*Tyto alba*)
- Fourie N (2003) Stable carbon and nitrogen isotope analysis of hair from small mammals from the arid Lowveld Bushveld, Phalaborwa District, South Africa. University of Cape Town, Honours Project
- Atyeo M (2004) Tracking stations as a method for assessing small mammal activity and bait uptake. University of Queensland, Australia Honours Project

These complementary studies, conducted with the assistance of the author, whilst not directly answering the questions posed in my research add contextual information on small mammals of the area and will be discussed in the context of my research in the following chapters.

# 5. Results

## *Comparison of study areas and sites*

### Floristic composition

As relatively homogenous sites were selected for the study (*Sclerocarya* dominated ridgetops) it was anticipated that all sites would be floristically similar. Whittaker Diversity studies (Mueller-Dombois 1974) revealed this to be the case in all sites, as summarised for each below:

### Kempiana

**Site A.** *Sclerocarya* grove with occasional *Dichrostachys cinerea* and *Terminalia sericea* open woodland. Grass layer dominated by *Themeda triandra*

**Site B.** *Sclerocarya* grove with occasional *Dichrostachys cinerea* open woodland. Grass layer dominated by *Panicum maximum*

**Site C.** *Sclerocarya* grove with occasional *Terminalia sericea* open woodland. Grass layer dominated by *Themeda triandra* and scattered *Heteropogon contortus*

**Site D.** *Sclerocarya* grove and *Dichrostachys cinerea* thicket. Grass layer dominated by *Themeda triandra*

### SAWC

**Site E.** *Sclerocarya* grove with occasional *Terminalia sericea* open woodland. Grass layer dominated by *Panicum maximum*

**Site F.** *Sclerocarya* grove with occasional *Terminalia sericea* and *Dichrostachys cinerea* open woodland. Grass layer dominated by *Panicum maximum* and *Themeda triandra*

**Site G.** *Sclerocarya* grove with occasional *Dichrostachys cinerea* open woodland. Grass layer dominated by *Themeda triandra*. Some *Digitaria eriantha* present.

## Welverdiend

**Site H.** *Sclerocarya* grove with adult and sub-mature trees, occasional *Terminalia sericea* open woodland. Grass layer dominated by *Aristida* sp.

**Site I.** *Sclerocarya* grove with scattered *Terminalia sericea* and *Dichrostachys cinerea* open woodland. Grass layer dominated by *Panicum maximum* with scattered *Themeda triandra*.

### *Grass biomass*

Average grass biomass was measured and calculated across all research areas with the disk pasture meter (Bransby & Tainton 1977). Between 50 and 100 disk pasture meter readings were taken per site (N), and an average density for each site and research area was calculated, summarised in Table 5-1.

**Table 5-1**: Average grass biomass (measured in tonnes/ha from a disk pasture meter) for the three research areas, Kempiana, SAWC and Welverdiend

| **Kempiana** | **N** | **Av. Density** (tonnes/ha) | **SAWC** | **N** | **Av. Density** (tonnes/ha) | **Welverdiend** | **N** | **Av. Density** (tonnes/ha) |
|---|---|---|---|---|---|---|---|---|
| Site A | 50 | 4,039 | Site E | 100 | 5,930 | Site H | 100 | 183 |
| Site B | 100 | 2,527 | | | | | | |
| Site C | 100 | 4,086 | Site F | 100 | 5,727 | Site I | 100 | 748 |
| Site D | 100 | 2,789 | Site G | 100 | 5,600 | | | |
| **Av. Density Kempiana study area** | 350 | **3,360** | **Av. Density SAWC study area** | 300 | **5,752** | **Av. Density Welverdiend study area** | 200 | **465** |

Average grass biomass was markedly different between all study areas, correlating with decreases in large herbivore abundance. These differences are demonstrated in the following Plates.

## Kempiana

In total, 350 grass biomass measurements were made using the disk pasture meter on the Kempiana property across four separate research plots. Average grass biomass was 3,360 tonnes per hectare.

**Plate 5-1:** Typical Kempiana granite ridgetop view (October 2000), showing *S. birrea* (centre left of picture), *T. sericea* and *D. cinerea* open woodland (mid – background). Grass sward grazed by indigenous large herbivores.

## SAWC

Altogether, 300 grass biomass measurements were made using the disk pasture meter across the three separate research plots. Average grass biomass was 5,752 tonnes per hectare.

**Plate 5-2:** Typical view in the SAWC large herbivore exclosure (October 2000). *S. birrea* in top left of picture. Note luxuriant grass cover in foreground.

### Welverdiend

In all, 200 grass biomass measurements were made using the disk pasture meter in the Welverdiend communal grazing area across the two separate research plots. Average grass biomass was 465 tonnes per hectare.

**Plate 5-3:** View of granite ridgetop (*S. birrea* in centre of picture) in Welverdiend communal grazing lands (October 2000). Note grass biomass greatly reduced and exposed soil patches.

In summary, the grass biomass readings of all sites show distinct differences, which can be visually seen in terms of the amount of grass, the number of exposed patches of soil, the extent of trampling and number of megaherbivore pathways.

## *Zoological – abundance and diversity of small mammals*

Sherman and Elliot live trapping over a period of 76 nights (4,300 trap nights) revealed 106 unique individuals of small mammal species captured across the three major study areas. The results of this trapping exercise are shown in Table 5-2.

**Table 5-2:** Trapping sites and trap nights used per site between all three study areas

| Site: | Number of trap nights | Number of traps/night | Trapping area | Different species captured | Individuals captured | Density of small mammals/ha |
|---|---|---|---|---|---|---|
| Site A (Kempiana) | 200 | 50 | 840 m$^2$ | 2 | 2 | 24 |
| Site B (Kempiana) | 300 | 50 | 840 m$^2$ | 2 | 2 | 24 |
| Site C (Kempiana) | 500 | 50 | 840 m$^2$ | 5 | 6 | 71 |
| Site D (Kempiana) | 450 | 50 | 840 m$^2$ | 3 | 10 | 119 |
| Site E (SAWC) | 550 | 50 | 840 m$^2$ | 7 | 25 | 298 |
| Site F (SAWC) | 450 | 50 | 840 m$^2$ | 8 | 20 | 238 |
| Site G (SAWC) | 850 | 50 | 840 m$^2$ | 6 | 29 | 345 |
| Site H (Welverdiend) | 500 | 100 | 1,680 m$^2$ | 2 | 3 | 18 |
| Site I (Welverdiend) | 500 | 100 | 1,680 m$^2$ | 3 | 7 | 42 |
| Trap nights total | 4,300 | Unique small mammals captured | | | 106 | |

Graphically, Figure 5-1 shows small mammal densities/ha summarised according to ascending site population densities (trap nights also represented in graph as blue dots).

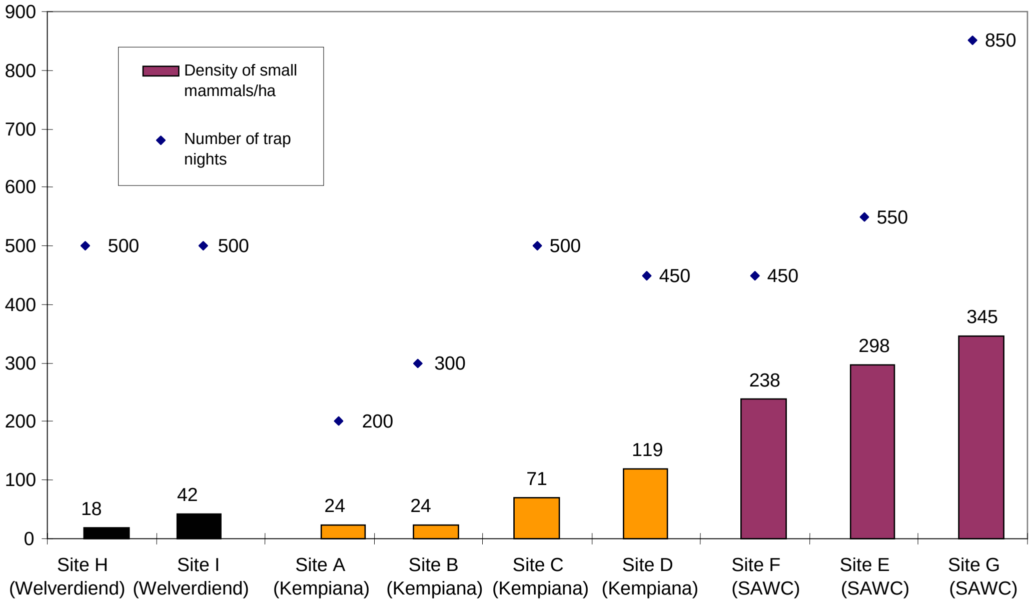

**Figure 5-1:** Approximated small mammal densities per ha and trapping nights in ascending order of densities (i.e.: Welverdiend, Kempiana and SAWC study areas).

Across each research area, summarised means of small mammal densities are demonstrated below.

**Table 5-3:** Summary of small mammal densities per ha on Kempiana, SAWC and Welverdiend study areas

| Study area | Average small mammals /ha |
|---|---|
| Kempiana | 60 |
| SAWC | 294 |
| Welverdiend | 30 |

Eleven separate species were captured, 10 of which are in the Order Rodentia, with one commonly captured insectivore, *Crocidura hirta*, the Lesser Dwarf Musk Shrew.

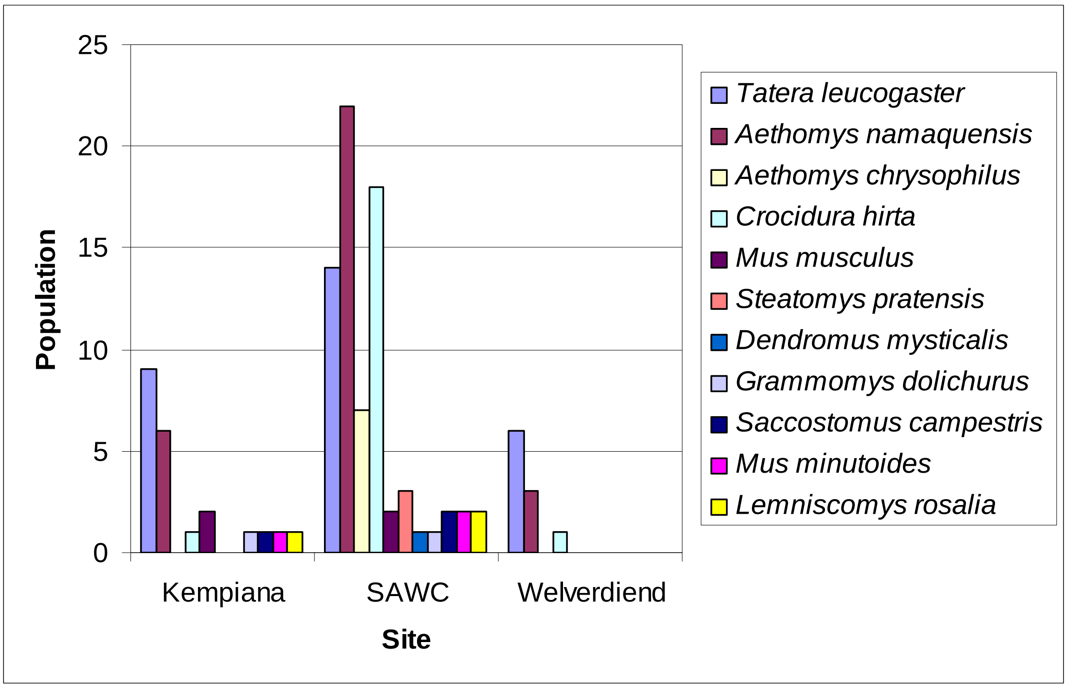

**Figure 5-3:** Unique Small mammal species captured across all study areas, Kempiana, SAWC and Welverdiend.

Figure 5.3 shows the overall predominance and diversity of small mammals on the SAWC study area, and a corresponding decline in numbers and species diversity for Kempiana, with these being even lower in Welverdiend.

**Table 5-4:** Most commonly captured small mammal species across all three study areas

| Abundance (individuals captured) | Name | Common name | Place captured |
|---|---|---|---|
| 1st (31) | *Aethomys namaquensis* **(Rodentia)** | Namaqua Rock Mouse | Kempiana (6)<br>SAWC (22)<br>Welverdiend (3) |
| 2nd (29) | *Tatera leucogaster* **(Rodentia)** | Bushveld Gerbil | Kempiana (9)<br>SAWC (14)<br>Welverdiend (6) |
| 3rd (20) | *Crocidura hirta* **(Insectivora)** | Lesser Red Musk Shrew | Kempiana (1)<br>SAWC (18)<br>Welverdiend (1) |
| 4th (7) | *Aethomys chrysophilus* **(Rodentia)** | Red Veld Rat | SAWC (7) |
| 5th (4) | *Mus musculus* **(Rodentia)** | Domestic Mouse | SAWC (4) |

The Red Veld Rat, *A. chrysophilus* was captured only on the SAWC sites, although in significant numbers to rank fourth in relative abundance. The only rodents captured across all three study areas were *A. namaquensis* and *T. leucogaster*.

## I. Comparative small mammal study 1: Study of *Tyto alba* pellets

In conjunction with trapping data from across sites Gregory (2000) conducted a study of small mammals as prey species for the barn owl (*Tyto alba*), across the study sites. Whilst not able to determine population size or physical locations for populations of small mammals, the analysis of *T. alba* diet aided in assessing the overall capture success of populations of small mammals in the trapping study. Overall species presence in pellets is summarised in Table I-1 where the two roosts (juvenile and adult occupied) pellets were collected

**Table I-1:** Small mammals identified from regurgitated pellets at two *Tyto alba* roosts (N = 143) on the SAWC Campus

| Prey species | Juvenile regurgitated pellets N = 56 | Adult regurgitated pellets N = 87 |
|---|---|---|
| *Tatera leucogaster* | 68.42% | 26.09% |
| *Mastomys natalensis* | 21.05% | 38.04% |
| *Crocidura hirta* | 10.53% | 30.43% |
| *Otomys angoniensis* | 0.00% | 1.09% |
| *Mus musculus* | 0.00% | 3.26% |
| *Aethomys chrysophilus* | 0.00% | 1.09% |

Gregory found significant numbers of *Mastomys natalensis* in the pellets, yet no *M. natalensis* were captured nor have been caught subsequently. It is possible that this species does not take the bait in the traps, or that the species is active diurnally when traps were closed (however, this is unlikely as personal observation showed that the owls tend to hunt at night). Alternately, *T. alba* may have hunted for species in habitat areas dissimilar to those of the trapping study (e.g.: river banks or open fields) where such species would be more commonly found. Hanney (1962) described potentially large hunting ranges for *T. alba* which would mean that the owls would indeed hunt across a very broad and diverse range, allowing access to small mammals beyond the immediate study area. Commonly captured prey species that confirmed trapping data included *T. leucogaster, C. hirta, A. chrysophilus* and *M. musculus. Otomys angoniensis* (the Angoni vlei rat) is an outlier not recorded in the habitat, possibly captured across a very broad hunting range or misidentified.

Other than the high abundance of *M. natalensis* as a prey item, Gregory's results support those I found by trapping

## II. Comparative small mammal study 2: Small mammal trapping (2004)

To aid in confirmation of trapping data collected in this experiment in 2000, Atyeo (2004) completed an additional small mammal abundance study at the SAWC Campus. Trapping results from this study are shown in Table II-1 in order of abundance

**Table II - 1:** Results of Atyeo (2004) small mammal trapping at SAWC Campus

| Species | Site 1 | Site 2 | Site 3 | Site 4 | Total |
|---|---|---|---|---|---|
| *Aethomys chrysophilus* | 3 | 17 | 10 | 6 | 36 |
| *Tatera leucogaster* | 14 | 3 | 4 | 5 | 26 |
| *Saccostromus campestris* | 0 | 3 | 0 | 0 | 3 |
| *Crocidura sp.* | 0 | 2 | 0 | 0 | 2 |
| *Paraxerus cepapi* | 0 | 0 | 0 | 2 | 2 |
| *Helogale parvula* | 0 | 0 | 0 | 1 | 1 |
| **Trap nights** | **43.5** | **44.5** | **33** | **36** | **157** |
| **Total captures** | **17** | **25** | **14** | **14** | **70** |

Similar to my findings, Atyeo captured a high proportion of *A. chrysophilus* and *T. leucogaster* within the SAWC Campus, although the *A. chrysophilus* population had grown significantly since 2000. In addition to the 2000 research, Atyeo trapped numerous *Paraxerus cepapi* (Sciuridae) and an example of *Helogale parvula* (dwarf mongoose). Both of these individuals, although not trapped in the earlier study, were commonly seen on the SAWC site in 2000. Considerably less trap nights during this later study yielded comparatively higher numbers of small mammals than in 2000, demonstrating high levels of fluctuation within small mammal populations in the area. Interestingly, no *A. namaquensis* were captured in 2004, yet were very predominant in 2000 – linking to predominant population cycles as discussed by Chesson *et al*. (2004).

### *Experimental error*

It is believed that the trapping exercise is a relatively accurate reflection of species abundance and diversity across the three study areas representing different management regimes. Comparative studies by Gregory and Atyeo assisted in confirming the reliability of the trapping study. Possible causes of error could include:

- Season of trapping was limited to spring/early summer. This may influence species abundance and diversity

- Trapping occurred across all study areas in rotation. Potential for error in trapping data may be exacerbated by change in season, or short duration effects such as phases of the moon, rainfall, etc., which could influence local small mammal numbers at any one site or all study areas at a particular period of time. As resources did not allow for simultaneous trapping on all sites, it is possible that a well moonlit night, for example, may have influenced results on all sites (van Henbergen & Martin 1993), despite the fact trapping was occurring in one study area at a time

- The year 2000 had significant rainfall events which may in turn effect small mammal populations though influence of water availability, food supply or plant growth

- Traps were commonly closed during the day due to animal welfare considerations. This may mean that potentially diurnal species (possibly such as *M. natalensis*) may not have been captured

- Whilst different site uses and grass biomasses have been recorded, the effects of fire on long term small mammal populations in all research sites has not been assessed in this experiment.

Despite these reservations I am confident that these results are an accurate reflection of the activities in each area, albeit a relative ‘snapshot’ in time of events. Data from comparative studies and the literature also generally confirm my findings

### *Seed and seedling predation*

The seed and seedling predation experiment was conducted between September and October 2000, utilising 23 individuals of the three most abundant small mammal species captured in the previous experiment. In total the following quantity of seeds and seedlings were offered to small mammal species:

**Table 5-5:** Seed and seedling offerings to captive small mammals

| Species | Seeds offered | Seedlings offered |
|---|---|---|
| *Acacia exuvialis* | 115 dehisced seeds | 18 |
| *Dichrostachys cinerea* | 23 seed pods (+/- 5 seeds per pod) | 14 |
| *Acacia nilotica* | 23 pods (5 seeds per pod) | 11 |
| *Terminalia sericea* | 115 seeds (within casing) | 8 |

Seed quantities were set per captive animal, and offered amounts were determined by factors including:

- Natural condition of seed – whether enclosed in pods or casings
- Size of seeds
- Perceived availability of seed for rodents in field (i.e. smaller dehisced seeds of *A. exuvialis* are considered to be more scattered and difficult to find on the ground than those enclosed within large pods such as *D. cinerea*)
- The amount of food eaten by each of these animals in a single sitting could not be found in the literature. Therefore numerous seeds were offered of each species to allow small mammals to consume at will.

The experiment revealed a variety of consumption patterns for *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* subject animals. Results are divided into groups for each increaser seed and seedling species.

### 1) *Dichrostachys cinerea*

#### *Seed predation*

In all 23 cafeteria experiments separate seed pods containing +/- 5 seeds per pod of *D. cinerea* were offered to the three predominant small mammals of the Kempiana property in the cafeteria experiment.

**Figure 5-2:** Predation of *D. cinerea* seeds by captive small mammals over a 24-hour period.

All captive small mammals showed a high level of interest in the cafeteria containing seeds of *D. cinerea*. Twenty-two of 23 seed pods were obviously chewed, of which 18 were partially consumed, four were entirely consumed and one was ignored. From this experiment *D. cinerea* seeds are considered to be highly palatable.

Evidence of considerable seed gnawing was found in and around the cafeteria including finely chewed and broken seed husks and pods. *A. chrysophilus* and *T. leucogaster* either partially (<50%) or significantly chewed (>50%) all *D. cinerea* seeds offered. *A. namaquensis* partially chewed eight of the nine samples of *D. cinerea* seeds offered. No intact seeds were found amongst debris of occupation, including in the rodent faeces.

### *Seedlings*

Twelve *D. cinerea* seedlings (germinated according to Tietema *et al*. 1992, Bell & van Staden 1993) were offered to the most abundant captured small mammal species of the Kempiana property; *A. namaquensis*, *A. chrysophilus* and *T. leucogaster*. Seedlings were placed in the cafeteria alongside various seed species, left for a 24 hour period and examined for damage after the captive animal was released. Where eaten seedlings were entirely consumed by captive mammals, i.e.: none were partially chewed as commonly occurred with seeds.

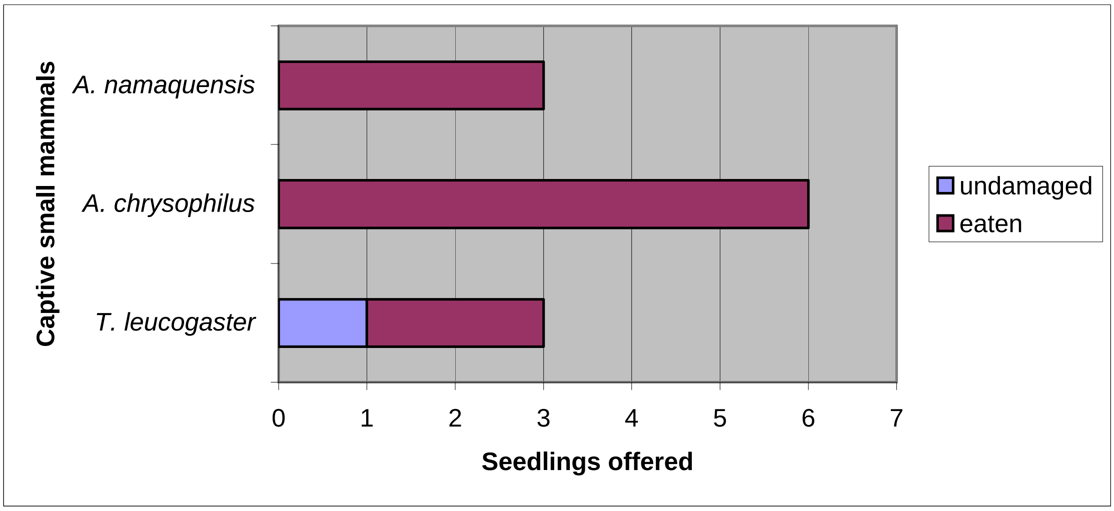

**Figure 5-3:** Predation of *D. cinerea* seedlings by captive small mammals over a 24-hour period.

All small mammals readily consumed *D. cinerea* seedlings. Of the 12 seedlings offered, all except one were consumed within the first 24 hours of captivity. It is apparent that *D. cinerea* seedlings are highly palatable for captured small mammals of this experiment, although *T. leucogaster* failed to consume one *D. cinerea* seedling as offered.

## 2) *Terminalia sericea*

### *Seed predation*

In all 115 separate seeds of *T. sericea* were offered in batches of five seeds to the three most common small mammals of the Kempiana property in the cafeteria experiment.

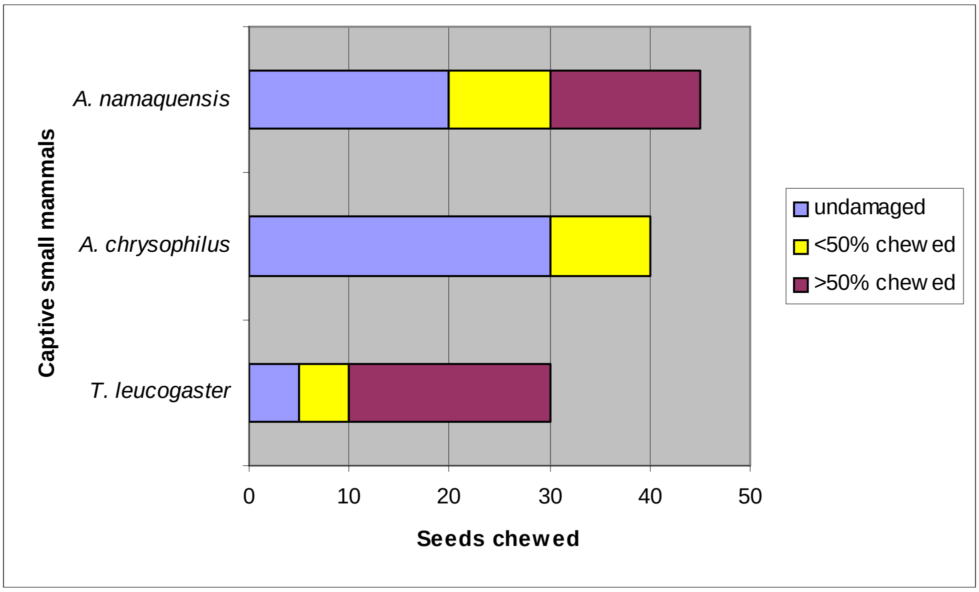

**Figure 5-4:** Predation of *T. sericea* seeds by captive small mammals over a 24-hour period.

All captive small mammals showed a high level of interest in the cafeteria containing seeds of *T. sericea*. Sixty of 115 offered seeds were obviously chewed, of which 25 (approximately one-fifth of all *T. sericea* seeds) were partially chewed; 35 (approximately one-third of all *T. sericea* seeds) were more than 50% chewed. Thirty-five *T. sericea* seeds were ignored by captive animals and not chewed at all. Evidence of considerable seed gnawing was found in and around the cafeteria including finely chewed and broken *T. sericea* seed husks. *T. leucogaster* was the most significant consumer of *T. sericea* seeds, either partially or totally chewing twenty-five of thirty offered seeds. *A. namaquensis* partially chewed 14 and totally chewed 15 samples of *T. sericea* seeds offered, ignoring 20 seeds entirely. *A. chrysophilus* partially chewed one-quarter (10) of the 40 *T. sericea* seeds offered.

All debris of occupation, including rodent faeces were examined for scattered, lost or cached seeds, and no viable removed *T. sericea* seeds were found within the cage. *T. sericea* seeds appear to be quite palatable for captured small mammal species in this experiment.

### *Seedlings*

Six *T. sericea* seedlings (germinated using guidelines from Tietema *et al*. 1992), were offered to the most abundant captured small mammal species of the Kempiana property, *A. namaquensis*, *A. chrysophilus* and *T. leucogaster*. Seedlings were placed in the cafeteria alongside various seed species, left for a 24 hour period and examined for damage after the captive animal was released. Where eaten seedlings were entirely consumed by captive mammals, i.e.: none were partially chewed as commonly occurred with seeds.

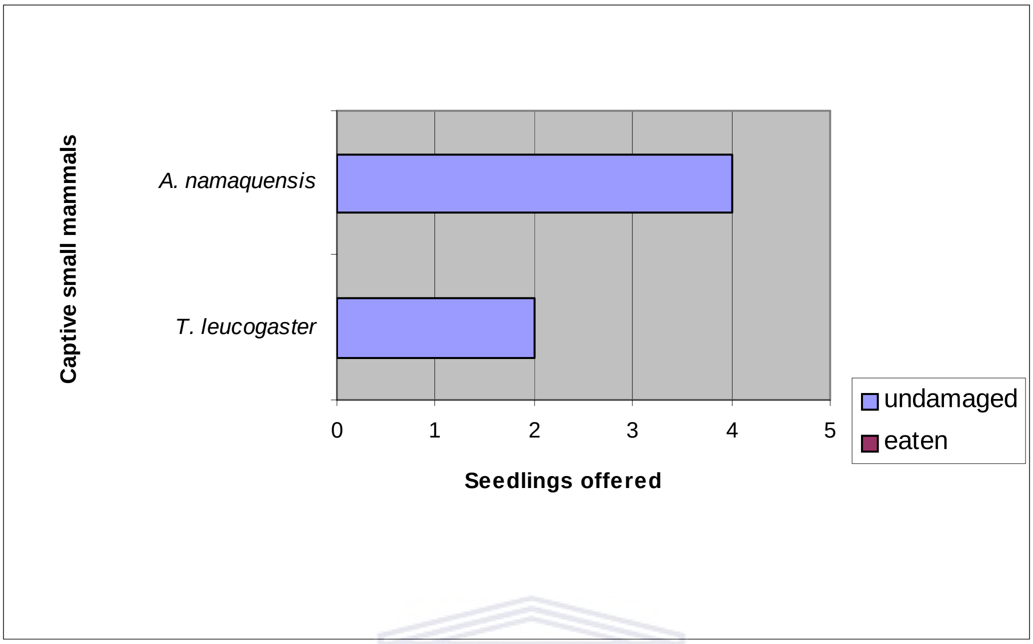

**Figure 5-5:** Predation of *T. sericea* seedlings by captive small mammals over a 24-hour period.

In this experiment neither *A. namaquensis* nor *T. leucogaster* readily consumed any of the offered *T. sericea* seedlings. A limited success rate of seedling propagation created a shortage of seedlings, meaning that *A. chrysophilus* was not offered *T. sericea* seedlings in this experiment. The capture and availability of *A. chrysophilus* and *T. sericea* seedlings did not co-incide fortuitously for this experiment.

## 3) *Acacia exuvialis*

### *Seed predation*

In all 115 separate seeds of *A. exuvialis* were offered in batches of five seeds to the three common small mammals of the area in the cafeteria experiment.

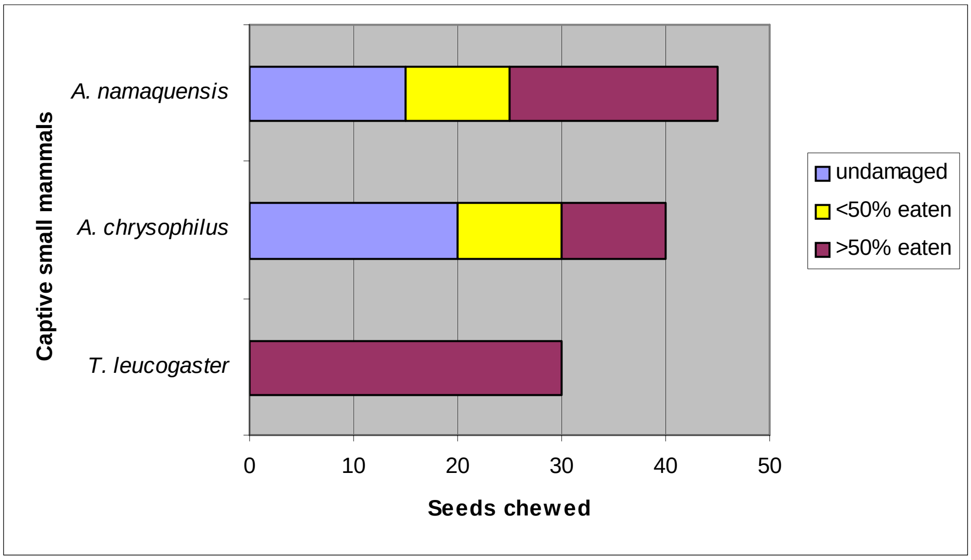

**Figure 5-6:** Predation of *A. exuvialis* seeds by captive small mammals over a 24-hour period.

All captive small mammals showed a high level of interest in the cafeteria containing seeds of *A. exuvialis*. Eighty of 115 offered seeds were obviously chewed, of which 20 were partially chewed, 60 (more than half of all *A. exuvialis* seeds) were more than 50% chewed. Thirty-five (one-third) of *A. exuvialis* seeds were ignored by captive animals and not chewed at all.

Evidence of considerable seed gnawing was found in and around the cafeteria including finely chewed and broken *A. exuvialis* seed coats and husks. *T. leucogaster* was the most significant consumer of *A. exuvialis* seeds, totally chewing (>50% damaged) all thirty offered seeds. *A. namaquensis* partially chewed 10 and totally chewed 20 samples of *A. exuvialis* seeds offered, ignoring 15 seeds entirely. *A. chrysophilus* partially chewed one-quarter (10), completely chewed (>50% damaged) one quarter (10) and ignored half (20) of the 40 *A. exuvialis* seeds offered.

All debris of occupation, including rodent faeces, were examined for scattered, lost or cached seeds, and no viable removed *A. exuvialis* seeds were found within the cage. Although remote, there is a likelihood of some lost seeds in this experiment, as *A. exuvialis* seeds were dehisced and loose in the cafeteria. It is possible that rodents could have scattered the seeds due to movement in the cafeteria, with some going missing. This may explain the divergent *A. chrysophilus* seed chewing results in this experiment.  It appears as if *A. exuvialis* seeds were highly palatable for captive small mammal species in this experiment.

### *Seedlings*

Seventeen *A. exuvialis* seedlings (germinated using guidelines from Tietema *et al.* 1992), were offered to the most abundant captured small mammal species of the Kempiana property, *A. namaquensis*, *A. chrysophilus* and *T. leucogaster*.  Seedlings were placed in the cafeteria alongside various seed species, left for a 24 hour period and examined for damage after the captive animal was released.  Where eaten seedlings were entirely consumed by captive mammals, i.e.: none were partially chewed as commonly occurred with seeds.

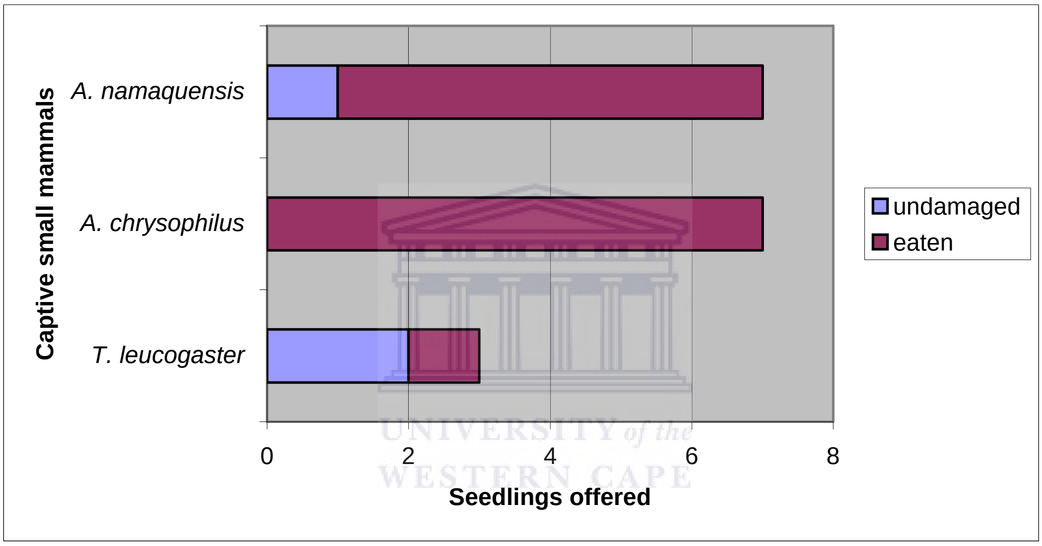

**Figure 5-7:** Predation of *A. exuvialis* seedlings by captive small mammals over a 24-hour period.

In this experiment all small mammals consumed *A. exuvialis* seedlings.  Of the 17 seedlings offered, 14 were consumed by small mammal species within the first 24 hours of captivity.  *A. chrysophilus* consumed 100% of seedlings, *A. namaquensis* consumed 85% of seedlings offered.  *T. leucogaster* only consumed one seedling from the three offered.  Overall, *A. exuvialis* seedlings appear a highly palatable food source for captive small mammal species.

## 4) *Acacia nilotica*

### *Seed predation*

Twenty three pods of *A. nilotica* (containing five viable seeds per pod – 115 seeds in total) were offered to the three predominant small mammals of the Kempiana property in the cafeteria experiment.

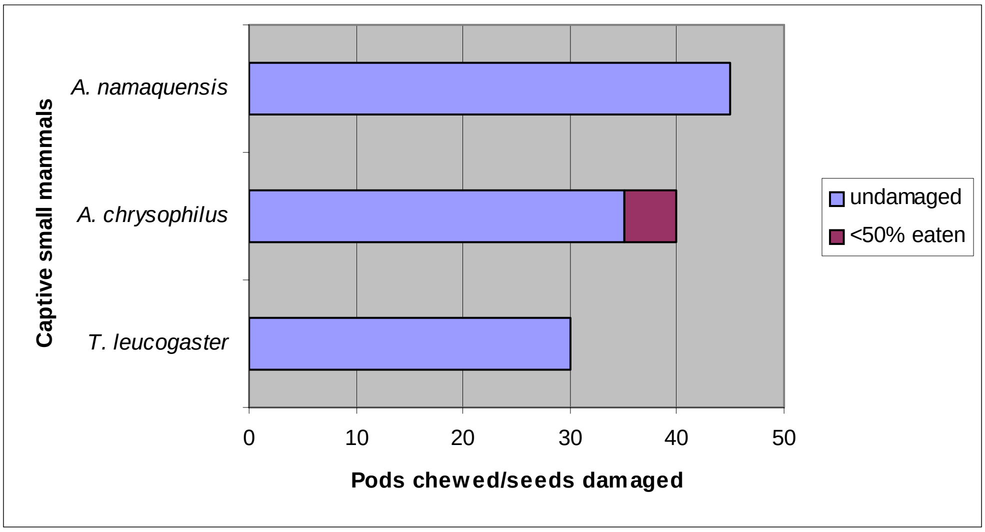

**Figure 5-8**: Predation of *A. nilotica* seeds by captive small mammals over a 24-hour period.

All captive small mammals showed a very low interest in the cafeteria containing seeds of *A. nilotica*. Five seeds within the 23 offered seed pods were obviously chewed where >50% damage had occurred to seeds within. Twenty-two pods, containing 110 *A. nilotica* seeds were ignored by captive animals and not chewed at all.

On one occasion a captive *A. chrysophilus* broke open one pod, extensively chewing all five seeds within. Considering the widespread ignorance of *A. nilotica* seed pods by all small mammal species, it is possible the seeds are considered unpalatable, or rodent species are unable/unwilling to chew the pod surrounding the seed reward. Predation of seeds was not significant for this species.

### *Seedlings*

Eleven *A. nilotica* seedlings (germinated using guidelines from Tietema *et al*. 1992), were offered to the most abundant captured small mammal species of the Kempiana property, *A. namaquensis*, *A. chrysophilus* and *T. leucogaster*. Seedlings were placed in the cafeteria alongside various seed species, left for a 24 hour period and examined for damage after the captive animal was released. Where eaten, seedlings were entirely consumed by captive mammals, i.e.: none were partially chewed as commonly occurred with seeds.

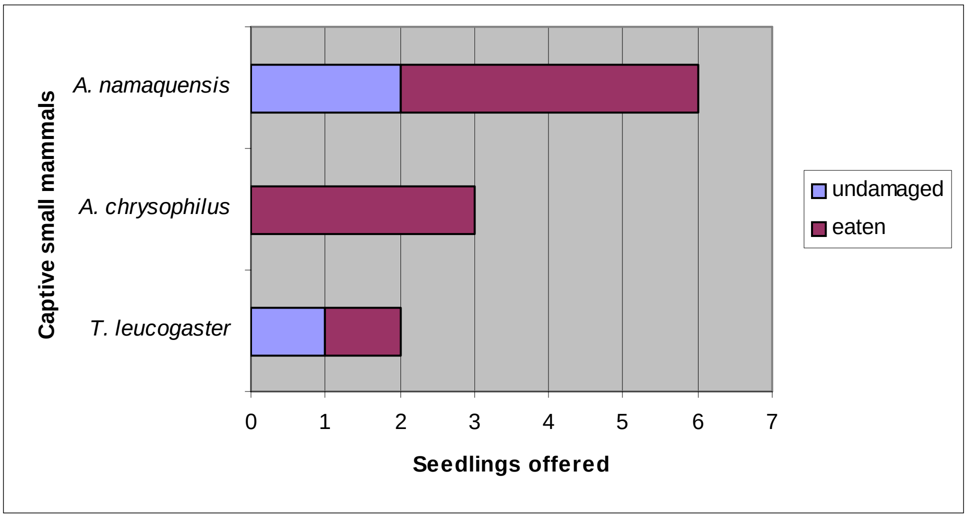

**Figure 5-9:** Predation of *A. nilotica* seedlings by captive small mammals over a 24-hour period.

In this experiment, all small mammals consumed *A. nilotica* seedlings. Of the 11 seedlings offered, eight were consumed by small mammal species within the first 24 hours of captivity. *A. chrysophilus* consumed 100% of offered seedlings, *A. namaquensis* consumed 66% of seedlings offered. *T. leucogaster* consumed 50% of seedlings offered.

### Total predation – seeds

Overall seed predation of captive small mammals varied with individual species, is summarised in Table 5-6 for all species

**Table 5-6:** Total seeds offered to captive small mammals

| | Unchewed | <50% chewed | >50% chewed | Total seeds offered |
|---|---|---|---|---|
| *A. namaquensis* | 81 | 28 | 35 | **144** |
| *A. chrysophilus* | 85 | 27 | 16 | **128** |
| *T. leucogaster* | 35 | 8 | 53 | **96** |
| | **201** | **63** | **104** | **368** |

Overall, all **three captive** small mammal species were **recognised as** partial or total consumers of seeds for commonly encroaching tree and shrub species of the area. A summary of seed chewing and/or predation by captive small mammal species is shown in Table 5-7:

**Table 5-7:** Average seed predation for all increaser species by captive small mammals

| Small mammal species | Percentage of seeds chewed or predated |
|---|---|
| *A. namaquensis* | 44% |
| *A. chrysophilus* | 34% |
| *T. leucogaster* | 64% |

## Total predation - seedlings

Total seedling predation was variable between captive small mammal species, although *A. chrysophilus* consumed all offered seedlings. These data are shown in Table 5-8 outlining total seedling preference

**Table 5-8:** Total seedlings offered to captive small mammals

| Small mammal species | Uneaten | Predated | Total seedlings offered |
|---|---|---|---|
| *A. namaquensis* | 6 | 4 | **10** |
| *A. chrysophilus* | 0 | 16 | **16** |
| *T. leucogaster* | 7 | 13 | **20** |
|  | **13** | **33** | **46** |

Overall, studied small mammal species were prominent consumers of seedlings for commonly encroaching tree and shrub species of the area, with overall percentage of consumption for each species shown in Table 5.9.

According to the results of the captive study all of the small mammal species tested are reliable predators of seedlings of local encroaching tree and shrub species in the Kempiana property. *A. chrysophilus* ate 100% of seedlings offered, acting as a ‘super’ seedling predator in this experiment. A summary of seedling predation by captive small mammal species is shown in Table 5-9:

**Table 5-9:** Overall predatory effects of captive small mammals on offered seedlings

| Small mammal species | Percentage of seedlings predated |
|---|---|
| *A. namaquensis* | 65% |

| | |
|---|---|
| *A. chrysophilus* | 100% |
| *T. leucogaster* | 40% |

All experimental small mammals displayed seedling predatory tendencies, although *A. chrysophilus* demonstrated the greatest seedling predation ability by eating all seedlings of species offered in the captive experiment.

### *Summary – seed and seedling predation*

Seed and seed predation tendencies for the subject small mammals are shown by species in Table 5.12.

**Table 5-10:** Overall results of captive small mammal and increaser species seed and seedling predation data

| | | ***Aethomys namaquensis*** | ***Aethomys chrysophilus*** | ***Tatera leucogaster*** | ***Average*** | ***Standard Deviation*** |
|---|---|---|---|---|---|---|
| ***Dichrostachys cinerea*** | Seeds offered | 9 | 9 | 6 | 7.67 | |
| | Seeds chewed | 8 | 9 | 6 | | 1.53 |
| | **Total chewed %** | **89%** | **100%** | **100%** | **96%** | |
| | Seedlings offered | 3 | 6 | 3 | 3.67 | |
| | Seedlings chewed | 3 | 6 | 2 | | 2.1 |
| | **Total chewed %** | **100%** | **100%** | **66%** | **89%** | |
| ***Terminalia sericea*** | Seeds offered | 45 | 40 | 30 | 19.33 | |
| | Seeds chewed | 24 | 10 | 24 | | 8.08 |
| | **Total chewed %** | **53%** | **25%** | **80%** | **53%** | |
| | Seedlings offered | 4 | 0 | 2 | 0 | |
| | Seedlings chewed | 0 | 0 | 0 | | 0 |
| | **Total chewed %** | **0%** | **n/a** | **0%** | **0%** | |
| ***Acacia exuvialis*** | Seeds offered | 45 | 40 | 30 | 26.77 | |
| | Seeds chewed | 30 | 20 | 30 | | 5.67 |
| | **Total chewed %** | **66%** | **50%** | **100%** | **72%** | |
| | Seedlings offered | 7 | 7 | 3 | 4.67 | |
| | Seedlings chewed | 6 | 7 | 1 | | 3.21 |
| | **Total chewed %** | **86%** | **100%** | **33%** | **73%** | |
| ***Acacia nilotica*** | Seeds offered | 45 | 40 | 30 | 1.67 | |
| | Seeds chewed | 0 | 5 | 0 | | 2.88 |
| | **Total chewed %** | **0%** | **12.5%** | **0%** | **4.2%** | |
| | Seedlings offered | 6 | 3 | 2 | 2.67 | |
| | Seedlings chewed | 4 | 3 | 1 | | 1.52 |
| | **Total chewed %** | **66%** | **100%** | **50%** | **72%** | |
| | Percentage predator | Seeds: 52%<br>(N=144)<br>Seedlings: 63% | Seeds: 46.8%<br>(N=128)<br>Seedlings: | Seeds:70%<br>(N=96)<br>Seedlings: | | |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | (N=20) | 100%<br>(N=16) | 37.3%<br>(N=10) |  |  |

The overall level of predation of seed and seedling species is summarised in Figure 5-10 to graphically show the impact of the select caged rodents on the subject seed and seedlings.

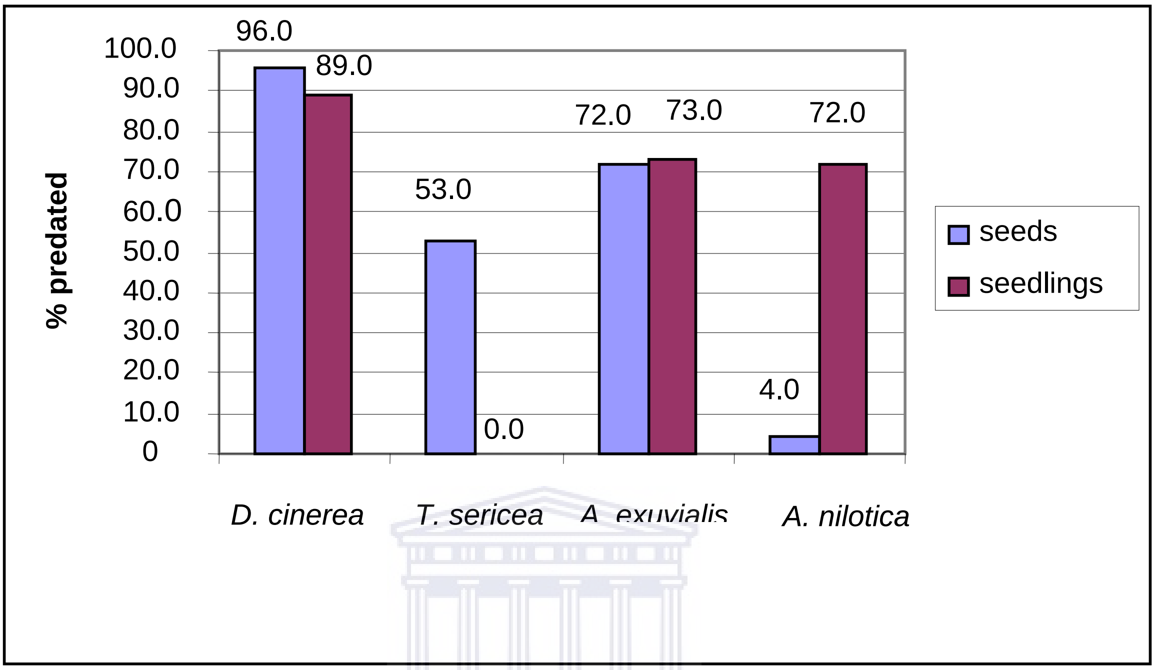

**Figure 5-10:** Overall predation percentages by captive rodents in the increaser tree species cafeteria experiment.

As we can see from the above graph, despite some considerable variability both *D. cinerea* and *A. exuvialis,* common tree seeds and seedlings in the area are commonly predated by captive small mammals.

- From this experiment, it is apparent that all three commonly occurring small mammal species of the Kempiana property are both common increaser seed and seedling consumers.

### *Experimental error*

A number of factors may have influenced results of this experiment:

- Lack of seedlings, due to unsuccessful plant propagation meant that more comprehensive seedling predation studies could not take place

- In the literature, little experimental feeding of wild captive mammals has taken place. Despite attempts to create an environment conducive to rodent requirements, the nature of captive experiments may make this hard to achieve. Possible social effects of captivity include additional stress on individuals that may create abnormal behavioural activity, such as lack of desire to eat offered seeds and seedlings.

- All rodents have an instinctive chewing action. It is possible that the seeds were chewed merely as they were available, convenient and favourable to chew, without necessarily being a food of choice. Extensive chewing was noted on the wooden cafeteria, wooden frame of the cage, and on the habitat materials within the cage (despite this the end result remains a chewed seed)

- Subject species diets and habitat requirements are not fully understood. Despite other sources of food within captivity (grass, bedding, leaves and leaf litter) it is likely that not all rodent food preferences were available. This may have forced caged individuals to consume the 'next best' choices which may give a false impression of food preferences

- Due to the reasonable volume of seeds offered, it is possible that the rodent species did not have sufficient time to consume all of the seeds offered in the 24 hour period, thus some were left unpredated.

Despite the potential for error I find it unlikely that this would have greatly impacted on the results of this experiment in any manner detrimental to my results.

### Statistical Analysis

The results of this study are an indication of the likely small mammal structures and activities in the Kempiana area. As a pilot study in this field, the aim of this experiment was to determine whether or not a link occurred between small mammals, their dietary patterns and woody plant establishment. The nature of the experiment, relatively self explanatory data and results lead me to believe that complex statistical analysis on these data would be impractical. In addition, the limited size of the study, alongside limitations of experimental design have meant that there is too little data (just over 100 individuals captured species three study areas over 4,300 trap nights) for comprehensive or meaningful statistical analysis (Dunne *pers comm*. 2006). A considerably greater sample size would allow such analysis to take place, although was not practical for this study. Eleven captures of two species over 1,000 trap nights in Welverdiend demonstrates the difficulty of attaining sufficient sample sizes for meaningful statistical analysis.

# 6. Discussion

## *Small mammal abundance and diversity*

Small mammal abundance and diversity varies over both space, time and habitat within the greater Kempiana area. Should such fluctuations occur on a broader scale this could lead to potential significant impacts on savanna ecosystem functioning. I shall investigate my findings and their implications both spatially and temporally.

### Spatial

### Land use and grass biomass

The three distinct land uses researched in this study comprised of various unique and relatively common land management practices of semi-arid savannas – conservation (Kempiana) and communal agriculture (Welverdiend), with the megaherbivore exclosure at SAWC serving as an experimental control area.

In floristic aspects study areas were all similar *Sclerocarya* granite ridgetops with varying abundance and diversity of understorey shrubs and grasses. Two of the study areas, Kempiana and Welverdiend, are subject to grazing and browsing by various herbivores and typify major types of land usage in the region. In Kempiana herbivores are resident in the form of a mix of indigenous grazers and browsers, and in Welverdiend's herbivores occur as grazing cattle with somewhat less numbers of browsers (goats). In my study Welverdiend reflected high levels of animal and fire disturbance that were demonstrated by a reduced herbaceous layer. Welverdiend's low levels of herbaceous material led to a higher proportion of bare ground and exposed soil.

Measurements by disc pasture meter confirmed that the impact of such stocking rates and management practice creates significantly different grass biomass levels at each study area. Considerable differences were recorded between overall grass biomass in Welverdiend with high numbers of domestic grazers (465 tonnes/ha), and Kempiana with indigenous megaherbivores (3,360 tonnes/ha). The SAWC study area has very high grass biomass levels (5,752 tonnes/ha) typical of a landscape when all megaherbivore disturbances are excluded.

**A direct link can be seen between the intensity of megaherbivore use across different management areas (as reflected by grazing impact) and levels of grass biomass on those study areas.**

### Grass biomass, grazing and rodent populations

It is apparent from my results that small mammal abundance has a direct linkage with habitat quality, in this case grass biomass. As the grassy component is reduced through grazing and trampling, the role that grass biomass and cover plays for small mammals such as rodents becomes reduced. In the SAWC study area, where no megaherbivore grazing was taking place and grass biomass was extremely high, small mammal abundance was significantly higher (+/- 294 individuals per hectare) than the other studied land uses (Kempiana and Welverdiend respectively +/- 60 individuals and +/- 30 individuals per hectare). High SAWC small mammal population levels were later confirmed by Atyeo (2004) in a similar abundance study of the same area.

As shown by Avenant (2000) high grass biomass creates a considerable cover for small mammals from predator species, especially birds of prey (such as *Tyto alba*). My research reinforces that the SAWC exclosure and its high grass biomass creates ideal habitats for small mammals, living in relative safety from such airborne predators. Conversely where grazing effects were highly concentrated by limited species (primarily domestic cattle) in Welverdiend, small mammal abundance is extremely low. In Welverdiend important habitat structural formations in the grassy layer have been destroyed through excessive trampling and grazing by large herbivores in the form of short grass grazer cattle and goats (Twine *et al*. 2002). Within Kempiana a combination of mixed feeding and diverse megaherbivores roaming over a far greater range than the cattle of Welverdiend also diminished grass biomass levels (to a slightly less degree), which has some limiting effect on small mammal abundance. In Kempiana, however, the size, scale and randomness of megaherbivore movements (when compared to regularly herded cattle in Welverdiend) has meant less habitat impacts for small mammal abundance and greater levels of intact grass cover serving as suitable habitat. As such the area supports an intermediate number of small mammals, although less than the SAWC but more than Welverdiend.

**Small mammal abundance shows a direct positive correlation to grass biomass understorey, which is in turn affected by the foraging activity of the megaherbivores active in the area.**

**Grass biomass, grazing and rodent diversity**

There appears to be a direct link between grass biomass, megaherbivore grazing activity and small mammal diversity on all study areas. For those small mammal species captured in this experiment, species diversity was highest (11 individuals) in areas of no megaherbivore or grazing activity and high grass biomass (5,752 tonnes/ha) in the SAWC exclosure. Species diversity was considered moderate (8 species) where a full range of indigenous herbivores roam on a regular basis with a moderate grass biomass (3,360 tonnes/ha) in Kempiana. Small mammal species diversity was lowest (3 species) in Welverdiend where domesticated *Bos taurus* are dominant grazers and grass biomass is very low (465 tonnes/ha).

The diversity of small mammals appears directly linked to grass biomass levels, which in turn are affected by grazing pressure. At the SAWC grazing impacts are restricted, and highly disturbance-sensitive rodents such as *A. chrysophilus* are abundant. As grazing impacts increase, the diversity of small mammals and overall abundance declines.

Across all locations I captured what is believed to be a representative sample of the small mammal species of the area, as confirmed by similar captures noted by Gregory (2000) in the *Tyto alba* prey study. In addition subsequent research by Atyeo (2004) found no new small mammal species in Kempiana or at the SAWC.

**Small mammal diversity shows a direct positive correlation to grass biomass, which is in turn is affected by the activity of the extant large herbivores active in the area.**

**Overall spatial effects**

As we have seen different land uses such as agriculture and conservation create different grass biomass conditions. These differing biomass conditions subsequently impact on small mammal populations and diversity of small mammal species. In short, where grass biomass is high small mammal abundance and diversity is high. Conversely where grass biomass is low, small mammal abundance and diversity is lower. Where megaherbivore activity is less concentrated it is possible that the balance between grazing activity and maintenance of some level of small mammal numbers could be reached, which in this experiment is best demonstrated in Kempiana. Kempiana provides a snapshot picture of an intermediate area, where a balance between wild herbivores and small mammals is retained and understorey habitats retain some structural integrity and grass biomass. In the SAWC exclosure small mammal populations are abundant and diverse, at levels considerably higher than the other study areas. Conversely in Welverdiend both diversity and abundance of small mammals is low, presumably restricted by lack of landscapes of sufficient structural diversity suitable for small mammals. As such the small mammals in these areas, restricted by paucity of suitable habitat, are limited in their movements and forage over smaller ranges and in vegetation islands, avoiding open spaces where I argue there is less food and cover protecting them from predators.

Savannas are inherently disturbance driven landscapes (Booysen & Tainton 1984), whereby repeatedly occurring small impacts (e.g.: grazing or browsing) and occasional large impacts (such as drought or fire) are responsible for maintaining a dynamic balance between vegetation structures (Booysen & Tainton 1984, Bothma 2004). In the case of this study, where the effects of grazing have been multiplied by the addition of many extra cattle, a formerly small impact has become a large one. Where grazers have eaten the grassy layer, the grass biomass is reduced to a point where organisms such as small mammals reliant on those grasses as structural habitats are either predated or move on.

**The SAWC, Kempiana and Welverdiend study areas symbolise significant spatial habitat differences which reflect in grass biomass data and in small mammal diversity and abundance data.**

## Temporal

### Season, disturbance and resource availability

It is well recorded in the literature that rodents are prone to highly variable population cycles (de Graaf 1981, Chesson *et al*. 2004). The small mammals in this study are no exception. Between 2000 and 2004 small mammal abundance increased at both the SAWC and Kempiana study areas.

Whilst this study is effectively a ‘snapshot in time’ it must be acknowledged that small mammal populations also fluctuate. Where seasons create resource pulses and enhanced plant growth, additional vegetation and grass biomass provides cover for small mammals. During such times small mammal populations grow significantly, as Atyeo noted in her 2004 study. Such conditions can favour certain individual species over and above others. For example, the most abundant rodent captured in the 2000 study, *A. namaquensis*, was entirely absent from research in Kempiana in 2004 (although still present at the SAWC). Despite their absence overall rodent abundance was significantly higher in 2004 than in 2000, with *T. leucogaster* and *A. chrysophilus* in greatly increased populations.

Each of the rodents studied have their own habitat and dietary preferences, creating subsequent micro-habitat impacts that play out over time. Interventions such as increased megaherbivore grazing impact in summer, or a fire event, act as a temporary agent in limiting small mammal activity. In Welverdiend where grazing disturbance occurs continuously and fires can be yearly or more frequent, small mammal diversity and abundance becomes continuously limited.

**Small mammal density and abundance of Kempiana (under ‘natural’ conditions) fluctuates according to season, disturbance and resource availability. Where disturbances such as fire and megaherbivore impacts are frequent, small mammal abundance and density declines.**

### *Summary – small mammal trapping across different management regimes*

The link between grass biomass and small mammal diversity and abundance is best summarised in Figure 6.1 where a positive correlation between all three indicators can be clearly seen.

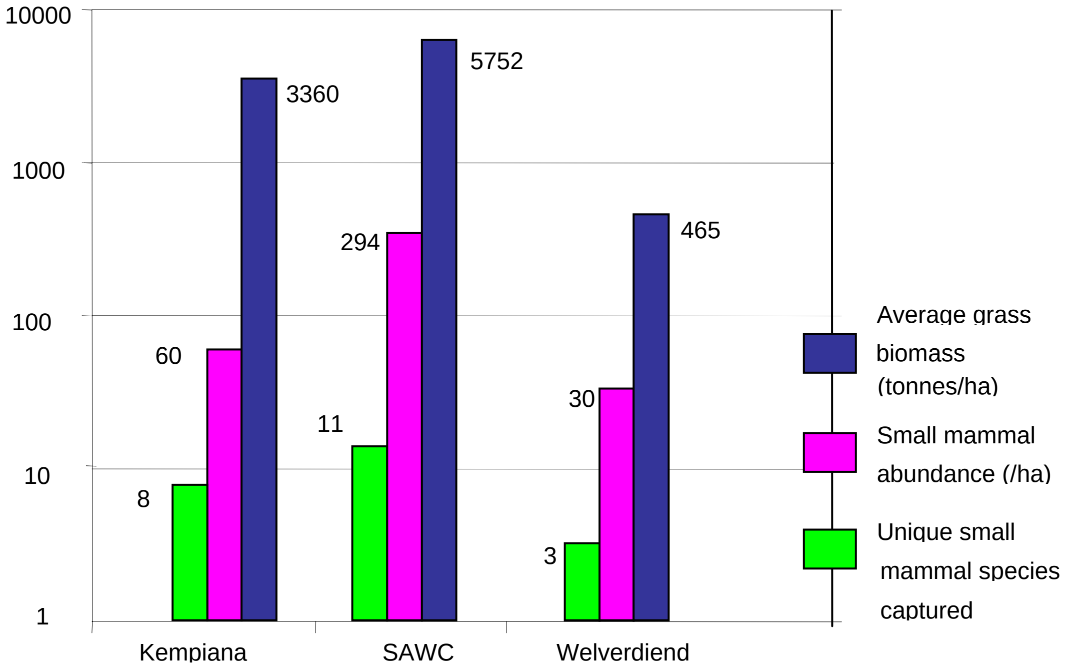

**Figure 6-1:** A logarithmic axis demonstrating the relationship between grass biomass, small mammal abundance and diversity for the three study areas, Kempiana, SAWC and Welverdiend.

## *Seed/seedling predation*

### Rodent and seeds/seedlings

Rodents are well known for their persistent chewing action. Evergrowing teeth, endothermy and fast metabolic processes stimulate a high energy demand and continuous foraging much of which is focused on energy rich food sources (Knight & Knight-Eloff 1986, Kerley 1992). Dietary records are most often based on visual observation, faecal analysis, and analysis of stomach contents of sacrificed animals (Monadjem 1997, Fourie *unpublished* 2003). Such studies assume the population studied is representative of the species as a whole, ignoring possible dietary and behavioural flexibility.

This experiment, a process of collecting common tree and shrub seeds of the area (most of which have been anecdotally described as ‘increasers’), germinating examples of each, then offering captive rodents a cafeteria style array of those seeds and seedlings, allows a small insight into seed and seedling predation behaviour in the local area. I have found that the Muridae inhabitants of this landscape are generally active consumers of tree and shrub seeds.

In addition to captive experiments, the results of carbon isotope analysis of the subject animals' hair by Fourie confirmed that small mammals of the area were indeed significant tree seed and seedling consumers, with *T. leucogaster* having an even contribution from $C_3$ and $C_4$ plants in its diet, *A. chrysophilus* exhibiting a 95% $C_3$ diet and *A. namaquensis* eating 35% $C_3$ plant material.

**This experiment revealed a relatively consistent and active effort on behalf of the captive rodents to target and eat both seeds and seedlings of the subject tree species.**

### Increaser seed survival

Research on semi-arid tree seeding activity and seed load is generally limited, however tree species resident in the study area generally produce a flush of potentially many thousands of seeds in an average year with species such as *A. nilotica* producing up to 30,000 in a favourable season (Tybirk 1989). In all likelihood, for all the seeds produced in the lifespan of an average tree only a tiny proportion will germinate, with even less surviving the process from germination through to adulthood. If we look at the example of *Dichrostachys*, my observations show that up to 50% of the seeds are parasitized by arthropods (e.g.: the Bruchid beetle) whilst still on the parent plant. This is corroborated by Miller who in review states that up to 36.5% of *A. nilotica* (Miller 1994), and 99% of related *Acacia* seeds (Miller 1995), are destroyed in this way. All remaining viable seeds are shed in pods directly under the parent tree where they many end up in shaded or nutrient deficient conditions unfavourable for germination and growth. Furthermore many such seeds require scarification, which will not happen if fire events are not forthcoming. Depending on the lifespan of the seeds, some will have to risk a waiting period (with various pathogens and parasites) for such fires, or appropriate germination conditions to present themselves. Seeds consumed by megaherbivores may be destroyed by chewing or the process of digestion, or surviving this be deposited in unsuitable areas for germination and growth.

Compounding the effects of seed mortality are the effects of small mammal predators. As seen by Fourie's (2003) results for two small mammal species; one (*A. chrysophilus*) is predominately $C_3$ plant consuming and the other (*T. leucogaster*) has a diet equally divided between $C_3$ and $C_4$ plants. In my captive dietary experiment, 53% of *T. sericea*, 72% of *A. exuvialis* and 96% of *D. cinerea* seeds were predated by the subject small mammals. In terms of seed eating behaviour in this experiment *T. leucogaster* (70%), *A. namaquensis* (52%) and *A. chrysophilus* (46.8%) all predated significant quantities of seed from those offered. These results concur with similar results in the literature and with the results from the study by Fourie (2003) on $C_3$/$C_4$ dietary composition for the small mammals. To extrapolate from the literature to my research I can infer that the local small mammals of the Kempiana area are indeed predators of indigenous tree propagules, and seeds certainly make up a significant component of their diets. Tree seeds, which are potentially the highest and most widespread nutritive source of $C_3$ material found within the foraging area are a significant source of food. Of all seeds tested only *A. nilotica* with a predation rate of 4% could be considered relatively unpalatable for small mammal species tested. In this case it is possible that subject mammals were unfamiliar with *A. nilotica* seeds because they were fed out of season or were not from that particular rodents home range.

**My data have shown studied small mammals resident of the central Lowveld are indeed significant consumers of woody plant seeds.**

### Increaser seedling survival

For seeds that may survive parasitism, predation and other effects to reach germination, the risks appear even more considerable. Upon germination seedlings have no ability to move to a more appropriate site, so initial suitability is crucial to survival. Those germinating under high cover, in infertile or unsuitable soils, on animal pathways (i.e. many germinating from dung), etc. have limited opportunity for survival. Even those germinating in appropriate sites will have to endure antagonistic grass-tree relationships as grasses ‘poach’ resources from germinating seedlings (Werger 1974). Any fires will kill seedlings not of a height to withstand burning events, increasingly hot fires will kill off newly developed root systems and any chance of subsequent germination. Furthermore, droughts, frosts and disease are all significant factors reducing seedling survival.

In my experiment predation by small mammals was a highly probable fate for germinating tree seedlings. Of seeds that germinated in this experiment, 73% of *A. exuvialis*, 89% of *D. cinerea*, and 72% of *A. nilotica* seedlings were predated by the captive small mammals.  In this case all three test mammal species were common consumers of seedlings - *T. leucogaster* (37%), *A. namaquensis* (63%), and *A. chrysophilus* (100%).  In this experiment *T. sericea* seedlings remained relatively untested due to failure to propagate.

It is apparent that seedlings of the Mimosaceae are in fact highly palatable for subject small mammals of the Kempiana region.  In this case *A. chrysophilus* could be considered a ‘super’ seedling predator.

**My study has revealed that all subject rodent species of the central Lowveld research area are significant predators of seedling material of local increaser tree species.**

### Predation of seeds and seedlings

Tree and shrub species are subject to intense damage or mortality from many factors at all stages from seed set to maturity.  My research shows that at the earliest and potentially most vulnerable stage - seeds and seedlings, small mammals such as rodents through consumption patterns, play a significant role impacting on their survival.  Whilst this seed/seedling predation study is limited in scope it does show a direct and common impact of predation on the local tree and shrub species studied by the most common small mammals of the area.

Moving beyond small mammals, the role of birds (also warm blooded with high energy demands) as seed and seedling predators should not be ignored.  Ground dwelling granivorous Francolin (*Francolinus* spp.), Helmeted Guinea Fowl (*Numida meleagris*), Quail and Buttonquail (*Coturnix* & *Turnix* spp.) are common in the study area, as are numerous other seed eaters such as canaries, buntings, quelea, etc.  Local Lagomorpha such as Hares (*Lepis saxatila*) are known seedling eaters and commonly recognised as agricultural pests because of this habit. Research into the seed and seedling predatory effects of these animals is beyond the scope of this study, but could well compliment my findings of small mammals playing a significant role as seed and seedling predators.

## *Implications of the findings*

Management paradigms and land use practices between the three study areas have created very different local habitats and environmental conditions. Should the current land management scenario in the Lowveld study areas continue, a number of trajectories of landscape development for each land use are possible. My results show a demonstrable link between grass biomass, small mammal abundance and diversity, and potential seed/seedling predatory activities.

Further review of the literature such as Noble (1997) and Weltzin *et al*. (1997) where interference with the population of small mammal seed predators led to broad scale thickening of the woody vegetation in both semi-arid Australia and Texas, USA allows me to predict the following scenarios for the study areas:

### 1. Kempiana

Presuming Kempiana continues to be managed as a ‘natural’ area the following trends are possible: It has been anecdotally noted that there has been an increase in megaherbivores in the Kempiana area (Pieterson *pers com*. 2000, Jones *pers com*. 2004). Recent media reports and South African National Parks are also claiming a large increase in certain megaherbivore species abundance – such as elephants. Should this trend continue Kempiana will undergo increased trampling and consumption of the grass understorey which in turn will potentially limit small mammal abundance and diversity (including the 97% $C_3$ reliant and ‘super’ seedling predator *A. chrysophilus* which is limited to areas of low understorey disturbance).

Additionally, primary factors (as suggested by Teague & Smit 1992) such as increasing levels of $CO_2$ in the atmosphere, plus an average increase in global temperatures, will favour growth of $C_3$ tree and shrub species over and above C4 grasses (Rogers *et al*. 1994). An increased density of woody plants will in turn encourage hotter fires which will in turn stimulate germination and growth of more woody plants in a positive feedback cycle. This would result in a slow decrease in grass biomass and small mammal abundance and diversity over time, inversely related to an increase in the woody component of the landscape.

It is possible that as the woody component thickens, remnant populations of small mammals will occupy these areas of higher vegetative cover (possibly utilising tree thickets as cover instead of grass cover).

Conversely with the advent of increased megaherbivore numbers, higher populations of elephants may create the opposite effect. In their role as a keystone herbivores elephants may become more important as they, in higher numbers, will possibly reduce overall tree and shrub cover through the process of shaping landscapes (as I have seen in Chobe National Park, Botswana where elephant populations are very high and the woody component of the landscape is heavily reduced through their direct impact) – also reported by Mosugelo *et al.* (2002). In Kempiana the role of browsing herbivores, especially the elephant may become more significant in terms of overall woody vegetation management in an increaser dominated environment.

In the longer term, should small mammal populations recover within woody thickets their predatory role as seed eaters may become significant as they consume a greater proportion of the increaser seeds shed each year. Without human management intervention Child (1995) believes the recovery process to a poorly-defined ‘normal’ savanna balance will take up to 1,000 years.

The management of secondary factors such as anthropogenic fires and grazing will become more important for maintaining a “balance” of vegetation within the landscape. In short, the dynamic savanna landscape would increase in woody plant density but remain dynamic, although at a new ratio of trees, shrubs and grasses, more in favour of the trees and shrubs. To keep the grassy component balance in the short term (i.e.: the next fifty years of known climate change) will require significant anthropogenic actions.

### *2. SAWC*

The high grass biomass will remain undisrupted by megaherbivores for the foreseeable future. However, yearly risk management burning drastically reduces biomass for a limited period, although fire events never burn the entire area. Unburnt areas serve as refuges for small mammals until grass growth occurs and understorey cover is restored. Such increased management fires may encourage the germination of woody shrub and tree seeds. However to survive, these seeds would have to germinate immediately after a fire event in an area of low grass biomass, demonstrate high growth rates, escape the resident predatory rodent population as they return to burnt areas, and avoid subsequent yearly fires to become established.

In non-fire parts of the year small mammal populations survive under high cover conditions supplied by the high grass biomass on the SAWC Campus (similarly described by Rowe-Rowe 1995). Small mammals have high densities in the area and are able to predate the significant majority of increaser seeds and seedlings, limiting plant recruitment to periods where small mammal numbers are naturally low (i.e.: rodents in a low population cycle).

As such the SAWC will not see significant numbers of germinating woody plants, except in years where fires are less severe/do not occur and small mammal abundance is at a low fluctuation. In that case a cohort of numerous tree species may become established for that year on the study area.

### *3. Welverdiend*

It is likely that the current intensive grazing management activity will continue or intensify and grass biomass will remain at low levels. Thickets of woody plants such as *Dichrostachys* and *Acacia* will expand at the cost of former grassy patches. Cattle will therefore be required to roam further afield for grazing, as foraging closer to the village become more nutritionally and economically marginal. Cattle will eventually become replaced with smaller economic units, specifically goats, who will then consume what remains of the understorey grass layer as well as the browse, which will be in increased supply from abundant woody vegetation clusters.

“Islands” of impenetrable thickets of increaser species will thus predominate, harbouring no grass species and allowing little light penetration. Small mammal species will become restricted to these islands as moving into the formerly grassy areas carries a high predation risk.

Subsequent fires will be hotter due to the increased woody biomass, killing what little grass remains and stimulating more tree growth, particularly highly flammable mutants (a scenario depicted by Bond & Keeley 2005). Cattle and goats will graze any surviving grass shoots until more trees dominate the formerly grassy patches. Large impenetrable woody thickets will come to dominate the landscape. The lack of megaherbivores, such as elephants means that anthropogenic management will be required to clear wooded sections for agriculture. Small mammal numbers and diversity will initially decline. However, those able to live under the protective cover of woody thickets will eventually inhabit these areas in the places where grassy habitat once occurred; and it is likely that their seed and seedling consuming habit may be continued, with declining affect away from the thicket edges (Ostfeld *et al.* 1997, Manson *et al.* 2001). As thickets grow larger these ‘islands’ will become bigger (logically seeds shed into bare patches will less likely be predated than those shed within, thus with improved survival chances will expand the ‘island’). Management intervention will be required at significant economic cost to encourage grass to return to these systems.

### General

Studies in semi-arid Texas and Australia have shown how the reduction in small mammal biomass of these habitats has led to a rise in the predominance of increaser species in those habitats. The high energy requirements of small mammals, alongside their continuous, if fluctuating abundance in the landscape is one of the many limiting effects on highly nutritive shrub and tree seeds and seedlings. Once those small mammal species (prairie dogs and marsupial bettongs) were removed, gradual changes in woody elements of these landscapes took place, to the point of substantial habitat modification and exclusion of commercially important animals and agriculture. In both cases, once the constant seed predating influence of these animals was removed, a window of opportunity for other species – in these cases woody shrubs – was opened. Amongst the many other causes of seed and seedling mortality in these areas, small mammals formerly played a significant role. My study draws many similarities in small mammal ecosystem function to those of Texas and Australia.

In terms of predatory effect, any scientific quantifying of the extent of seed and seedling predation would be problematic to quantify and thus lies beyond the scope of this study. However, the slow accruing nature of bush encroachment only requires the survival of one extra offspring per tree per year (remembering that potentially 30,000 seeds can be shed per tree in one season), incrementally over a decade to create impenetrable thickets of shrubs. Removal of small mammal species through habitat alteration may well, alongside fire, overgrazing, climate change and other factors be complicit in the increasing densification of woody shrub and tree species in Kempiana, its surrounds and other similar southern African savannas.

# 7. Sources of information

## *References*

Acocks JPH (1953) Veld Types of South Africa. Memoirs of the Botanical Survey of South Africa 28

Anon (May 2000) Nguni cattle set for a comeback? Farmers Weekly Magazine

Archer SR (1995) Have South Texas savannas been converted to woodlands in recent history? American Naturalist 134: 545-561

Atyeo M (2002) Tracking stations as a method for assessing small mammal activity and bait uptake. Unpublished report

Avenant NL (2000) Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. South African Journal of Wildlife Research 30 (1): 26-32

Bazzaz FA, McConnaughay KDM (1992) Plant-plant interactions in elevated $CO_2$ environments. Australian Journal of Botany 40: 547-563

Bell WE, van Staden J (1993) Seed structure and germination of *Dichrostachys cinerea*. South African Journal of Botany 59 (1): 9 – 13

Bond WJ, Ferguson M, Forsyth G (1980) Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. Southern African Journal of Zoology 15: 34-43

Bond WJ, Breytenbach GJ (1985) Ants, rodents and seed predation in Proteaceae. South African Journal of Zoology 20: 150 - 154

Bond WJ, Keeley JE (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20 (7) 387-394

Booysen P de V, Tainton NM (1984) The ecological effects of fire in South African ecosystems. Ecological studies 48: Springer-Verlag, Heidelberg

Bothma J du P (ed.) (2004) Game Ranch Management. Van Schaik Publishers, Pretoria

Bowers MA, Dooley JL (1993) Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94 (2): 247-254

Bransby DI, Tainton NM (1977) The disc pasture meter: possible applications in grazing management. In: Procedures of the Grassland Society of South Africa 12: 115 - 118

Bredenkamp GJ (1986) Ecological profiles of potential bush encroacher species in the Manyeleti Game Reserve. South African Journal of Botany 52 (1): 53-58

Chesson P, Gebauer RLE, Schwinning S, Huntly R, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) Pulse events and arid ecosystems - resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments**.** Oecologia 141(2): 236 – 253. Springer Berlin / Heidelberg

Child G (1995) Wildlife and people: the Zimbabwean success. Wisdom Foundation, Harare

Coates Palgrave (1977) Trees of southern Africa. Struik, Cape Town

Curtin CG, Kelt DA, Frey TC, Brown JH (2000) On the role of small mammals in mediating climatically driven vegetation change. Ecology Letters (3) 4: pg 309

Damm G (2002) The conservation game. Safari Club International

Dean WRJ, Milton SR, Jeltsch F (1999) Large trees, fertile islands, and birds in arid savanna. Journal of Arid Environments 41: 61-78

Dean WRJ, Milton SJ (1991) Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. Journal of Arid Environments 20: 231-237

De Graaff G (1981) Order Rodentia, In: The Complete Book of Southern African Mammals, eds G. Mills & L. Hess, Struik, Cape Town

Flannery T (1994) The Future Eaters. Reed Books Australia

Fourie NH (2003) Stable carbon and nitrogen isotope analysis of hair from small mammals from the arid lowveld bushveld, Phalaborwa District, South Africa. Honours project, unpublished, University of Cape Town

Gertenbach WPD (1983) Landscapes of the Kruger National Park. Koedoe 26: 9-121

Gill AM, Groves RH & Noble IR (eds) (1981) Fire and the Australian biota. Australian Academy of Science, Canberra

Gregory I (2000) The diet of the Barn Owl (Tyto alba) at the Southern African Wildlife College (unpublished)

Guy PR (1981) Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. Journal of Applied Ecology 18: 507-519

Hanney P (1962) Observations on the food of the Barn Owl (*Tyto alba*) in Southern Nyasaland. Annual Magazine of Natural History 13 (6): 305-313

Hickman CP, Roberts, LS, Larson A (1993) Integrated principles of Zoology, Ninth Edition. Mosby Year Book, St Louis USA

Higgens SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. Journal of Ecology 88 (2): 213-229

Honeyguide CC (2005) Kruger National Park (Map). Nelspruit

Hudak AT (1999) Rangeland Mismanagement in South Africa: Failure to Apply Ecological Knowledge Human Ecology 27 (1): 55-78 Springer Netherlands

Hugo ML (2004) Environmental Management. Ecoplan, Pretoria

Hulme PE (1994) Seedling herbivory in grassland, relative impact of vertebrate and invertebrate herbivores. Journal of Ecology 82 (4): 873-880

Jacobs OS, Biggs R (2001) The effect of different fire treatments on the population structure and density of the Marula, *Sclerocarya birrea* (A. Rich.) subsp. *caffra* (Sond.) *kokwaro* (Kokwaro & Gillet 1980) in the Kruger National Park. In: African Journal of Range and Forage Science (18): 13-23

Jeltsch F, Milton SJ, Dean WRJ, Rooyen N (1996) Tree Spacing and Coexistence in Semiarid Savannas**.** Journal of Ecology 84 (4): 583-595

Jeltsch F, Milton SJ, Dean WRJ, Rooyen N, Moloney KA (1998) Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. Journal of Ecology 86 (5): 780-793

Jooste JF, Palmer NG (1981) The distribution and habitat preference of some small mammals in the Rolfontein Nature Reserve. South African Journal of Wildlife Research 12 (1)

Kerley GIH (1991) Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. Journal of Arid Environments 20: 63 - 69

Kerley GIH (1992) Small mammal seed consumption in the Karoo, South Africa: further evidence for divergence in desert biotic processes. Oecologia 89: 471 - 475

Knight MH & Knight-Eloff AK (1986) Rodents – the ‘little people’ in a world of giants. Custos 16 (8)

Leung LKP, Clark NM (in press), 'Bait avoidance and habitat use by the roof rat, *Rattus rattus,* in a piggery', International Biodeterioration and Biodegradation

Linzey AV, Kesner MH (1997) Small Mammals of a woodland savanna ecosystem in Zimbabwe. 1. Density and habitat occupancy patterns, in Journal of Zoology, London 243: 137 - 152

Long ME (1998) The vanishing prairie dog – shoot them or save them? In National Geographic 193 (4)

Low B, Rebelo A (1996) Biomes of South Africa Map. Ecology and Conservation Department, National Botanical Institute; Cape Town

Manson RH, Ostfeld RS, Canham CD (2001) Long term effects of rodent herbivores on tree invasion dynamics along forest field edges. Ecology 82 (12): 3320-3329

Maron, JL, Simms EL (1997) Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*) Oecologia 111 (1): 76 - 83

McNaughton SJ (1992) The propagation of disturbance in savannas through food webs. Journal of Vegetation Science (3): 301 – 314

Miller MF (1994) Seed predation by nocturnal rodents in an African savanna ecosystem. South African Journal of Zoology 29 (4): 262 - 265

Miller MF (1995) *Acacia* seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. African Journal of Ecology (33): 194 - 210

Miller MF (1996) Dispersal of *Acacia* seeds by ungulates and ostriches in an African Savanna Journal of Tropical Ecology 12: 345 – 356. Cambridge University Press

Monadjem (1997) Stomach contents of 19 species of small mammals from Swaziland. South African Journal of Zoology 32 (1): 22 - 25

Monadjem A, Perrin MR (1998) The effect of supplementary food on the home range of the multimammate mouse *Mastomys natalensis*. South African Journal of Wildlife Research 28 (1)

Mosseau M, Saugier B (1992) The effects of increased $CO_2$ on gas exchange and growth of forest tree species. Journal of Experimental Botany 43 (253): 1121 - 1130

Mosugelo DK, Moe SR, Ringrose S, Nellemann C (2002) Vegetation changes during a 36 year period in northern Chobe National Park, Botswana. African Journal of Ecology 40: 232 – 240

Mucina L, Rutherford MC, Powrie L (eds) (2005) Vegetation map of South Africa, Lesotho and Swaziland 1:100,000 scale sheet maps; SANBI, Pretoria ISBN 1-919976-22-1

Mueller-Dombois D, Ellenberg H (1974) Aims and Methods of Vegetation Ecology, John Wiley & Sons, USA

Mushasha LL (1998) The ecology of four common rodent species at the Wits Rural Facility, Northern Province. Thesis Report (unpublished), University of the Witwatersrand

Newenham J (2000) Kruger to Canyons biosphere reserve application for funding to UNESCO. Unpublished

Noble J (1997) The delicate and noxious scrub – CSIRO studies on native tree and shrub proliferation in the semi-arid woodlands of eastern Australia. CSIRO Division of Wildlife and Ecology, Canberra

Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78 (5): 1531 - 1542

Palmer E, Pitman AA (1977) Trees of southern Africa. Balkeane Publishing, Cape Town

Parsons DAB, Shackleton CM, Scholes RJ (1997) Changes in herbaceous layer condition under contrasting land use systems in the semi-arid lowveld, South Africa. Journal of Arid Environments 37 (2): 319-329

Perrin MR, Swanepoel PS (1987) Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. South African Journal of Zoology 22: 218-227

Perrin, MR, Curtis BA (1980) Comparative morphology of the digestive system of 19 species of southern African myomorph rodents in relation to diet and evolution. South African Journal of Zoology 15: 22-33

Perrin MR, Johnson SJ (1999) The effect of supplemental food and cover availability on a population of the striped mouse. South African Journal of Wildlife Research 29 (1): 15 - 18

Pickett STA, White PS (1985) The ecology and natural disturbance of patch dynamics. Academic Press, San Diego

Pieterson E (1998) Kempiana Management Plan. Unpublished.

Raven PH, Evert RF, Eichhorn SE (1986) Biology of Plants. Fourth Edition, Worth Publishers, New York

Ridley HN (1930) The dispersal of plants throughout the world. L. Reeve & Co. Kent

Rogers HH, Runion GB, Krupa SV (1994) Plant responses to atmospheric CO2 enrichment with emphasis on roots and the rhizosphere. In: Environmental Pollution 83(1-2): 155-189

Rowe-Rowe DT, Lowry PB (1982) Influence of fire on small mammal populations in the Natal Drakensberg, in South African Journal of Wildlife Research 12 (4)

Rowe-Rowe DT (1995) Small mammal recolonization of a fire exclusion catchment after unscheduled burning. South African Journal of Wildlife Research 25 (4): 133 - 137

SAPPI (1999) Lowveld tree spotter. South Africa Pulp and Paper Industries, Johannesburg

Savory CAR (1978) A holistic approach to ranch management using short-duration grazing. In: DN Hyder (ed.) Proceedings of the First International Rangelands Congress. Society for Range Management, Denver. pp. 555-557.

Scholes RJ (1986) A guide to bush clearing in the Eastern Transvaal Lowveld, Second Edition, University of the Witwatersrand. Johannesburg

Shackleton CM (1993) Demography and dynamics of the dominant woody species in a communal and protected area of the eastern Transvaal Lowveld. South African Journal of Botany 59 (6): 569-574

Shackleton CM (1993) Are the communal rangelands in need of saving? Development Southern Africa 10: 65-78

Shackleton CM (2000) Comparison of plant diversity in protected and communal lands in the Bushbuckridge lowveld savanna, South Africa. Biological Conservation 94: 273-285

Sinclair I, Hockey P (1996) The larger illustrated guide to birds of southern Africa. Struick Publishers, Cape Town

Skinner JD, Smithers RHN (1990) The mammals of the Southern African subregion. Second Edition, University of Pretoria

Smit R, Bokdam J, den Ouden J, Olff H, Schot-Opschoor H, Schrijvers M (2001) Effects of introduction and exclusion of large herbivores on small rodent communities. Plant Ecology 155 (1): 119-127

Smit GN, Richter CGF, Aucamp AJ (1999) Bush encroachment: an approach to understanding and managing the problem, in Tainton N (ed) 1999 Veld Management in South Africa

Tainton N (ed) (1999) Veld Management in South Africa. University of Natal Press, Pietermaritzburg

Teague WR, Smit GN (1992) Relations between woody and herbaceous components and the effects of bush-clearing in southern Africa. Journal of the Grassland Society of Southern Africa

Thomson R (1992) The Wildlife Game. Nyala Wildlife Publications Trust, Durban

Tietema T, Merkesdal E, Schroten J (1992) Seed germination of indigenous trees in Botswana. African Centre for Technology Studies, Nairobi

Trollope WSW (1981) in Tainton NM (1981) (ed) Veld and pasture management in South Africa. Shuter & Shooter; University of Natal Press, Pietermaritzburg

Trollope WSW (1982) Ecological effects of fire in South African savannas. Ecology of Tropical Savannas (eds Huntley BJ & Walker BH) 292–306. Springer-Verlag, New York, NY

Twine W, Gray V, Owen-Smith N (2002) The effect of prolonged heavy grazing pressure on the regrowth of two perennial grass species in a semi-arid communal rangeland. African Journal of Range and Forage Science 19: 129-130

Twine W, Moshe D, Netshiluvi TR, Shipugu V (2000) Direct use values of non timber forest products from the rural area of Mametja, Northern Province, RSA. Unpublished report, University of the Witwatersrand

Tybirk K (1989) Flowering, pollination and seed production of *Acacia nilotica*. Nordic Journal of Botany 9 (4): 375 - 381

Van der Wal SB, Kuhn KM, Gworek JR (2005) Two phase seed dispersal: linking the effects of frugivorous birds and seed caching rodents. Oecologia 145 (2): 281 – 286

Van Hensbergen HJ, Martin SC (1993) Climatic factors affecting trapping success of some South African small mammals. South African Journal of Wildlife Research 23 (3): 87 – 94

Van Vegten (1984) Thornbush invasion in a savanna system in eastern Botswana. Plant Ecology 56 (1): 3 -7

Venter F, Venter J (1996) Making the most of indigenous trees. Briza Publications, Pretoria

Walker BH, Ludwig D, Holling CS, Peterman RM (1981) Stability of Semi-Arid Savanna Grazing Systems. Journal of Ecology 69 (2): 473-498

Walter H (1979) Vegetation of the earth and ecological systems of the biosphere. Second edition, Springer-Verlag

Weltzin JF, Archer S, Heitschmidt RK (1997) Small mammal regulation of vegetation structure in a temperate savanna. Ecology 78 (3): 751-763

Werger MJA (1974) On concepts and techniques applied in the Zurich-Montpellier method of vegetation survey. Bothalia 11: 309 - 323

Williams PA, Karl BJ, Bannister P, Lee WG (2000) Small mammals as potential seed dispersers in New Zealand. Austral Ecology (25) 5: 523 - 532

Williamson BR (1975) The condition and nutrition of elephant in Wankie National Park. Arnoldia Rhodesia 7 (12): 1 - 20

Witt GB, Moll EJ, Beeton RJS (1998) Sheep faeces under shearing sheds: a documentary of vegetation change using stable carbon isotope analysis. The Rangeland Journal 19 (1): 109 - 115

Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. In: Biological Conservation 122: 351–359

Young , JZ (1981) The life of vertebrates, Oxford University Press, New York

**Personal communications**

Ivan Groenhof (2005) Director, Alien Clearing Project Management Services, Cape Town

Professor Bruce Hewitson (2006) Climate Change Specialist, University of Cape Town

Professor Tim Dunne (2006) Professor of Statistical Sciences, Universty of Cape Town

Mr Brian Jones (2004) Moholoholo Wildlife Rehabilitation Centre, Hoedspruit

Dr Eugene Moll (2000) Southern African Wildlife College, Hoedspruit

Mr Trevor Pezet (2006) Seed and crop technologist; Enza-Zaden Seeds, Narramine NSW, Australia

Mr Errol Pieterson (2000) former Section Ranger, Kingfisherspruit Kruger National Park

Mr Ross Turner (2005) Botanist, Cape Town

Dr Ian Whyte (2000) Kruger National Park Ecologist, South Africa