Among Rodents and Rhinos:

Interplay between Small Mammals and Large Herbivores in a South African Savanna

Onder knaagdieren en neushoorns:
Wisselwerking tussen kleine zoogdieren en grote herbivoren
in een Zuid-Afrikaanse savanne

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Interplay between Small Mammals and Large Herbivores in a South African Savanna

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Abstract

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Mankind has caused species extinction of many groups of organisms through the transformation and fragmentation of once continuous natural habitats. In order to protect and restore natural biodiversity hotspots such as the African savannas we need to understand the determinants of their community structure and species diversity. Evidence has accumulated that body size differences that balance species facilitation and competition interactions as well as spatial heterogeneity may be key factors in the functioning of these ecosystems. This study explores the ecological consequence of the interplay between murid rodents and large herbivore species in a South African savanna and investigates the effect of abiotic factors on community interactions.

The herbivores studied showed strong interactions that were influenced by both fire and rainfall. Exclusion of large herbivores resulted in plant species composition changes and grass cover modifications, leading to higher rodent abundances. Middle-sized and large herbivore species responded to short-term postfire succession patterns with large species being the pioneers on recently burnt vegetation patches. Both middle-sized and large species affect murid rodents in the time of recolonisation burnt areas, mostly through increasing and prolonging their predation risk via grass cover changes. Additionally, the grass cover played a major role in the habitat selection and space use of grass-eating rodents, although the availability of high quality food resources was also important, especially with male and females having different priorities. Furthermore, the recruitment of the encroaching woody species *Dichrostachys cinerea* was not only positively (less competition for water and light with grasses) and negatively (higher risk of being trampled or desiccation) affected by large herbivores and rainfall but also influenced through predation by invertebrates and murid rodents. The findings of this study suggest that herbivore communities from very small (murid rodents) to very large (elephant) potentially interact in a South African savanna and that this interplay is of importance for the maintainance of the biodiversity in these ecosystems. Large herbivores influence murid rodents mainly through top-down effects (via grass cover modifications) rather than through competitive and facilitative interactions for food (bottom-up). Additionally, by changing the vegetation structure large herbivores may have an impact on the woody species recruitment, but to what extent this imposes a feedback on them remains unclear. Furthermore, the study supports the hypothesis that herbivores, in interaction with abiotic factors, strongly modify African savanna ecosystems. Under low rainfall conditions woody species recruitment is mostly limited by seed predators and browsers, while fire plays a bigger role under high rainfall conditions. However, fire seems to be one possible management tool to maintain spatial heterogeneity in savannas in order to sustain coexistence opportunities for different-sized herbivore species.

Key words: African savanna, biodiversity, *Dichrostachys cinerea*, different-sized herbivores, fire, herbivore interactions, murid rodents, spatial heterogeneity.

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Chapter 1

General introduction

The global biodiversity crisis

Large areas of the earth's surface have been transformed by human activity over the past centuries (Vitousek et al. 1997). Humans have modified biogeochemical cycles (Schlesinger 1991), have transformed and fragmented once continuous natural habitats and thus reduced the mobility of organisms (Chapin et al. 1991) by creating dispersal barriers. As a consequence, other species on earth are increasingly restricted to smaller areas of poorer quality which in turn leads to rapid losses in biodiversity. Mankind has caused the extinction of 5-20% of the species in many groups of organisms (Pimm and Raven 2000, Woodruff 2001), the largest species loss since the extinction of the dinosaurs. This process is continuing: the world population is expected to grow by another 60% in the next 50 years (Anonymous 2006), especially in those tropical areas that host the highest biodiversity (Myers et al. 2000, Lutz et al. 2001). In order to protect and restore biodiversity we need to understand the principal determinants of the structure and diversity of species in ecological communities. Unfortunately, after almost a century of ecological research no theory that yields quantitive predictions on the community structure and species diversity has been found (Brown 1981, May 1988, Schluter and Ricklefs 1994, Huston 1994, Hubbell 2001), although responses of biological diversity to factors such as the number of available niches in space (Hutchinson 1959, Hutchinson and Mac Arthur 1959, MacArthur 1964, Morse et al. 1985, May 1988), productivity (Rosenzweig and Abramsky 1994, Tilman and Pacala 1994, Rosenzweig 1995), area (Rosenzweig 1995), species' body size (Hutchinson and MacArthur 1959, Brown et al. 1993, Siemann et al. 1996, Belovsky 1997, Prins and Olff 1997) and habitat fragmentation (Verboom et al. 1993, Quinn and Harrison 1988) are well-known. However, the complexity of interactions between species in ecological communities has made such predictions very difficult until now as many species are involved (5-50 million) of which many have not been described yet. The ecological requirements and behaviour of most described species are unclear and the ecological interactions between known species are often non-linear and thus very complex.

The African savanna

Half of the area of the African continent is covered by savannas (Okigbo 1985, Werner et al. 1990, Sankaran et al. 2005), about 13 million square kilometres. African savannas are diverse complex ecosystems that host a high diversity and density of different-sized mammalian herbivores (Prins and Olff 1997, Olff et al. 2002) and are therefore of major importance when it comes to the conservation of biodiversity on the earth. Despite the establishment of many protected areas, savannas are still subject to many threats. Increasing human populations, land use change and land claims in natural areas often result in ecosystem fragmentation, habitat loss and thus species extinction (Prins and Olff 1997). To be able to protect and restore savanna ecosystems and predict the effects of management interventions more accurately, insight into the principal determinants of their community structure and species diversity is necessary.

The study of the patterns and causes of variation of species-richness in herbivore assemblages has been the focal point of savanna ecology for a decade (Prins and Douglas-Hamilton 1990, Prins and Olff 1997). Several studies have linked rainfall, soil fertility and primary productivity to herbivore species richness (Western and Ssemakula 1981, East 1984, Huston 1994, Rosenzweig 1995, Danell and Niemela 1996, Olff et al. 2002). Until now very little is known how savannas can sustain such a large concentration of herbivores, but there is a growing recognition that herbivore body size may be a key factor in the functioning of these ecosystems (Du Toit and Owen-Smith 1989, McNaughton and Georgiadis 1986, Prins and Olff 1997, Olff et al. 2002). Body size is a critical parameter in the scaling of animal physiology, life history and behaviour (Peters 1983, Brown 1995), including metabolic rate and digestive capacity (Demment and van Soest 1985), home range size (Mysterud et al. 2001, Haskell et al. 2002) and herbivore foraging parameters (Peters 1983, Belovsky 1997, Wilmshurst et al. 2000).

In savannas body sizes of different species in herbivore assemblages have a certain regularity, which might be related to the balance between facilitation and competition interactions (Prins and Olff 1997, Arsenault and Owen-Smith 2002). Facilitation has been well described for different assemblages of native African herbivores (Lamprey 1963, Bell 1970, Leuthold 1978, Jarman and Sinclair 1979) and can occur when herbivores show enough difference in body sizes to select different diets (Prins and Olff 1997, Olff et al. 2002) regarding their foraging selectivity and food quality requirements. Large herbivores can only graze on multiple plants as their lowest level of selection and tolerate coarser, lower quality food (Demment and van Soest 1985, French 1985, Illius and Gordon 1992, Olff et al. 2002) whereas small herbivores like rodents can feed on individual plants or even plant parts (Ritchie and Olff 1999). Rodents have a higher energy demand per gram body mass (Kleiber 1961) and a shorter digestive tract, therefore they need a higher plant nutrient content than bulk feeders to meet their food requirements (Van Soest 1982, Belovsky 1997, Hamback et al. 2002) and may profit from grazing by large herbivores through improved quality or accessibility of their food source (Huisman and Olff 1998, Arsenault and Owen-Smith 2002). On the other hand, rodents maintain the vegetation biomass at a low level (Keesing 1997, 2000), hence improving food resource quality for larger grazers. It has been hypothesised that species that are ‘too similar’ in body mass might not profit sufficiently from facilitation interactions leading to compensatory effects within the assemblage (Prins and Olff 1997): the decline of one species of herbivore may be compensated by an increase in other species (Prins and Douglas-Hamilton 1990). Especially under fluctuating conditions (e.g., annual variation in rainfall) the competitive balance might vary between years. The ‘optimal’ body mass difference for a given habitat is therefore likely to depend on primary productivity, vegetation biomass-quality relationships, and environmental fluctuations.

Aim of the study

Many South African parks that were established to protect the high biodiversity of savanna ecosystems are fenced and relatively small in size, animals cannot migrate to outside the park, for instance in times when food sources are scarce. In these small parks spatial heterogeneity seems to be particularly important for the coexistence of different herbivore species (Du Toit and Owen-Smith 1989, Belovsky 1997, Wilmshurst et al. 2000, Cromsigt and Olff in press), especially on small scales. It is therefore crucial to gain knowledge about the principal determinants of the functioning of savanna ecosystems in order to provide authorities appropriate strategies for its conservation.

The distinctive vertebrates of African savannas have long been studied, but research on community interactions has focussed almost exclusively on larger herbivores, primarily ungulates (Bell 1970, Jarman 1974, Sinclair 1977, Sinclair and Norton-Griffiths 1979, Owen-Smith 1988, Prins and Douglas-Hamilton 1990, Sinclair and Arcese 1995). Most ecological research on smaller herbivores like rodents has been done on the abiotic factors and the resulting density-independent population processes influencing their population dynamics (Neal 1977, Hubert and Adam 1983, Leirs et al. 1996). Up to now interactions between small and large herbivore savanna communities are comparatively poorly known. Recent research has demonstrated that savanna rodents in East Africa may strongly interact with native ungulates and cattle (Keesing 1997, 1998, 2000). However, the interplay of savanna rodents with high densities of diverse indigenous herbivore species greatly varying in body size has not been investigated yet.

In spite of its consequence for the community interactions between different herbivore species in African savannas, information on murid rodent diet is very limited (Monadjem 1997, Metz and Keesing 2001), whereas the diet of larger herbivore species is comparatively well-known (Hofmann and Stewart 1972, Jarman and Sinclair 1979, Hansen et al. 1985, Hofmann 1989). Predominantly grass-eating rodent species may be influenced by larger grazers in their abundance or even their habitat selection and space use patterns due to food resource competition. In contrast, primarily granivorous rodent species may not be influenced through food resource availability by larger grazers as they do not compete for food. However, studies on the diet choices of rodents are of crucial importance in order to draw the right conclusions about community interactions between small and large herbivore species in African savannas.

The present study aims to get insight into the interactions between small and large herbivore species communities (Fig. 1) and to explore the ecological consequence of these interactions for the maintenance of the savanna ecosystem. This is crucial in order to make predictions whether the disappearance of a certain species may cause the extinction of other species, resulting in disproportional loss of biodiversity in the savanna ecosystem. This study wants to make a contribution to the fundamental understanding of biodiversity in African savannas and provides some relevant implications for its conservation.

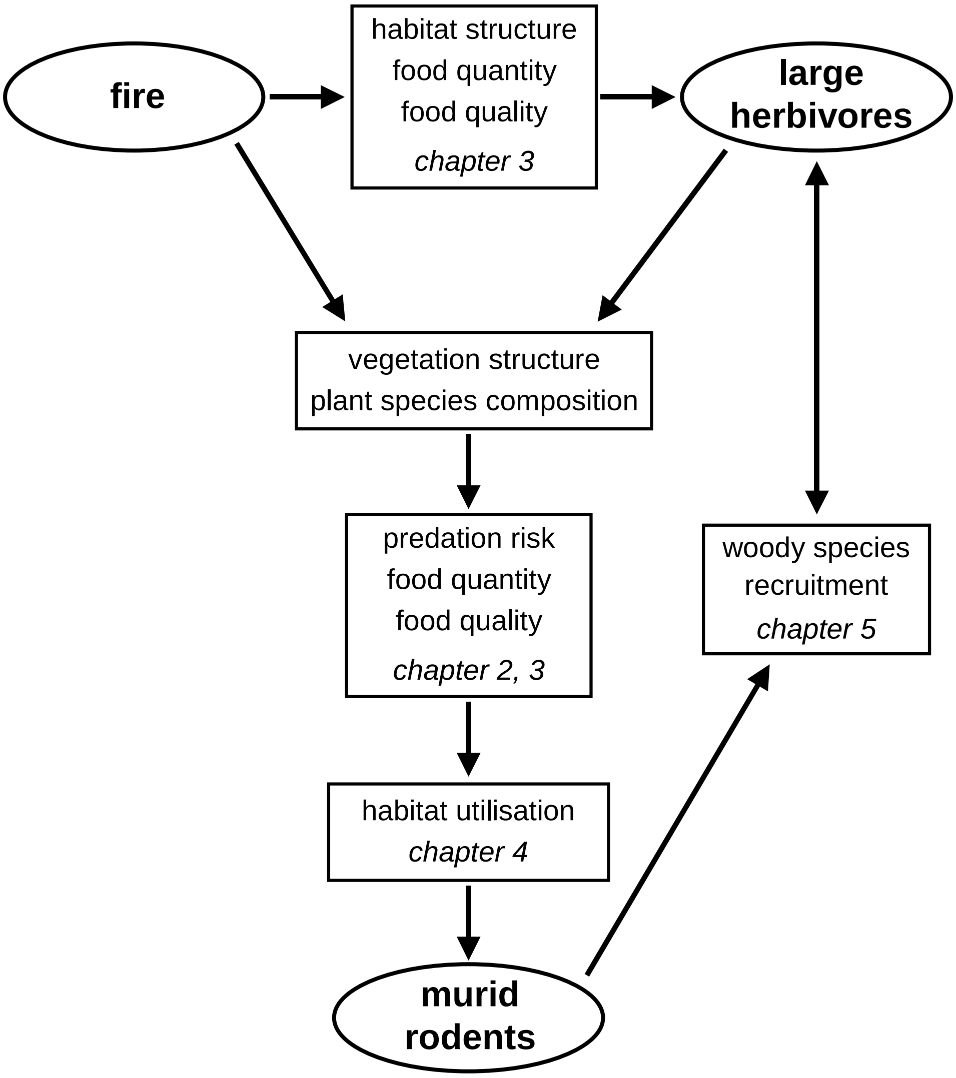


Fig 1 Interaction web investigated in this study.

Study site

The research for this thesis was performed in the Hluhluwe-iMfolozi Park (HiP; formerly called Hluhluwe-Umfolozi Park) which is situated in KwaZulu-Natal, South Africa (28°13’S and 32°00’E). HiP is a 90,000 ha fenced protected area and consists of the Hluhluwe Game Reserve in the North and the iMfolozi Game Reserve in the South (Fig. 2). The altitude in the park ranges from 60 m to 750 m (Conway et al. 2001). The climate is coastal and seasonal, temperatures range from an average of 13 °C to an average of 35 °C. Rain primarily falls between October and March. A rainfall gradient can be seen from North (985 mm/y) to South (650 mm/y). The vegetation mainly consists of open grasslands to closed *Acacia* and broad-leaved riparian woodlands. Furthermore *Dichrostachys cinerea* (legume of the Mimosoidae), a deciduous multistemmed shrub/small tree is an important bush encroacher in HiP, invading large areas of previously open grasslands (Skowno et al. 1999). Dominant grass species are *Digitaria longiflora* (Retz.) Pers., *Eragrostis curvula* (Schrad.) Nees, *Eragrostis superba* Peyr., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) A. Robyns & Tournay, *Sporobolus nitens* Stent, *Themeda triandra* Forsk, *Urochloa mosambicensis* (Hack.) Dandy. Fire is an important management tool in the park, where different areas are burnt with different frequencies. The aim of this fire management regime is to control bush encroachment and alien plants (Balfour and Howison 2001) but also to remove moribund grass material and thus improve quality and quantity of food resources for herbivores. HiP harbours a high diversity and biomass of indigenous large herbivores with important conservation value (Brooks and MacDonald 1983) including elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus),* kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasi*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus aethiopicus*). Mammalian carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*) and smaller carnivores such as white-tailed mongoose (*Ichneumia albicauda*) and slender mongoose (*Gallerella sanguinea*). Common snakes encountered in this habitat are Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*). Important raptors in HiP predating on rodents are black-shouldered kite (*Elanus caerulus)* and spotted eagle owl (*Bubo africanus*).

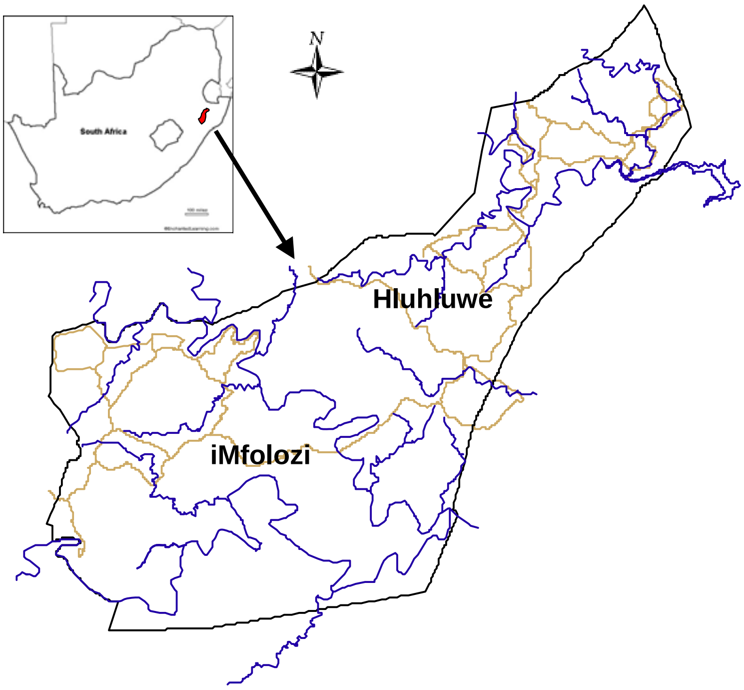
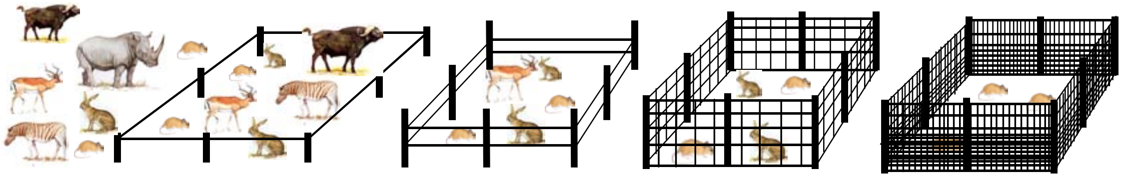


Fig 2 Location and geographical features of the Hluhluwe-iMfolozi Park in South Africa.

Experiments

My core experiment involved a ‘Russian doll approach’ meaning that I made use of plots from which vertebrate herbivores had been permanently excluded stepwise from large to small from 40 m x 40 m blocks of savanna vegetation by using fences with different height and mesh width (Fig. 3). Outside the exclosure about 42 species of mammalian herbivores were potentially present. A single cable at 50 cm height excludes only white and black rhino (rhino fence); whereas two cables at 0.7 m and 1 m height additionally excludes zebra, wildebeest, waterbuck, buffalo, but allows impala, kudu and nyala to jump over (zebra fence). A coarse wire mesh of 2.5 m height additionally excludes impala, kudu, nyala; but allows duiker, hares and porcupines to go through (impala fence), finally a coarse wire mesh of 2.5 m height combined with a chicken mesh of 1 m height excludes hares and all larger species; only small mammals like rodents have access (hare fence). I could use these herbivore exclusion experiments by courtesy of Prof. William Bond of the University of Cape Town, South Africa, and Prof. Han Olff of the University of Groningen, The Netherlands. Small mammal capture and vegetation measurements were conducted in the herbivore exclosure treatments from July 2002 until December 2004. For chapter 2 and 5 the experiment consisted of four replicates, in chapter 3 the experiment started with seven replicates but continued with four replicates until the end of the experiment. Study sites were located in both Hluhluwe and iMfolozi. In Hluhluwe the sites included all five exclosure treatments, whereas in iMfolozi the sites contained only three exclosure treatments (control, rhino fence and hare fence). During the period of the study the sites were burnt in 2002 and 2004.



Control	Rhino fence	Zebra fence	Impala fence	Hare fence
White rhino	-	-	-	-
Buffalo	Buffalo	-	-	-
Zebra	Zebra	-	-	-
Wildebeest	Wildebeest	-	-	-
Impala	Impala	Impala	-	-
Nyala	Nyala	Nyala	-	-
Duiker	Duiker	Duiker	Duiker	-
Hares	Hares	Hares	Hares	-
Rodents	Rodents	Rodents	Rodents	Rodents

Fig 3 Design of the exclosures where different-sized herbivore groups are stepwise permanently excluded from 40 m x 40 m blocks of savanna vegetation by using fences with different height and mesh width.

In chapter 3 large scale herbivore observations were conducted while driving transects by car that were chosen to cross areas that differed in their fire history. Herbivore locations were calculated and the structural vegetation type of their habitats was recorded from July 2003 until April 2005. Furthermore, a small scale experiment in two open bunch grassland sites that were burned in 2002 and 2004 was performed. Both the visitation of different size groups of herbivores (middle-sized herbivores: warthog, nyala and impala; and large herbivores: white rhino, buffalo, zebra and wildebeest) and the vegetation height at the sites were monitored for 3 years. Murid rodents were equipped with radio-collars for three months to telemetrically determine their location within their habitat with triangulation in chapter 4. In chapter 5 seed and seedlings of the encroaching savanna shrub *Dichrostachys cinerea* were planted in clipped and unclipped grass, with and without large herbivores present. Seed germination, seedling survival and predation were then monitored for eight months.

Outline of the thesis

Large herbivores in tropical savannas can have both positive and negative effects on small herbivores. For instance, intense grazing by large herbivores could improve the vegetation structure and thus food quality for smaller grazers (Farnsworth et al. 2002, Arsenault and Owen-Smith 2002) as it creates vegetation mosaics with short grazing lawns that consist of high quality plant species. On the other hand, selective larger herbivores could decrease the number of high quality plant species available for smaller herbivore species and so negatively influencing them through food resource competition (Keesing 1998). Additionally, large herbivores may restrict the habitat available to small herbivores as grazing and trampling reduces the vegetation cover, leading to higher exposure of small herbivores to their predators and therefore increase their predation risk (Hughes and Ward 1993, Brown 1999). *Chapter 2* investigates the effect of large herbivores on the vegetation structure and plant species composition in a tropical savanna and how this in turn influences the quantity and quality of food recourses available to murid rodents and the predation risk they experience in this system (Fig. 1).

High herbivore densities and re-occurring fire are important natural phenomenons that determine the structure and functioning of African savannas. Herbivores may be affected by small scale fire patterns in their seasonal dynamic of landscape use in the short-term as they generally prefer to forage on young regrowth (Sinclair 1977) but species may respond differently in time after a burn depending on their body size (Wilsey 1996). Middle-sized herbivore species (e.g., warthog, nyala and impala) selectively feed on high quality food resources, can deal with low food quantities shortly after a fire and may therefore be the pioneer species on the burnt vegetation patches. Large herbivore species (e.g., white rhino, buffalo, zebra and wildebeest) can survive on lower food quality but need high food quantities (Jarman 1974, Van Soest 1982, Belovsky 1986, 1997). They may only re-occur on burnt patches several months after the fire. Both, large and middle-sized herbivores could influence rodents when they recolonise burnt areas through changing both their predation risk and the quality of food resources available to them. Furthermore, fires together with herbivores are also important in creating large scale landscape mosaics in the long-term. Intense grazing in most recent burnt areas by different-sized herbivores may maintain fire-caused structural habitat changes in the system for several years. *Chapter 3* examines the response of herbivores greatly varying in sizes to short- and long-term fire succession patterns on small and landscape scales and resulting community interactions between them (Fig.1).

The coexistence of many herbivore species in tropical savannas may promote high numbers of diverse avian, mammalian and reptilian predators. Rodents may be particularly important for the ecosystem as they form the basis of the food web for higher trophic levels, such as small carnivores, raptors and snakes; hence the diversity of these species may depend on rodent abundance. To understand the ecological patterns in complex ecosystems like South-African savannas it is important to get insight into the habitat utilisation and spatial movements of rodents and the ecological factors influencing their spacing behaviour. Rodent space use may be affected by both large grazing herbivores and rodent predators. Food is an important component that determines the habitat selected by rodents (Monadjem and Perrin 1998) and also their home range size (Andrzejewski & Mazurkiewicz 1976, Taitt 1981, Zubaid & Gorman 1993). Herbivorous rodents selectively feed on high quality food resources and may therefore preferentially utilise vegetation patches with abundant high quality plant species created by large grazing herbivores. On the other hand, high grazing pressure by large herbivores reduces the vegetation cover and may therefore restrict the suitable habitat available to rodents as they prefer abundant cover that could be used as antipredation refuge. But savanna rodents face predators with different hunting tactics, which cause spatially varying predation risk and therefore dense habitat structure may not always be perceived as safer habitat. *Chapter 4* explores the habitat utilisation patterns of rodents in a South-African savanna and considers the habitat characteristics influencing their spatial distribution (Fig. 1).

Not only do large herbivores and fire potentially indirectly affect small herbivores through the vegetation composition, also *vice versa* effects are expected. Rodents influence the ecological interactions in savannas as they may change the tree-grass ratio by inhibiting the recruitment of woody species through predation of seeds and seedlings (Weltzin et al. 1997). Seed and seedling predation by rodents can be particularly important when it comes to encroaching woody species that invade areas of previously open savanna grasslands. A large woody biomass can alter soil moisture (Pressland 1973), intensity of fires (Higgins et al. 2000, van Langevelde et al. 2003), nutrient and microclimate conditions (Belsky 1992), and suppress grass productivity (Stuart-Hill & Tainton 1989) and therefore negatively affect herbivores that highly depend on abundant grass for food. But not only rodents influence the tree-grass ratio, also large herbivores and fire can positively and negatively affect seed germination and seedling establishment of encroaching woody species and thus drive vegetation dynamics in savannas. *Chapter 5* studies the interacting effects of herbivory and vegetation height on the establishment of the encroaching woody species *Dichrostachys cinerea* in savanna grassland (Fig. 1). *Chapter 6* will provide the synthesis of the thesis.

References

Andrzejewski R, Mazurkiewicz M (1976) Abundance of food supply and size of the bank vole’s home range. Acta theriol 21:237-253

Anonymous (2006) Incredible shrinking countries; declining populations. The Economist 378:12

Arsenault R, Owen-Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313-318

Balfour DA, Howison OE (2001) Spatial and temporal variation in a mesic savanna fire regime: response to variation in annual rainfall. African Journal Range and Forage Science 19:45-53

Bell RHV (1970) The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A (ed). Animal populations in relation to their food resources. Symposium of the British Ecological Society, Aberdeen 1969. Blackwell Scientific Publications, Oxford, p 111-124

Belovsky GE (1986) Generalist herbivore foraging and its role in competitive interactions. American Zoologist 26:51-69

Belovsky GE (1997) Optimal foraging and community structure: the allometry of herbivore food selection and competition. Evolutionary Ecologist 11:641-672

Belsky AJ (1992) Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. Tropical Grasslands 26:12-20

Brooks PM, Macdonald IAW (1983) The Hluhluwe-Umfolozi Reserve: an ecological case history. In: Management of large mammals in African conservation areas. Haum Educational Publishers, Pretoria, p 51-77

Brown JH (1981) Two decades of homage to Santa Rosalia: towards a general theory of diversity. American Zoologist 21:877-888

Brown JH (1995) Macroecology. University of Chicago Press, Chicago

Brown JS (1999) Vigilance, patch use and habitat selection: Foraging under predation risk. Evolutionary Ecology Research 1:49-71

Brown JH, Marquet P, Taper M (1993) Evolution of body size: consequences of an energetic definition of fitness. American Naturalist 142:573-584

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynold HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (1991) Consequences of changing biodiversity. Nature 405:234-242

Conway A, Balfour D, Dale T, Hartley P, Morrison P, Howison R, Galli N, Wadge M (2001) Hluhluwe-Umfolozi Park Management Plan 2001. Ezemvelo KwaZulu-Natal Wildlife

Cromsigt JPGM, Olff H (in press) Resource partitioning amongst large grazerm mediated by local heterogeneity: an experimental approach

Danell KLP, Niemela P (1996) Species richness in mammalian herbivores: patterns in the boreal zone. Ecography 19:404-409

Demment MW, van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. American Naturalist 125:641-672

Du Toit JT, Owen-Smith N (1989) Body size, population metabolism and habitat specialisation among large African herbivores. American Naturalist 133:736-740

East R (1984) Rainfall, nutrient status and biomass of large African savannah mammals. African Journal of Ecology 22:245-270

Farnsworth KD, Focardi S, Beecham JA (2002) Grassland-herbivore interactions: How do grazers coexist? American Naturalist 159:24-39

French NR (1985) Herbivore overlap and competition in Kenya rangelands. African Journal of Ecology 23:259-268

Hamback PA, Grellmann D, Hjalten J (2002) Winter herbivory by voles during a population peak: the importance of plant quality. Ecography 25:74-80

Hansen RM, Mugambi MM, Bauni SM (1985) Diets and trophic ranking of ungulates of the Northern Serengeti. Journal of Wildlife Management 49:823-829

Haskell JP, Ritchie ME, Olff H (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418:527-530

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

Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226-240

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants. A comparative view of their digestive system. Oecologica 78:443-457

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Hubert B, Adam F (1983) Outbreaks of *Mastomys erythroleucus* and *Taterillus gracilis* in the Sahelo-Sudanien zone in Senegal. Acta Zool Fenn 46:137-166

Hughes JJ, Ward D (1993) Predation risk and distance to cover affect foraging behavior in Namib Desert gerbils. Animal Behaviour 46:1243-1245

Huisman J, Olff H (1998) Competition and facilitation in multispecies plant-herbivore systems of productive environments. Ecology Letters 1:25-29

Huston MA (1994) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:145-159

Hutchinson GE, Mac Arthur RH (1959) A theoretical model of size distributions among species of animals. American Naturalist 93:117-125

Illius AW, Gordon IJ (1992) The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56:989-999

Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48:215-267

Jarman PJ, Sinclair ARE (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair ARE, Norton-Griffitths N (eds). Serengeti: dynamics of an ecosystem. Chicago University Press, Chicago, p 130-163

Keesing F (1997) Ecological interactions between small mammals, large mammals and vegetation in a tropical savanna of Central Kenya. PhD thesis, University of California, Berkeley

Keesing F (1998) Impacts of ungulates on the demography and diversity of small mammals in central Kenya. Oecologia 116:381-389

Keesing F (2000) Cryptic consumers and the ecology of an african savanna. BioScience 50:205-215

Kleiber M (1961) The fire of life: an introduction to animal energetics. Wiley, New York

Lamprey HF (1963) Ecological separation of the large mammal species in Tarangire Game Reserve, Tanganyika. East African Wildlife Journal 1:63-92

Leirs H, Verhagen R, Verheyen W, Mwanjabe P, MbiseT (1996) Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. Journal of Applied Ecology 33:937-943

Leuthold E (1978) Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241-252

Lutz W, Sanderson W, Scherbov S (2001) Nature 412:543-545

MacArthur RH (1964) Environmental factors affecting bird species diversity. American Naturalist 98:387-397

May RM (1988) How many species are there on earth? Science 241:1441-1449

McNaughton SJ, Georgiadis NJ (1986) Ecology of african grazing and browsing mammals. Ann Rev Ecol Syst 17:39-65

Metz MR, Keesing F (2001) Dietary choices of the pouched mouse (Saccostomus mearnsi) in central Kenya. Biotropica 33:182-187

Monadjem A (1997) Stomach contents of 19 species of small mammals in Swaziland. African Journal of Ecology 35:64-72

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)

Morse D, Stork NE, Lawton JH (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature 314:731-732

Myers N, Mittelmeier RA, Mittelmeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Mysterud A, Pérez-Barbería FJ, Gordon IJ (2001) The effect of season, sex and feeding style on home range areas versus body mass scaling in temperate ruminants. Oecologia 127:30-39

Neal BR (1977) Reproduction of the multimammate rat, *Praomys (Mastomys) natalensis* (Smith), in Uganda. Zeitschrift fuer Saugetierkunde 42:221-231

Okigbo BN (1985) Land use and production potentials of African savanna. In: Ecology and management of the world’s savannas (eds. Tothill JC, Mott JC). Australian Academy of Sciences, Canberra, pp 384

Olff H, Ritchie M, Prins HHT (2002) Global environmental control of diversity in large herbivores. Nature 415:901-904

Owen-Smith N (1988) Megaherbivores. The influence of very large body size on Ecology. Cambridge University Press, Cambridge

Peters RH (1983) The ecological implications of body size. Cambridge University Press, New York

Pimm SL, Raven P (2000) Biodiversity – Extinction by numbers. Nature 403:843-845

Pressland AJ (1973) Rainfall partitioning by an arid woodland (Acacia anura F. Muell.) in southwestern Queensland. Australian Journal of Botany 21:235-245

Prins HHT, Douglas-Hamilton I (1990) Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83:392-400

Prins HHT, Olff H (1997) Species richness of African grazer assemblages: towards a functional explanation. In: Dynamics of tropical communities. (eds. Newbery D, Prins HHT, Brown ND), Blackwell, Oxford, p 448-490

Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557-560

Quinn JF, Harrison SP (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75:132-140

Rosenzweig ML, Abramsky Z (1994) in: Species diversity in ecological communities: Historical and geographical perspectives (eds. Schluter D and Ricklefs R). University Chicago Press, Chicago, p 52-65

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. Nature 436:846 – 849

Schlesinger WH (1991) Biogeochemistry: An analysis of global change. Academic Press, San Diego

Schluter D, Ricklefs R (1994) Species diversity in ecological communities: Historical and geographical perspectives. University Chicago Press, Chicago

Siemann E, Tilman D, Haarstad J (1996) Insect species diversity, abundance and body size relationships. Nature 380:704-706

Sinclair ARE (1977) The African buffalo. University of Chicago Press, Chicago, p 355

Sinclair ARE, Norton-Griffiths M (1979) Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, pp 389

Sinclair ARE, Arcese P (1995) Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, pp 665

Skowno AL, Midgley JJ, Bond WJ, Balfour D (1999) Secondary succession in Acacia nilotica (L.) savanna in the Hluhluwe Game Reserve, South Africa. Plant Ecology 145:1-9

Stuart-Hill GC, Tainton NM (1989) The competitive interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. Journal of Applied Ecology 26:285-298

Taitt MJ (1981) The effect of extra food on small populations. 1. Deer mice (Peromyscus maniculatus). Journal of Animal Ecology 50:111-1124

Tilman D, Pacala SW (1994) in: Species diversity in ecological communities: Historical and geographical perspectives (eds. Schluter D and Ricklefs R). University Chicago Press, Chicago, p 13-25

Van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore A, Hearne J, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350

Van Soest PJ (1982) Nutritional ecology of the ruminant: Ruminant metabolism, nutritional strategies, the cellulolytic fermentation and the chemistry of forages and plant fibres. O & B Books, Corvallis

Verboom J, Metz JAJ, Meelis E (1993) Metapopulation models for impact assessment of fragmentation. In: Vos CC, Opdam P (eds). Chapman and Hall, London, p 172-191

Vitousek PM, Mooney HA, Lubchenko J, Melillo JM (1997) Human domination of the Earth's ecosystem. Science 277:494-499

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

Werner PA, Walker BH, Stott PA (1990) Introduction. Journal of Biogeography 17:343-344

Western D, Ssemakula J (1981) The future of savanna ecosystems: ecological islands of faunal enclaves? African Journal of Ecology 19:7-19

Wilmshurst JF, Fryxell JM, Bergmann CM (2000) The allometry of patch selection in ruminants. Proceedings of the Royal Society of London 267:345-349

Wilsey BJ (1996) Variation in use of green flushes following burns among African ungulate species: The importance of body size. African Journal of Ecology 34:32-38

Woodruff DS (2001) Declines of biomes and biotas and the future of evolution. Proceedings of National Academy of Science 98:5471-5476

Zubaid A, Gorman ML (1993) The effect of supplementary feeding upon the sizes of the home ranges of wood mice Apodemus sylvaticus living on a system of maritime sand dunes. Journal of Zoology, London 231:233-237

Chapter 2

Effect of large herbivores on murid rodents in a South African savanna

N. Hagenah, H. Olff, H. H.T. Prins

Abstract

Savanna ecosystems host a high diversity and size variety of herbivores. Considerable scientific interest therefore arises in the community ecology and ecosystem functioning of these complex systems. Until now studies on community interactions in savannas have been centred almost exclusively on large ungulates. Very little information exists, however, about how small and large herbivore communities interact. To asses the effects of large herbivores on murid rodents in a South African savanna, different-sized large herbivores were excluded from plots of vegetation. At four study sites, located in an either high or low rainfall area, rodents were captured inside the herbivore exclosures with live traps and vegetation changes in absence of large herbivores were recorded. The exclusion of large herbivores lead to changes in both the plant species composition and vegetation structure. Decreasing large herbivore numbers and increasing vegetation height resulted in an increasing rodent abundance. On the other hand, no impact of large herbivores was found on the grass species composition in the diet of the most frequently captured rodent species, *Lemniscomys rosalia spinalis*. Furthermore large herbivores had no effect on rodent body weight or on distances they moved. It appeared, however, that rodent species composition may be influenced by a rainfall gradient rather then by large herbivores. Our findings exhibited that different-sized large herbivores and rodents strongly interact in South African savannas. Rodent abundance may be mainly affected by large grazing herbivores through the reduction of the vegetation cover and the subsequent increased exposure of rodents to predators. Furthermore our results may provide evidence that rainfall differences can have an effect on the small mammal community and their interaction with larger herbivores.

Nomenclature: *Aristida congesta* Roem. & Schult., *Botriochloa insculpta* (A. Rich.) A. Camus, *Digitaria longiflora* (Retz.) Pers., *Eragrostis curvula* (Schrad.) Nees, *Eragrostis superba* Peyr., *Heteropogon contortus* (L.) Beauv. ex Roem. and Schult., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) A. Robyns & Tournay, *Sporobolus nitens* Stent, *Themeda triandra* Forsk., *Urochloa mosambicensis* (Hack.) Dandy.

Introduction

Savannas harbour a high diversity of herbivores of different sizes. Despite the establishment of many protected areas, savannas are still subject to many threats. Increasing human populations, land use change, and land claims in natural areas often result in ecosystem fragmentation, habitat loss and thus in species extinction (Prins and Olff 1997). To be able to protect savanna ecosystems better and predict the effects of management interventions more accurately, insight into the determinants of species coexistence is necessary. Niche partitioning based on body size differences has been suggested to facilitate the coexistence of savanna herbivore species (Owen-Smith 1988, Prins and Olff 1997, Olff et al. 2002). However, up to now research on community interactions in savannas has focussed mostly on large ungulates, such as buffalo and elephant (Owen-Smith 1988, Prins and Douglas-Hamilton 1990). Until recently very little was known about interactions between small and large herbivore communities. Recent studies in East African savannas suggest that large herbivores can have strong and rapid impacts on rodent abundance and diversity (Keesing 1997, 1998b, 2000). Keesing (1998b) found that the exclusion of native ungulates and cattle resulted in an overall increase in rodent abundance. She suggested that rodents and large herbivores in these ecosystems compete for food resources and that habitat quality was higher for rodents when ungulates were absent. However, the effects of community interactions between different-sized indigenous herbivores and rodents in savannas have not been further explored.

In the present study we investigate the impact of large herbivores on murid rodent abundance and diversity in a South African savanna by selectively excluding different-sized herbivore species from plots of vegetation. We hypothesise that the exclusion of large herbivores may have both positive and negative effects on rodent abundance due to several possible mechanisms. For instance, trampling by large herbivores causes soil disturbance which may therefore positively affect rodents by loosening the hard soil top layer making it easier for them to dig burrows. Intense grazing could improve the vegetation structure for smaller grazers (Farnsworth et al. 2002, Arsenault and Owen-Smith 2002) as it leads to the development of patchy vegetation with short grazing lawns. Short patches of vegetation are less likely to burn or, if they do, will have less intense fires due to small fuel loads. This in turn may have positive short- term effects on rodents as fewer individuals get killed by fires. Furthermore, the establishment of short grazing lawns may have positive long-term effects on rodents by improving the food quality as grazing lawns consist of high quality plant species. On the other hand, selective larger herbivores (e.g., impala) could decrease the number of high quality plant species available for smaller herbivore species and thus negatively influencing them through competition for food resources (Keesing 1998b). Additionally, vegetation modifications by large herbivores may restrict the habitat available to rodents as grazing and trampling reduces the vegetation cover (Grant et al. 1982; Bock et al. 1984, Roques, O'Connor and Watkinson 2001, Goheen et al. 2004). A decrease of vegetation cover could lead to higher exposure of rodents to their predators and therefore increase their predation risk (Birney et al. 1976, Edge, Wolff and Carey 1995, Peles and Barret 1996).

In this study, we experimentally excluded different size classes of large herbivores from plots of savanna vegetation and monitored small mammal abundances and vegetation characteristics to explore their interplay.

Material and methods

Study site

This study was conducted between July 2002 and December 2004 in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa (28°13'S and 32°00'E). HiP is a 90,000 ha fenced protected area and consists of the Hluhluwe Game Reserve in the North and the iMfolozi Game Reserve in the South. The altitude in the park ranges from 60 m to 750 m (Conway et al. 2001). The climate is coastal and seasonal, with temperatures from ± 13 °C to ± 35 °C. Rains generally fall between October and March with mean annual rainfall ranging from 985 mm in the northern to 650 mm in the southern areas. The amount of rainfall during the study period in both areas appeared not to be different from that of previous years. The park is characterised by savanna vegetation ranging from open grasslands to closed *Acacia* and broad-leaved riparian woodlands. Dominant grass species are *Digitaria longiflora*, *Eragrostis curvula, Eragrostis superba*, *Panicum maximum*, *Sporobolus africanus*, *Sporobolus nitens, Themeda triandra* and *Urochloa mosambicensis*. A fire management regime is simulating natural fires in the park, where different areas are burnt with different frequencies. HiP harbours a high diversity and biomass of indigenous large herbivores including elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus),* kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasi*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus aethiopicus*). Mammalian carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*) and smaller carnivores such as white-tailed mongoose (*Ichneumia albicauda*) and slender mongoose (*Gallerella sanguinea*). Common snakes encountered in this habitat are Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*). Important raptors in HiP predating on rodents are black-shouldered kite (*Elanus caerulus)* and spotted eagle owl (*Bubo africanus*).

Experimental design

Herbivore exclosures

Our experiment was established in early 2000 (Bond and Olff, unpubl.). Different-sized herbivores were permanently excluded in a nested design from 40 m x 40 m blocks of savanna vegetation by using fences with different height and mesh width. Two study sites were located in Hluhluwe and two study sites were located in iMfolozi. The experiment consisted of four replicates with five herbivore exclosure treatments each (only dominant species listed):

1. control: no fence, about 42 species of mammalian herbivores potentially present
2. rhino fence: single cable at 50 cm height (excludes only white and black rhino)
3. zebra fence: two cables at 0.7 m and 1 m height (additionally excludes zebra, wildebeest, waterbuck, buffalo; allows impala, kudu and nyala to jump over)
4. impala fence: 2.5 m high (additionally excludes impala, kudu, nyala; but allows duiker, hares and porcupines to go through)
5. hare fence: with chicken mesh lower 1 m (excludes hares and all larger species; only rodents such as mice, rats, gerbils and insects have access)

The study sites in Hluhluwe included all five exclosure treatments, whereas the study sites in iMfolozi contain only three exclosure treatments (control, rhino fence and hare fence). Dung counts conducted in the control and the exclosure treatments indicated that the fence successfully excluded the target groups.

The four study sites were chosen to compare the results along a high to low rainfall gradient (Hluhluwe - high rainfall; iMfolozi - low rainfall). The study sites were burned once every two years as part of the fire regime management in the park. During the period of this study they were burned in August 2002 and August 2004.

Vegetation characterisation

Vegetation characteristics were measured in March 2003 in one half of each exclosure treatment in a grid with measuring points spaced 1 m apart from each other (200 points). To measure vegetation height a wooden disk with a diameter of 46 cm was fully lifted to the top of a pole with a height scale and then dropped onto the vegetation. The most dominant grass species was determined and the height at which the disk was resting on the vegetation was measured. To determine the quality of rodent food sources we collected a total of 112 samples of green leaves of the most dominant grass species from all exclosures and control in which they occurred. We analysed each sample for its N, P, Ca, Mg and Na content and then calculated the average content of each nutrient per grass species in order to avoid any treatment effects. We discriminated the grass species by their growth forms and placed them into two categories (1. bunch grasses and 2. lawn grasses, Table 1). We then calculated the weighted average contents of the nutrients in the samples and then classified them in two nutritional quality categories (1. high quality grasses, 2. low quality grasses).

Small mammal surveys

We established a permanent small mammal trapping grid inside each of the four replicates of the exclosure treatments. Each 40 m x 40 m plot contained a trapping grid of 25 (5 x 5) traps located 8 m spacing apart from each other. Traps were not placed closer than three meters to a fence. We conducted nine trapping sessions of four to five consecutive nights each, using PVC live-traps, with one trap per station. Traps were placed on flat ground and baited with a mixture of oatmeal, raisins, water, oil and salt and checked in the morning and evening, re-baited and reset if necessary. Captured animals were identified to species and permanently individually marked with glass fibre transponders (Telinject$^{®}$, ID 100, Römerberg, Germany). Other data recorded included sex, age, weight, and reproductive condition (after Gurnell and Flowerdew 1990, Barnett and Dutton 1995). Additionally, dung of the most frequently captured small mammal species was collected from the traps for diet analysis. Due to the fact that rodents were able to move between all exclosures and therefore may have fed in different exclosures the components of their diet were only analysed for differences between study sites and not for treatment effects. Captured animals were always released at their trapping location after measurements were taken. To estimate the differences in the use of space by individual rodents in response to changes in predation risk and food quality in the fencing treatments, we compared the maximum distances moved between captures for males and females that were captured more than once. Small mammal trapping and marking in HiP was approved by Ezemvelo KZN Wildlife.

Data-analysis

A Pearson's Chi-square test was used to test for the effect of large herbivores and rainfall on both plant and small mammal species composition between fences and study sites. The impact of the rainfall gradient on both overal diet composition of rodents and rodent graminoid diet components were analysed with Pearson's Chi-square test. Furthermore the influence of large herbivore grazing on the vegetation structure and on rodent body weight as well as plant nutrient concentration differences were calculated using a one-way ANOVA followed by Tukey HSD tests. A one-way ANOVA followed by Tukey HSD tests was also used to test for differences in both effects of large herbivores and rainfall on rodent numbers and trapping success and for differences in distances rodents moved between trapping locations between either fences or study sites. Relations between trapping success and vegetation structure was analysed with logistic regression with small mammal presence/absence as the dependent variable and vegetation height as a predictor.

Results

Vegetation analysis

Plant species quality

Lawn grass species had significantly higher average N ($F_{1, 110} = 11.154$, $P = 0.001$), P ($F_{1, 110} = 17.893$, $P < 0.001$), Ca ($F_{1, 110} = 12.621$, $P = 0.001$), Mg ($F_{1, 110} = 25.947$, $P < 0.001$) and Na contents ($F_{1, 110} = 274.497$, $P < 0.001$) than bunch grass species (Table 1) and are therefore determined as high quality grass species. However, some bunch grasses are high quality as well (such as *P. maximum*).

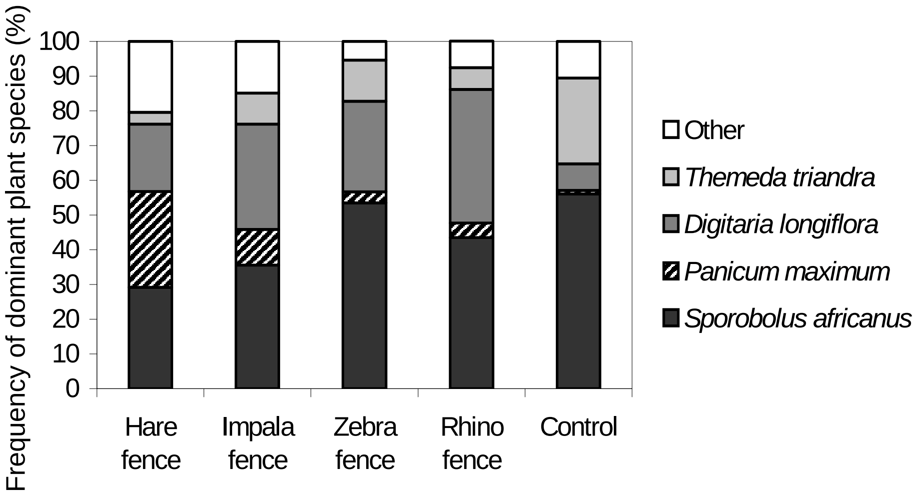
Plant species composition

The grass species most frequently dominant at the Hluhluwe sites occurring in all exclosure treatments and control are *S. africanus* and *D. longiflora* (Fig. 1A), representing 67 % of the recorded plant species. Other frequently recorded grass species included *P. maximum* and *T. triandra*. We found an increasing occurrence of *P. maximum* when more groups of large herbivore species were excluded ($X^2_{12} = 377.141$, $P < 0.001$). The most abundant dominant grass species at the iMfolozi sites were *P. maximum* and *U. mosambicensis* recorded at 49 % of the measurement points (Fig. 1B), however *S. nitens* and *T. triandra* were also recorded frequently. Also at the iMfolozi sites, the high quality *P. maximum* was recorded more often as dominant species the more groups of large herbivore species were excluded ($X^2_6 = 139.498$, $P < 0.001$).

Table 1 Mean leaf nutrient concentrations of the dominant grasses at the study sites, the number of samples taken and growth form-category of each species (bunch grass and lawn grass). * : is expected to be neglected by herbivores due to a bitter taste (van Oudtshoorn 1992).

Species	Growth form-category	N	N (%)		P (%)		Ca (%)		Mg (%)		Na (mg/kg)	
			Mean	SDs	Mean	SDs	Mean	SDs	Mean	SDs	Mean	SDs
Digitaria longiflora	lawn grass	10	1.71	0.54	0.27	0.12	0.37	0.15	0.22	0.07	6313	1213.37
Sporobolus nitens	lawn grass	9	2.61	0.82	0.28	0.1	0.38	0.75	0.22	0.04	5407	1881.46
Urochloa mosambicensis	lawn grass	13	2.67	0.99	0.35	0.12	0.65	0.16	0.35	0.14	9471	3888.36
Aristida congesta	bunch grass	5	1.97	0.46	0.16	0.07	0.22	0.09	0.13	0.05	604	349.29
Botriochloa insculpta *	bunch grass	11	2.18	0.33	0.25	0.03	0.38	0.06	0.23	0.09	446	483.98
Eragrostis curvula	bunch grass	10	1.43	0.29	0.19	0.05	0.25	0.07	0.1	0.03	997	310.36
Eragrostis superba	bunch grass	13	1.99	0.42	0.24	0.06	0.55	0.15	0.19	0.05	971	387.12
Heteropogon contortus	bunch grass	7	1.65	0.32	0.18	0.04	0.31	0.08	0.2	0.07	334	162.70
Panicum maximum	bunch grass	16	2.49	0.51	0.3	0.09	0.46	0.15	0.24	0.05	2077	968.82
Sporobolus africanus	bunch grass	10	1.33	0.31	0.21	0.05	0.26	0.04	0.12	0.02	383	175.27
Themeda triandra	bunch grass	8	1.49	0.18	0.17	0.03	0.28	0.05	0.16	0.05	372	210.80

A)



B)

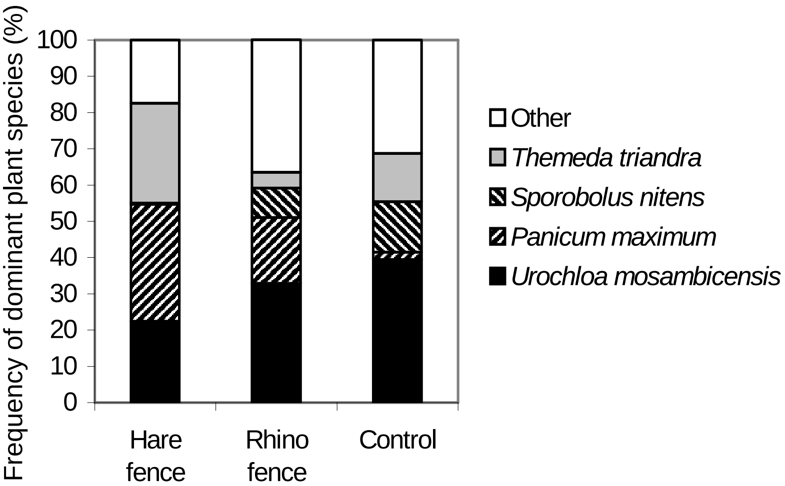


Fig 1 Frequency of occurrence of dominant grass species for the different fence types at the Hluhluwe (A) and iMfolozi sites (B) measured in March 2003. The grass species composition was significantly different between the fencing treatments at both the Hluhluwe (n = 200, $X^2_{12} = 377.141$, $P < 0.001$) and the iMfolozi sites (n = 200, $X^2_6 = 139.498$, $P < 0.001$).

Vegetation structure

The vegetation height at both Hluhluwe sites decreased with increasing herbivore size present, although this was not the case for the hare fence and the impala fence ($F_{4, 1974} = 68.21$, $P < 0.001$; Fig. 2A). At the iMfolozi sites the vegetation height also significantly reduced with the size of herbivores present ($F_{2, 1078} = 507.5$, $P < 0.001$; Fig. 2B).

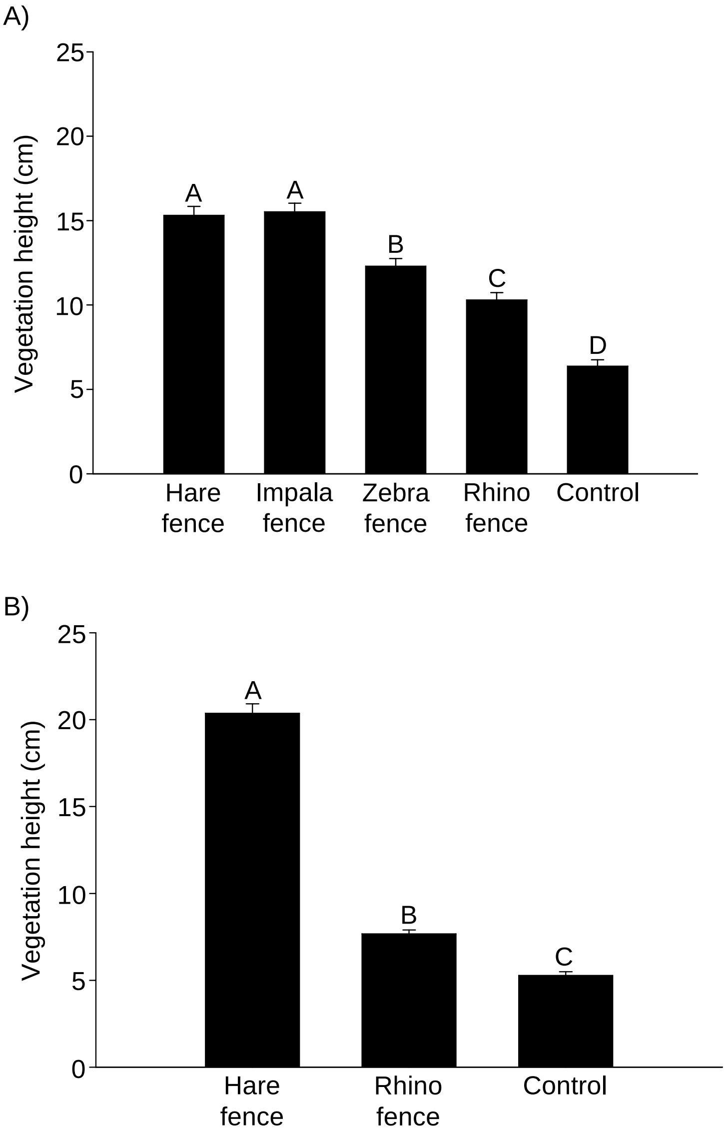
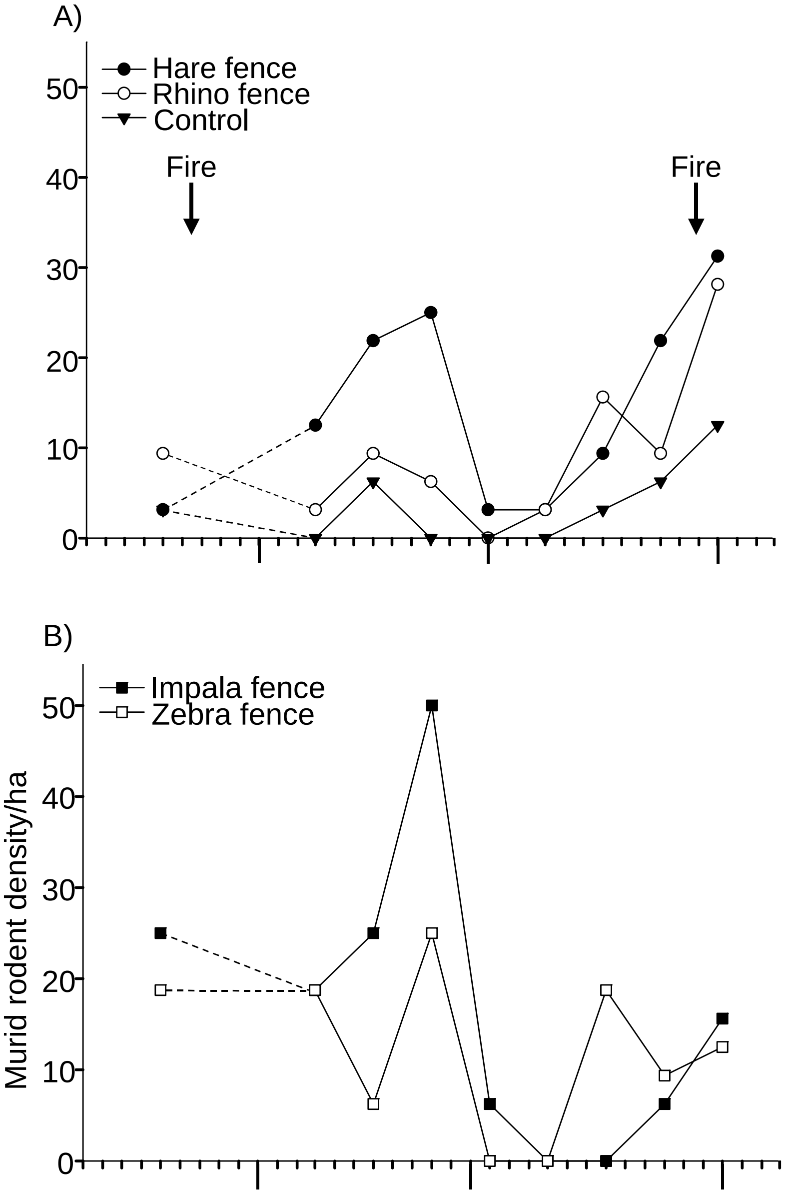


Fig 2 Mean vegetation height for the different fence types at Hluhluwe (A) and iMfolozi sites (B; ± SE, n = 200) measured in March 2003. Different letters show significant differences, $P < 0.001$.

Small mammal analysis

Between July 2002 and December 2004, we captured a total of 387 murid rodents, comprising four species. The most frequently captured species in the exclosure treatments of all study sites was the single-striped mouse *(Lemniscomys rosalia spinalis*), a murid rodent that is widespread in bushveld habitats (Taylor 1998) south of the Sahara. In HiP the single-striped mouse represented about 75% of all captures. Other small mammal species captured and identified included the natal multimammate mouse (*Mastomys natalensis)*, the pouched mouse (*Saccostomus* *campestris*) and bush-rats (*Aethomys* spp). However, several captured rodents could not be identified on a species level. Overall, the exclusion of different size groups of larger herbivores lead to a significant increase of total rodent numbers ($F_{32, 32}$ = 1.99, *P* = 0.028; Figs 3A and B) at the Hluhluwe sites. At the iMfolozi sites rodents were more abundant after the exclusion of different-sized larger herbivores during the different trapping periods (Fig. 3C), although these differences appeared not to be significant ($F_{32, 32}$ = 1.085, *P* = 0.41).



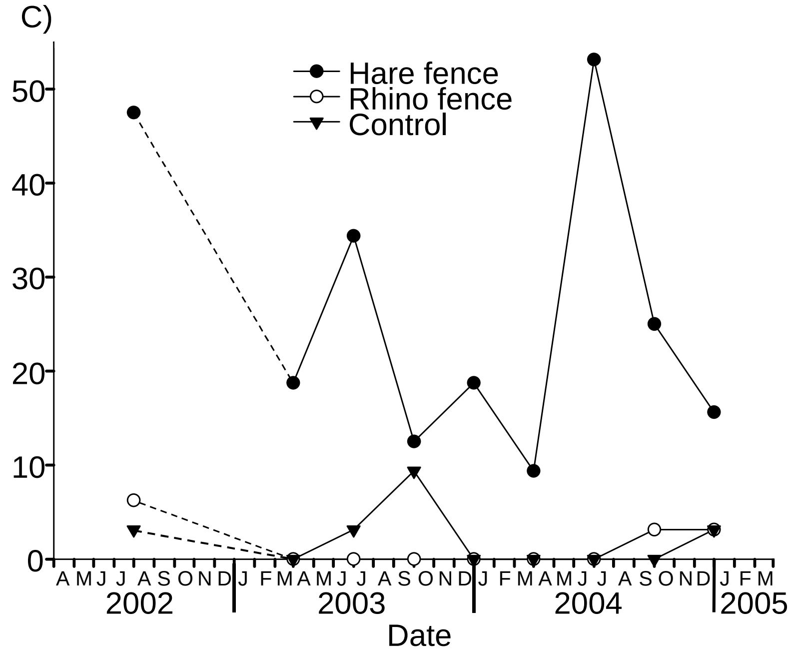


Fig 3 Density of murid rodents (total number of individuals over all species) for the different fencing treatments at the Hluhluwe (A and B) and iMfolozi sites (C) for July 2002 to December 2004. Overall, differences in numbers between treatments are statistically significant (Repeated Measures ANOVA, $F_{32, 32} = 1.99$, $P = 0.028$) at the Hluhluwe sites

We found no impact of fire on the abundance of rodents at either Hluhluwe or iMfolozi. Overall, the trapping success increased with decreasing large herbivore numbers at both the Hluhluwe sites ($F_{4, 85} = 2.688$, $P = 0.037$) and iMfolozi sites ($F_{2, 51} = 12.567$, $P < 0.001$). Rodents moved significantly longer distances between trapping locations in the presence of all large herbivores at the Hluhluwe sites ($F_{4, 109} = 3.489$, $P = 0.01$; Fig. 4A). No effect of the presence or absence of large herbivores on the distance rodents moved between trapping locations was found at the iMfolozi sites ($F_{2, 147} = 0.535$, $P = 0.587$; Fig. 4B).

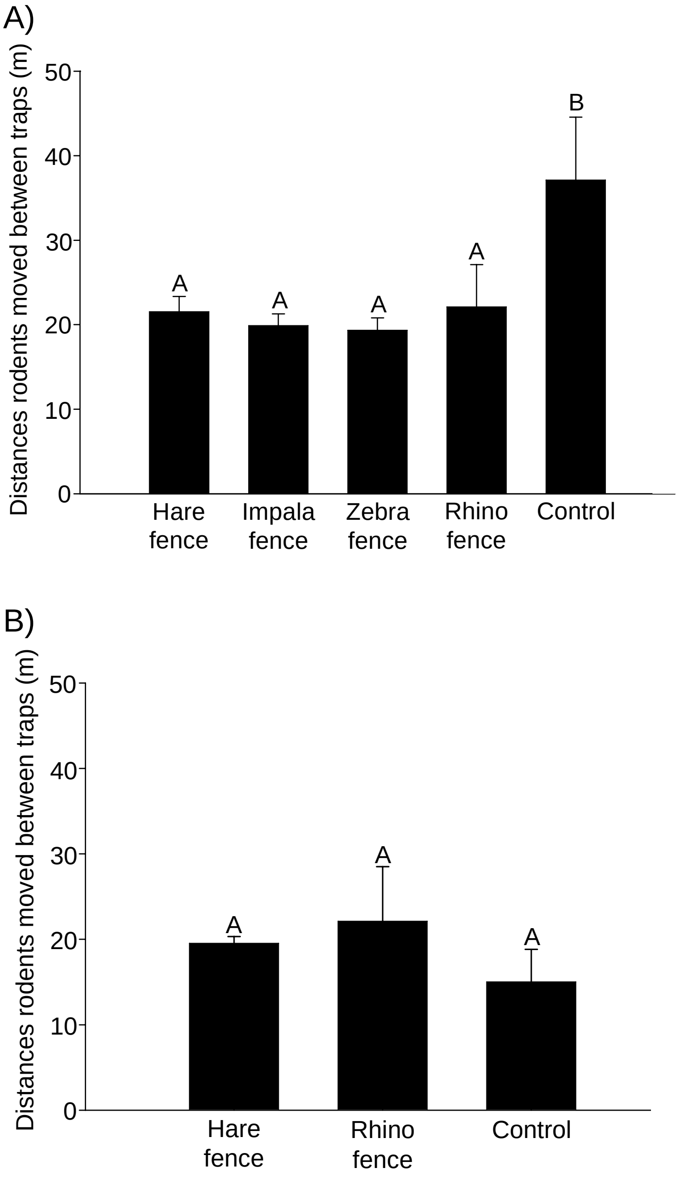


Fig 4 Mean distances murid rodents moved between trapping locations at the Hluhluwe (A) and iMfolozi sites (B) over all trapping periods (± SE, n = 9). Different letters show significant differences, $P = 0.01$.

The diet of *L. rosalia spinalis* consists mainly of graminoid leafs and stems, fruits and arthropods (Fig. 5). However, their overall diet composition is significantly different between the Hluhluwe and iMfolozi sites ($X^2_4 = 20.708$, $P = 0.001$).

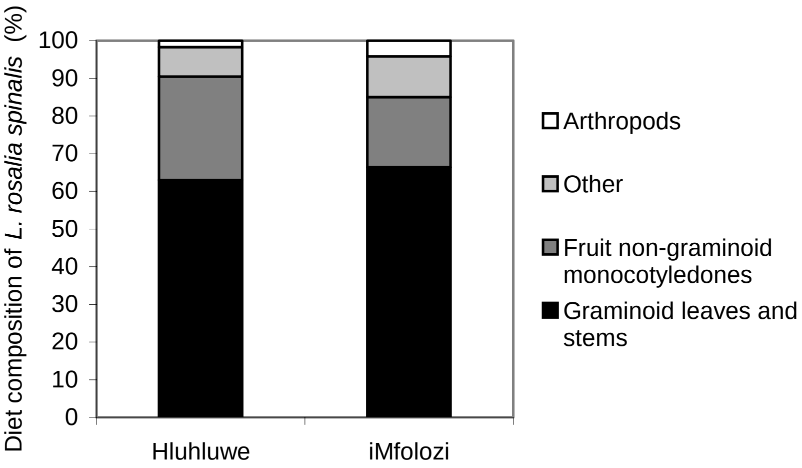


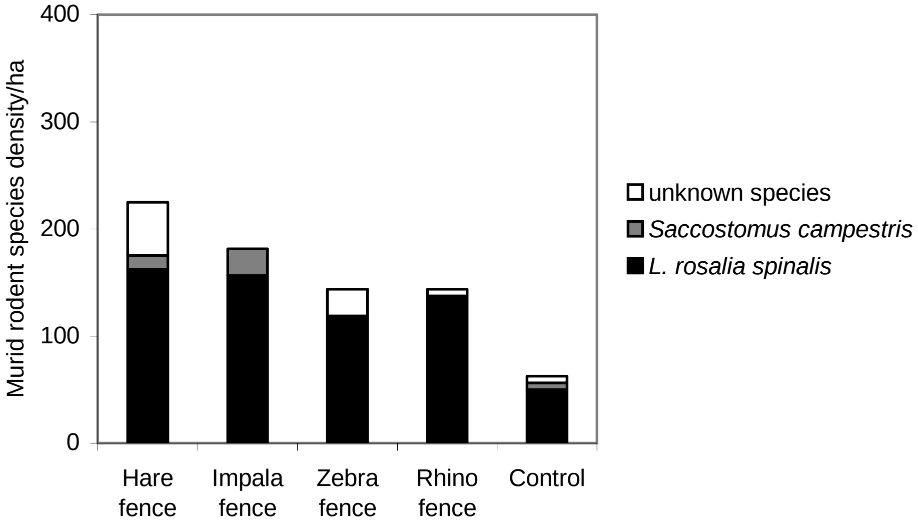
Fig 5 Diet composition of *L. rosalia spinalis* at the Hluhluwe and iMfolozi sites in July 2002. The diet composition was significantly different between the Hluhluwe and iMfolozi sites (n = 12, $X^2_4 = 20.708$, $P = 0.001$).

Considering only the graminoid diet components, *L. rosalia spinalis* consumed significantly different grass species at the Hluhluwe than at the iMfolozi sites ($X^2_9 = 708.29$, $P < 0.001$). At the Hluhluwe sites they mostly fed on two low quality bunch grass species, *S. africanus* and *E. curvula* (Fig. 6), as well as on the high quality lawn grass *S. nitens*. At the iMfolozi sites they mostly fed on the high quality lawn grass species *U. mosambicensis* (Fig. 6), however *T. triandra*, a lower quality bunch grass species, was also detected in their diet. No differences in the body weight of rodents were found in the presence or absence of larger herbivores at either the Hluhluwe ($F_{4, 176} = 0,814$, $P = 0.52$) or iMfolozi sites ($F_{2, 162} = 0.257$, $P = 0.77$).

Fig 6 Grass species composition of the *L. rosalia spinalis* diet at the Hluhluwe and iMfolozi sites in July 2002. The grass species composition was significantly different between the Hluhluwe and iMfolozi sites (n = 12, $X^2_9 = 708.29$, $P < 0.001$).

The vegetation height had a significant impact on the trapping success at both the Hluhluwe sites (Waldl = 5.49, $P = 0.019$) and iMfolozi sites (Waldl = 38.36, $P < 0.001$). A significant higher trapping success was measured with increasing vegetation height. Overall, the composition of rodent species showed different responses to the exclusion of different-sized large herbivores. *L. rosalia spinalis* was present in all fencing treatments at both the Hluhluwe and iMfolozi sites, while *S. campestris* was captured only after exclusion of herbivores larger than antelopes, and only at the Hluhluwe sites (Fig. 7A). *M. natalensis* and *Aethomys* spp. were captured only in large herbivore absence at the iMfolozi sites (Fig. 7B). Overall, the composition of the rodent species assemblage in the presence or absence of different-sized larger herbivore species at the Hluhluwe sites were significantly different ($X^2_8 = 29.594$, $P < 0.001$), whereas no significant differences were detected at the iMfolozi sites ($X^2_6 = 9.184$, $P = 0.164$). In addition, the composition of the rodent species assemblage was significantly different between Huhluwe and iMfolozi sites ($X^2_4 = 60.704$, $P < 0.001$).

A)



B)

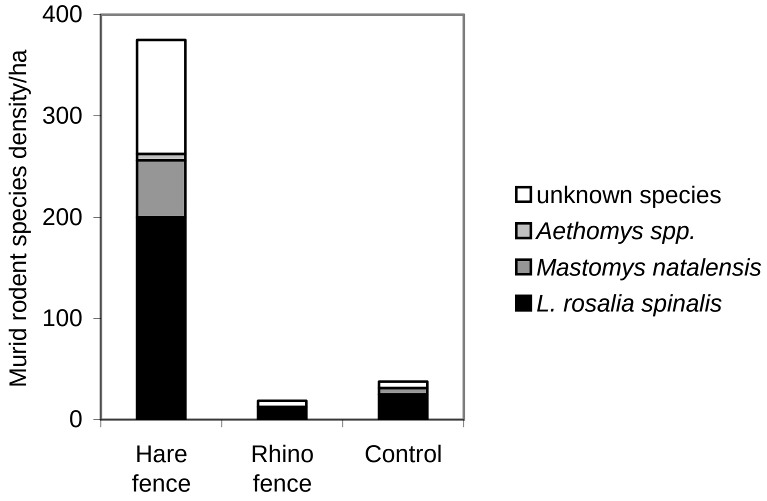


Fig 7 Density of murid rodent species captured in the different fencing treatments at the Hluhluwe (A) and iMfolozi sites (B) for July 2002 to December 2004. The rodent species composition was significantly different between the fencing treatments at the Hluhluwe sites (A) (n = 9, $X^2_8 = 29.594$, $P < 0.001$).

Discussion

The exclusion of large herbivores strongly affected the plant species composition and height of the vegetation. Rodent abundance increased with decreasing large herbivore numbers and increasing vegetation height. Large herbivores had no impact on the grass species composition in the diet of *L. rosalia spinalis*, rodent body weight or on distances they moved. However, rodent species composition appeared to be influenced by rainfall rather than by large herbivores. We conclude therefore that rodents may be influenced by their interactions with larger herbivores and through the indirect effects of microclimate and soil characteristics.

Effects of large herbivores on murid rodents

It has been suggested that large herbivores could cause soil disturbance through trampling (Keesing 1998b), which may affect murid rodents positively by loosening the soil and allowing them to more easily dig burrows. In our study we found that rodents did dig and use burrows (see also Keesing 1998a), but that the opportunity to dig or use burrows had no impact on rodent numbers or diversity (Hagenah et al., unpubl. data), therefore this effect seems unlikely to be a major factor.

Heavy grazing results in areas with short vegetation that are less likely to burn or that have less intense fires (van de Vijver 1999, van Langevelde et al. 2003). Rodents living in habitats with short vegetation would be expected to be safer from being killed by fires and therefore might occur in higher numbers. In this study we did not find any evidence that fire had an impact on the abundance and diversity of rodents.

Grazing herbivores play an important role in creating mosaic patches of short and long vegetation (Vesey-FitzGerald 1969, 1972; Beecham et al. 1999, Cromsigt and Olff in press) that differ in quality and quantity. Therefore it has been predicted that the removal of large herbivores would lead to changes in the quantity and quality of food available to rodents. In the presented study the exclusion of large herbivores lead to changes in both food quantity and plant species composition, increasing the abundance of high quality plant species available to rodents. Furthermore all rodents captured were mostly herbivorous and therefore potentially competing with large herbivores for food resources. They maintained the same body weights and moved the same distances regardless of higher numbers when large herbivores were absent. However, no large herbivore-induced differences in the vegetation composition were reflected in the diet of *Lemniscomys rosalia spinalis*. They revealed a strong preference for the most abundant grass species occurring in their habitat, rather than for high quality grass species. The cause of this is yet unclear.

Trampling and grazing by large herbivores have been shown to reduce vegetation cover (Grant et al. 1982, Bock et al. 1984, McInnes et al. 1992, Pacala and Crawley 1992), but the amount of cover is considered important for protecting rodents from predators (Cook 1959, Birney et al. 1976, Edge et al. 1995, Peles and Barret 1996). We therefore expected that the exclusion of large herbivores would result in increased vegetation cover, and that rodents would be less exposed to predators which could lead to an increase in their abundance. The present study showed that the exclosure of large herbivores lead to an increase in vegetation height, and that rodents became more abundant with decreasing large herbivore numbers and increasing vegetation cover. Smit et al. (2001) also found taller vegetation and higher rodent density after the exclusion of large herbivores. It appeared that the vegetation height was correlated with the rodent density; a higher vegetation height may imply a better habitat for rodents as they benefit from closed vegetation cover through a lower predation risk (Kotler 1984, Kotler and Blaustein 1995). In some habitats, however, small mammal numbers increase in the absence of larger herbivores despite detectable differences in vegetation cover (Heske and Campbell 1991, Keesing 1998a, 1998b, 2000). Nevertheless, we conclude that large grazing herbivores most likely influence rodent abundance through the reduction of the vegetation cover and the subsequent increase in their exposure to predators, especially raptors, which are abundant in HiP.

Effect of the rainfall gradient on herbivore interactions

It has often been suggested that high amounts of plant-available moisture leads to increased plant productivity, whereas little amount of plant-available moisture results in low plant productivity (e.g., Walker and Langridge 1997, Olff et al. 2002), and that this in turn may affect the herbivore community interactions. This study revealed that the rainfall gradient in combination with high grazing pressure of large herbivores may be a possible explanation for the differences in the small mammal species composition. The most abundant species *L. rosalia spinalis* was found at both the

Hluhluwe (high rainfall area) and iMfolozi sites (low rainfall area), whereas *Saccostomus campestris* was found at the Hluhluwe sites exclusively and *Mastomys natalensis* was only captured at the iMfolozi sites. *L. rosalia spinalis* are known to occupy herbivore niches as they tend to be herbivorous (Monadjem 1997b). Their most important requirement seems to be the presence of dense ground cover of long grass (Monadjem 1997a, Taylor 1998) and they avoid recently burnt areas (Monadjem and Perrin 1997) as they appear to breed in surface grass nests (De Graaff 1981). High rainfalls at Hluhluwe may promote tall bunch grasses and thus high plant biomass production in spite of heavy grazing by large herbivores. Tall bunch grasses in turn provide good shelter and rodents living in these habitats are therefore less exposed to their predators. *Saccostomus campestris* are slow moving animals that often fall prey to carnivores (Taylor 1998). Therefore it is likely that this species prefers tall bunch grass dominated habitat rather than a habitat dominated by short grazing lawn grasses. At iMfolozi low rainfalls combined with high grazing pressure of large herbivores leads to a vegetation dominated by short grazing lawn grass species that produce little plant biomass. Rodents in these habitats are more exposed to predators as there is not much shelter. *Mastomys natalensis* is known to be a pioneer species in the colonisation of heavily overgrazed areas (Meester, Lloyd and Rowe-Rowe 1979) and seems therefore to be able to successfully colonise these areas. Therefore we think that rainfall differences in combination with predation may affect the interactions of small and large herbivores in this savanna.

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References

Arsenault R, Owen-Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313-318

Barnett A, Dutton J (1995) Expedition field techniques:Small mammals (excluding bats). Expedition Advisory Centre, London, England

Beecham JA, Oom SP, Hester AJ, Maudsley M, Marshall J (1999) The role of animal decisions in the development of vegetation dynamics. Heterogeneity in landscape ecology:pattern and scale, Proceedings of the eighth Annual Conference of the International Association for Landscape Ecology, Bristol

Birney EC, Grant WE, Baird DD (1976) Importance of vegetative cover to cycles of Microtus Populations. Ecology 57:1043-1051

Bock CE, Bock JH, Kenney WR, Hawthrone VM (1984) Responses of birds, rodents, and vegetation to livestock exclosure in a semi desert grassland site. Journal of Range Management 37:239-242

Conway A, Balfour D, Dale T, Hartley P, Morrison P, Howison R, Galli N, Wadge M (2001) Hluhluwe-Umfolozi Park Management Plan 2001. Ezemvelo KwaZulu-Natal Wildlife

Cook SF (1959) The effects of fire on a population of small rodents. Ecology 40:102-108

Cromsigt JPGM, Olff H (in press) Resource partitioning amongst large grazerm mediated by local heterogeneity: an experimental approach

De Graaf G (1981) The rodents of southern Africa. Pretoria: Butterworths

Edge WD, Wolff JO, Carey RL (1995) Density-dependent responses of gray-tailed voles to moving. Journal of Wildlife Management 59:245-251

Farnsworth KD, Focardi S, Beecham JA (2002) Grassland-herbivore interactions: How do grazers coexist? American Naturalist 159:24-39

Goheen JR, Keesing F, Allan BF, Ogada DL, Ostfeld RS (2004) Net effects of large mammals on Acacia seedling survival in an African savanna. Ecology 85:1555-1561

Grant WE, Birney EC, French NR, Swift DM (1982) Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetation cover. Journal of Mammalogy 63:248-260

Gurnell J, Flowerdew JR (1990) Live trapping small mammals. A practical guide. Occassional Publications of the Mammal Society of London 3:1-39

Heske EJ, Campbell M (1991) Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, south-eastern Arizona. Southwest Naturalist 36:89-93

Keesing F (1997) Ecological interactions between small mammals, large mammals, and vegetation in a tropical savanna of central Kenya. PhD thesis, University of California, Berkeley

Keesing F (1998a) Ecology and behaviour of the pouched mouse (Saccostomus mearnsi) in central Kenya, Journal of Mammalogy 73:919-931

Keesing F (1998b) Impacts of ungulates on the demography and diversity of small mammals in central Kenya, Oecologia 116:381-389

Keesing F (2000) Cryptic consumers and the ecology of an african savanna. BioScience 50:205-215

Kotler BP (1984) Risk of predation and the structure of desert rodent communities. Ecology 65:689-701

Kotler BP, Blaustein L (1995) Titrating food and safety in a heterogeneous environment: when are risky and safe patches of equal value? Oikos 74:251-258

McInnes PF, Naiman RJ, Pastor J, Cohen Y (1992) Effects of moose browsing on vegetation and litter of the boreal forest isle Royale Michigan, USA. Ecology 73:2059-2075

Meester J, Lloyd CNV, Rowe-Rowe DT (1979) A note on the ecological role of Praomys natalensis. South African Journal of Science, 75, 183-184

Monadjem A (1997a) Habitat preferences and biomasses of small mammals in Swaziland. African Journal of Ecology 35:64-72

Monadjem A (1997b) Stomach contents of 19 species of small mammals in Swaziland. African Journal of Ecology 35:64-72

Monadjem A, Perrin MR (1997) Population dynamics of Lemniscomys rosalia (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. South African Journal of Zoology 32:129-135

Olff H, Ritchie M, Prins HHT (2002) Global environmental control of diversity in large herbivores. Nature 415:901-904

Owen-Smith N (1988) Megaherbivores. The influence of very large body size on Ecology. Cambridge University Press, Cambridge

Pacala SW, Crawley MJ (1992) Herbivores and plant diversity. American Naturalist 140:243-260

Peles JD, Barrett GW (1996) Effects of vegetation cover on the population dynamics of meadow voles. Journal of Mammalogy 77:857-869

Prins HHT, Douglas-Hamilton I (1990) Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83:392-400

Prins HHT, Olff H (1997) Species richness of African grazer assemblages: towards a functional explanation. in: Dynamics of tropical communities. (ed. by D. Newbery, H.H.T. Prins, & N.D. Brown), pp. 448 - 490. Blackwell, Oxford

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

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 155:119-127.

Stuart C, Stuart T (2003) A field guide to the tracks and signs of Southern and East African Wildlife. Struik Publishers

Taylor P (1998) The smaller mammals of KwaZulu-Natal, University of Natal Press, Pietermaritzburg

Van de Vijver CADM (1999) Fire and life in Tarangire. Effects of burning and herbivory on an East African savanna system. PhD thesis. Wageningen University, Wageningen, the Netherlands

Van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroossnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337-350

Van Oudtshoorn FP (1992) Guide to grasses of South Africa. Briza Publications, Arcadia, South Africa

Vesey-FitzGerald DF (1969) Utilization of the habitat of the buffalo in Lake Manyara National Park. East African Wildlife Journal 7:131-145

Vesey-FitzGerald DF (1972) Fire and animal impact on vegetation in Tanzania National Parks. Proceeding of Tall Timbers Fire Ecological Conference 11:297-317

Walker BH, Langridge JL (1997) Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): A case study from Australia. Journal of Biogeography 24:813-825

Chapter 3

Response of different-sized herbivores to fire history

N. Hagenah, J.P.G.M. Cromsigt, H. Olff, H.H.T. Prins

Abstract

High herbivore densities and re-occurring fires are natural phenomenons that determine the structure and functioning of African savannas. Traditional burning practices have been intensified over the past years due to increased herbivore numbers. Insight how animals respond to fire is important to understand ecosystem functioning and for the use of fire as management tool. Until now studies have centred mainly on spatial relationships between herbivores and fires. Very little information exists on effects of temporal fire patterns on herbivore communities. To assess the effect of fire succession on herbivore species greatly differing in body mass we conducted experiments and observational studies on smaller scales and landscape scales. We investigated the response of herbivores on both short-term and long-term succession patterns. Rodent densities were affected by the presence of larger herbivores rather than by seasonal patterns and increased with the absence of large herbivores and increasing vegetation height. Both middle-sized and large herbivore species responded on short-term post-fire patterns with large species being the pioneer species on burnt patches, whereas buffalo was the only species that also responded on long-term post-fire patterns. Our results indicate that larger herbivores in interaction with fire influence rodents by both increasing and prolonging the predation risk they experience in these habitats. Furthermore grazer presence and the amount of rainfall may be two interacting factors that prolong fire patterns in the landscape. Particularly buffalo responded to fire patterns, most likely due to the higher intake levels of digestible plant material and increased forage efficiency.

Nomenclature: *Digitaria longiflora* (Retz.) Pers., *Eragrostis curvula* (Schrad.) Nees, *Eragrostis superba* Peyr., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) A. Robyns & Tournay, *Themeda triandra* Forsk.

Introduction

African savannas are affected by a high diversity of different-sized herbivores and re-occurring fires (Sankaran et al. 2005) since millennia. Herbivory and fire are two interacting factors that determine the structure and functioning of these systems (Walker 1981, van de Vijver 1999, Roques et al. 2001, van Langevelde et al. 2003). Increased herbivore numbers have resulted in the intensification of burning practices, in order to provide herbivores with an abundant grass vegetation of high quality (West 1965, 1972, Vogl 1974, Frost and Robertson 1987), as a consequence many areas burn annually. Insight how animals respond to fire has therefore important implications not only for understanding ecosystem functioning but also for the use of fire to manage these savanna systems. Facilitation (Vesey-Fitzgerald 1960, de Boer and Prins 1990) and resource partitioning between herbivores (Jarman and Sinclair 1979, Voeten and Prins 1999) in fire-created mosaics may be an important explanation for the high density and diversity of mammalian wildlife in African savannas. However, most previous studies have focussed mainly on spatial relationships between fires and herbivores, not on the temporal patterns. The risk of drawing conclusions only from spatial relations is that these may be confounded with soil factors, distance to water etc. So far, it is not known how long temporal fire patterns in the landscape affect herbivore communities. Van de Vijver (1999) suggested that fire creates temporal landscape patterns but that any prolonged physical effects of fire on the vegetation disappear several months after the burn. This certainly applies for the knowledge of the effect of temporal fire patterns on small and large herbivores.

In the present study we investigate the effect of post-fire succession on different-sized savanna herbivore species and the community interactions between them. Additionally we looked for seasonal patterns in the response of herbivores to the fire history in order to explore the influence of rainfall. We hypothesise that temporal small and large scale fire patterns may affect the seasonal dynamics of landscape use of herbivores due to several possible mechanisms: In the short term fire can have small scale homogenising effects on the landscape (Hobbs et al. 1991) because after a burn any grazing patterns are eliminated (Adler et al. 2001) and the burned patch consists of short high quality regrowth. Herbivores generally prefer to forage on post-fire regrowth, the ‘green flush’ (Sinclair 1977, Moe et al. 1990, Stein et al 1992, Pfeiffer and Hartnett 1995, Sparks and Masters 1996, van de Vijver 1999) but species may respond differently in time after a burn depending on their body size (Wilsey 1996). Middle-sized herbivore species (e.g., warthog, nyala and impala) selectively feed on high quality food resources and thus leading to an overall short-term decline in the forage quality through removal of high quality items. They can deal with low food quantities shortly after the fire and are therefore expected to be the pioneer species on the regrowth of burnt vegetation patches. Large herbivore species (e.g., white rhino, buffalo, zebra and wildebeest), on the other hand, are more generalist feeders and can survive on lower food quality. They need high food quantities and may therefore only reoccur on burnt patches several months after the fire to achieve their feeding acquirements, especially after rains have promoted new biomass production. Both, large and middle-sized herbivores, may affect small herbivores (such as rodents) when they recolonise burnt areas through changing both their predation risk and the quality of food resources available to them (Fig. 1).

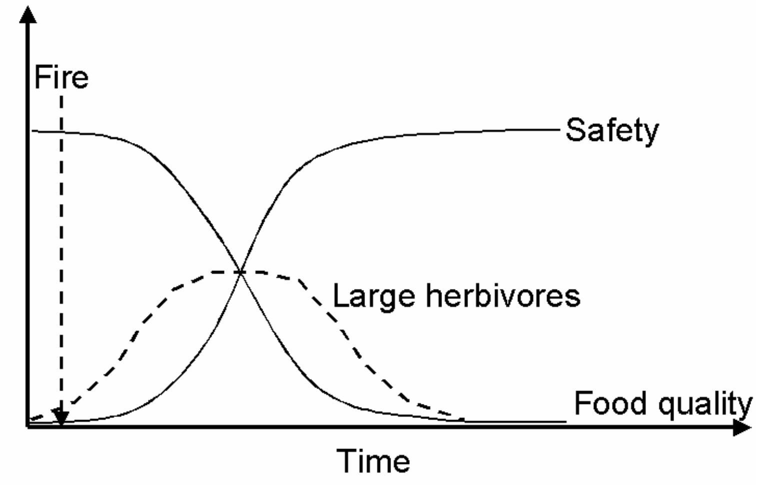


Fig 1 Impact of fire succession and larger herbivores on savanna rodents.

We hypothesised that shortly after the fire food quality for rodents is enhanced but the safety, especially regarding avian predators, is very low. In the course of the post-fire season food quality decreases but safety increases until several months after the fire conditions for rodents are optimal. After that optimum conditions for rodents may further improve in terms of safety but impair in terms of food quality.

Fires together with herbivores are important in creating large scale landscape mosaics in the long-term (Hochberg et al. 1994, Hobbs 1996, HilleRisLambers et al. 2001, Rietkerk et al. 2002, van Langevelde et al. 2003, Archibald et al. 2005). Fires in areas with huge fuel loads of dry plant material can cause severe damage or even death of shrubs and trees (Bond and van Wilgen 1996, Trollope et al. 2002) and thus may lead to structural open habitats after a burn. Extended temporal fire patterns may be maintained in the system for several years through the foraging behaviour of herbivores as they preferentially graze in areas of the most recent fire years. The effects of intense herbivore grazing may be displayed through preserved changes in the vegetation structure, species composition and plant nutritional status after a fire. Therefore the effects of fire may be indirectly maintained (Higgins et al. 2000) for periods longer than initially suspected. However, the degree to which herbivores maintain this process may be also linked to larger scale ecosystem properties such as seasonal rainfall (Rietkerk et al. 2002, van Langevelde et al. 2003, Sankaran et al. 2005) and whether herbivores make seasonal different choices regarding their foraging areas.

In this study, we experimentally investigated the seasonal response of different size groups of savanna herbivore species (small herbivores: rodents; middle-sized herbivores: warthog, nyala and impala; and large herbivores: white rhino, buffalo, zebra and wildebeest) to fire on a small scale. Furthermore we studied the effect of large scale fire patterns on the dynamics of herbivores and resulting community interactions between them.

Material and methods

Study site

This study was conducted between July 2003 and June 2005 in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa (28°13'S and 32°00'E). HiP is an 90,000 ha fenced protected area and the altitude in the park ranges from 60 m to 750 m (Conway et al. 2001). The climate is coastal, with temperatures from ± 13 °C to ± 35 °C. Vegetation growth is seasonal, rains generally fall between October and March with mean annual rainfall ranging from 985 mm in the northern to 650 mm in the southern areas. The park is characterised by savanna vegetation ranging from open grasslands to closed *Acacia* and broad-leaved riparian woodlands. Dominant grass species are *Digitaria longiflora*, *Eragrostis curvula, Eragrostis superba*, *Panicum maximum*, *Sporobolus africanus and Themeda triandra*. Fire is an important management tool in the park, where different areas are burnt with different frequencies. The aim of this fire management regime is to control bush encroachment and alien plants (Balfour and Howison 2001) but also to remove moribund grass material and thus improve quality and quantity of food resources for herbivores. It also has been predicted that the creation of habitats of different post fire ages would favour different herbivore species (Balfour 1999). HiP harbours a high diversity and biomass of indigenous large herbivores including white rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), nyala (*Tragelaphus angasi*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus aethiopicus*).

In this study we aimed to measure the effect of fire succession on several herbivore species greatly differing in sizes, from small rodents up to large herbivores like white rhino. We wanted to investigate whether herbivore species respond differently on succession patterns, depending on spatial scale or time after burn. In order to take these factors into account several experiments were conducted. Data presented will be categorised according to seasons: early wet season (EW), late wet season (LW), early dry season (LD) and late dry season (LD). Furthermore larger herbivores species are classified in groups according to their body masses (Tab. 1; large herbivores: white rhino, buffalo, zebra and wildebeest; middle-sized herbivores: warthog, nyala and impala).

Table 1 Feeding behaviour, body mass and total numbers (in 2004) of the most dominant large and middle-sized herbivore species in HiP. See for body mass: Prins and Olff 1997, feeding behaviour: Kingdon 1997, herbivore numbers: Cromsigt & Olff in press.

Species	Scientific name	Feeding behaviour	Body mass (kg)	Total numbers in HiP (2004)
White Rhino	*Ceratotherium simum*	Grazer	1875	1731
Buffalo	*Syncerus caffer*	Grazer	631	3152
Zebra	*Equus burchelli*	Grazer	235	3389
Wildebeest	*Connocheates taurinus*	Grazer	226	3082
Warthog	*Phacochoerus aethiopicus*	Grazer	74	3184
Nyala	*Tragelaphus angasi*	Browser	56	7490
Impala	*Aepyceros melampus*	Mixed-feeder	53	24471

Small scale experiments

Short-term response during post-fire succession

Rodent survey

Fences excluded all herbivore species larger than hares from 40 x 40 m plots of vegetation since late 1999 (Bond & Olff, unpubl. data). In an earlier study it was recorded that the exclusion of large herbivores lead to both increased grass height and higher abundances of high quality grass species such as *P. maximum* (*chapter 2*). To quantify rodent densities permanent trapping grids inside and outside the exclosure treatment were established (*chapter 2*). We conducted in total ten trapping sessions of four to five consecutive nights each from July 2002 until December 2004. The first trapping session was conducted at seven sites, the second and third trapping session at five sites and then trapping was continued at four sites until the end of the study. No trapping was conducted in the early wet season in 2002. The study sites were burned at the end of the early dry season in 2002 and 2004.

Large herbivore measurements

We selected two open *Themeda triandra* dominated bunch grassland sites (Mnqabatheki and Hlaza), each several hectares in size. In each grassland site we marked a one ha plot and laid out 10 fixed line transects, 10 meter apart, where we monitored vegetation height from the early dry season 2002 until the late wet season in 2005. Once per month we measured the height of the vegetation with a wooden disk of 46 cm in diameter that was fully lifted to the top of a pole with a height scale and then dropped onto the vegetation. The height at which the disk was resting on the vegetation was measured every meter along the 10 transects, resulting in 1000 measuring points per site per month. In each ha plot we created five fixed 1x5 meter sand beds around each side of the one ha plots to be able to count spoors of animals that visited the plots. To create these spoor plots we removed the top grass layer, creating a bed of a few cm deep. Thereafter, the bed was refilled with loamy sand from a local quarry. We checked the spoor plots for animal tracks once or twice a week between the late dry season 2002 until the early wet season 2005. Instead of counting individual tracks we counted individual track pathways. After each observation we wiped the spoor plots with a rake. During the period of the study the sites were burned at the end of the early dry season in 2002 and 2004.

Landscape scale observations on spatio-temporal patterns

We conducted herbivore observations while driving transects by car that were chosen to cross areas that differed in their fire history. Observations were done for three to four consecutive days per month for approximately seven hours per day from July 2003 until April 2005. We recorded the species, number of individuals, sex, age, behaviour and also the structural vegetation type of the area where animals were observed. Other data included the distance and compass direction towards the animal(s). The observer position was determined, using a GPS, in order to calculate the exact position of the herbivores with regard to the burn history of the different areas. During the period of the observations different areas along the transects were burnt in either 2003 or 2004. In order to take this into account we categorised these areas into classes, starting with zero for areas that were burnt in the year of observation and ending with the highest number for areas that were least recently burnt in the year of observation (Tab. 2).

Table 2 Size (in hectare) and classes of the areas with the most recent fires that were crossed during observations in 2003 and 2004.

year of last fire	observation year 2003	observed total area (hectare)	observation year 2004	observed total area (hectare)
2004	n.a.	n.a.	0	650.52
2003	0	535.03	1	442.69
2002	1	801.31	2	288.81
2001	2	218.81	3	344.10
2000	3	429.24	4	394.44
1999	4	320.93	5	167.06
1998	5	115.98	6	209.50
1997	6	116.14	7	108.84
1996	7	102.78	8	100.89
1995	8	120.00	9	30.36
1994	9	20.81	10	0.81
1993	10	0.00	11	21.07
1992	11	1.28	12	1.28
1991	12	4.72	13	26.74
1990	13	0.00	14	0.00

Areas of 2004 observations were categorised in the same class plus one as for 2003 observations. To analyse whether herbivores preferentially occurred in areas of a particular fire history we first estimated the total size of the different most recent fire patches along the transects within a buffer zone of 200 m. Then we calculated the proportion of each patch in comparison to the total size of the buffer zone and multiplied by the proportion of the herbivore occurrence in that area with the proportion of the fire patch according to Manly et al. (2002). However, only areas that measured at least 100 hectare were considered in further analysis. Additionally the structural vegetation type were recorded every 100 m within an area of approximately 50 m at both sides of the observation transects. To investigate both short- and long-term post-fire succession effects on the different herbivore species the data were analysed in two different ways. On a short-term level we particularly looked at the herbivore response within the first two years after a fire occurred in an area. To study long-term fire succession effects we also compared herbivore responses to areas that were burnt up to eight years ago.

Data-Analysis

The effect of the fence, the season within the post-fire succession and interaction effects of these factors on rodent abundance, survivorship and trapping probability (repeated capture of the same individuals) was tested with a univariate ANOVA followed by Tukey HSD tests. A three-way ANOVA followed by Tukey HSD tests was used to test for effects of the fence, season, sex or interaction effects of these factors on rodent body weight. Furthermore relations between trapping probability and vegetation height was analysed with logistic regression with small mammal presence/absence as the dependent variable and vegetation height as a predictor. A Pearson’s Chi-square test was used to test whether large herbivores or post-fire seasons affected rodent assemblages. To test whether the fire history of the areas affected the short-term response of middle-sized and large herbivore species on landscape scales a Pearson’s Chi-square test was used. Landscape scale short- and long-term vegetation type modifications due to fire and the effect of fire on the vegetation type middle-sized and large herbivores preferred to forage were also calculated by a Pearson’s Chi-square test. The long-term response of middle-sized and large herbivore species on landscape scale post-fire succession patterns was tested with a generalised linear model (linear regression).

Results

Small scales

Description of short-term post-fire succession

Rodent response on fire succession and larger herbivores
Between July 2002 and December 2004, we captured a total of 492 murid rodents, comprising of five species. The most frequently captured species was the single-striped mouse *(Lemniscomys rosalia spinalis*), representing about 73% of all captures. Other rodent species captured and identified included the natal multimammate mouse (*Mastomys natalensis)*, the pouched mouse (*Saccostomus*

campestris), norway rat (*Rattus norvegicus*) and bush-rats (*Aethomys* spp). Several captured rodents could not be identified on a species level.

Overall, the exclusion of larger herbivores lead to an significant increase in rodent abundance ($F_{1, 64}$ = 13.641, $P < 0.000$, Fig. 2), but neither seasonal differences ($F_{9, 64}$ = 0.915, $P = 0.518$) nor significant interactions between the season and the fence was detected ($F_{9, 64}$ = 0.406, $P = 0.927$).

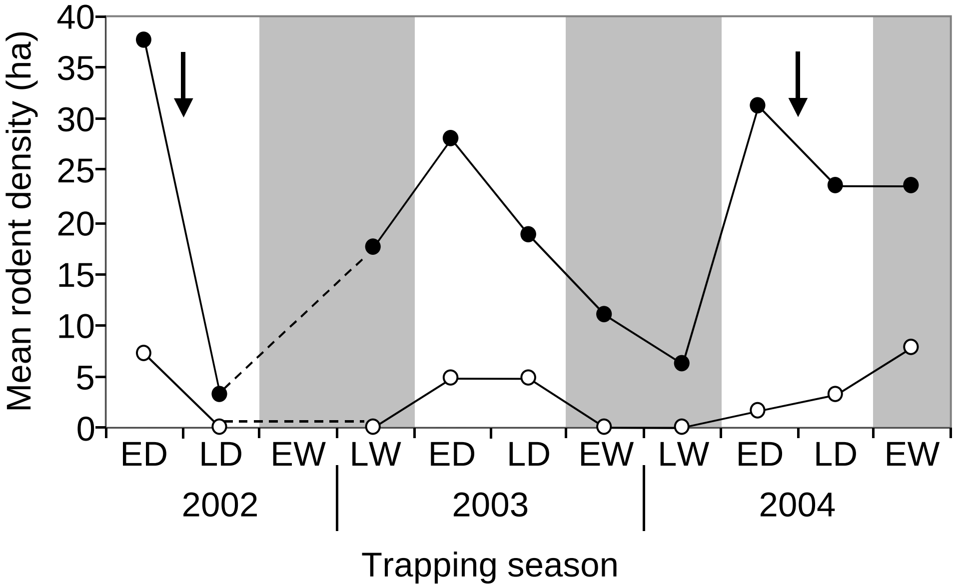


Fig 2 Mean abundance of murid rodents in presence (open circles) and absence of larger herbivores (solid circles) from the early dry season 2002 to early wet season 2004. Overall, the absence of larger herbivores lead to an significant increase in rodent abundance ($F_{1, 64}$ = 13.641, $P < 0.000$). Grey shaded areas represent wet seasons, arrows indicate fire events.

The probability that rodents were captured was also higher when larger herbivores were excluded ($F_{1, 62}$ = 11.676, $P = 0.001$), but again, no differences in season ($F_{9, 62}$ = 1.348, $P = 0.232$) nor significant season and fence interaction was revealed ($F_{9, 62}$ = 1.003, $P = 0.447$). Furthermore, the trapping probability increased with vegetation height (Waldl = 37.786, $P < 0.000$, Fig. 3). We detected no significant effect of the fence ($F_{1, 190}$ = 0.086, $P = 0.769$), season ($F_{9, 190}$ = 1.233, $P = 0.282$) or sex ($F_{1, 190}$ = 2.305, $P = 0.131$) nor interaction effects ($F_{3, 190}$ = 1.387, $P = 0.240$) on the body weight of rodents.

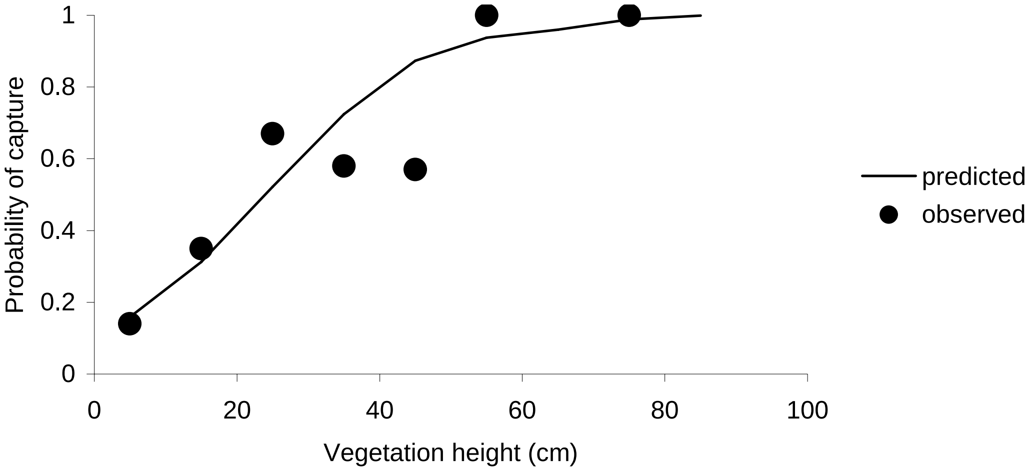


Fig 3 Overall trapping probability of rodents in different vegetation heights. The trapping probability significantly increased with vegetation height (Waldl = 37.786, $P < 0.000$).

Rodent survivorship was not affected by fence ($F_{1, 58} = 3.745$, $P = 0.058$), season ($F_{9, 58} = 1.10$, $P = 0.377$) or interaction affects ($F_{9, 58} = 1.297$, $P = 0.221$). Overall, the composition of rodent species was not influenced by the presence or absence of larger herbivores ($X^2_5 = 4.116$, $P = 0.533$, Fig 4).

Fig 4 Total murid rodent species composition in presence and absence of larger herbivores from July 2002 to December 2004. The composition of the species was not significantly different in absence or presence of larger herbivores ($X^2_5 = 4.116$, $P = 0.533$).

Impact of post-fire succession on larger herbivores and vegetation

In this small scale experiment larger herbivores responded strongly to the fire events at both study sites, Mnqabatheki and Hlaza. White rhino, buffalo, zebra and wildebeest were the first species found at the sites after the fire in both years 2002 and 2004. High densities were recorded within the first four months after the burns, during the late dry and early wet season (Fig. 5 A-D). In comparison, middle-sized herbivores such as warthog and nyala hardly occurred, while impala visitation increased in the early wet season shortly after the burn but decreased again to very low levels (Fig. 5 E-G). High densities of large herbivore species were recorded again in the early wet season 2003 and late wet season 2004, 15 to 19 months after the fire. Furthermore the overall herbivore density was higher at Hlaza than at Mnqabatheki.

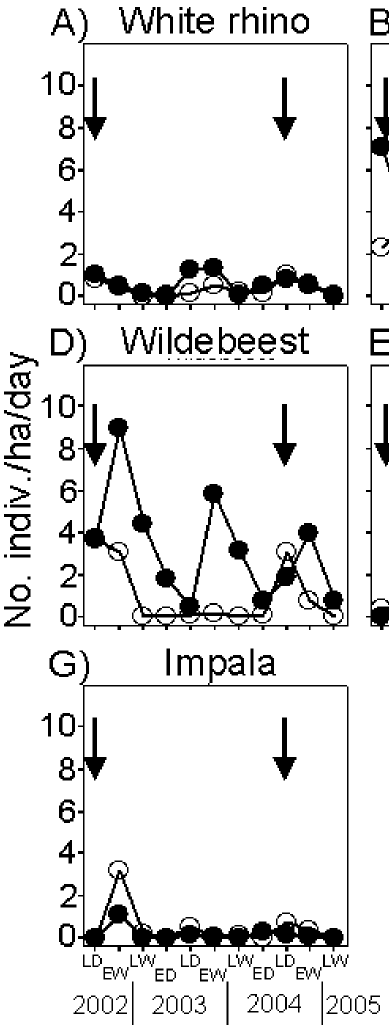


Fig 5 Total density of large (A to D) and middle-sized herbivore species (E to G) for Hlaza (solid circles) and Mnqabatheki (open circles) over the course of the post-fire succession from the late dry season 2002 to late wet season 2005 per hectare per day. Arrows indicate fire events.

The post-fire succession was also characterised by seasonal shifts in the grass height at both study sites, although patterns were less clear at Hlaza. In both late dry seasons in 2002 and 2004, the grass height sharply decreased immediately after the fire and stayed short for about six months, until beginning of the late wet season (Fig. 6).

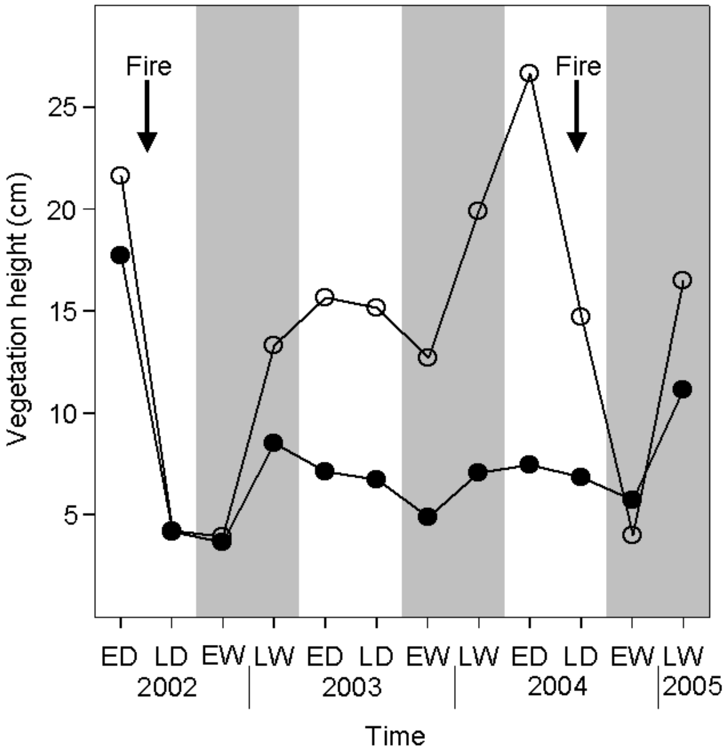


Fig 6 Seasonal mean vegetation height for Hlaza (solid circles) and Mnqabatheki (open circles) over the course of the post-fire succession from early dry season 2002 to late wet season 2005. Grey shaded areas represent wet seasons.

At the end of the late wet season in 2003 the grass height increased again until the early dry season, about 14 months after the burn. Then the grass height decreased again for four months and decreased drastically again after the second fire. Comparing the grass height between the two sites it appeared that generally grass was higher at Mnqabatheki than it was at Hlaza.

Landscape scale

Short-term post-fire succession of large herbivores

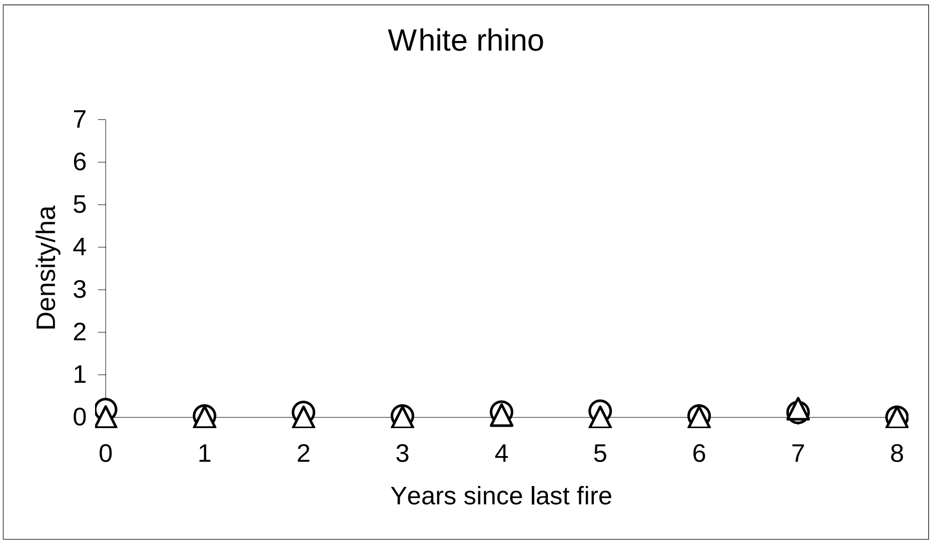
The herbivore observations revealed that the post-fire succession leads to different responses of the herbivore size groups (X^2_{138} = 1687.764, P < 0.00), if we consider the herbivore response within the first two years after the fire. Again large herbivores were the first species found on the burnt patches. High numbers were recorded within the first two months after the fire and again three months later. Middle-sized herbivores, on the other hand, firstly occurred in high densities about three months after the patches burnt and preferentially graze there for three months.

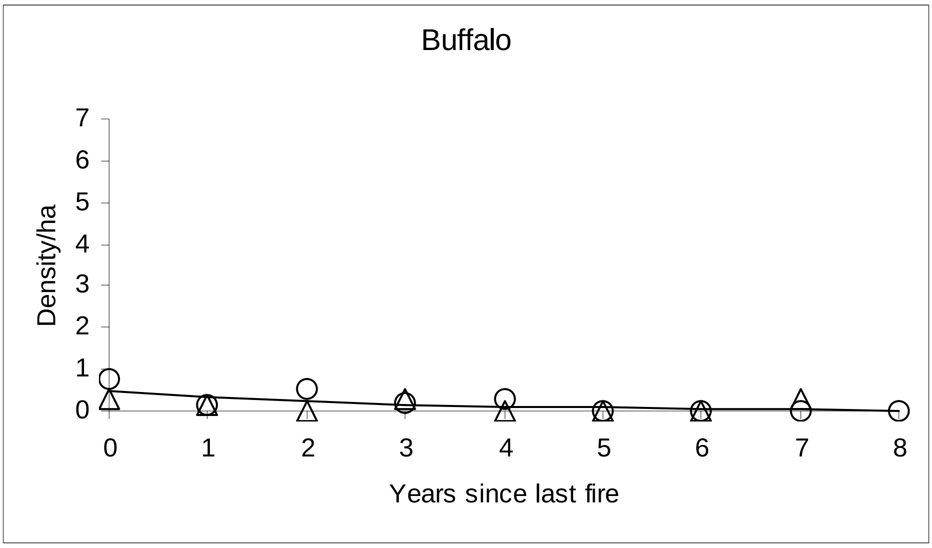
We found no shift in structural vegetation types due to a post-fire succession during the first two years after the fire. However, the post-fire succession lead to a shift in vegetation types the size groups of herbivore species preferred to forage (X^2_{18} = 705.997, $P < 0.00$). Within the first nine months after the fire 90 % of the forage activities of middle-sized herbivores took place in grasslands and open woodlands, whereas large herbivores only spent 75 % of their foraging time in those habitats. However, after that period both large and middle-sized herbivores almost exclusively feed in grasslands and open woodlands for the next 15 months.

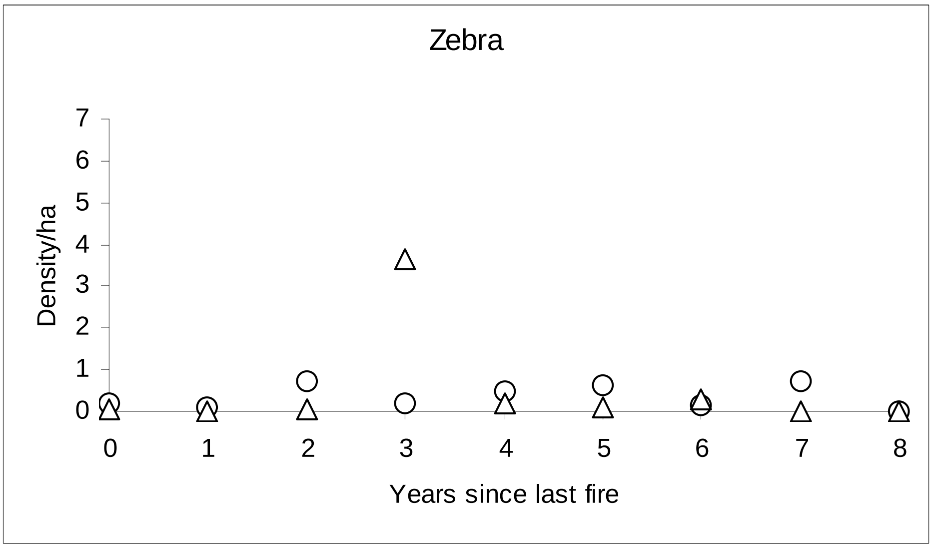
Long-term post-fire succession of large herbivores

The herbivore observations indicated that buffalo was the only species that showed in the wet season a significant trend for patches of the most recent fire year (linear regression: -0.371594, Wald: 7.267, $P = 0.007$, Fig 7A), if we take the long-term herbivore response into account. Impala, on the other hand, occurred in high numbers in areas that were burnt two years ago in the wet season 2003, whereas in the wet and dry season 2004 high numbers were found in areas that were burnt three years ago. All other species seemed to prefer vegetation patches that were burnt approximately three years ago, especially in the dry season 2004.

A)




Buffalo
Density/ha
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
8
Years since last fire


Zebra
Density/ha
7
6
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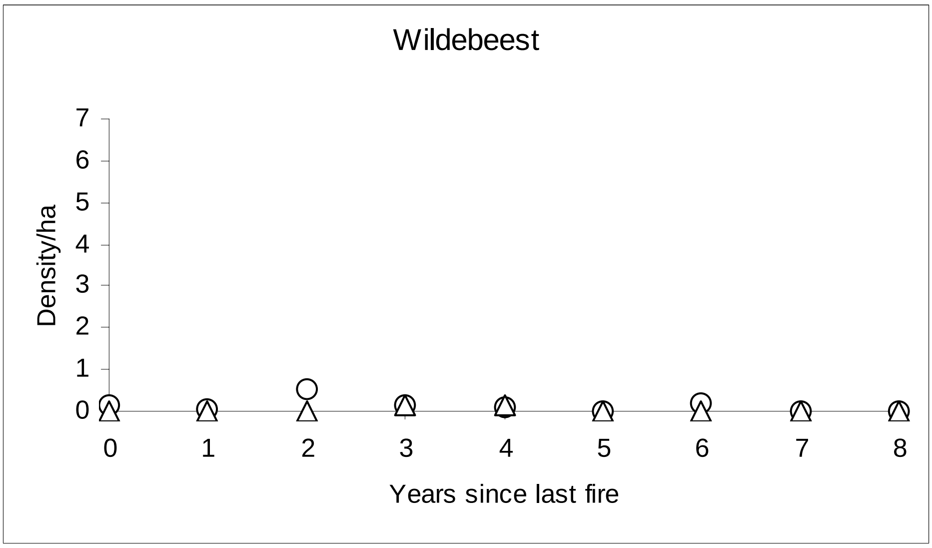
Years since last fire


Wildebeest
Density/ha
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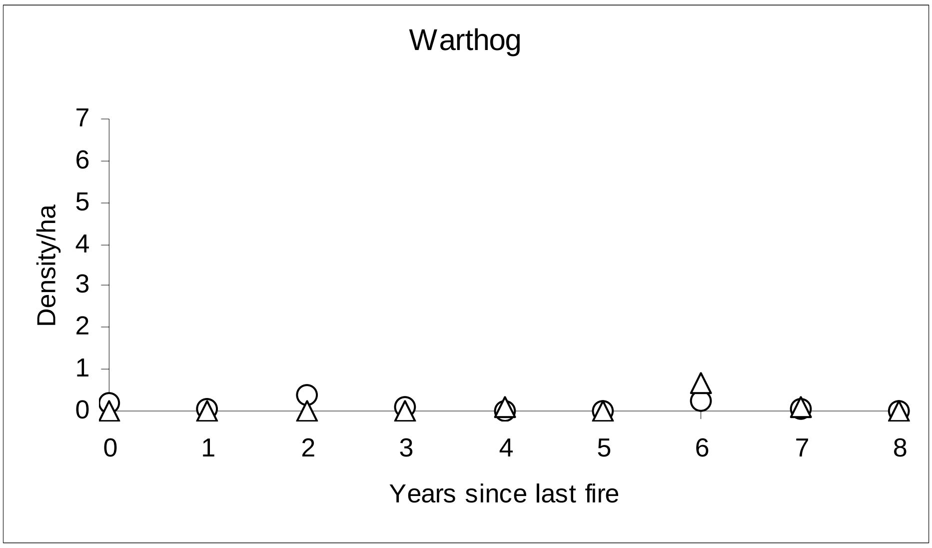
Years since last fire


Warthog
Density/ha
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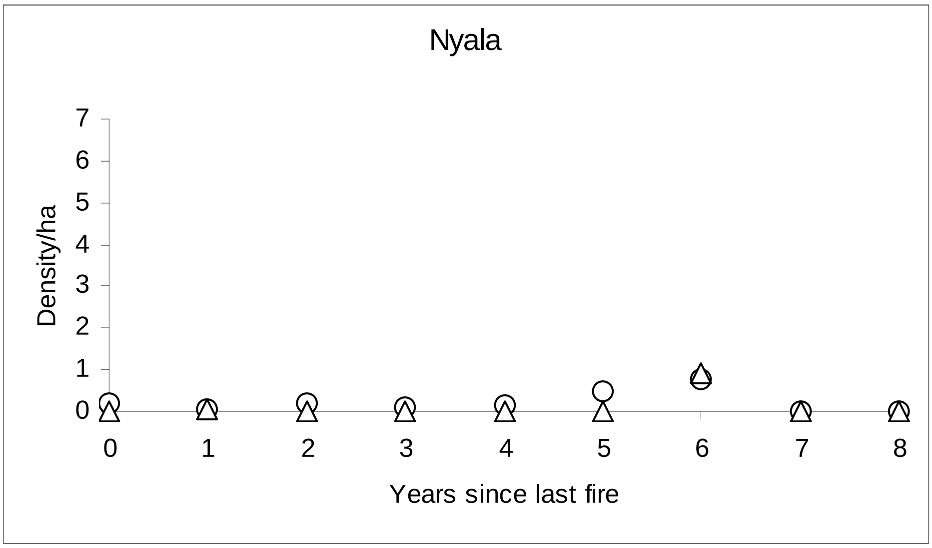
Years since last fire


Nyala
Density/ha
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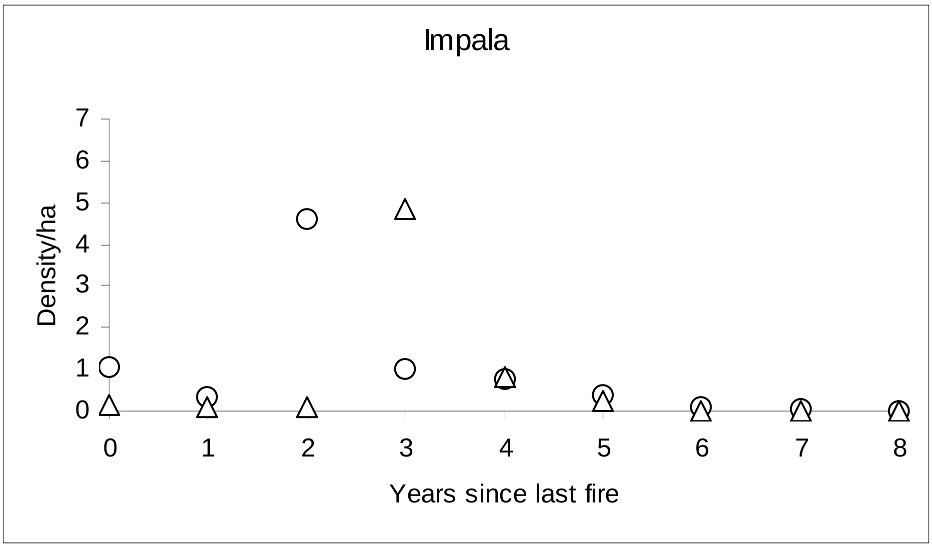
Years since last fire


Impala
Density/ha
0
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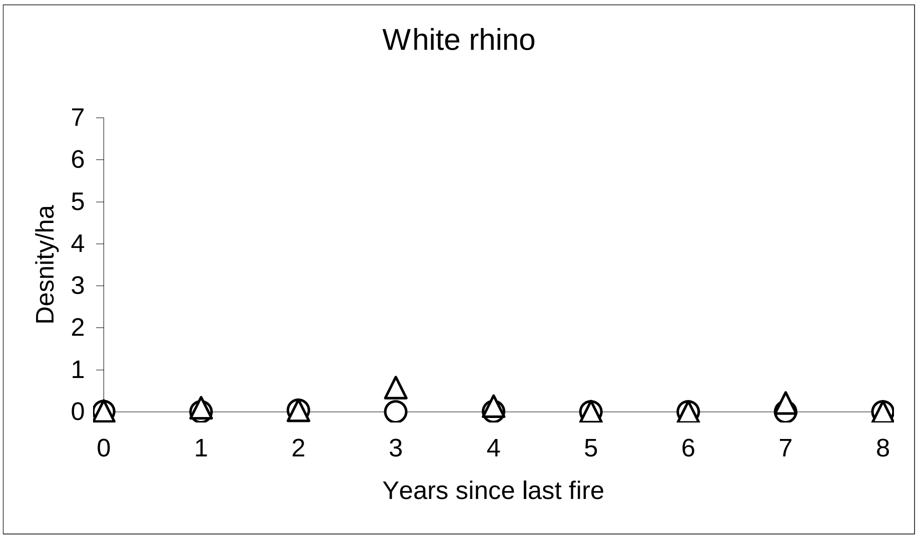
Years since last fire

B)


White rhino
Desnity/ha
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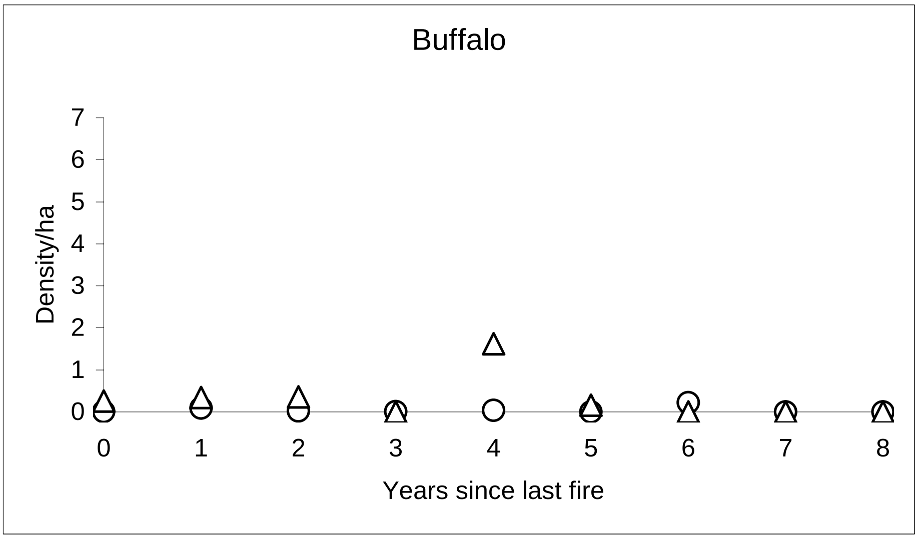
Years since last fire


Buffalo
Density/ha
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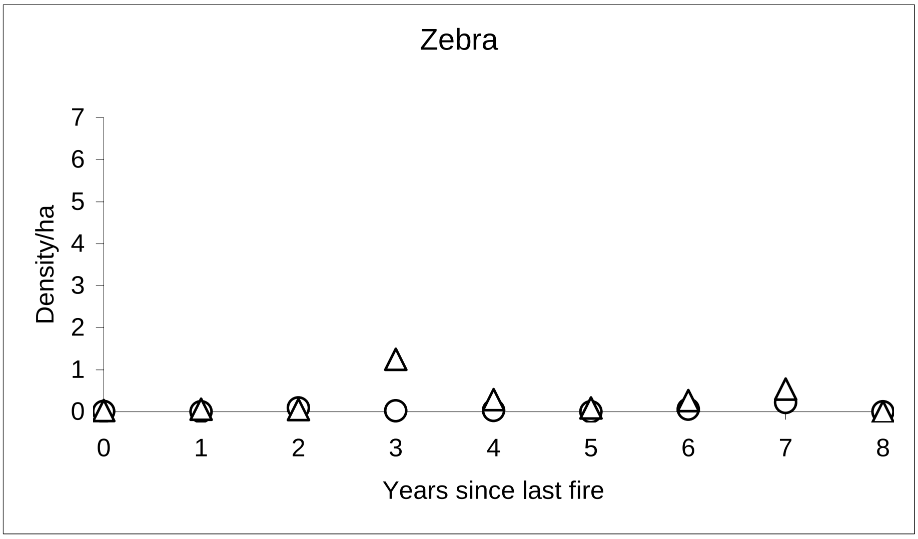
Years since last fire


Zebra
Density/ha
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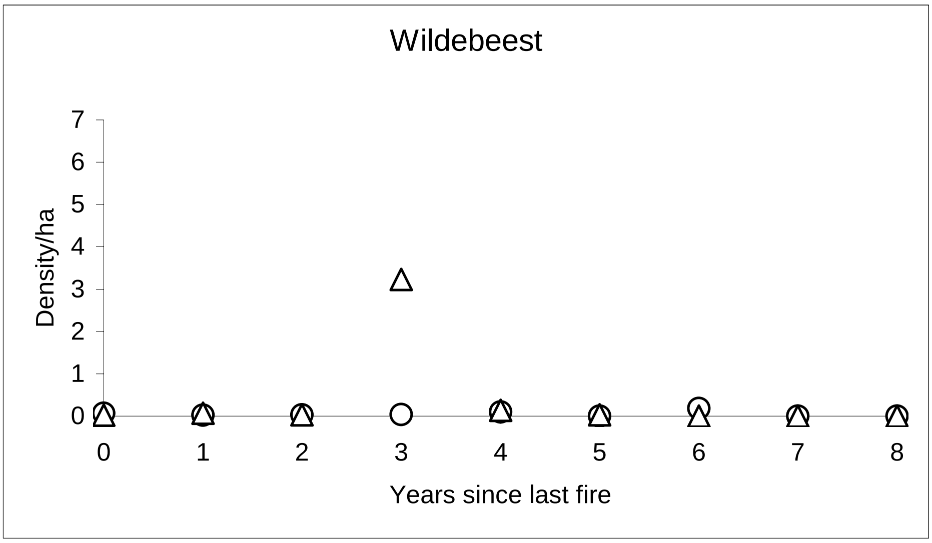
Years since last fire


Wildebeest
Density/ha
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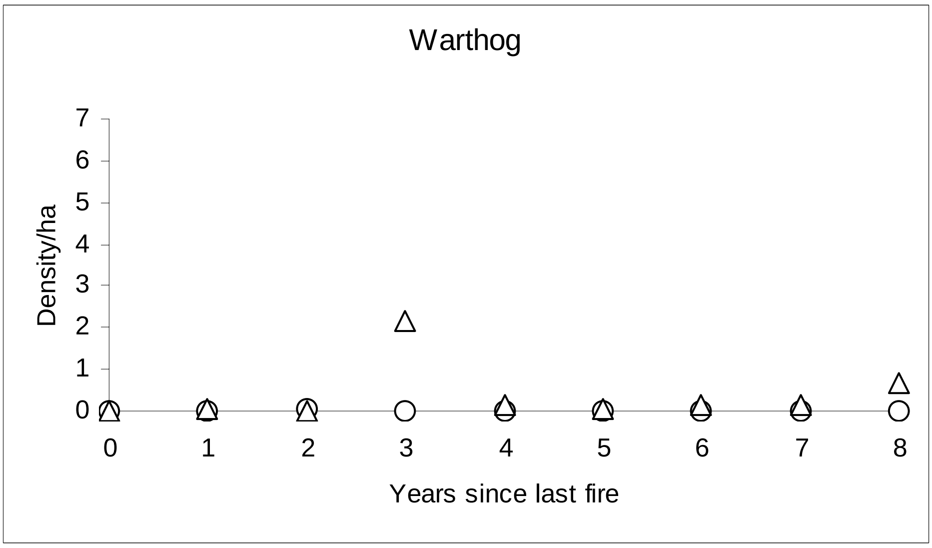
Years since last fire


Warthog
Density/ha
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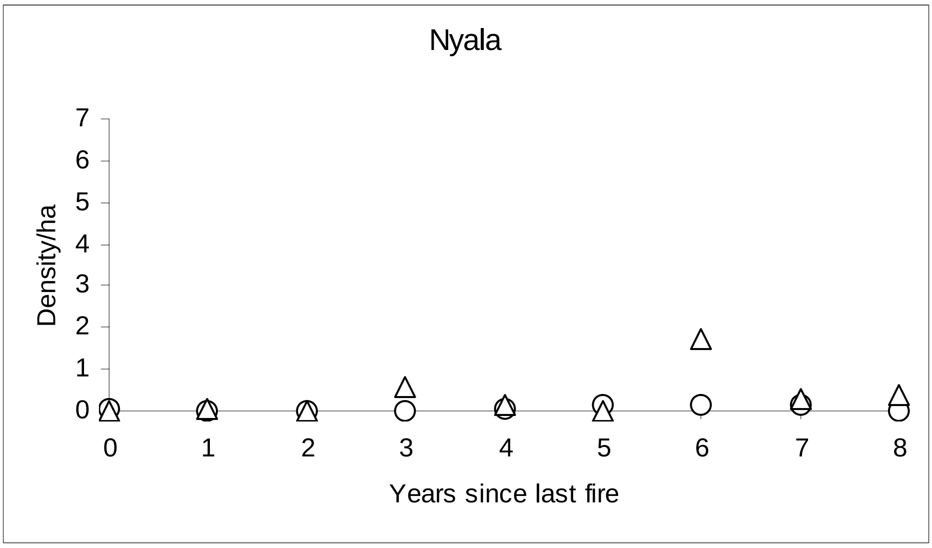
Years since last fire


Nyala
Density/ha
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Years since last fire

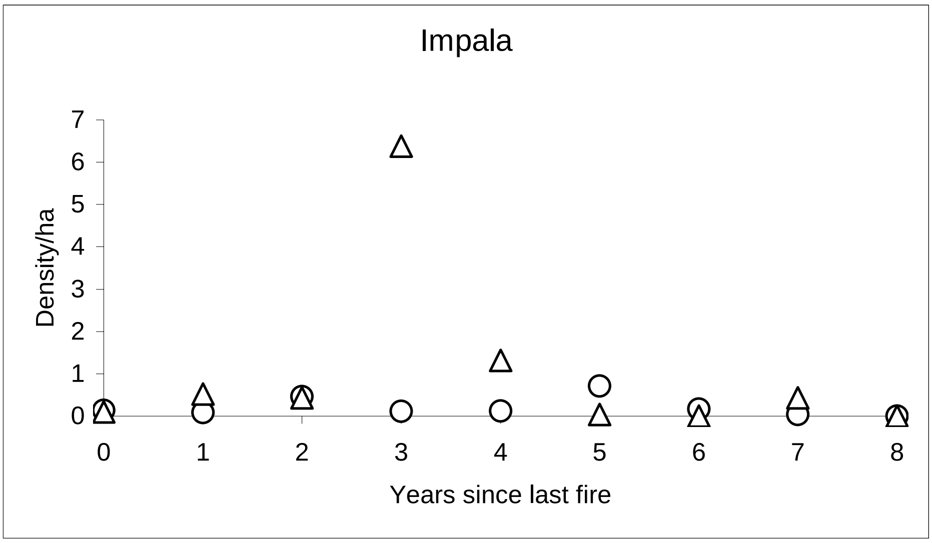


Fig 7 Number of individual herbivore species within eight years since the last burn for the wet (A) and dry season (B) in 2003 (circles) and 2004 (triangles). Buffalo was the only species that showed in the wet season a significant preference for patches of the most recent fire year (linear regression: -0.371594, Wald: 7.267, *P* = 0.007).

The post-fire succession was also characterised by a shift in structural vegetation types (X^2_{36} = 272.248, *P* < 0.00). Structural open vegetation types such as grasslands and open woodlands were mainly found within five years after the burn (Fig. 8).

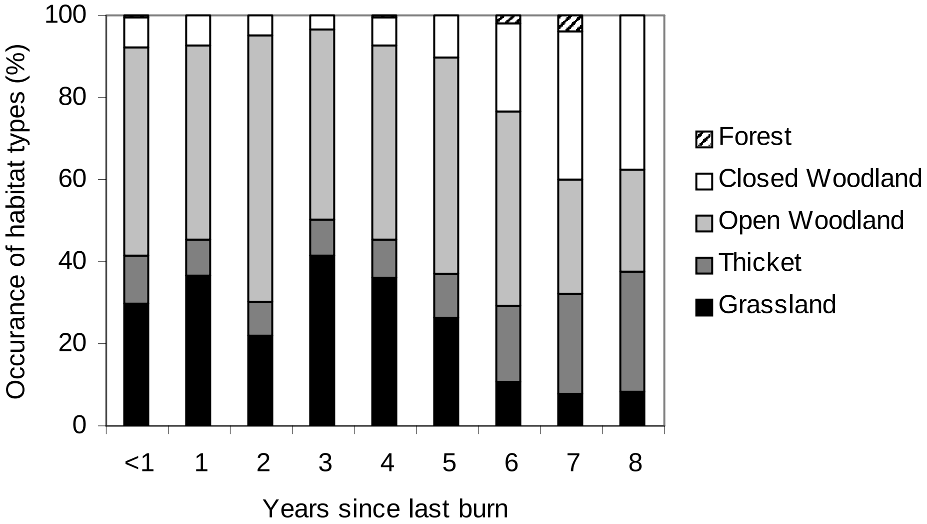
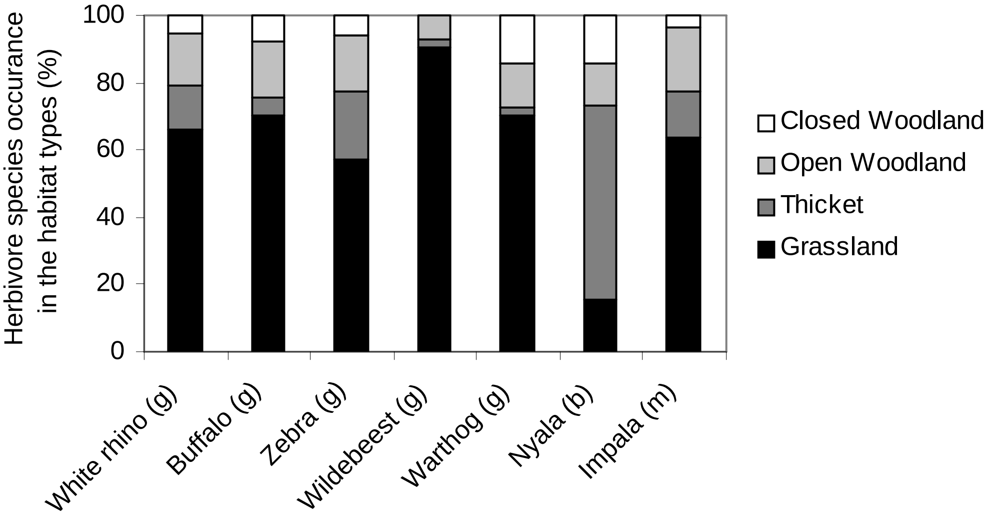


Fig 8 Frequency of occurrence of main habitat types (based on vegetation structure) within eight years since the last burn. The vegetation types showed a significantly shift over the course of the post-fire succession (X^2_{36} = 272.248, *P* < 0.00).

Additionally we found that the different-sized herbivore species preferred specific vegetation types for their foraging activities. In the wet season both middle-sized and large herbivore species preferred to forage in grasslands and open woodlands, but however, nyala foraged mainly in thickets and closed woodlands (X^2_{18} = 433.446, $P <$ 0.00, Fig. 9A).

A)



B)

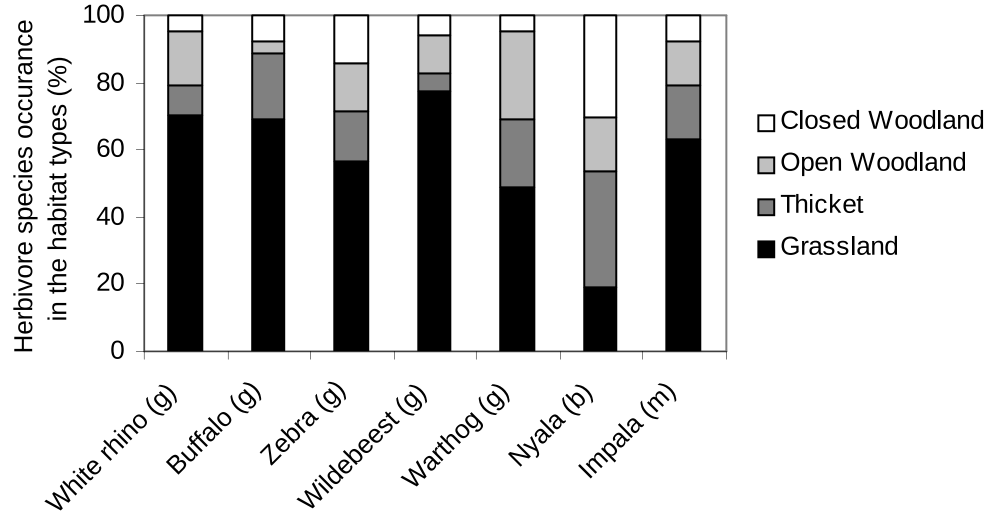


Fig 9 Frequency of occurrence that herbivore species chose to forage in a particular habitat type (based on vegetation structure) for the wet (A) and dry season (B) within eight years since the last burn. The herbivore species showed significantly different preferences in the vegetation types they foraged, in both wet (X^2_{18} = 433.446, $P <$ 0.00) and dry season (X^2_{18} = 278.055, $P <$ 0.00). Herbivore species in the figure are indicated as grazers (g), browser (b) or mixed-feeder (m).

Overall, we found the same forage patterns also for the dry season, although it appeared that all size groups of herbivores tended to forage more in structural denser vegetation types (X^2_{18} = 278.055, $P < 0.00$, Fig. 9B).

Discussion

Rodent abundance was affected by the presence of larger herbivores rather than seasonal patterns and increased with the absence of larger herbivores and increasing vegetation height. Middle-sized and large herbivore species responded on short-term post-fire patterns with large species being the pioneer species on burnt patches, but however, buffalo was the only species that also responded on long-term post-fire patterns.

Impact of post-fire succession and larger herbivores on savanna rodents

It was predicted that both large herbivores and the post-fire succession patterns may influence rodents by changing the food resources available to them and through changes in the predation risk they experience. Our results indicated that rodents were affected by larger herbivore induced habitat modifications rather than seasonal post-fire patterns. However, herbivores and fire are strongly interrelated in African savanna ecosystems (Norton-Griffiths 1979, Pellew 1983) since fire is an important environmental force in those systems (Daubenmire 1968, Vesey-Fitzgerald 1972). In many ways the effects of fire on the savanna ecosystem functioning are comparable with the effects of herbivory (van de Vijver 1999). Like herbivores, fire ‘consumes’ large amounts of plant material and thus may be viewed as a major generalist herbivore (Bond and van Wilgen 1996, Bond and Keeley 2005). But, however, fire is not selective, removes all plant parts dry enough to burn and replaces them with high quality regrowth, while the majority of herbivores are selective feeders, removing specific species and plant parts, live grass leaves in particular (van de Vijver 1999). Therefore fire makes the vegetation probably more uniform than grazing. High herbivore densities also may lead to a compensatory feedback on favourable graze through altering the nutrient cycle via their grazing and dung and urine deposition (Bailey 1996) and thus enhancing the net primary production (Day and Detling 1990, Hobbs 1996, Adler et al. 2001). Furthermore burns in combination with herbivores could result in plant species replacement with the high quality species after being removed initially, being protected in increasingly thick thickets and in clumps of low quality species. The absence of large herbivores can lead to changes in both food quantity and plant species composition, increasing the abundance of high quality grass species available to small herbivores (*chapter 2*). However, the diet of the most abundant rodent species *L. rosalia spinalis* revealed a strong preference for the most abundant grass species occurring in their habitat, rather than for high quality grass species. They may have been highly selective by only taking the best parts of the food resources available regardless of quality. However, we suggest that larger herbivores in interaction with fire are a rather minor factor influencing the quantity and quality of food resources available to small herbivores.

Both fire and large herbivores are important factors that play a role in terms of heterogeneity through creating spatial and temporal landscape patterns. Fire is important in creating long term spatial patterns in the landscape, but it also has short term effects through a homogenising influence on the landscape (Hobbs et al. 1991). After a burn any pattern, especially patterns created by grazing herbivores (Adler et al. 2001), are eliminated and the entire area consists of short regrowth. Grazing herbivores in savannas are attracted to the green regrowth after a fire (Moe et al. 1990, Scholes and Walker 1993, Pearson et al. 1995, van de Vijver 1999, Tomor and Owen-Smith 2002, Traill 2004) and high grazing pressure may result in a suppress of biomass and thus a prolonged persistence of the ‘fire signature’ in the landscape (Archibald et al. 2005). The absence of large herbivores on the other hand leads to an increase in vegetation height and thus increased small herbivore numbers (*chapter 2*). We therefore conclude that large herbivores in interaction with fires most likely influence small herbivores by both increasing and prolonging the predation risk they experience in these habitats.

Response of different-sized large herbivores to post-fire succession patterns

Fire can influence the dynamics of landscape use by herbivores (Pearson et al. 1995, Bailey 1996) but the degree of influence may depend on the temporal persistence of the fire pattern. In our study different-sized herbivore species preferentially foraged in areas that were burnt most recently at both small and landscape scales for up to two years. It has been reported in many studies that savanna herbivores are attracted to the green regrowth after a fire (Sinclair 1977, McNaughton 1985, Moe et al. 1990, Stein et al. 1992, Pfeiffer and Hartnett 1995, Sparks and Masters 1996, Wilsey 1996). Therefore the role of herbivores and fire on the vegetation and hence landscape pattern and progress are closely inter-related in savannas (Walker 1981). Owen-Smith (pers. comm.) noted that large herbivores aggregate on recently burnt areas for up to one year. Therefore we conclude that post burn patterns in the landscape influence large herbivore distributions but the extent of impact may depend on the temporal persistence of the fire pattern.

The persistence of a ‘fire signature’ in the landscape may have a close inter-relationship with the presence of grazers and the amount of rainfall. In our study post-fire dynamics of the grass height were clearly influenced by both herbivores and the rainfall season as interacting factors. Grazers can have important interactions with the ecosystem and therefore play a role in structuring ecosystem patterns (Naiman et al. 2000). But fire has the potential to have a short term homogenizing effect on the landscape (Hobbs et al. 1991) as after a burn any pattern, especially patterns created by grazing (Adler et al. 2001) are eliminated and the entire area consists of short regrowth. The response of vegetation production to burning may then primarily related to rainfall (Tainton and Mentis 1984, Briggs and Knapp 1995). High rainfall results in high productivity and an extended temporal pattern may be preserved in the system through the grazing behaviour of the herbivores and can be displayed through the changes in the grass height. Higher densities of grazers maintain 'fire signature' on the vegetation by grazing down the grass to recovery, if grazer density is low grass height grows very quickly. Furthermore herbivore aggregations could cause a compensatory feedback on favourable grazing lawns through the cumulative interactions of grazing and dung and urine deposition (Bailey 1996) and thus indirectly sustain these post-fire areas for longer periods (Archibald et al. 2005). Our study showed that the presence of grazers and the amount of rainfall may be two interacting factors that persist post-fire patterns in the landscape.

It has been suggested that fire creates temporal landscape patterns but that any prolonged physical effects of fire on the vegetation disappear several months after the burn (van de Vijver 1999). In our study small scale post-fire patterns like grass height differences were recorded for up to two years. But it also appeared that differences on larger scales such as shift of habitat types may be caused by a post-fire succession, and these effects lasted for approximately five years after the burn. We therefore conclude that a post-fire vegetation succession may remain in the landscape for longer than previously expected or ever recorded.

It has been mentioned that a variety of herbivore species travel long distances to feed on post-burn vegetation (Philip 1965) but, however, herbivore species may differ in the level that post-fire landscape patterns affect their land use dynamics. Our results revealed that especially large but also middle-sized herbivore species responded to short-term post-fire patterns and occurred in high densities on patches that were most recently burnt at both small and landscape scales. But however, buffalo was the only species that also responded on long-term post-fire patterns, whereas all other species, especially impala, appeared to prefer patches that were burnt approximately three years ago. The quality versus quantity trade off may be such that large species are forced to make their grazing choices to maximise bulk gains (Senft et al. 1987). Compared to unburned vegetation, leaf bulk densities on post-fire regrowth is higher for several months after the burn primarily due to higher levels of digestible plant material (Hungate 1975, Hobbs and Spowart 1984, Hobbs et al. 1991), increased foraging efficiency as a result of improved structural sward characteristics which regulate herbivore forage selection time (Prins 1996, Heitkoenig and Owen-Smith 1998) and to a lesser extent higher nutrient concentrations (Hill 1972, Daubenmire 1968, 1975, McNaughton 1985, Smith and Kadlec 1985, Frost an Robertson 1987, Moe and Wegge 1997). Furthermore grazers are less bothered by flies, ticks and other parasites (Sutherst 1987, Spickett et al. 1992) for some time after the burn. Therefore grazing on post-fire regrowth leads to higher body mass gains then when they would graze on unburned vegetation (Miller and Watson 1974, Woolfolk et al. 1975, Anderson 1979, Svejcar 1989). However, why buffalo distinguished between burnt areas even several years after the fire remains unclear as our study showed that any prolonged physical small scale effects of fire on the vegetation disappear after approximately two years after the fire.

Our results may also suggest that small scale experiments on temporal fire succession effects on herbivores are necessary in order to exclude confounding effects. For instance, impala occurred in the wet season of 2003 in high numbers in areas that were burnt two years ago, but in the wet and dry season of 2004 they favoured areas that were burnt three years ago. Also, several other species had a preference for areas that were burnt about three years ago, but this preference mainly appeared in the dry season of 2004. It seems rather unlikely that most of the species investigated favour areas of a particular year after a fire has occurred. We believe that this favour presented in our study is rather caused by confounding area specific effects e.g., due to a water source nearby or soil factors, rather than by any prolonged fire effects. Furthermore, HiP is a fenced park of relatively small size, animals cannot migrate to outside the park and therefore herbivores may be forced to focus their foraging on particular areas, especially in times when food sources are scarce. We therefore conclude that particularly buffalo are influenced by temporal post-fire landscape patterns, most likely due to higher levels of digestible plant material and increased forage efficiency.

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References

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465-479

Anderson RC (1979) An evolutionary model summarising the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: An end paper. In: JR Estes, RJ Tyrl and JN Brunken (eds). Grass and grasslands. University of Oklahoma press, Norman, USA, pp 297-308

Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire – grazer interactions in an African savanna. Ecological Application 15:96-109

Bailey DW (1996) Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400

Balfour DA (1999) The management of fire in Hluhluwe-Umfolozi Park. Part D, Appendix 16

Balfour DA, Howison OE (2001) Spatial and temporal variation in a mesic savanna fire regime: response to variation in annual rainfall. African Journal of Range Forage Science 19:45-53

Bond WJ, van Wilgen BW (1996) Fire and Plants. Chapman and Hall, London, Glasgow, Weinheim, New York, Tokyo, Melbourne, Madras, 263 p

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

Briggs JM, Knapp AK (1995) Interannual variability in primary production in tall grass prairie: Climate, soil moisture, topographic position, and fire as determinants of above-ground biomass. American Journal Botany 82:1024-1030

Conway A, Balfour D, Dale T, Hartley P, Morrison P, Howison R, Galli N, Wadge M (2001) Hluhluwe-Umfolozi Park Management Plan 2001. Ezemvelo KwaZulu-Natal Wildlife

Cromsigt JPGM, Olff H (in press) Resource partitioning amongst large grazerm mediated by local heterogeneity: an experimental approach

Daubenmire RF (1968) Ecology of fire in grasslands. Advances in Ecological Research 5, 209-266

Daubenmire RF (1975) Plants and Environment. A Textbook on plant autoecology. John Wiley and Sons, New York, USA, 422 p

Day TA, Detling JK (1990) Grasslands patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188

De Boer WF, Prins HHT (1990) Large herbivores that strive mightily but eat and drink as friends. Oecologia 82:264-274

Frost PGH, Robertson F (1987) The ecological effects of fire in savannas. In: B.H. Walker (ed). Determinants of tropical savannas. IRL Press, Oxford, pp 93-140

Gillon D (1983) The fire problem in tropical savannas. In: F. Bourlière (ed) Ecosystems of the world: 13. Tropical savannas. Elsevier Scientific Publishing Company, Amsterdam, Netherlands, pp 617-641.

Heitkoenig IMA, Owen-Smith N (1998) Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. African Journal of Ecology 36:57-70

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

Hill P (1972) Grass forage: Food for fauna or fuel for fire or both? Proceedings Tall Timbers Fire Ecology Conference 11:337-357

HilleRisLambers R, Rietkerk M, van den Bosch F, Prins HHT, de Kroon JCJM (2001) Vegetation pattern formation in semi-arid grazing systems. Ecology 82:50-61

Hobbs NT (1996) Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713

Hobbs NT, Spowart RA (1984) Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551-560

Hobbs NT, Schimel DS, Owensby CE, Ojima DS (1991) Fire and grazing in the tall gras prairie: contingent effects on nitrogen budgets. Ecology 72:1374-1382

Hochberg ME, Menaut JC, Gignoux J (1994) The influences of tree biology and fire in the spatial structure of the West African savanna. Journal of Ecology 82:217-226

Hungate RE (1975) The rumen microbial ecosystem. Annual Review Ecology Syst 6:39-66

Kingdon J (1997) Field guide to African Mammals. Princeton University Press

Jarman PJ, Sinclair ARE (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: ARE Sinclair and N Norton Griffiths (eds) Serengeti: Dynamics of an ecosystem. Chicago University press, Chicago, pp 130-163

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals. Statistical design and analysis for field studies. 2nd Edition, Kluver Academic Publishers

McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. Ecologial Monographs 55:259-294

Miller GR, Watson A (1974) Some effect of fire on vertebrate herbivores in the Scottish Highlands. Proceedings Tall Timbers Fire Ecology Conference 13:39-65

Moe SR, Wegge P, Kapela EB (1990) The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. African Journal of Ecology 28:35-43

Moe SR, Wegge P (1997) The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. Journal of Tropical Ecology 13:279-292

Naiman RJ, Elliott SR, Helfield JM, O'Kneefe TC (2000) Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. Hydrobiologia 410:79-86

Pearson SM, Turner MG, Wallace LL, Romme WH (1995) Winter habitat use by large ungulates following fire in northern Yellowstone National Park. Ecol Appl 5:744-755

Pfeiffer KE, Hartnett DC (1995) Bison Selectivity and Grazing Response of Little Bluestem in Tall grass Prairie. Journal of Range Management 48:26-31

Philip JFV (1965) Fire as Master and Servant: It's Influence in the Bioclimatic Regions of Trans-Saharan Africa. Proceedings Tall Timbers Fire Ecology Conference 4:7-109

Prins HHT (1996) Ecology and behaviour of the African buffalo: social inequality and decision making. Chapman and Hall, London, 239 p

Prins HHT, Olff H (1997) Species richness of African grazer assemblages: towards a functional explanation. in: Dynamics of tropical communities. (ed. by D. Newbery, H.H.T. Prins, & N.D. Brown), pp. 448 - 490. Blackwell, Oxford

Rietkerk M, Boerlijst M, van Langevelde F, HilleRisLambers R, van de Koppel J, Kumar L, Prins HHT, de Roos AM (2002) Self-organization of vegetation in arid ecosystems. American Naturalist 160, 4: 524-530

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence, Journal of Applied Ecology 38:268-280

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. Nature 436:846 – 849

Scholes RJ, Walker BH (1993) An African Savanna: Synthesis of the Nylsvley Study. Cambridge University Press, 306 p

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological Hierarchies. BioScience 37:789-799

Sinclair ARE (1977) The African buffalo. University of Chicago Press, Chicago, 355 p

Smith LM, Kadlec JA (1985) Fire and herbivory in a great salt lake march. Ecology 66:259-265

Sparks JC, Masters RE (1996) Fire seasonality effects on vegetation in mixed-, tall- and south-eastern pine grassland communities: A review. In: KG Wadsworth, RE McCabe (eds). Transactions of the 61'st North American Wildlife and Natural Resources Conference, pp 246-255

Spickett AM, Horak IG, Vanniekerk A, Braack LEO (1992) The effect of veld-burning on the seasonal abundance of free-living Ixodid ticks as determined by drag-sampling. Onderstepoort Journal of Veterinary Research 59:285-292

Stein SJ, Price PW, Abrahamson WG, Sacchi CF (1992) The effects of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. Oikos 65:190-196

Sutherst RW (1987) Ectoparasites and herbivore nutrition. In: JB Hacker, JH Ternouth (eds). The nutrition of herbivores. Academic Press Australia, pp 191-209

Svejcar TJ (1989) Animal performance and diet quality as influenced by burning on tall grass prairie. Journal of Range Management 37:392-397

Tainton NM, Mentis MT (1984) Fire in grassland. In: P de V Booysen, NM Tainton (eds). Ecological effects of fire in South African ecosystems. Springer Verlag, Berlin, pp 115-147

Tomor BM, Owen-Smith N (2002) Comparative use of grass order following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. African Journal of Ecology 40:2001-2204

Traill LW (2004) Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. South African Journal of Wildlife Research 34:13-24

Trollope WSW, Trollope LA, Hartnett DC (2002) Fire behaviour a key factor in the fire ecology of African grasslands and savannas. In: Viegas X (ed) Forest Fire Reseach and Wildland Fire Safety. Millpress, Rotterdam

Van de Vijver CADM (1999) Fire and life in Tarangire. Effects of burning and herbivory on an East African savanna system. PhD thesis. Wageningen University, Wageningen, the Netherlands

Van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore A, Hearne J, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350

Vesey-Fitzgerald DF (1960) Grazing succession among East African game animals. Journal of Mammalogy 41:161-171

Vesey-FitzGerald DF (1972) Fire and animal impact on vegetation in Tanzania National Parks. Proceedings Tall Timbers Fire Ecology Conference 11:297-317

Voeten MM, Prins HHT (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120:287-294

Vogl RJ (1974) Effects of fire on grasslands. In: TT Kozlowski and CE Ahlgren (eds) Fire and Ecosystems. Academic Press New York, San Francisco, pp 139-194

Walker BH (1981) Is succession a viable concept in African savanna ecosystems? In: DC West, HH Shugart and DB Botkin (eds), Forest Succession. Springer Verlag, Berlin, pp 431-447

Werger MJA (1983) Tropical grasslands, savannas, woodlands: natural and man-made. In: W Holzner, MJA Werger, I Ikusima (eds). Man's impact on vegetation. Dr. W Junk Publ, The Hague, The Netherlands, pp 107-137

West O (1965) Fire in Vegetation and its use in Pasture Management; with special reference to tropical and subtropical Africa. Mineographed Publication 1, Commonwealth Bureau of Pastures and Field Crops. CAB, 53 p

West O (1972) Fire, man and wildlife as interacting factors limiting the development of climax vegetation in Rhodesia. Proceedings Tall Timbers Fire Ecology Conference 11:121-145

Wilsey BJ (1996) Variation in use of green flushes following burns among African ungulate species: The importance of body size. African Journal of Ecology 34:32-38

Woolfolk JS, Smith EF, Schalles RR, Brent BE Habera LH, Owensby CE (1975) Effects of nitrogen fertilizer and late spring burning of bluestem range on diet and performance of steers. Journal of Range Management 28:1

Chapter 4

Habitat utilisation of rodents in a savanna mosaic

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Abstract

African savannas host high densities of different-sized herbivores and diverse predators. Despite of its importance in understanding the ecological interplay of coexisting species, habitat utilisation and spatial movement patterns of very small herbivores like rodents are not well known. So far, studies have concentrated mostly on rodent space use patterns in temperate ecosystems, very little information exist on how rodents in complex heterogeneous ecosystems like savannas utilise their habitat. To investigate rodent spatial movement and habitat utilisation patterns capture-mark-release methods and radio-tracking were used. Furthermore habitat characteristics were recorded to explore ecological factors potentially influencing their distribution. Overall, high quality food resources were more abundant and grass height was higher in rodent home ranges than compared to the surrounding, but females and males may have different priorities. Males and females were different in the distances moved and home range sizes. Our results suggest that the local vegetation cover is the most important factor determining the habitat selection of savanna rodents but food resource availability also plays an important role in rodent space use. However, females and males may have different priorities in the trade-off between foraging and predation risk.

Nomenclature: *Digitaria longiflora* (Retz.) Pers., *Eragrostis curvula* (Schrad.) Nees, *Eragrostis superba* Peyr., *Heteropogon contortus* (L.) Beauv. ex Roem. and Schult., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) A. Robyns & Tournay, *Sporobolus nitens* Stent, *Themeda triandra* Forsk., *Urochloa mosambicensis* (Hack.) Dandy.

Introduction

Studies that seek to explore the habitat utilisation and spatial movement patterns of rodents have mainly concentrated on microtine rodents (voles) in temperate ecosystems (Ims 1987; Norrdahl & Korpimaeki 1998, 2000; Banks et al. 2000, 2002; Johnson et al. 2000, 2002). Very few studies investigate the space use patterns of rodents in rather complex ecosystems like African savannas (Keesing 1998, 2001). Compared to temperate ecosystems African savannas harbour high densities of many different species of herbivores. It has been suggested that intense grazing of large herbivores in this system leads to mosaics of spatial heterogeneous vegetation (Vesey-Fitzgerald 1969, 1972; Beecham et al. 1999, Cromsigt & Olff in press) and thus creates habitats for other smaller herbivores, hence facilitates the coexistence of species (Owen-Smith 1988, Prins and Olff 1997, Olff et al. 2002). The coexistence of many herbivore species in turn may promote high numbers of diverse avian, mammalian and reptilian predators. Despite its importance in understanding ecological patterns in savannas, space use by rodents is not well known. Very few studies on the habitat utilisation and spatial movement patterns of rodents in African savannas have been conducted yet. Particularly detailed ecological information on the single-striped mouse (*Lemniscomys rosalia spinalis*), a dominant murid rodent (*chapter 2 and 3*) in southern African savannas, is very limited. Recent studies revealed that the space use and movement patterns of rodents in East Africa are strongly influenced by the availability of food resources and vegetation cover (Leirs et al. 1996, Monadjem 1998). However, the habitat utilisation and spatial movement patterns of savanna rodents have not been further explored.

In spite of its urgency in understanding community interactions between different herbivore species in African savannas, information on the diet choices of murid rodents is very limited (Monadjem 1997, Metz and Keesing 2001). In contrast, the diet of larger herbivore species is well-known (Hofmann and Stewart 1972, Jarman and Sinclair 1979, Hansen et al. 1985, Hofmann 1989). Predominantly grass-eating murid rodent species may be affected by larger herbivores in their habitat selection and space use patterns through food resource competition. Primarily granivorous murid rodent species, on the other hand, may not be influenced by larger herbivores through food resource availability as they do not compete for food. However, studies on the diet choices of murid rodents are crucial in order to draw the right conclusions from the information on the community interactions between small and large herbivore species in African savannas.

In the present study we determine the spatial movement patterns of herbivorous rodents in a savanna ecosystem in South Africa. Furthermore we investigate space use of the dominant rodent species, *Lemniscomys rosalia spinalis*, and habitat characteristics influencing its spatial distribution. We hypothesise that in South African savannas both large herbivores and their predators may affect rodent habitat utilisation and movement patterns due to several possible mechanisms: Grazing large herbivores play an important role in creating mosaic patches of short and long vegetation (Vesey-Fitzgerald 1969, 1972; Beecham et al. 1999, Cromsigt & Olff in press) that differ in quality and quantity. Intense grazing may improve the food quality and vegetation structure for smaller herbivores (Farnsworth et al. 2002, Arsenault & Owen-Smith 2002) when it leads to the development of patches with short grazing lawns of high quality plant species. Monadjem & Perrin (1998) suggested that food is an important component in the habitat selected by rodents. Herbivorous grazing rodents selectively feed on high quality food resources and may therefore preferentially utilise vegetation patches with abundant high quality plant species. Additionally the quantity of food resources may affect the space use of rodents. Several studies indicated that foraging for food is a major determinant of the home range size in African rodents (Andrzejewski & Mazurkiewicz 1976, Taitt 1981, Zubaid & Gorman 1993). On the other hand, high grazing pressure reduces the vegetation cover (Grant et al. 1982, Bock et al. 1984, Roques et al. 2001, Goheen et al. 2004) and may therefore restrict the suitable habitat available to rodents. Many rodent species in temperate ecosystems show a preference for habitats with abundant cover that is used as anti predator refuge (Kaufman et al. 1983, Drickamer 1990, Kotler et al. 1991). Studies on rodents in Africa have shown the amount of vegetation cover being especially important for rodents (Bowland & Perrin 1989).

But rodents in savannas may face different type of predators with different hunting tactics, which cause spatially varying predation risk. Therefore dense habitat structure may not always be perceived as safer habitat by prey (Lima 1992)), and it is a combination of the predator’s hunting tactics and the response of the prey to these that will determine the prey’s patterns of behaviour (Hopcraft et al. 2005).

Female and male rodents in savannas may show different habitat utilisation and spatial movement patterns. In temperate ecosystems the habitat composition of female home ranges was significantly different from that available, whereas male home ranges did not differ from availability (Cameron & Spencer 1985). Additionally female home range size has been shown to depend on food availability (Ims 1987; Johnsson et al. 2002). Furthermore female and male rodents may show different behavioural adaptations regarding the predation risk they face. It has been found that avian predators selectively preyed more on male rodents, whereas carnivores selectively preyed on females, which may be due to the differences in the use of senses. However, herbivorous rodents may solve the problem of trade-off between foraging and protection from predators attack by selecting a home range with shelter for inactive periods and an adjacent area of rich short grass in which to forage (Cassini & Galante 1992).

In this study capture-mark-release methods were used to investigate the distances savanna rodents moved. Furthermore we conducted radio-tracking to estimate the home range size of the most abundant rodent species. Additionally habitat characteristics like trees, shrubs, rock formations and termite mounds occurring in the study area were determined to explore ecological factors potentially influencing their spatial distribution.

Material and methods

Study site

This study was conducted between March and June 2003 in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa (28°13'S and 32°00'E). HiP is a 90,000 ha fenced protected area and the altitude in the park ranges from 60 m to 750 m (Conway et al. 2001). The climate is coastal, with temperatures from ± 13 °C to ± 35 °C. The vegetation growth is seasonal, rains generally fall between October and March with mean annual rainfall ranging from 985 mm in the northern to 650 mm in the southern areas. The park is characterised by savanna vegetation ranging from open grasslands to closed *Acacia* and broad-leaved riparian woodlands. Dominant grass species are *Digitaria longiflora*, *Eragrostis curvula, Eragrostis superba*, *Panicum maximum*, *Sporobolus africanus and Themeda triandra*. A fire management regime is simulating natural fires in the park, where different areas are burnt with different frequencies. The area at the study site was burned in September 2002. HiP harbours a high diversity and biomass of indigenous large herbivores including white rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), nyala (*Tragelaphus angansi*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus aethiopicus*). Common snakes encountered in this habitat are Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*). Important raptors in HiP predating on rodents are black-shouldered kite (*Elanus caerulus)* and spotted eagle owl (*Bubo africanus*).

Experimental design

Small mammal survey

A permanent trapping grid was established, covering a total area of 1.4 ha. In March the trapping grid consisted of 100 PVC live-traps, with one trap per station, but was extended to 144 traps in the second trapping session. We conducted three trapping sessions of 10 consecutive days in the first trapping session and six consecutive days in the two following trapping sessions. Traps were placed on flat ground with approximately 10 m spacing apart from each other and checked in the morning and evening, re-baited and reset if necessary. Captured animals were identified to species and permanently individually marked with glass fibre transponders (Telinject®, ID 100, Römerberg, Germany). Other data recorded included sex, age, weight, and reproductive condition (after Gurnell and Flowerdew 1990, Barnett and Dutton 1995). Captured animals were always released at their trapping location after measurements were taken. Small mammal trapping and marking in HiP was approved by Ezemvelo KZN Wildlife.

Radio-telemetry

To estimate home range sizes and spatial movement patterns five individuals of the most dominant small mammal species captured at the study site were radio-collared with TW-4 button cell tags of 2.5 g (Biotrack, Wareham, UK). Only adult individuals that were captured in the core of the trapping grid were radio-collared and movement patterns were telemetrically determined by using a portable TR-4 receiver and a RA-14 K antenna (Telonics Inc. Impala, Arizona, USA). We conducted three radio-tracking sessions in total from April until June 2003. The location of all individuals was determined with triangulation using the ‘homing-in’ method (see White & Garrott 1990). We estimated the approximate location of all radio-collared individuals by measuring the direction of the received signal from three different points. We repeated this procedure several times shortly after dusk and before dawn but the intervals, number of bearing points used for each location and the amount of data collected varied within and between tracking sessions. Small mammal trapping, marking and collaring in HiP was approved by Ezemvelo KZN Wildlife.

Habitat characterisation

Vegetation characteristics were measured in March 2003 at five points around each trapping location, an additional measurement was taken between all trapping locations. To measure vegetation height a wooden disk with a diameter of 46 cm was fully lifted to the top of a pole with a height scale and then dropped onto the vegetation. The three most dominant grass species were determined and the height at which the disk was resting on the vegetation was measured. To determine the quality of rodent food sources we collected a total of 112 samples of green leaves of the most dominant grass species from all exclosures and control in which they occurred. We analysed each sample for its N, P, Ca, Mg and Na content and then calculated the average content of each nutrient per grass species in order to avoid any treatment effects. We discriminated the grass species by their growth forms (bunch grasses and lawn grasses) and classified them in two nutritional quality categories (high quality grasses and low quality grasses; for more details see *chapter 2*). It appeared that all lawn grass species (*Digitaria longiflora*, *Sporobolus nitens* and *Urochloa mosambicensis*) are high quality grasses and most of the bunch grass species (*Aristida congesta*, *Eragrostis curvula*, *Eragrostis superba*, *Heteropogon contortus*, *Sporobolus africanus*, *Themeda triandra*) are low quality grass species (except *Botriochloa insculpta* and *Panicum maximum*). Additionally the location, number and species of all shrubs and trees occurring at the study area were recorded, including data on height, stem diameter at approximately 1.5 m height and the number of branches. Furthermore habitat features such as dead trees, rock formations and termite mounds were recorded, including diameter of rock formations and termite mounds.

Data analysis

A one-way ANOVA followed by Tukey HSD tests was used to test for differences between species in the mean distances rodents moved and rodent home range sizes, a t-test was used to look for differences in the mean distances rodents moved and rodent home ranges between sex. Furthermore grass height differences between home ranges of both sexes and the surrounding were tested with a one-way ANOVA followed by Tukey HSD tests. A Pearson's Chi-square test was used to test whether the grass species composition and frequency of grass quality classes in female and male home ranges differed from the surrounding. Differences in the tree species composition and other habitat features in female and male home ranges compared to the surrounding were also tested using a Pearson's Chi-square test. Relations between trapping probability (repeated capture of the same individuals) and vegetation structure was analysed for females and males with logistic regression with small mammal presence/absence as the dependent variable and vegetation height as a predictor.

Results

Small mammal analysis

Between March and June 2003, we captured a total of 49 murid rodents of which 38.1% were females and 61.9% were males. The predominant grass-eating single-striped mouse *(Lemniscomys rosalia spinalis*) represented 61% of all captures, but also the pouched mouse (*Saccostomus campestris*), that primarily feeds on forbs during the dry season and on seeds following the rains (Keesing 1998) was captured frequently (29% of all captures). However, several captured murid rodents could not be identified to a species level. The number of rodents was approximately four individuals per hectare in March and June, in May rodent numbers slightly increased with approximately nine individuals per hectare.

Rodent movement patterns

The mean distance *L. rosalia spinalis* moved between trapping locations was approximately 32 m, whereas *S. campestris* and the other species moved shorter distances (Fig. 1). However, distances species moved were not significant different. Overall, females moved shorter distances between trapping locations than males ($F_{1, 38} = 9.34$, $P = 0.002$; Fig. 2).

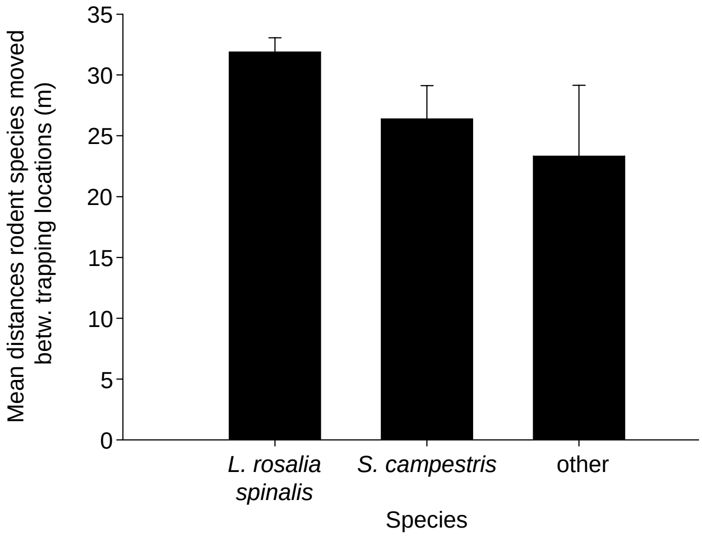

Fig 1 Mean distances rodent species moved between trapping locations over all trapping periods (± SE, n = 3). Distances species moved were not significantly different ($F_{3,42}$ = 2.11, *P* = 0.098).

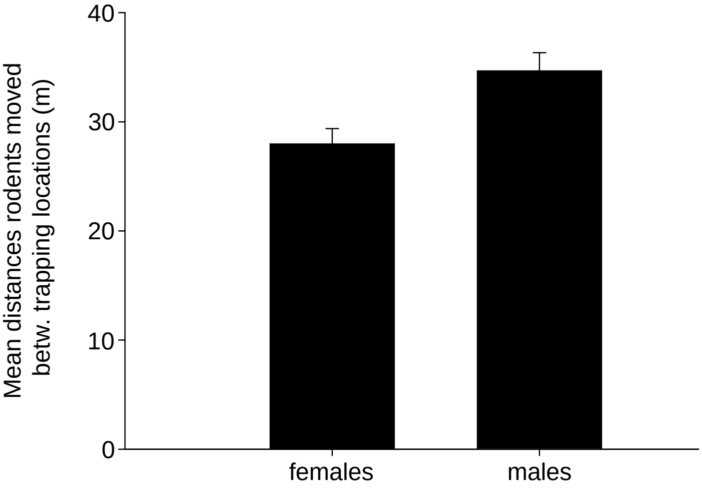

Fig 2 Mean distances female and male rodents moved between trapping locations over all trapping periods (± SE, n = 2). Distances moved were significantly different between sex ($F_{1,\ 38}$ = 9.34, *P* = 0.002).

The home range size of *L. rosalia spinalis* varied between approximately 1060 m^2 for females and 1615 m^2 for males. However, no significantly differences in home range sizes were found (Fig. 3). The home ranges were generally evenly distributed within the trapping grid (Fig. 4).

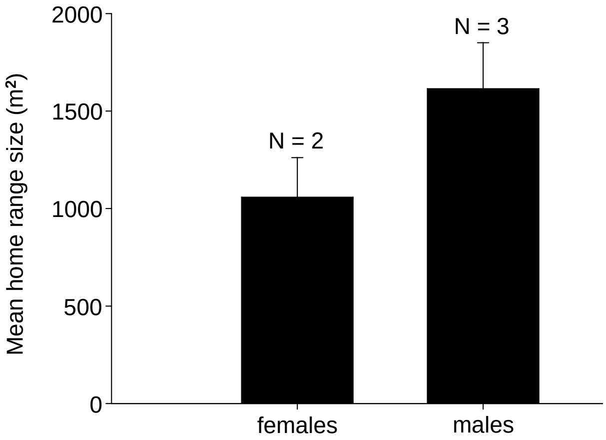

Fig 3 Mean home range sizes of female and male *L. rosalia spinalis* (± SE). Home range sizes were not significantly different between sexes ($F_{1,3}$ = 2.69, *P* = 0.20).

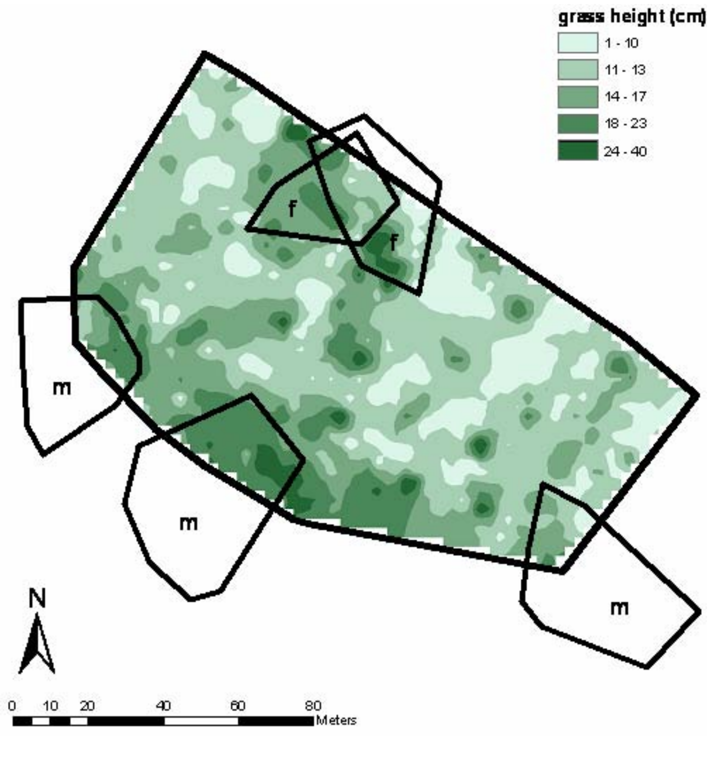

Fig 4 Distribution of female (f) and male (m) home ranges of *L. rosalia spinalis* within the trapping grid.

Female home ranges overlapped and lay almost completely within the trapping grid, whereas male home range did not overlap and mostly lay outside the trapping grid. The distance between male home ranges was approximately 53 m, distances between the female and male home ranges were approximately 65m.

Habitat analysis

In total 25 different grass species were recorded within the study site. The most frequently dominant grass species occurring in the trapping grid were the low quality bunch grasses *Themeda triandra*, *Eragrostis curvula* and *Sporobolus africanus*, representing approximately 40 % of the recorded grass species (Tab. 1). Overall, 66 % of the grass species recorded within the trapping grid was low quality bunch grasses (Fig. 5).

Table 1 Frequency of occurrence of dominant grass species in the trapping grid and in female and male home ranges of *L. rosalia spinalis*. The grass species composition was significantly different between the trapping grid and the home ranges of both sexes (n = 510, $X^2_{20} = 83.10$, $P < 0.000$). Quality classes of grass species are according to chapter 2.

Grass species	Quality class	Frequency in trapping grid (%)	Frequency in female home ranges (%)	Frequency in male home ranges (%)
Digitaria longiflora	lawn grass, high quality	4.5	8.5	6.3
Sporobolus nitens	lawn grass, high quality	3.3	9.5	5.3
Urochloa mosambicensis	lawn grass, high quality	0.3	9.0	10.3
Eragrostis curvula	bunch grass, low quality	14.4	10.0	11.3
Eragrostis superba	bunch grass, high quality	6.8	13.5	8.6
Heteropogon contortus	bunch grass, low quality	2.6	2.5	7.0
Panicum maximum	bunch grass, high quality	7.4	18.0	11.6
Sporobolus africanus	bunch grass, low quality	9.2	10.0	15.9
Themeda triandra	bunch grass, low quality	17.1	9.0	15.2
other	no data	34.1	10.0	8.6

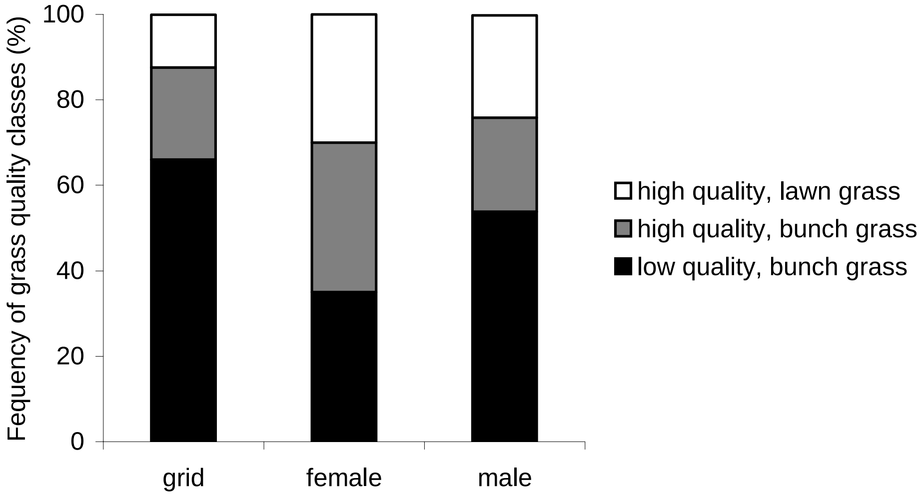

Fig 5 Frequency of occurrence of high and low quality grass species in the trapping grid and in female and male home ranges of *L. rosalia spinalis*. The composition of grass species was significantly different between the trapping grid and the home ranges of both sexes (n = 510, $X^2_4 = 26.041$, $P < 0.000$).

The height of the grass in the trapping grid varied between 0 – 50 cm with an average height of about 11 cm (Fig. 6). We recorded 189 individual trees, consisting of seven species respectively. The most abundant tree species were *Acacia nilotica* and *A. karroo*, representing 55 % of all recorded woody species. The mean height of all trees recorded was approximately 3 m. Furthermore 48 rock formations, five termite mounds and seven dead trees were found at the study site.

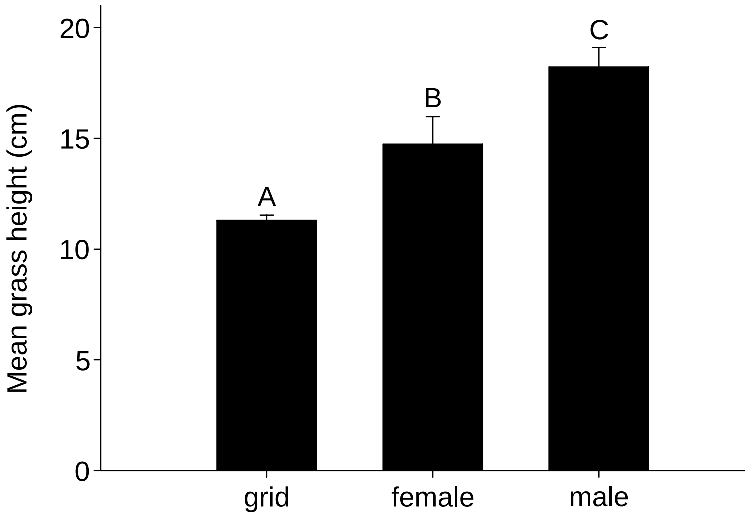

Fig 6 Mean grass height in the trapping grid and in female and male home ranges of *L. rosalia spinalis* (± SE, n = 514). Different letters show significant differences, $P < 0.000$.

Habitat characteristics of rodent home ranges

We found significant differences in the grass species composition between the trapping grid and the home ranges of both sexes of *L. rosalia spinalis* ($X^2_{20} = 83.10$, $P < 0.000$). In female home ranges mostly high quality bunch grasses such as *Panicum maximum* and *Eragrostis superba* were found (Tab. 1), whereas in male home ranges low quality bunch grasses such as *S. africanus* and *T. triandra* were recorded most often. Furthermore the frequency of high and low quality grass species was different between the trapping grid and the home ranges of females and males ($X^2_4 = 26.041$, $P < 0.000$). Females had a higher abundance of high quality grass species in their home ranges than had males (Fig. 5). The grass height was significantly higher in the home ranges of both female and male *L. rosalia spinalis* than compared to the trapping grid ($F_{2, 514} = 49.017$, $P < 0.000$; Fig. 6) and had a significant impact on the trapping probability of males (Waldl = 6.506, $P = 0.011$; Fig. 7). A significant higher trapping probability was measured with increasing grass height. However, no significantly impact of the grass height on the trapping probability of females was found (Waldl = 0.954, $P = 0.329$).

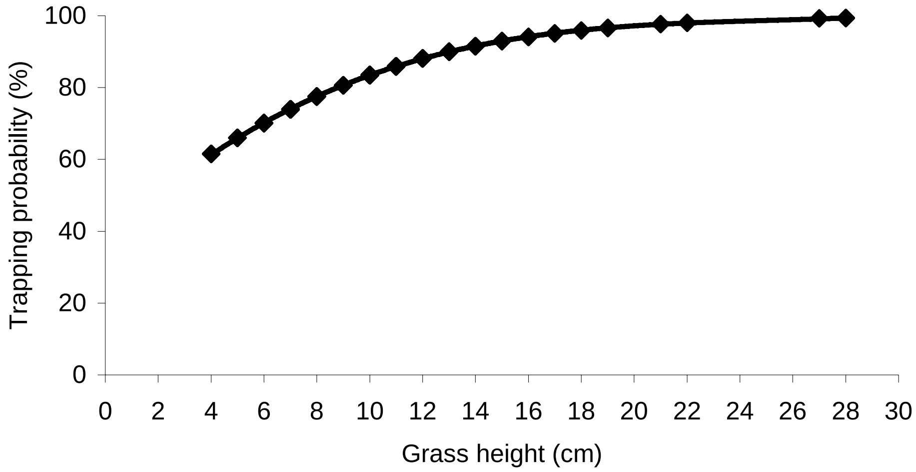

Fig 7 Trapping probability of male rodents in the different grass heights (cm). The trapping probability significantly increased with grass height (Wald = 6.506, P = 0.011).

We recorded 38 trees within the home ranges of *L. rosalia spinalis*, consisting of four species respectively. The number of trees per home range varied between three and 13. The most abundant tree species was *A. nilotica*, but the tree species composition in the home ranges of both females and males was not significant different from the trapping grid ($X^2_{14} = 18.588$, $P = 0.181$). Also, eight rock formations and two dead trees were found within the home ranges of *L. rosalia spinalis*, but no significant differences were detected ($X^2_6 = 4.244$, $P = 0.644$).

Discussion

Overall, the composition of *L. rosalia spinalis* home ranges was significantly different from the generally available habitat. High quality grass species were more abundant in their home ranges than compared to the surrounding. Furthermore the grass height within their home ranges was higher than in the rest of the grid. Additionally differences in the distances moved as well as in their home range sizes were found between sexes. For females high quality grass species seemed to be primarily important, whereas for males high vegetation cover appeared to be most important.

Habitat utilisation patterns

Food resources may be important components in the habitat selected by small herbivores in Africa (Monadjem & Perrin 1998) as they are expected to be highly selective feeders. It was therefore predicted that savanna rodents may preferentially utilise vegetation patches with abundant high quality grass species created by large grazing herbivores. On the other hand, larger herbivore species may limit the habitat choice of savanna rodents, especially that of predominantly grass-eating species, through food resource competition. In the present study the grass species composition in the home ranges of *L. rosalia spinalis* was significantly different from the rest of the trapping grid. A higher abundance of high quality grass species was found within the home ranges compared to the surrounding. Although the role of food resource availability in southern African rodent communities is poorly understood (Delany 1986), it has been suggested that food resources are clearly a limiting factor for East African rodents (Monadjem & Perrin 1998) and may therefore strongly affect the habitat utilisation of these selective feeders. For instance, the availability of suitable food resources influenced the distribution, numbers, reproduction, and mass of rodents in Swaziland (Leirs & Verheyen 1995, Monadjem & Perrin 1996). But although *L. rosalia spinalis* would be expected to selectively feed on high quality food resources analysis of their diet generally revealed a preference for the most abundant grass species occurring in their habitat, rather than for high quality grass species (*chapter 2*). The cause of this is yet unclear. They may have been highly selective by only taking the best parts of the food resources available regardless of quality. However, the food resources *L. rosalia spinalis* feed on may also depend on factors that have not been addressed in this study (e.g., sex, breeding condition, season etc.). Therefore we suggest that grass-eating savanna rodents in South Africa are influenced in their habitat utilisation by the availability of food resources in the vegetation patches created by large grazing herbivores, but it seems unlikely to be the major factor in the habitat that savanna rodents select.

Habitat preferences of rodents in East Africa are determined primarily by the type of cover available to them (Rowe-Rowe & Mester 1982, Iyawe 1988). We therefore expected that the habitat selection of savanna rodents would be mainly affected by the vegetation cover patchiness induced by large grazing herbivores. Results of our study supported this expectation as we found the grass height, and thus the vegetation cover, within the home ranges of *L. rosalia spinalis* being higher than in the rest of the grid. Furthermore results of an earlier study demonstrated that *L. rosalia spinalis* became more abundant with denser vegetation cover (*chapter 2*). Many studies on habitat selection have found that vegetation cover is an important determinant of rodent distribution not only in Africa (Bond, Ferguson & Forsyth 1980, Leirs & Verheyen 1995, Leirs, Verheyen & Verhagen 1996, Monadjem 1997) but also in temperate and boreal zones (e.g. Eadie 1953, Kaufman et al. 1983, Desy et al. 1990, Drickamer 1990, Kotler et al. 1991, Dickman 1992). The preference for high cover has been suggested to be most likely an adaptation for reducing predation risk, especially imposed by birds of prey (Kotler and Blaustein 1995, Korpimaeki et al. 1996, Thorson et al. 1998). Owing to its diurnal habits (Skinner & Smithers 1990) *L. rosalia spinalis* may be particularly prone to predation by diurnal birds of prey (e.g., black shouldered kite) which are abundant in the study area. The results of our study support the hypothesis that the patchiness of the vegetation cover created by large herbivores is the most important factor determining the habitat selection of *L. rosalia spinalis* in the South African savanna.

Space use patterns and spatial distributions of males and females

It was predicted that habitat utilisation and spatial movement patterns of savanna rodents may also depend on the individual sex. In our study we found that females had smaller home ranges and moved shorter distances than males. Furthermore the major determinant for the habitat selected by females was abundant high quality grass species, whereas for males high vegetation cover appeared to be most important. In small mammals it is well known that average male home ranges are larger than average female home ranges (Kikkawa 1964, Bergstedt 1966, Jewell 1966, Crawley 1969, Andrzejewski & Mazurkiewicz 1976). The spacing behaviour of females is suggested to depend on the distribution and abundance of food (Ostfeld 1985, 1990, Ims 1987, Maher & Lott 2000, Johnsson et al. 2002), indicating that the habitat composition (and quality) is a major determinant of their home range size. Additionally, it has been demonstrated that the habitat composition of female rodent home ranges was significantly different from that available, whereas that of males did not differ from availability (Cameron & Spencer 1985). The habitat utilisation and spacing behaviour of males, on the other hand, may be mainly influenced by their search for potentially mating partners. The mobility of rodents has been demonstrated to be significantly associated with predation risk (Norrdahl & Korpimaeki 1998). Rodents with high mobility and thus larger home ranges may have a higher chance of being killed than rodents with lower mobility. The high mobility of males makes them particularly vulnerable to avian predators (Norrdahl & Korpimaeki 1998) which mainly use vision in hunting. Therefore the preference of male rodents for high cover may be an adaptation for reducing predation risk by birds of prey (Kotler and Blaustein 1995, Korpimaeki et al. 1996, Thorson et al. 1998). This clearly indicates that dense vegetation cover rather than food resource availability determines the habitat selected by males. However, both female and male rodents may solve the problem of trade-off between foraging and protection from predators attack by selecting a home range with shelter for inactive periods and an adjacent area of rich short grass in which to forage.

Acknowledgement

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References

Andrzejewski R, Mazurkiewicz M (1976) Abundance of food supply and size of the bank vole’s home range. Acta Theriol 21:237-253

Arsenault R, Owen-Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313-318

Banks PB, Norrdahl K, Korpimaeki E (2000) Nonlinearity in the predation risk of prey mobility. Proceedings to the Royal Society of London 267:1621-1625

Banks PB, Norrdahl K, Korpimaeki E (2002) Mobility decisions and the predations risks of reintroduction. Biological Conservation 103:133-138

Beecham JA, Oom SP, Hester AJ, Maudsley M, Marshall J (1999) The role of animal decisions in the development of vegetation dynamics. Heterogeneity in landscape ecology: pattern and scale, Proceedings of the eighth Annual Conference of the International Association for Landscape Ecology, Bristol

Bergstedt B (1966) Home ranges and movements of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linné) in southern Sweden. Oikos 17:150-157

Bock CE, Bock JH, Kenney WR, Hawthorne VM (1984) Responses of birds, rodents, and vegetation to life stock exclosure in a semi desert grassland site. Journal of Range Management 37:239-242

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

Bowland AE, Perrin MR (1989) The effect of overgrazing on the small mammals in Umfolozi Game Reserve. Zeitschrift fuer Saeugetierkunde 54:251-260

Cameron GN, Spencer SR (1985) Assessment of space-use patterns in the hispid cotton rat (*Sigmodon hispidus*). Oecologia 68:133-139

Cassini MH, Galante ML (1992) Foraging under predation risk in the wild guinea pig: the effect of vegetation height on habitat utilization. Annual Zool Fennici 29:285-290

Conway A, Balfour D, Dale T, Hartley P, Morrison P, Howison R, Galli N, Wadge M (2001) Hluhluwe-Umfolozi Park Management Plan 2001. Ezemvelo KwaZulu-Natal Wildlife

Crawley MC (1969) Movements and home-ranges of *Clethrionomys glareolus* (Schreber) and *Apodemus sylvaticus* L. in north-east England. Oikos 20:310-319

Cromsigt JPGM, Olff H (in press) Resource partitioning amongst large grazerm mediated by local heterogeneity: an experimental approach.

Delany MJ (1986) Ecology of small rodents of southern Africa. Mammal Review 16:1-41

Desy EA, Batzli GO, Liu J (1990) Effects of food and predation on behaviour of prairie voles: a field experiment. Oikos 58:159-168

Dickman CR (1992) Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313-322

Drickamer LC (1990) Microhabitat preferences of two species of deer mice Peromyscus in a north-eastern United States deciduous hardwood forest. Acta Theriol 35:241-252

Eadie WR (1953) Response of Microtus to vegetative cover. Journal of Mammalogy 34:263-264

Farnsworth KD, Focardi S, Beecham JA (2002) Grassland-herbivore interactions: How do grazers coexist? American Naturalist 159:24-39.

Goheen JR, Keesing F, Allan BF, Ogada DL, Ostfeld RS (2004) Net effects of large mammals on Acacia seedling survival in an African savanna. Ecology 85:1555-1561.

Grant WE, Birney EC, French NR, Swift DM (1982) Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetation cover. Journal of Mammalogy 63:248-260

Hansen RM, Mugambi MM, Bauni SM (1985) Diets and trophic ranking of ungulates of the Northern Serengeti. Journal of Wildlife Management 49:823-829

Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226-240

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants. A comparative view of their digestive system. Oecologica 78:443-457

Hopcraft JGC, Sinclair ARE, Packer C (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559-566

Ims RA (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. Journal of Animal Ecology 56:341-349

Iyawe JG (1988) Distribution of small rodents and shrews in a lowland rain forest zone of Nigeria, with observations on their reproductive biology. African Journal of Ecology 26:189-195

Jarman PJ, Sinclair ARE (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair ARE, Norton-Griffitths N (eds). Serengeti: dynamics of an ecosystem. Chicago University Press, Chicago, p 130-163

Jewell PA (1966) The concept of home range in mammals. Symposium of the zoological Society, London 18:85-109

Jonsson P, Koskela E, Mappes T (2000) Does risk of predation by mammalian predators affect the spacing behaviour of rodents? Two large-scale experiments. Oecologia 122:487-492

Johnsson P, Hartikainen T, Koskela E, Mappes T (2002) Determinants of reproductive success in voles: use in relation to food and litter size manipulation. Evolution and Ecology 16:455-467

Kaufman DW, Peterson SK, Fristik R, Kaufman GA (1983) Effect of microhabitat features on habitat use by Peromyscus leupocus. American Midland Naturalist 110:177-185

Keesing F (1998) Ecology and behaviour of the pouched mouse, Saccostomus mearnsi, in central Kenya. Journal of Mammalogy 79:919-931

Keesing F (2001) Impacts of density and large mammals on space use by the pouched mouse (Saccostomus mearnsi) in central Kenya. Journal of Tropical Ecology 17:465-472

Kikkawa J (1964) Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodlands. Journal of Animal Ecology 33:259-299

Korpimaeki E, Koivunen V, Hakkarainen H (1996) Microhabitat use and behaviour of voles under weasel and raptor predation risk: predator facilitation? Behavioral Ecology 7:30-34

Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behaviour and rates of owl predation. Ecology 72:2249-2260

Kotler BP, Blaustein L (1995) Titrating food and safety in a heterogeneous environment: when are risky and safe patches of equal value? Oikos 74:251-258

Leirs H, Verheyen N (1995) Population ecology of Mastomys natalensis (Smith, 1834). Implications for rodent control in Africa. Belgian Administration for Development Cooperation. Agricultural Edition Nr. 35

Leirs H, Verheyen W, Verhagen R (1996) Spatial patterns in Mastomys natalensis in Tanzania (Rodentia, Muridae). Mammalia 60:545-555

Lima SL (1992) Strong preferences for apparently dangerous habitats – a consequence of differential escape from predators. Oikos 64:597-600

Maher CR, Lott DF (2000) A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1-29

Monadjem A (1997) Habitat preferences and biomasses of small mammals in Swaziland. African Journal of Ecology 35:64-72

Monadjem A (1998) Effects of supplemental food on the habitat selected by Mastomys natalensis (Muridae:Rodentia) in a subtropical grassland in Swaziland. South African Journal of Zoology 33:172-177

Monadjem A, Perrin MR (1996) The effects of additional food on the demography of rodents in a subtropical grassland in Swaziland. Mammalia 60:785-789

Monadjem A, Perrin MR (1997) Population dynamics of Lemniscomys rosalia (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. South African Journal of Zoology 32:129-135

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

Monadjem A, Perrin MR (1998b) Effects of food supplementation and fire on small mammal community structure in a Swaziland grassland. South African Journal of Science 94 (2)

Norrdahl K, Korpimaeki E (1998) Does mobility or sex of voles affect predation risk by mammalian predators? Ecology 79:226-232

Norrdahl K, Korpimaeki E (2000) The impact of predation risk from small mustelids on prey populations. Mammal Review 30:147-156

Ostfeld RS (1985) Limited resources and territoriality in microtine rodents. American Naturalist 126:1-15

Ostfeld RS (1990) The ecology of territoriality in small mammals. Trends in Ecology & Evolution 5:411-415

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

Rowe-Rowe DT, Mester J (1982) Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. South African Journal of Zoology 17:202-209

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

Taitt MJ (1981) The effect of extra food on small populations. 1. Deer mice (*Peromyscus maniculatus*). Journal of Animal Ecology 50:111-1124

Thorson JM et al. (1998) Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. Behavioral Ecology 9:157-161

Vesey-FitzGerald DF (1969) Utilization of the habitat of the buffalo in Lake Manyara National Park. East African Wildlife Journal 7:131-145

Vesey-FitzGerald DF (1972) Fire and animal impact on vegetation in Tanzania National Parks. Proceedings of Tall Timbers Fire Ecological Conference 11:297-317

White GC, Garrott RA (1990) Analysis of Wildlife Radio-Tracking Data. Academic Press, London

Zubaid A, Gorman ML (1993) The effect of supplementary feeding upon the sizes of the home ranges of wood mice Apodemus sylvaticus living on a system of maritime sand dunes. Journal of Zoology, London 231:233-237

Chapter 5

Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub

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Abstract

Shrub encroachment is a widely observed problem in Southern African savannas. Although the effects of herbivory and grass height on the recruitment of woody species in savannas have been studied individually, very little information exists about how these factors interact. In this study seeds and seedlings of the encroaching shrub *Dichrostachys cinerea* were planted in clipped and unclipped grass plots, with and without large herbivores present in a savanna with a full assemblage of grazers and browsers. Seed germination, seedling survival and seedling predation were monitored for eight months. Both seed germination and seedling survival of *Dichrostachys cinerea* was promoted by clipping the grass and excluding large herbivores. Taller grass positively affected seedling survival when large herbivores were present. We also found some evidence that higher rainfall promoted both seed germination and seedling survival in this ecosystem. Invertebrates were found to be primary consumers of *D. cinerea* seedlings but also rodents consumed them. The recruitment of *D. cinerea* was strongly influenced by the interplay of grass height and herbivory. It appeared that the positive effects of large grazing herbivores on seed germination and seedling survival (reducing competition with grasses for water and light) may outweigh the associated negative effects (higher risk of being grazed or trampled by herbivores and desiccation).

Nomenclature: *Dichrostachys cinerea* (L.) Wight & Arn., *Digitaria longiflora* (Retz.) Pers., *Eragrostis curvula* (Schrad.) Nees*, Eragrostis superba* Peyr., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) A. Robyns & Tournay, *Sporobolus nitens* Stent*, Themeda triandra* Forsk.*, Urochloa mosambicensis* (Hack.) Dandy.

Introduction

Trees in savannas are important for the functioning of savanna ecosystems through their effects on nutrient cycling, water availability (Belsky et al. 1993, Belsky 1994) and patterns of space use by wildlife (Traill 2004). Bush- and tree encroachment poses significant problems for farmers and wildlife managers in many parts of the world and has been well documented in North America (Hobbs & Mooney 1986, Archer et al. 1988, Archer 1995), South America (Adamoli et al. 1990), Australia (Burrows et al. 1990) and Africa (Van Vegten 1983, Watson & MacDonald 1983, Skarpe 1990, Prins & van der Jeugd 1993, Moleele et al. 2002). Particularly in formerly open grasslands an increase in woody plant biomass can alter the water balance (Pressland 1973), fire intensity (van Langevelde et al. 2003), nutrient cycling (Belsky 1992), and primary productivity of the grass layer (Stuart-Hill & Tainton 1989). As livestock and large herbivores are highly dependent on the quality and quantity of grass (Witkowski & Garner 2000), they are also likely to be negatively affected by bush encroachment. In South Africa it has been estimated that 13 million ha of savanna have been subject to recent bush encroachment (Trollope et al. 1989) due to changed grazing and fire regimes. Herbivores and fire are major interacting drivers of tree-grass dynamics in African savannas (Pellew 1983, Dublin 1991, McNaughton 1992). For instance, grazers can indirectly and positively affect tree seedling establishment by reducing the surrounding grass cover (Roques et al. 2001, Goheen et al. 2004). This decreases the competition with grasses for resources such as water, nutrients and light (Belsky & Blumenthal 1997) and prevents seedlings from burning through reducing fuel loads (Walker et al. 1981, van Vegten 1983, Archer 1995, Milton & Dean 1995). Fire may additionally promote the regeneration of woody species by promoting the release (Lamont et al. 1991) and germination (Brown and van Staden 1997, Keeley and Fortheringham 2000, Brown et al. 2003) of seeds from otherwise sealed pods. Consumption of seed pods followed by defecation of intact seeds by browsers can also promote shrub recruitment (Brown & Archer 1987, Reyes et al. 1994) as scarification through ingestion is known to break seed dormancy (van Staden et al. 1994b). On the other hand, large herbivores can inhibit tree establishment through browsing, uprooting or trampling of seedlings (Dublin et al. 1990, Mwalyosi 1990, Sinclair 1995). High browsing pressure by selective herbivores (as impala) can prevent the establishment and recruitment of woody seedlings (Prins & van der Jeugd 1993) and make them more exposed to fire (Mills 1983). Furthermore intense grazing can lead to a drier microclimate and lower soil moisture which increases the risk of seedling desiccation, especially in the dry season. In addition to large herbivores, smaller consumers (e.g. rodents and insects) have been reported to negatively influence recruitment of woody species via seed- and seedling predation (Sullivan 1979, Anderson & Lonsdale 1990, Ostfeld &

Canham 1993, Miller 1994, Auld 1995, Crawley & Long 1995, Harju & Tahvanainen 1997, Weltzin et al. 1997, Manson et al. 2001), especially during population peaks (Pusenius et al. 2000). Although the effects of herbivory and grass height on the recruitment of woody species in savannas have been studied individually (Walker et al. 1981, Trollope 1984, Prins & van der Jeugd 1993, O'Connor 1995), the importance of interactions of these factors is still poorly understood, and experimental studies are rare.

The leguminous shrub *Dichrostachys cinerea* is an important bush encroacher in South African savannas (van Vegten 1983, O'Connor 1995, Roques et al. 2001, Moleele et al. 2002). In the present study we investigate the interaction of herbivores and grass height on *D. cinerea* seed germination and seedling survival in a South African savanna. To determine the interacting direct effects of herbivores (browsing) and indirect effects through grass layer we manipulated both the grazing intensity by excluding large herbivores and the grass height by clipping at four study sites (two in mesic and two in arid savanna). In tall grass patches seedlings would be protected from browsing herbivores, but might compete with grasses for light and water. In contrast, in short grass seedlings may suffer less from competition with grasses for light and water, but grazing herbivores may graze them along with the grasses and thus also make them more visible for browsers. This may cause the effect of grass clipping to be either positive or negative. We expected that the presence of large herbivores decreases seedling establishment by predation particularly in clipped grass where seedlings are more visible. Previous studies have shown that the exclusion of large herbivores leads to increased small mammal densities (chapter 2) which in turn may have a negative impact on tree seedling survival.

Methods

Study site

This study was conducted between March and December 2004 in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa (28°13'S / 32°00'E). HiP is a 90,000 ha fenced protected area and consists of the Hluhluwe Game Reserve in the North and the iMfolozi Game Reserve in the South. The altitude in the park ranges from 60 m to 750 m (Conway et al. 2001). The climate is coastal and seasonal, with temperatures from ± 13 °C to ± 35 °C. Rainfall varies greatly and generally falls between October and March. The mean annual rainfall (measured from 1980-2004) for Hluhluwe is 985 mm (min: 68 mm, max: 4060 mm), whereas in iMfolozi it is 650 mm (min: 2 mm, max: 3200 mm). The park is characterised by savanna vegetation ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Brooks and McDonald 1983). Skowno et al. (1999) documented that the woody plant biomass in HiP has rapidly increased over the last 40 years. *Dichrostachys cinerea* (legume of the Mimosoidae), a deciduous multistemmed shrub/small tree (Van Wyk 1972, Pooley 1993) is an important bush encroacher in HiP, invading large areas of previously open grasslands (Skowno et al. 1999). The shrub produces highly nutritious leaves and pods and the infructescence have a strong rich aroma which attracts browsers (van Staden et al. 1994a). The seeds of *D. cinerea* are impermeable to water and dormant at release (van Staden et al. 1994b, Witkowski & Garner 2000). Dormancy is mainly broken through diurnal temperature fluctuations, by scarification through ingestion and by bruchid exit holes (van Staden et al. 1994b). A fire management regime is simulating natural fires in the park, where different areas are burnt with different frequencies. HiP harbours a high diversity and biomass of indigenous large herbivores including elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis L.*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus),* kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angansi*), impala (*Aepyceros melumpus*) and warthog (*Phacochoerus aethiopicus*).

Experimental design

The present study utilised herbivore exclosures established at four study sites in HiP within the context of a different study (Bond & Olff, unpublished). Fences 2.50 m tall excluded all mammalian herbivores larger than hares from 40 x 40 m plots of vegetation since early 2000. To quantify small mammal densities, permanent trapping grids inside and outside the exclosure treatment were established (n = 8). The absence of large herbivores leads to an increase in small mammal numbers although these differences appeared not to be significant (chapter 2). Furthermore the exclusion of large herbivores resulted in increased grass height at all sites. The grass species most frequently dominant in the mesic savanna were *Sporobolus africanus* and *Digitaria longiflora*, other frequently dominant grasses included *Panicum maximum* and *Themeda triandra* (chapter 2). For the arid savanna the dominant grass species were *Urochloa mosambicensis* and *P. maximum*, but also *T. triandra* and *Sporobolus nitens* were found frequently (all mentioned grass species are C4 species). The amount of rainfall was measured at 10 weather stations situated closest to our study sites. The rainfall varied greatly between seasons (Fig. 1). The amount of rainfall in 2004, however, was not significantly different from that of previous years since 1980. The soils at all study sites were similar lithosols with 17 % clay content (FAO). All study sites are burned every second year, in 2004 they were burnt approximately four months after seeds and seedlings were planted. *D. cinerea* can survive bushfires and resprouts easily after burning (Bond, pers. convers.).

Seed-germination and seedling survival experiments

Fresh seeds of *D. cinerea* were collected during July to September 2003 from more than 50 trees well spread over the HiP. Seeds were stored in a sealed box in a fridge for several days, scarified between sandpaper to break dormancy and imbibed in water for 12 hours. A pre-germination test of *D. cinerea* seeds under controlled conditions revealed a germination rate of approximately 20 %.

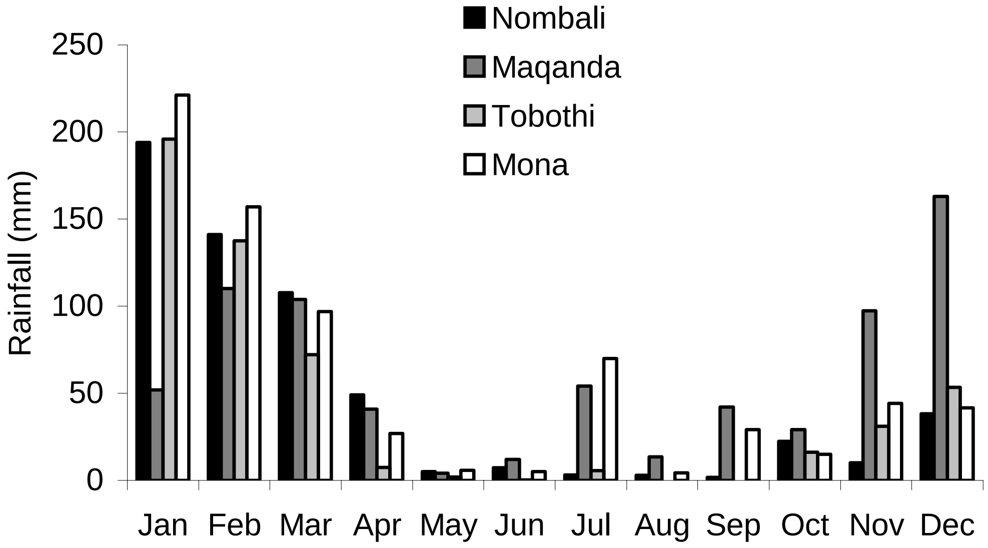


Fig 1 Mean monthly rainfall (mm) at the four study sites in the Hluhluwe-iMfolozi Park from January to December 2004. *Dichrostachys cinerea* seeds were planted mid of March 2004.

Experiment 1: Germination and seedling and survival of planted seeds

To examine the effects of herbivory and grass height on tree seedling germination and survival two study sites each were established in mesic savanna in Hluhluwe (Nombali and Maqanda) and in arid savanna in iMfolozi (Mona and Tobothi). Each study site had two large herbivore treatments: herbivore exclusion and not. Within the herbivore treatments four 1 x 1 m plots with tall grass and four 1x 1 m plots with short grass were created by clipping the vegetation in half of the plots to approximately 8 cm grass height. A total of 64 plots were thus established. Plots inside and outside the herbivore exclosure were assigned with at least 10 m spacing, however, plots in unclipped and clipped grasses were established using a paired set-up. Approximately mid of March 25 imbibed seeds were planted in each plot (resulting in 1600 planted seeds in total) approximately 1 cm deep in the soil and watered. Seedling germination, survival and herbivory were monitored and vegetation height recorded in the plots on a monthly basis throughout the experiment (eight months). Seedlings were considered to be damaged by mammalian herbivores when their stems, leaves, or branches had been cut off and by invertebrates when leaves were partly eaten. Wilted seedlings were also recorded.

Experiment 2: Survival of transplanted seedlings

For this experiment one study site in mesic savanna (Nombali) and one study site in arid savanna (Mona) was used. Each study site had two herbivore treatments: herbivore exclusion and not. Within the herbivore treatments three 1x 0,5 m plots with tall grass and three 1x 0,5 m plots with short grass were created by clipping the vegetation to approximately 8 cm grass height. A total of 24 plots were thus established. Plots inside and outside the herbivore exclosure were established with at least 10 m spacing, however, plots in unclipped and clipped grasses were established using a paired set-up. The plots were treated as described for experiment 1. Imbibed seeds were planted separately approximately one cm deep in plastic trays with soil from the park and stored in a nursery. Seeds were left to germinate and watered daily. After eight weeks seedlings were approximately two cm in height. Nine seedlings were then transplanted in each 0.5 x 1 m plot into the field (resulting in 216 seedlings in total) and watered once a week during the first month. Herbivory was monitored as described for experiment 1.

Data-analysis

Seed germination and seedling survival rate were analysed using a Cox regression hazard model (after Kleinbaum 1996) and log-linear models with either germination time or survival time as time factor, the status either ‘germinated’ or ‘alive’ as event and fence type (fenced vs. unfenced), clipping treatment (clipped vs. unclipped) and site as predictors. We used logistic regression to analyse the effect of the vegetation height on the seedling survival with seedling presence/absence as the dependent and vegetation height as a predictor. Seedling growth was tested using a one-way ANOVA with fence type or clipping treatment as predictors. Furthermore a Pearson’s Chi-square test was used to analyse the overall differences of seedling predation in fenced/unfenced plots and clipped/unclipped plots.

Results

Experiment 1 - Seed germination

The rate of germination was not affected by the clipping treatment over the course of the experiment (Table 1), but overall significantly more seeds germinated in clipped than in unclipped grass (Table 2, Fig. 2). The effect of the large herbivore exclusion on the seed germination (no. of seedlings present) varied among sites (significant site x fence interaction, Table 1 and 2). At Nombali the seed germination rate was approximately 20% to 32% higher than at the three other sites, for unfenced and fenced plots respectively (Fig. 2).

Table 1 Interacting effects of site, fence (fenced vs. unfenced) and clipping treatment (clipped vs. unclipped) on germination rate and seedling survival of *D. cinerea* over the course of the experiment (eight months), analysed with Cox regression hazard model.

Source of variation	df	Germination rate		Seedling survival of planted seeds		Seedling survival of transplanted seedlings	
		Waldl	*P*	Waldl	*P*	Waldl	*P*
Site	1	6.953	0.008	0.169	0.681	3.674	0.055
Fence	1	3.631	0.057	7.771	0.005	1.351	0.245
Clipping treatment	1	0.387	0.534	0.135	0.714	0.275	0.60
Site x Fence	1	4.295	0.038	12.733	0.000	3.522	0.61
Site x Clipping treatment	1	2.658	0.103	3.607	0.058	3.621	0.57
Fence x Clipping treatment	1	0.009	0.926	7.948	0.005	2.778	0.096
Site x Fence x Clipping treatment	1	0.001	0.970	9.546	0.002	0.513	0.474

Table 2 Interacting effects of site, fence (fenced vs. unfenced) and clipping treatment (clipped vs. unclipped) on germination rate and seedling survival of *D. cinerea*, analysed with a log-linear model.

Source of variation	df	Germination rate		Seedling survival of planted seeds		Seedling survival of transplanted seedlings	
		Waldl	*P*	Waldl	*P*	Waldl	*P*
Site	3	112.859	0.000	0.009	0.999	0.002	0.966
Fence	1	2.262	0.133	0.000	0.999	0.000	0.999
Clipping treatment	1	10.513	0.001	0.006	0.939	0.002	0.966
Site x Fence	3	10.042	0.018	0.004	0.999	0.000	0.999
Site x Clipping treatment	3	3.975	0.264	0.002	1.000	0.002	0.966
Fence x Clipping treatment	1	0.011	0.915	0.001	0.974	0.000	0.999
Site x Fence x Clipping treatment	3	1.529	0.676	0.002	1.000	0.000	0.999

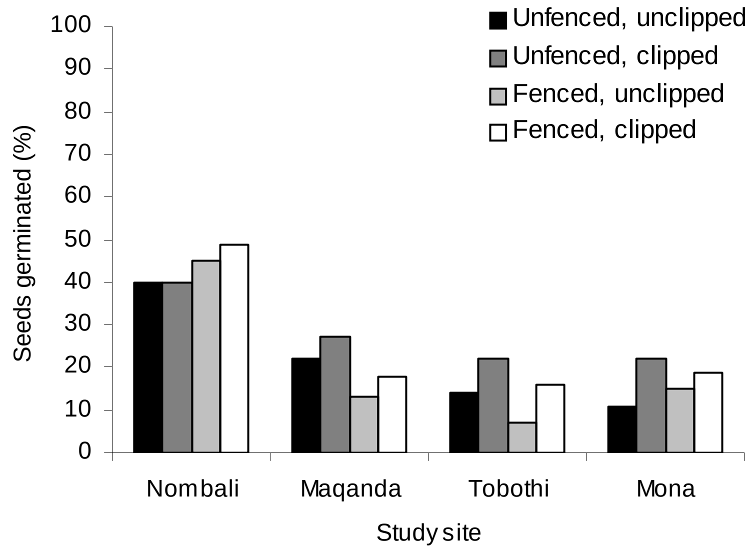
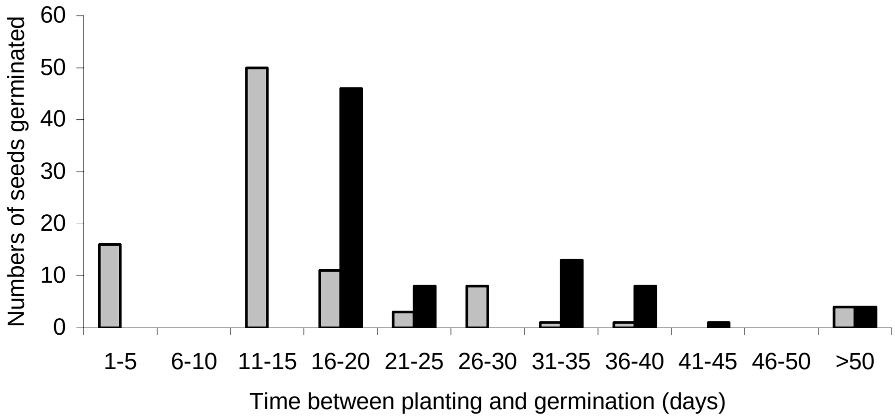


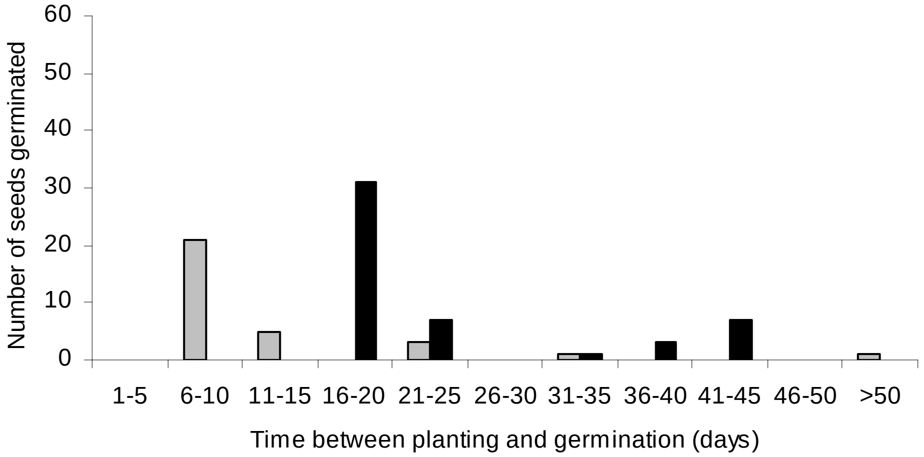
Fig 2 Interacting effects of the clipping treatment (clipped vs. unclipped) and large herbivores (fence vs. unfenced) on the total percentage of *D. cinerea* seeds that germinated at the two mesic sites (Nombali and Maqanda) and two arid sites (Tobothi and Mona). Significantly more seeds germinated in clipped than in unclipped plots (N = 380, Waldl = 10.513, *P* = 0.001). The effect of large herbivores on seed germination varied significantly among sites (N = 380, Waldl = 10.042, *P* = 0.002).

Within 15 days after seed planting both the precipitation and the germination rate of seeds in fenced/unfenced plots was similar at all sites (Fig. 1 and 3 A-D). However, 16 to 25 days after seed planting the precipitation as well as the seed germination rate was higher at the mesic sites than at the arid sites.

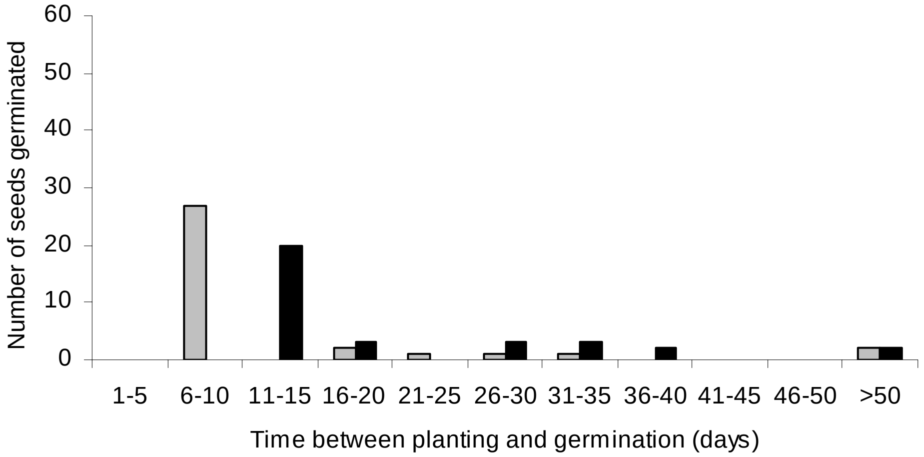
A) Nombali



B) Maqanda



C) Mona



D) Tobothi

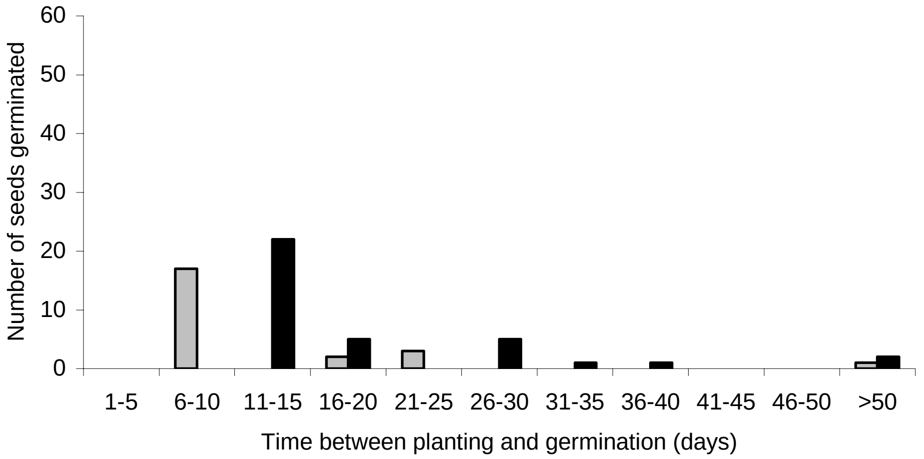


Fig 3 (opposite page) Total number of seeds that germinated in fenced (grey shaded bars) and unfenced plots (black shaded bars) within a given period after planting at the two mesic sites Nombali and Maqanda (A and B) and two arid sites Mona and Tobothi (C and D; N = 380).

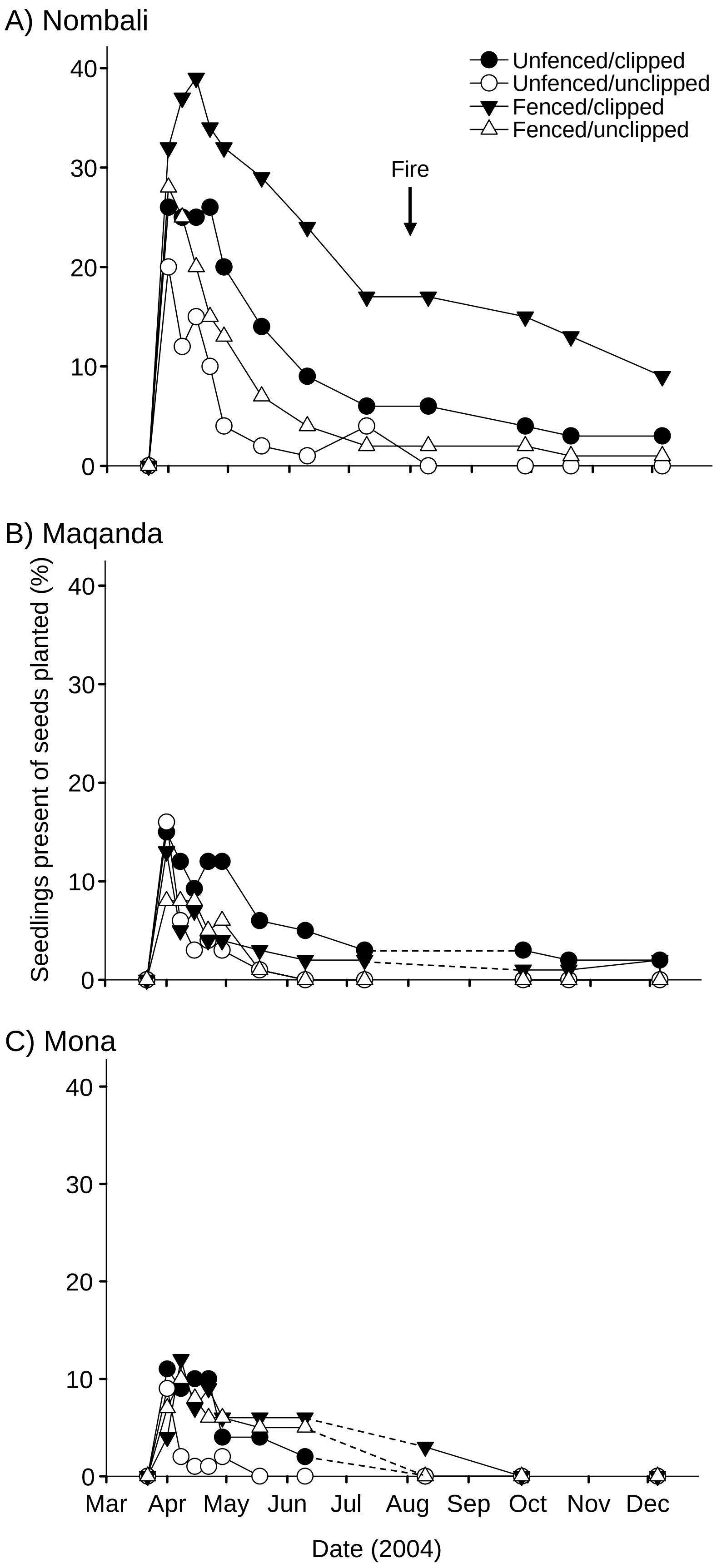
Experiment 1 - Survival of seedlings established from planted seeds

Interacting effects of grass height, herbivores and site

The combined effects of the grass clipping treatment and herbivore exclusion on the survival rate of *D. cinerea* seedlings varied among sites over the course of the experiment (significant site x clipping treatment x fence interaction; Table 1). Seedling survival was higher in plots where the grass was clipped than in unclipped plots (Fig. 4 A-D). Furthermore, higher numbers of seedlings survived when large herbivores were excluded. However, overall the number of surviving seedlings in clipped plots increased with increasing grass height when large herbivore were present (Waldl = 18.46, $P < 0.000$) but no effect of increasing grass height on seedling survival was found when large herbivores were excluded (Waldl = 1.551, P = 0.213). In total only 21 seedlings that established from planted seeds were still alive at the end of the experiment of which 13 were found at the mesic site Nombali (4 A). Nombali was therefore the only site where enough survivors remained to do further analysis. For this site, we found a significantly higher proportion of seedlings in clipped grass compared to unclipped grass (Waldl = 4.949, $P = 0.026$).

Cause of damage to seedlings

Overall, 32 % of seedlings alive were damaged over the course of the experiment. We observed significant differences in the predation types that seedlings experienced in the different treatments ($X^2_9 = 808.957$, $P < 0.000$, Fig. 5). Most of the damage was caused by invertebrates but also rodents were found to be predators of seedlings. Furthermore, both invertebrates and rodents damaged more seedlings in clipped than in unclipped grass, whereas the presence or absence of larger herbivores had no effect. However, for all treatments the cause of damage to seedlings often could not be determined.


A) Nombali
Unfenced/clipped
Unfenced/unclipped
Fenced/clipped
Fenced/unclipped
Fire
40
30
20
10
0
B) Maqanda
Seedlings present of seeds planted (%)
40
30
20
10
0
C) Mona
40
30
20
10
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date (2004)

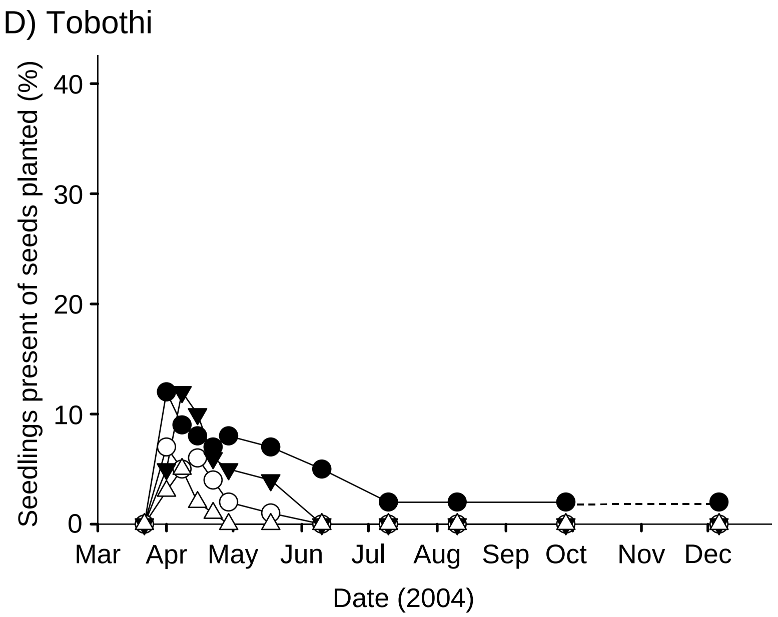


Fig 4 Interacting effects of the clipping treatment (clipped vs. unclipped) and large herbivores (fence vs. unfenced) on the survival of *D. cinerea* seedlings at the two mesic sites Nombali and Maqanda (A and B) and two arid sites Mona and Tobothi (C and D) for March to December 2004. The combined effects of the clipping treatment and large herbivore exclusion varied significantly among sites (N = 4 plots per treatment, Waldl = 9.546, *P* = 0.002).

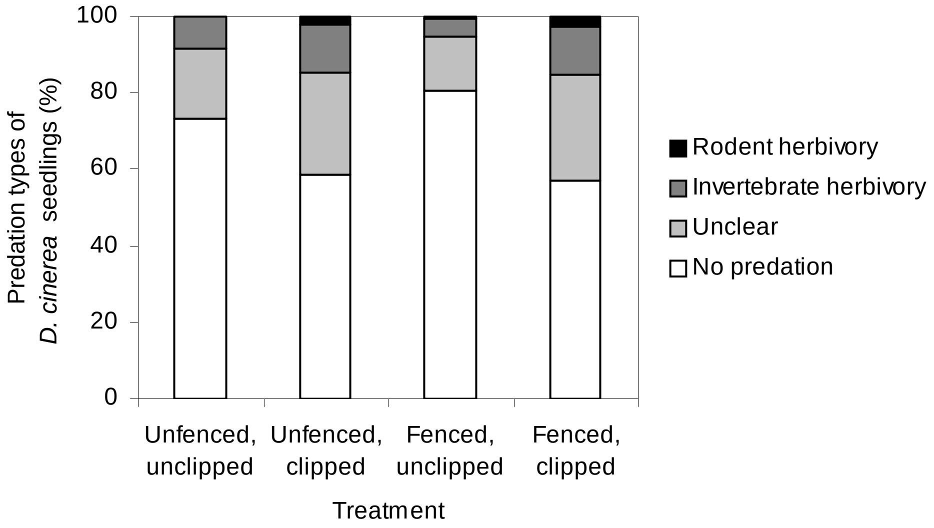


Fig 5 Percentage of different predation types of *D. cinerea* seedlings for the different treatments at all sites for March to December 2004. Seedling predation was significantly different between treatments (N = 890, X^2_9 = 808.957, *P* < 0.000).

Experiment 2: Survival of transplanted seedlings

Effects of grass height, herbivores and site

The seedling survival rate was not significantly affected by the clipping treatment or large herbivore exclusion over the course of the experiment (Table 1 and 2, Fig. 6 A and B). However, seedling survival was generally higher when large herbivores were excluded.

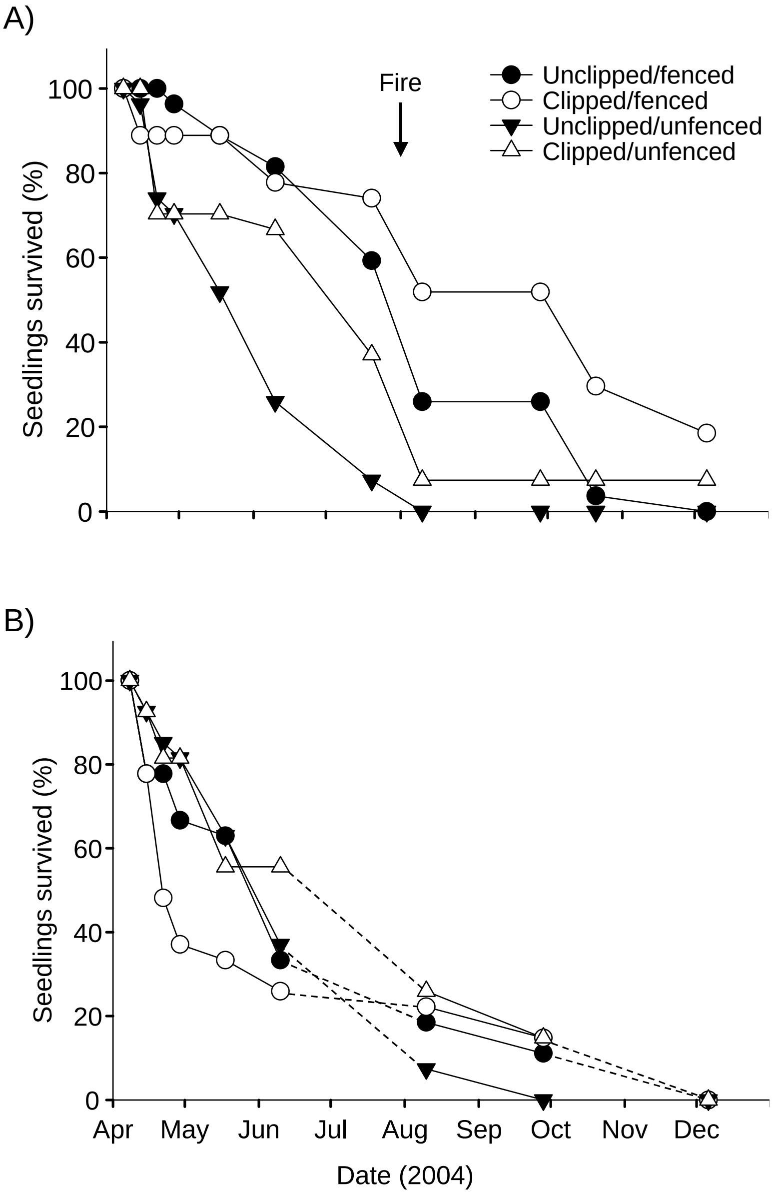


Fig 6 Interacting effects of large herbivores (fence vs. unfenced) and clipping treatment (clipped vs. unclipped) on the survival of transplanted *D. cinerea* seedlings at the mesic site Nombali (A) and arid site Mona (B) for April to December 2004. The seedling survival at the two sites was not significantly influenced by the combined effects of the clipping treatment and large herbivore exclusion (N = 3 plots per treatment, Waldl = 0.513, *P* = 0.474).

Furthermore, when large herbivores were present the number of surviving seedlings increased with increasing vegetation height not only in clipped plots (Waldl = 48.881, $P < 0.000$) but also in unclipped plots (Waldl = 98.442, $P < 0.000$). Only six transplanted seedlings were still alive at the end of the experiment, all of them were recorded at the mesic site Nombali (Fig 6A). All survivors were found in clipped grass but herbivore absence also positively affected seedling survival.

Seedling growth

Overall, seedling growth (as measured by height) was affected by both clipping treatment and site. Seedlings in clipped grass grew more than in unclipped grass plots ($F_{1,\ 181} = 26.29$, $P < 0.001$) and seedling growth was higher at the mesic savanna site Nombali than at the arid savanna site Mona ($F_{1,\ 181} = 10.06$, $P = 0.002$). We found no evidence that seedling growth was influenced by large herbivores.

Cause of damage to seedlings

Overall, 20 % of the seedlings alive were damaged over the course of the experiment. Significant differences in the types of damage to seedlings in the different treatments were observed ($X^2_9 = 96.056$, $P < 0.000$, Fig. 7). Most of the damage was caused by invertebrates, rodent-type damage to the seedlings was rarely observed. Furthermore, more seedlings were damaged in unclipped than in clipped grass, and more seedlings were damaged in the absence of large herbivore than in their presence. However, for all treatments the cause of predation/loss of seedlings often remained unclear.

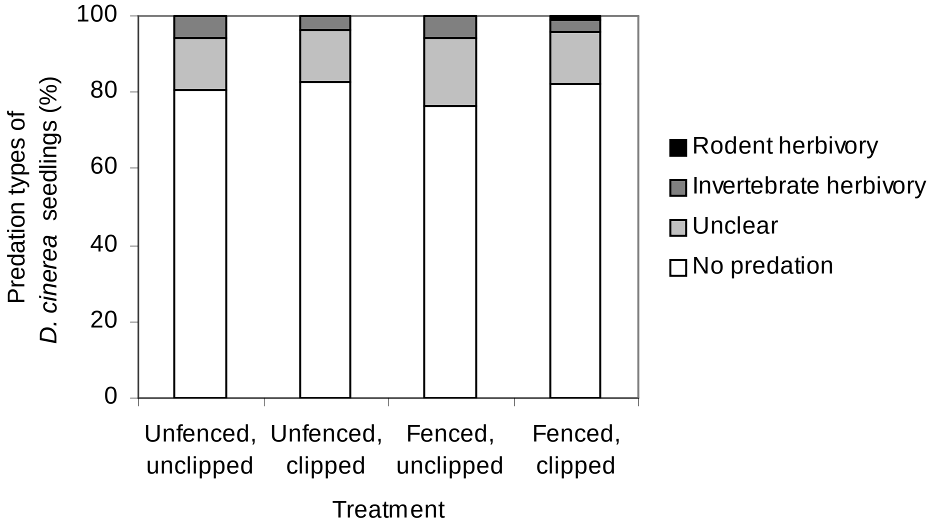


Fig 7 Percentage of different predation types of *D. cinerea* seedlings for the different treatments at both sites for April to December 2004. Seedling predation was significantly different between treatments (N = 1330, $X^2_9 = 96.056$, $P < 0.000$).

Discussion

In this study, both seed germination and seedling survival of *Dichrostachys cinerea* were promoted by simulated grazing of the grass layer in the absence of grazers and by excluding large herbivores. Increasing grass height however positively affected seedling survival when large herbivores were present, suggesting that the benefits of protection to large herbivore grazing was not fully compensated by the negative effect of enhance competition by the grasses. Additionally, our results suggest that rainfall may be another factor that positively influences seed germination as well as the survival of seedlings. Invertebrates were primary consumers of *D. cinerea* seedlings but also rodents were found to be seedling predators.

Seed germination and seedling survival

It is often suggested that competitive inhibition by the grass layer may be a crucial filter for tree recruitment in grasslands (Davis et al. 1999) and savannas (Sankaran et al. 2004) but also herbivores have been considered important (Pellew 1983, Dublin 1991, McNaughton 1992, van Langevelde et al. 2003) as they may affect woody-plant invasion both positively (Van der Wall 1994) and negatively (Bowers 1993) by indirectly changing resource availability for plants through their foraging (McNaughton 1983, Dublin et al. 1990, Ritchie & Tilman 1995, Hobbs 1996, Augustine & McNaughton 1998). In the present study seed germination and seedling survival of *D. cinerea* was affected by an interplay of competition between trees and grasses for resources and habitat modifications caused by grazing large herbivores. For instance, by suppressing the growth of graminoids through intense grazing, herbivores may indirectly facilitate seed germination and seedling survival through improved light conditions. It has been shown that high light levels can improve seed germination and seedling survival (Denslow 1987, Brokaw 1985, Fischer et al. 1991, Belsky & Blumenthal 1997). On the other hand the ‘two-layer hypothesis’ of grass-tree interactions in savannas states that grasses generally are superior competitors for water in the upper soil layer (Walker et al. 1981), leaving only limited amounts to penetrate to deeper layers, where it is exclusively available to trees and shrubs (Skarpe 1990). When the grass sward is damaged, e.g., by overgrazing, above- and below-ground biomass is reduced (Holland & Detling 1990) more water could become available for woody plants (Caldwell et al. 1987) that could otherwise have been utilised by the grasses (Walker & Noy-Meir 1982, Bland 1985). Water relations have been indicated to be particularly important during seed germination (Hoffmann 1996) but also for seedling survival. Therefore intense grazing by large herbivores may indirectly facilitate seed germination and seedling survival by suppressing the growth of competing grasses and thus accelerate tree recruitment through improved light and water availability.

On the other hand grazing can also have negative effects on seedling survival. For instance, overgrazing often results in a significant decrease of the vegetation cover and the lack of protective cover in turn may increase the seedlings’ risk of being directly killed through trampling of large grazing herbivores. Additionally large grazers could graze them along with grasses and make them more visible to browsers. Furthermore, less shade levels in overgrazed areas may lead to higher desiccation which may increase seedling mortality compared with a shady environment (Gerhardt 1996). In our study the vegetation cover was generally lower in presence of large herbivores and seedling survival was higher with increasing grass height when large herbivores were present indicating that trampling, direct grazing of seedlings and desiccation may be limiting factors influencing seedling survival. However, in our study it appears that the positive effects of by large grazing herbivores created short grass on *D. cinerea* seed germination and seedling survival (less competition for water and light) may outweigh its negative effects (higher risk of being trampled by herbivores and desiccation).

Browsing mammals have been suggested to have a relatively low impact on tree seedling recruitment, while invertebrates may account for most of the herbivory (Miller 1994, Mucunguzi 1995, Meiners et al. 2000, Shaw et al. 2002). We observed that invertebrates were responsible for most of the herbivory on *D. cinerea*. Additionally, rodents were found to be seedling predators whereas large browsers were only of minor importance. This coincides with the observation of Roques et al. (2001) who found that large browsers only had a minor impact on *D. cinerea* dynamics in Swaziland. In African savannas the reported role of rodents in influencing tree recruitment ranges from potentially important (e.g., Miller 1994) to negligible (e.g., Barnes 2001). Shaw et al. (2002) found that rodents in East African savannas have only relatively little effects on *Acacia drepanolobium* seedling survival, whereas insect were considered to be important agent of seedling mortality.

Implications of the study

There is considerable debate on how rainfall (Fensham & Holman 1999, Fernandez-Gimenez & Allen-Diaz 1999, Fynn & O’Connor 2000) and grazing (Hulme et al. 1999, Bokdam & Gleichman 2000, Sternberg et al. 2000) should be taken into account in terms of management of shrub encroachment. The results from this study indicate that effective reductions in shrub cover may occur when drought acts in concert with light grazing. Drought might inhibit germination of seeds and seedling survival. Light grazing may result in a closed grass sward and has therefore the potential to reduce or prevent shrub encroachment (Roques et al. 2001). When the grass sward has sufficient above- and below-ground biomass the grasses would be able to utilise the water in the upper soil that otherwise would have been used by the woody species. Furthermore increased plant growth could lead to both increased fire frequencies (Roques et al. 2001) and intensities (Norton-Griffiths 1979) and fire would thus be another important tool to suppress bush encroachment. While managers can influence the fire-grazing mechanism, they have little control over drought and self-thinning. This suggests that the reversal of encroachment may be possible through fine-tuning fire management to rainfall patterns.

Acknowledgement

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References

Adamoli J, Sennhauser E, Acero JM, Resica A (1990) Stress and disturbance: vegetation dynamics in the dry region of Argentina. Journal of Biogeography 17:491-500

Anderson AN, Lonsdale WM (1990) Herbivory by insects in Australian tropical savannas: a review. Journal of Biogeography 17:433-444

Archer S, Scifres CJ, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical savanna: conversion of grassland to a thorn woodland. Ecological Monographs 58: 111-127

Archer S (1995) Tree-grass dynamics in a *Prosopis*-thornshrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83-99

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183

Auld TD (1995) Seedling survival under grazing in the arid perennial *Acacia oswaldii*. Biological Conservation 72:27-32

Balfour DA, Howison OE (2001) Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. African Journal of Range and Forage Science 19:43-51

Barnes ME (2001) Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. Journal of Arid Environments 49:541-554

Belsky AJ (1992) Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. Tropical Grasslands 26:12-20

Belsky AJ, Mwonga SM, Amundson RG, Duxbury JM, Ali AR (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low rainfall savannas. Journal of Applied Ecology 30:143-155

Belsky AJ (1994) Influences of trees on savanna productivity: test of shade, nutrients, and tree-grass competition. Ecology 75:922-932

Belsky AJ, Blumenthal DM (1997) Effects of livestock grazing and stand dynamics and soils in upland forests of the interior West. Conservation Biology 11:315-327

Bland G (1985) Bush encroachment in the integrated farming pilot project (IFPP) areas of Botswana. MSc dissertation, School of Development Studies, University of East Anglia, Norwich

Bokdam J, Gleichman JM (2000) Effects of grazing by free-ranging cattle on vegetation dynamics in a continental NW-European heathland. Journal of Applied Ecology 37:415-431.

Bowers MA (1993) Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. Oikos 67:129-141

Brokaw NVL (1985) Gap-phase regeneration in a tropical forest. Ecology 66:682-687

Brooks PM, Macdonald IAW (1983) The Hluhluwe- Umfolozi Reserve: An ecological case history. Management of large mammals in African conservation areas. Haum Educational Publishers, Pretoria 1983

Brown JR, Archer S (1987) Woody plant seed dispersal and gap information in a north-American sub-tropical savanna woodland: the role of domestic herbivores. Vegetatio 73:73-80

Brown NAC, van Staden J (1997) Smoke as a germination cue: a review. Plant Growth Regulation 22:115-124

Brown NAC, van Staden J, Daws MI, Johnson T (2003) Patterns in the seed germination response to smoke in plants from the Cape Floristic Region, South Africa. South African Journal of Botany 69:514-525

Burrows WH, Beale IF, Silcock RG, Pressland AJ (1990) Prediction of tree and shrub population changes in a semi-arid woodland. Ecology and Management of the Worlds Savannas (eds J.C. Tothill & J.J. Mott), pp. 207-211. Australian Academy of Science, Canberra, Australia

Caldwell MM, Richards JH, Manwaring JH, Eissenstat DM (1987) Rapid shifts in phosphate acquisition show direct competition between neighboring plants. Nature 327:615-616

Conway A, Balfour D, Dale T, Hartley P, Morrison P, Howison R, Galli N, Wadge M (2001) Hluhluwe-Umfolozi Park Management Plan 2001. Ezemvelo KwaZulu-Natal Wildlife

Crawley MJ, Long CR (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. Journal of Ecology 83:683-696

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annual Review Ecological Systems 18:431-451

Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mar woodlands, Journal of Animal Ecology 59:1147-1164

Dublin HT (1991) Dynamics of the Serengeti-Mara woodlands, Forest and Conservation History 35:169-178

FAO (1995) Digital soil map of the world and derived soil properties. Food and Agriculture Organization of the United Nations, FAO

Fensham RJ, Holman JE (1999) Temporal and spatial patterns in drought-related tree dieback in Australien savanna. Journal of Applied Ecology 36:1035-1050

Fernandez-Gimenez ME, Allen-Diaz B (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. Journal of Applied Ecology 36:871-885

Fischer BL, Howe HF, Wright SJ (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understorey. Oecologia 86:292-297

Fynn RWS, O'Connor TG (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle-performance in a semi-arid savanna, South Africa. Journal of Applied Ecology 37:491-507

Gerhardt K (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonl dry forest. Forest Ecology and Management 82: 33-48

Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. Ecology 85:555-1561

Harju A, Tahvanainen J (1997) Palatability of silver birch seedlings to root voles *Microtus oeconomus*. Ecography 20:83-87

Hobbs NT (1996) Modification of ecosystems by ungulates, Journal of Wildlife Management 60:695-713

Hobbs RJ, Mooney HA (1986) Community changes following shrub invasion of grasslands. Oecologia 70:508-513

Hoffmann WA (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. Journal of Ecology 84:383-393

Holland EA, Detling JK (1990) Plant response to herbivory and below ground nitrogen cycling. Ecology 71:1040-1049

Hulme PD, Pakeman RJ, Torvell L, Fisher JM, Gordon IJ (1999) The effects of controlled sheep grazing on the dynamics of upland *Agrostis-Festuca* grassland. Journal of Applied Ecology 36:886-900

Janzen DH (1971) Seed predation by animals. Annual Review Ecological Systems 2:465-492

Keeley JE, Fortheringham CJ (2000) Role of fire in regeneration from seed. In Seeds: The ecology of Regeneration in Plant Communities (Fenner, M., ed.), pp. 311-330, CABI

Kleinbaum DG (1996) Survival analysis. A self learning text. Springer

Kozlowski TT, Kramer PJ, Pallardy ST (1991) The Physiological Ecology of Woody Plants. Academic Press, San Diego

Loth PE (1999) The vegetation of Manyara: Scale-dependent states and transitions in the African Rift Valley. PhD thesis, Wageningen University

Ludwig F (2001) Tree-grass Interactions on an East African Savanna: The effects of competition, facilitation and hydraulic lift. PhD hesis, Wageningen University

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

McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contigency in community organization. Ecological Monographs 53:291-320

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

Meiners SJ, Handel SN, Pickett STA (2000) Tree seedling establishment under insect herbivory: edge effects and inter-annual variation. Plant Ecology 151:161-170

Miller MF (1994) Large African herbivores, bruchid beetles, and their interactions with *Acacia* seeds. Oecologia 97:265-270

Mills JN (1983) Herbivory and seedling establishment in post-fire southern California chaparral. Oecologia 60:267-270

Milton MJ, Dean WRJ (1995) South Africa's arid and semiarid rangelands: Why are they changing and can they be restored? Environmental Monitoring and Assessment 37:245-264

Moleele NM, Ringrose S, Matheson W, Vanderpost C (2002) More woody plants? The status of bush encroachment in Botswana's grazing areas. Journal of Environmental Management 64:3-11

Mucunguzi P (1995) Effects of bruchid beetles on germination and establishment of *Acacia* species. African Journal of Ecology 33:64-70

Mwalyosi, RBB (1990) The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. African Journal of Ecology 28:189-199

Norton-Griffiths M (1979) The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Serengeti: Dynamics of an Ecosystem (eds A.R.E Sinclair & Norton-Griffiths), pp. 310-352. Chicago university Press, Chicago, IL

O'Connor TG (1995) Acacia karoo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. Oecologia 103:214-223

Ostfeld RS, Canham CD (1993) Effects of meadow vole population density on tree seedling survival in old fields. Ecology 74:1792-1801

Peet NB, Watkinson AR, Bell DJ, Sharma UR (1999) The conservation management of *Imperata cylindrica* grassland in Nepal with fire and cutting: an experimantal approach. Journal of Applied Ecology 36:374-387

Pellew RA (1983) The impact of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. African Journal of Ecology 21:41-74

Pooley E (1993) The complete field guide to trees of Natal, Zululand and Transkei. Natal Flora Publication Trust, Durban

Pressland AJ (1973) Rainfall partitioning by an arid woodland (*Acacia anura* F. Muell.) in southwestern Queensland. Australian Journal of Botany 21:235-245

Prins HHT, Van der Jeugd HP (1993) Herbivore population crashes and woodland structure in East African Journal of Ecology 81:305-314

Pusenius J, Ostfeld RS, Keesing F (2000) Patch selection and tree-seedling predation by resident vs. immigrant meadow voles. Ecology 81:2951-2956

Reyes F, Gonzalez E, Hernandez D, Carbello M, Mendoza C (1994) Effect of ruminal ingestion on germination of seeds of tropical legumes. Pastos Y Forrajes 17:283-286

Ritchie M, Tilman D (1995) Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. Ecology 76:2648-2655

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

Shaw MT, Keesing F, Ostfeld RS (2002) Herbivory on *Acacia* seedlings in an East African savanna. Oikos 98:385-392

Sinclair ARE (1995) Equilibria in plant-herbivore interactions. - In: sinclair, A.R.E. and Arcese, P. (eds), Serengeti II: dynamics, management, and conservation of an ecosystem. Univ. of Chicago Press, pp. 91-113

Skarpe C (1990) Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. Journal of Aplied Ecology 27:873-885

Skowno AL, Midgley JJ, Bond WJ, Balfour D (1999) Secondary succession in Acacia nilotica (L.) savanna in the Hluhluwe Game Reserve, South Africa. Plant Ecology 145:1-9

Sternberg M, Gutman M, Perevolotsky A, Ungar ED, Kigel J (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional approach. Journal of Applied Ecology 37:1-15

Stuart-Hill GC, Tainton NM (1989) The competitive interactions between Acacia karroo and the herbaceous layer and how it is influenced by defoliation. Journal of Applied Ecology 26:285-298

Sullivan TP (1979) Use of alternative foods to reduce conifer seed predation by the deer mouse (*Peromyscus maniculatus*). Journal of Applied Ecology 16:475-495

Traill LW (2004) Seasonal utilisation of habitat by large grazing herbivores in semi-arid Zimbabwe. South African Journal of Wildlife Research 34:13-24

Trollope WSW (1984) Fire in Savanna, in Ecological Effects of Fire in South African Ecosystems. In: Booysen, P.de V. and Tainton, N.M. (eds), Springer-Verlag, Berlin, pp. 199-306

Trollope WSW, Hobson FO, Danckwerts JE, van Niekerk JP (1989) Encroachment and control of undesirable plants. Veld Management in the Eastern Cape (eds J.E. Danckwerts & W.R. Teague), pp. 73-89. Department of Agriculture and Water Supply, Pretoria, South Africa

van der Wall SB (1994) Seed fate pathways of Antelope Bitterbrush - Dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911-1926

van Langevelde F, Van de Vijver CADM, Kumar L, Van de Koppel J, De Ridder N, Van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337-350

van Staden J, Kelly KM, Bell WE (1994a) Chemical-composition of pods and seeds of *Dichrostachys cinerea* as a basis of seed dispersal. Plant Growth and Regulation 14:73-277

van Staden J, Kelly KM, Bell WE (994b) The role of natural agents in the removal of coat-imposed dormancy in *Dichrostachys cinerea* (L.) Wight et Arn. seeds. Plant Growth and Regulation 14:51-59

van Vegten JA (1983) Thornbush invasion in a savanna ecosystem in eastern Botswana. Vegetatio 56:3-7

Walker BH, Ludwig D, Holling CS, Peterman RM (1981) Stability of semi-arid savanna grazing systems. Journal of Ecology 69:473-498

Walker BH, Noy-Meir I (1982) Aspects of the stability and resilience of savanna ecosystems. Ecology of Tropical Savannas (eds B.J. Huntly & B.H. Walker), pp. 555-590. Springer-Verlag, Berlin, Germany

Walter H (1971) Ecology of Tropical and Subtropical Vegetation. Oliver and Boyd, Edinburgh, UK

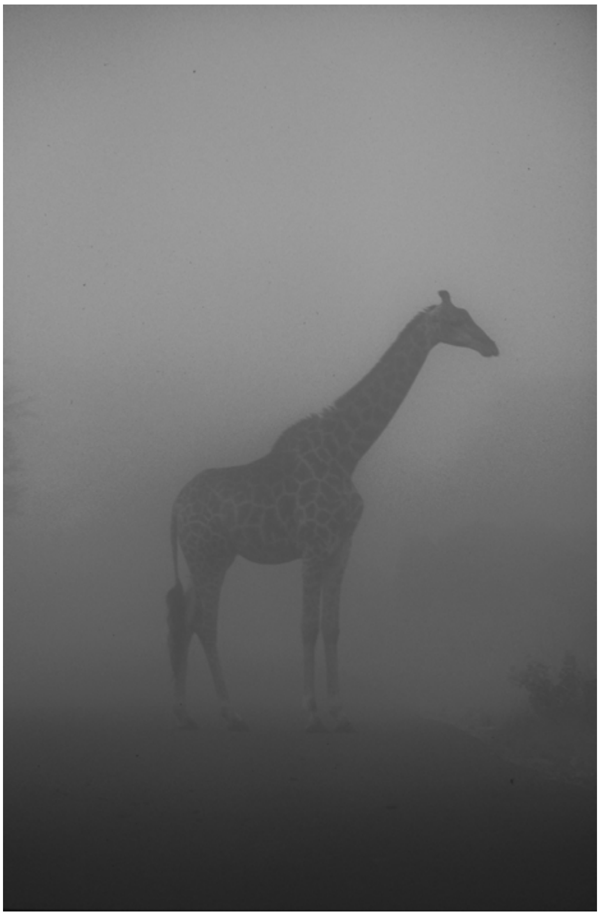
Watson HK, MacDonald IAW (1983) Vegetation changes in the Hluhluwe-Umfolozi Game Reserve Complex from 1937 to 1975. Bothalia 14:265-269

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

Whateley A, Porter RN (1983) The woody vegetation communities of the Hluhluwe- Corridor-Umfolozi Game Reserve Complex. Bothalia 14:745-758

Wilson TB, Witkowski ETF (1998) Water requirements for germination and early seedling establishment in four African savanna woody plant species. Journal of Arid. Environment 38:541-550

Witkowski ETF, Garner RD (2000) Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites. Plant Ecology 149:91-106



Chapter 6

Synthesis

In the previous chapters I showed how different-sized large herbivores and rodents interact in the studied savanna ecosystem and found that these interactions are influenced by fire and rainfall. The stepwise exclusion of large herbivore groups resulted in changes of the plant species composition and increased grass height and thus cover, hence leading to higher abundances of rodents. Middle-sized and large herbivore species responded to short-term post fire succession patterns in savannas. Large herbivore species were the pioneer species on recently burnt vegetation patches. Middle-sized and large herbivores influenced rodents when they recolonised burnt areas mainly through increasing and prolonging their predation risk via grass cover modifications. Additionally, the grass cover was the most important factor determining the habitat selection of predominantly grass-eating savanna rodents but food resource availability also seemed to play a role, especially since male and females have different priorities. Furthermore, the recruitment of the encroaching woody species *Dichrostachys cinerea* is influenced by both the positive effects (less competition with grasses for water and light) and negative effects (higher risk of being trampled by herbivores and desiccation) of grazing large herbivores and the amount of rainfall but also through predation by invertebrates and murid rodents. In this chapter I will try to connect all these aspects of the interplay between small and large herbivores in African savannas and explore the ecological consequence of this interplay for the maintenance of this ecosystem.

Top-down or bottom-up, that is the question!

Animal communities may be controlled by the availability of their resources (bottom-up control) or by their predators (top-down control, Hutchinson 1959, Hairston et al. 1960, Hunter and Price 1992, Power 1992). The largest herbivores in savannas like elephant, hippo, rhino’s and buffalo have been suggested to be generally limited by resources (Hairston et al. 1960, Hanks and McIntosh 1973, Sinclair et al. 1985, Drent and Prins 1987, Owen-Smith 1988, Phillipson 1992), but there are many ideas on how small herbivores like rodents are controlled and none is widely accepted. Some of these hypotheses include food as controlling (Kalela 1962, Heske et al. 1994) others suggest predators (Lima and Valone 1986, Lima and Dill 1990, Cassini 1991, Holmes 1991) being the main determinant of rodents. Therefore one aim of my thesis was to find the controlling factors for murid rodent communities in a complex ecosystem like the South African savanna.

Large herbivores in savannas have often been suggested to improve the vegetation structure and thus food quality for smaller herbivores (Farnsworth et al. 2002, Arsenault and Owen-Smith 2002) as their intense grazing leads to the development of mosaics with short and long vegetation patches (Vesey-FitzGerald 1969, 1972; Cromsigt and Olff in press) that differ in quality and quantity. On the other hand, selective larger grazing herbivores could decrease the number of high quality plant species available for smaller primarily grass-eating herbivore species and so negatively influencing them through food resource competition (Keesing 1998). Small herbivores like rodents have a high energy demand per gram body mass (Kleiber 1961) and have a short digestive tract; they need a high plant nutrient content to meet their food requirements (Bell 1982, Van Soest 1982, Belovsky 1986, 1997, Wilmshurst et al. 2000, Hamback et al. 2002) and may therefore depend on high quality food resources. Food resources are important components in the habitat selected by rodents (Monadjem 1998, Monadjem and Perrin 1998) and foraging for food is a major determinant of the space use and movement patterns in African rodents (Andrzejewski and Mazurkiewicz 1976, Taitt 1981, Zubaid and Gorman 1993). It was therefore predicted that the absence of large grazing herbivores would result in changes of the rodent food resource availability and that rodents preferentially utilise vegetation patches with abundant high grass species created by large herbivores. I showed that the exclusion of large herbivores lead to changes in both food quantity and plant species composition, increasing the abundance of high quality plant species available to rodents (*chapter 2*). All rodents captured in this study were primarily grass-eaters (or at least seasonal grass-eaters) and therefore potentially competing with large grazing herbivores for food resources. The grass species composition in the home ranges of the most dominant rodent species *Lemniscomys rosalia spinalis* was significantly different from the rest of the trapping grid (*chapter 4*). A higher abundance of high quality grass species was found within the home ranges than compared to the surrounding. The role of food resource availability in southern African rodent communities is poorly understood (Delany 1986). Monadjem and Perrin (1998) found that in southern Africa food is clearly a limiting factor for rodents and may therefore strongly affect the habitat utilisation of these selective feeders. This may be especially true for the driest savannas (below 600 mm annual rainfall). For instance, the availability of suitable food resources influenced the distribution, numbers, reproduction, and mass of rodents in Swaziland (Leirs and Verheyen 1995, Monadjem and Perrin 1996). However, no large herbivore-induced differences were reflected in the graminoid diet components of *L. rosalia spinalis* (*chapter 2*). Their home ranges consisted mainly of the most abundant grass species occurring in their habitat, rather than high quality grass species. This may mean that they have been highly selective by only taking the best parts of the food resources available regardless of quality. This suggests that forage quality is not an important limiting factor for *L. rosalia spinalis* in this habitat.

High grazing pressure and trampling by large herbivores reduces the vegetation cover and may then restrict the suitable habitat available to rodents (Grant et al. 1982; Bock et al. 1984, McInnes et al. 1992, Pacala and Crawley 1992, Roques et al. 2001, Goheen et al. 2004) as the decrease of vegetation cover could lead to a higher exposure of rodents to their predators and therefore increase their predation risk (Birney et al. 1976, Edge et al. 1995, Peles and Barret 1996). I therefore expected that the absence of large herbivores would result in increased vegetation cover, leading to high rodent numbers as they mostly utilise these dense habitats. The present study showed that large herbivore absence lead to an increase in grass height, and that rodents became more abundant when there was sufficient vegetation cover (*chapter 2*). Furthermore the vegetation cover within the home ranges of *L. rosalia spinalis* was higher than in the rest of the grid (*chapter 4*). Several other studies on habitat selection have found that vegetation cover is the primarily determinant of rodent distribution not only in Africa (Bond et al. 1980, Rowe-Rowe and Mester 1982, Iyawe 1988, Leirs and Verheyen 1995, Leirs et al. 1996, Monadjem 1997a) but also in temperate and boreal zones (e.g., Kaufman et al. 1983, Desy et al. 1990, Drickamer 1990, Kotler et al. 1991, Dickman 1992). The amount of vegetation cover is especially important for rodents (Bowland and Perrin 1989) and has been suggested to be most likely an adaptation for reducing predation risk, especially imposed by birds of prey (Kotler and Blaustein 1995, Korpimaeki et al. 1996). Owing to its diurnal habits (Skinner and Smithers 1990) *L. rosalia spinalis* may be particularly prone to predation by diurnal birds of prey (e.g., black shouldered kite) which are abundant in the study area. Summarising, my results and the available literature suggest that large herbivores in this ecosystem mostly affect murid rodents through modifying their predation risk (top-down, by changing the structure of the vegetation) rather than through facilitative or competitive interactions for food (bottom-up).

The precipitation gradient as a determinant

It has been often documented that precipitation and fire are important environmental forces (Daubenmire 1968, Vesey-Fitzgerald 1972) that, in a strong interaction with herbivores, modify African savanna ecosystems (Norton-Griffiths 1979, Pellew 1983). Precipitation variations affect ecosystem processes as high amounts of plant-available moisture increases productivity but reduces plant nutrient contents (Walker and Langridge 1997, Olff et al. 2002), whereas little amount of plant-available moisture results in low plant productivity with high nutrient content. This in turn affects the carrying capacity of an ecosystem not only regarding animal species diversity (Olff et al. 2002) but also with regard to animal biomass (Watson 1972). Fire affects vegetation production and nutrient status (Daubenmire 1975, Smith and Kadlec 1985, Frost and Robertson 1987, Moe and Wegge 1997) and reduces the cover of the savanna woody component (Vesey-Fitzgerald 1972, Werger 1983) and therefore influence herbivore distribution as they tend to concentrate on post-fire regrowth (Sinclair 1977, Moe et al. 1990, Stein et al. 1992, Pfeiffer and Hartnett 1995, Sparks and Masters 1996, Wilsey 1996, van de Vijver 1999). It was hypothesised in this study that general ecosystems processes in African savannas may be determined by a precipitation gradient. Results of this thesis provide evidence that precipitation and fire events in African savannas affect herbivore abundance, distribution and species composition (*chapter 2 and 3*). Furthermore, the tree-grass ratio in savannas is strongly directly and indirectly influenced through the foraging behaviour of herbivores but precipitation and fire also play a role (*chapter 3 and 5*).

The most abundant rodent species *Lemniscomys rosalia spinalis* was found at both the Hluhluwe (high rainfall area) and iMfolozi sites (low rainfall area), whereas *Saccostomus campestris* was found in Hluhluwe exclusively and *Mastomys natalensis* was only captured in iMfolozi. *L. rosalia spinalis* are predominantly grass-eating (*chapter 2*) and known to occupy herbivore niches (Monadjem 1997b). Their most important requirement seems to be the presence of dense ground cover of long grass (*chapter 2 and 4*, but see also Monadjem 1997a, Taylor 1998) and may therefore avoid recently burnt areas (*chapter 3*, see also Monadjem and Perrin 1997). The high rainfall in Hluhluwe promotes a high productivity of mostly low quality (*chapter 2*) bunch grasses in spite of heavy grazing by larger herbivores. Furthermore, tall bunch grasses provide good shelter for rodents and living in these habitats may therefore result in less exposure to their predators (*chapter 2 and 4*). *Saccostomus campestris* are slow moving rodents that often fall prey to carnivores (Taylor 1998). This species may generally utilise habitats with dense cover (*chapter 2*). The high rainfall in the Hluhluwe area not only promotes grass productivity but also tree seed germination and seedling establishment (*chapter 5*), which in combination with large grazing herbivores may improve conditions for the invasion of encroaching woody species. But big fuel loads in turn results in frequent and intense fires, which leads to short- and long-term vegetation shifts on small and landscape scales, affecting the foraging behaviour of middle-sized (warthog, nyala and impala) and large herbivores (white rhino, buffalo, zebra and wildebeest). Fire caused an immediate sharp reduction of grass height (*chapter 3*). Especially large species preferentially foraged on recently burnt grass patches (see in contrast to this Wilsey 1996) and kept the grass short until it, promoted by rainfall, grew back to the originally height after approximately two years (*chapter 3*). Furthermore, fire kills all trees and shrubs below a height of approximately three meter (Trollope et al. 2002) and thus modifying long-term large scale tree-grass ratios. It appeared that the intense foraging of middle-sized and large herbivores had the potential to keep habitats structurally open for up to five years, although they then turn into structural closed habitats (*chapter 3*).

At iMfolozi low rainfall combined with very intense grazing by large herbivores results in a vegetation that is dominated by short grazing lawn grass species which produce little plant biomass (*chapter 2*). Murid rodents in these habitats may be more exposed to predators as there is not much shelter. *Mastomys natalensis* is known to be a pioneer species in the colonisation of heavily overgrazed areas (Meester, Lloyd and Rowe-Rowe 1979) and seems therefore to be able to successfully colonise these areas although it seems to avoid recently burnt areas (*chapter 3*). Low precipitation does not only slow grass productivity (Birkett and Stevens-Wood 2005) but also suppresses seed germination and seedling establishment of encroaching woody species (*chapter 5*). Furthermore, tree seeds and seedlings in heavily overgrazed areas are particularly vulnerable to desiccation due to too high light levels (*chapter 5*). Intense grazing by middle-sized and large herbivores often results in patches of short vegetation (*chapter 2*) that are less likely burn or, if they do, will have less intense fires due to small fuel loads. Seedlings in those vegetation patches may be protected from burning (Walker et al. 1981, van Vegten 1983, Archer 1995, Milton and Dean 1995) and therefore seedling predators like vertebrate and invertebrate herbivores may be particularly important in preventing woody species recruitment (*chapter 5*, see also van de Koppel and Prins 1989). I conclude that my study supports the idea that woody species recruitment is mostly limited by seed predators and browsers under low rainfall conditions, while fire plays a bigger role under high rainfall conditions.

The functional importance of rodents in South African savannas

The results of my study suggest that the interplay of rodents and larger herbivores may be of functional importance for the African savanna ecosystem. Recent research in East African savannas demonstrated that rodents interact strongly with native ungulates and cattle (Keesing 1997). Keesing (1998, 2000) suggested that savanna community dynamics are dominated by large herbivores, most likely through their negative influence on food resources available to rodents. However, rodents also had a pronounced effect on the vegetation (Keesing 1998, 2000) available to their larger counterparts and are therefore important members of the savanna herbivore community. At the beginning of this study I hypothesised that the interplay between rodents and different-sized herbivores is characterised by various ‘two-way interactions’ and that rodents are functionally important for the maintenance of African savanna ecosystems. In this study I found that the different-sized herbivores had a significant impact on rodent abundance and habitat utilisation patterns through vegetation modifications, most likely due to their increased exposure to predators (*chapters 2, 3 and 4*). Rodents, on the other hand, may have the potential to influence the tree-grass ratio by inhibiting the recruitment of woody species and thus positively affecting large grazers (*chapter 5*). However, invertebrates may also play an important role in suppressing woody species recruitment. The findings of this study coincide with Smit et al. (2001) who also found that rodent densities were strongly influenced by the vegetation changes induced by large grazing herbivores. Furthermore, modifications of the vegetation structure through large grazers (Prins and van der Jeugd 1993) can have a pronounced impact on the habitat utilisation of rodents (Putman 1986). In contrast, rodents in African savannas can have significant effects on vegetation dynamics. Especially via seed (Keesing 2000, 2001) and seedling predation (Ostfeld and Canham 1993, Shaw et al. 2002, Goheen et al. 2004), rodents can have a major impact on the tree-grass ratio by inhibiting the recruitment of woody species and thus positively affect larger herbivores that highly depend on abundant grass for food. If rodent activity is clumped in ‘safe sites’, their effect on seedlings and herbaceous vegetation may be highly heterogeneous in these areas with keeping trees out of grass patches. As a result, determinants of the abundance and distribution of rodents may indirectly influence patterns of plant establishment. However, in African savannas the reported role of rodents in influencing tree recruitment ranges from potentially important (e.g., Miller 1994) to negligible (e.g., Barnes 2001, Shaw et al. 2002). In summary, I conclude that large herbivores affect murid rodents in this ecosystem through modifying the vegetation structure, which may affect tree recruitment. To which extent this imposes a feedback on larger herbivore species needs to be further explored.

Potential consequences for biodiversity

The findings of my thesis suggest that herbivore communities from very small (rodents) to very large (elephant) potentially interact in South African savannas and that this interplay may have ecological importance in maintaining the high biodiversity of these complex ecosystems. The global policy for biodiversity conservation and restoration in savannas has changed over the past decades since there is an increasing understanding in the functioning of these ecosystems (Du Toit and Owen-Smith 1989, Prins and Olff 1997, Sinclair and Arcese 1995). Until recently, many savanna conservation authorities focussed on the protection of particular highly endangered key herbivore species such as white rhino, black rhino or elephant. Nowadays authorities aim to conserve the biodiversity of the ecosystem as a whole and therefore take both animal species interactions and their response to the environment into account. Whereas it is possible to directly influence the abundance and species diversity of large herbivore species through e.g., reintroduction or culling, it appears to be difficult to conserve smaller species as they only can be influenced indirectly (e.g., with fire management). It is therefore important to get insight into the principal determinants of the functioning of the savanna ecosystem in order to provide authorities appropriate strategies for its conservation.

This has interesting consequences for ecosystem dynamics if indeed murid rodents affect tree recruitment, and large herbivores affect murid rodents and respond to trees. The extinction of particular herbivore species might disrupt the interplay between other species and their environment and thus trigger a chain reaction which may result in a long-term shift of the savanna ecosystem: The extinction of a large herbivores species, e.g., white rhino, would lead to a significant increase of the grass height and thus generates a general less heterogen vegetation as formerly short grazing lawns may turn into tall bunch grass vegetation in the long term. This is turn may favour rodents and therefore their densities increase as they preferentially utilise areas with high grass cover. But abundant grass cover also coincides with big fuel loads, resulting in both more frequent and more intense large scale fires in the dry seasons that may have effects on rodents. Rodent numbers, habitat selection and space use may be restricted by the lack of sufficient grass cover that would otherwise protect them from predators. But however, precipitation of the next rainy season promotes plant productivity, generating dense grass cover which in turn promotes a general high rodent density. High densities of granivorous rodents may have the potential to affect the tree-grass ratio by predating seedlings of trees (Shaw et al. 2002, Goheen et al. 2004) and may in the long term turn the savanna into open grassland that consists of tall bunch grass and very few trees. This in turn will generally favour grazing herbivore species but impair conditions for browsers, leading to the extinction of browsing herbivore species. Since the availability and concentration of all major nutrients is much higher under trees compared to open grassland (Ludwig et al. 2004) smaller herbivore species selectively feeding on nutrient-rich herbs and grasses that grow under trees would experience a lack of high quality food resources. Furthermore, the low tree seed availability only promotes low numbers of seed-dispersing herbivores; fewer seeds will be dispersed and germinate which then again leads to fewer trees. This may cause more species extinction in the long run as then the same number of selective feeder have to share less abundant high quality food. Additionally, if the abundance of predominantly seed-eating rodents outside parks is stimulated, e.g., through crop fields of human beings, it can result in a significant increase of rodents in that area. This may lead to more seed and seedling predation of trees, and hence to a (further) decline of woody cover. In this scenario parks are ‘safe islands’ for woody species as seed and seedling predation is less strong through lower small rodent numbers. However, further experimental and observational evidence is needed to support these arguments.

The opposite scenario, the extinction of small herbivores like rodents can cause ecosystem shifts through feedbacks (see Scheffer et al. 2001). The absence of granivorous rodents may generate an increase of woody species in that habitat as fewer seedlings get killed by predation. Selective herbivore species that previously competed with grass-eating rodents for high quality grasses and herbs growing under trees would then experience better feeding conditions and may therefore increase in abundance. Furthermore, the densities of seed-dispersing herbivores may increase due to improved habitat conditions, more seeds will be dispersed and germinate, again rising the number of trees. This in turn may shift the tree-grass ratio of the habitat from an open savanna to closed woodland in the long term that favours browsing herbivore species which increase in their abundance in that system. The trees will outshade the grasses which reduces the fire intensity. In this situation, fires fail to prevent bush encroachment and can neither control alien plants nor improve food resources for large grazers anymore. Conditions especially for large grazers strongly impair due to a lack of sufficient food resources. This reasoning is, however, quite speculative, and is worthwhile to be investigated further.

Fire seems to be one possible management tool to maintain spatial heterogeneity of savannas in order to sustain coexistence opportunities for different-sized herbivores. But however, an appropriate fire regime is of crucial importance for the balance of the positive and negative effects of fire desired by managers (Van de Vijver 1999, Trollope et al. 2002). Rare but intensive, large scale fires, for instance, could lead to a rather structural open landscape in the long term as it causes severe damage or even death to shrubs and trees (Bond and van Wilgen 1981). The positive effects of fire (increased forage quality for herbivores) are short term (Van de Vijver 1999), while the negative effects (homogeneous landscape patterns) are longer lasting and may even lead to substantial declines in browser populations. In contrast, several small scale fires may result in a heterogeneous landscape with alternating mosaics of structurally open but also dense habitats. In these habitats the intense foraging by herbivore aggregations on post-fire regrowth may have the potential to indirectly sustain the fire-created mosaics in the system for several years (Rietkerk et al. 2002, van Langevelde et al. 2003, Archibald et al. 2005) through the cumulative interactions of foraging and dung and urine deposition (Bailey 1996). These extended fire-created mosaics may in turn promote various herbivore species as they support both grazing and browsing species through facilitation and resource partitioning (Cromsigt and Olff in press).

References

Andrzejewski R, Mazurkiewicz M (1976) Abundance of food supply and size of the bank vole’s home range. Acta Theriol 21:237-253

Archer S (1995) Tree-grass dynamics in a Prosopis-thornshrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83-99

Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire – grazer interactions in an African savanna. Ecological Applications 15:96-109

Arsenault R, Owen-Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313-318

Bailey DW (1996) Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400

Barnes ME (2001) Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. Journal of Arid Environment 49:541-554

Bell RHV (1982) The effect of soil nutrient availability on community structure in African ecosystems. In: Ecology of tropical savannas (eds. Huntly BJ, Walker BH). Springer, Berlin, 193-216

Belovsky GE (1986) Generalist herbivore foraging and its role in competitive interactions. American Journal of Zoology 26:51-69

Belovsky GE (1997) Optimal foraging and community structure: the allometry of herbivore food selection and competition. Evolution and Ecology 11:641-672

Birney EC, Grant WE, Baird DD (1976) Importance of vegetative cover to cycles of Microtus Populations. Ecology 57:1043-1051

Birkett A, Stevens-Wood B (2005) Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. African Journal of Ecology 43:123-130

Bock CE, Bock JH, Kenney WR, Hawthorne VM (1984) Responses of birds, rodents, and vegetation to life stock exclosure in a semi desert grassland site. Journal of Range Management 37:239-242

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

Bond WJ, van Wilgen BW (1996) Fire and Plants. Chapman and Hall, London, Glasgow, Weinheim, New York, Tokyo, Melbourne, Madras, 263 p

Bowland AE, Perrin MR (1989) The effect of overgrazing on the small mammals in Umfolozi Game Reserve. Zeitschrift fuer Saeugetierkunde 54:251-260

Cameron GN, Spencer SR (1985) Assessment of space-use patterns in the hispid cotton rat (Sigmodon hispidus). Oecologia 68:133-139

Cassini MH (1991) Foraging under predation risk in the wild guinea pig *Cavia aperea*. Oikos 62:20-24

Crawley MC (1969) Movements and home-ranges of *Clethrionomys glareolus* (Schreber) and *Apodemus sylvaticus* L. in north-east England. Oikos 20:310-319

Cromsigt JPGM, Olff H (in press) Resource partitioning amongst large grazers mediated by local heterogeneity: an experimental approach.

Daubenmire RF (1968) Ecology of fire in grasslands. Advances in Ecological Research 5:209-266

Daubenmire RF (1975) Plants and Environment. A Textbook on plant autoecology. John Wiley and Sons, New York, USA, 422 p

Delany MJ (1986) Ecology of small rodents of southern Africa. Mammal Review 16:1-41

Desy EA, Batzli GO, Liu J (1990) Effects of food and predation on behaviour of prairie voles: a field experiment. Oikos 58:159-168

Dickman CR (1992) Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313-322

Drent RH, Prins HHT (1987) The herbivore as a prisoner of its food supply. In: Van Andel J, Bakker JP, Snaydon RW (eds) Disturbance in grasslands. Junk, Dordrecht, pp 131-147

Drickamer LC (1990) Microhabitat preferences of two species of deer mice Peromyscus in a north-eastern United States deciduous hardwood forest. Acta Theriol 35:241-252

Du Toit JT, Owen-Smith N (1989) Body size, population metabolism and habitat specialisation among large African herbivores. American Naturalist 133:736-740

Edge WD, Wolff JO, Carey RL (1995) Density-dependent responses of gray-tailed voles to moving. Journal of Wildlife Management 59:245-251

Farnsworth KD, Focardi S, Beecham JA (2002) Grassland-herbivore interactions: How do grazers coexist? American Naturalist 159:24-39

Frost PGH, Robertson F (1987) The ecological effects of fire in savannas. In: B.H. Walker (ed). Determinants of tropical savannas. IRL Press, Oxford, 93-140 pp

Goheen JR, Keesing F, Allan BF, Ogada DL, Ostfeld RS (2004) Net effects of large mammals on Acacia seedling survival in an African savanna. Ecology 85:1555-1561

Grant WE, Birney EC, French NR, Swift DM (1982) Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetation cover. Journal of Mammalogy 63:248-260

Hairston NG, Smith FE, Slobodkin LB 1960 Community structure, population control and competition. American Naturalist 94:421-425

Hamback PA, Grellmann D, Hjalten J (2002) Winter herbivory by voles during a population peak: the importance of plant quality. Ecography 25:74-80

Hanks J, McIntosh JEA (1973) Population dynamics of the African elephant (*Loxodonta africana*). Journal of Zoology Lond 169:29-38

Heske EJ, Brown JH, Mistry S (1994) Long-term experimental study of a chihuahuan desert rodent community – 13 years of competition. Ecology 75:438-445

Holmes WG (1991) Predation risk affects foraging behaviour of pikas: observational and experimental evidence. Animal Behaviour 42:111-119

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:145-159

Iyawe JG (1988) Distribution of small rodents and shrews in a lowland rain forest zone of Nigeria, with observations on their reproductive biology. African Journal of Ecology 26:189-195

Johnsson P, Hartikainen T, Koskela E, Mappes T (2002) Determinants of reproductive success in voles: use in relation to food and litter size manipulation. Evolution and Ecology 16:455-467

Kalela O (1962) On the fluctuation in the numbers of arctic and boreal small rodents as a problem of production biology. Annual Academy Sci Fenn Ser A IV, 66:38 pp

Kaufman DW, Peterson SK, Fristik R, Kaufman GA (1983) Effect of microhabitat features on habitat use by *Peromyscus leupocus*. American Midland Naturalist 110:177-185

Keesing F (1997) Ecological interactions between small mammals, large mammals, and vegetation in a tropical savanna of central Kenya. PhD thesis, University of California, Berkeley

Keesing F (1998) Ecology and behaviour of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. Journal of Mammalogy 79:919-931

Keesing F (2000) Cryptic consumers and the ecology of an african savanna. BioScience 50:205-215

Keesing F (2001) Impacts of density and large mammals on space use by the pouched mouse (*Saccostomus mearnsi*) in central Kenya. Journal of Tropical Ecology 17:465-472

Kleiber M (1961) The fire of life: an introduction to animal energetics. Wiley, New York

Korpimaeki E, Koivunen V, Hakkarainen H (1996) Microhabitat use and behaviour of voles under weasel and raptor predation risk: predator facilitation? Behavioral Ecology 7:30-34

Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behaviour and rates of owl predation. Ecology 72:2249-2260

Kotler BP, Blaustein L (1995) Titrating food and safety in a heterogeneous environment: when are risky and safe patches of equal value? Oikos 74:251-258

Leirs H, Verheyen N (1995) Population ecology of Mastomys natalensis (Smith, 1834). Implications for rodent control in Africa. Belgian Administration for Development Cooperation. Agricultural Edition Nr. 35

Leirs H, Verheyen W, Verhagen R (1996) Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). Mammalia 60:545-555

Lima SL (1992) Strong preferences for apparently dangerous habitats – a consequence of differential escape from predators. Oikos 64:597-600

Lima SL, Valone TJ (1986) Influence of predation risk on diet selection: a simple example in the grey squirrel. Animal Behaviour 34:536-544

Lima SL, Dill L (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640

Ludwig F, de Kroon H, Berendse F, Prins HHT (2004) The influence of savanna trees on nutrient, water and light availbility and the understorey vegetation. Plant Ecology 170:93-105

Maher CR, Lott DF (2000) A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1-29

McInnes PF, Naiman RJ, Pastor J, Cohen Y (1992) Effects of moose browsing on vegetation and litter of the boreal forest isle Royale Michigan, USA. Ecology 73:2059-2075

Meester J, Lloyd CNV, Rowe-Rowe DT (1979) A note on the ecological role of Praomys natalensis. South African Journal of Science 75:183-184

Miller MF (1994) Large African herbivores, bruchid beetles, and their interactions with Acacia seeds. Oecologia 97:265-270

Milton MJ, Dean WRJ (1995) South Africa’s arid and semiarid rangelands: Why are they changing and can they be restored? Environmental Monitoring and Assessment 37:245-264

Moe SR, Wegge P, Kapela EB (1990) The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. African Journal of Ecology 28:35-43

Moe SR, Wegge P (1997) The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. Journal of Tropical Ecology 13:279-292

Monadjem A (1997a) Habitat preferences and biomasses of small mammals in Swaziland. African Journal of Ecology 35:64-72

Monadjem A (1997b) Stomach contents of 19 species of small mammals in Swaziland. African Journal of Ecology 64-72

Monadjem A (1998) Effects of supplemental food on the habitat selected by Mastomys natalensis (Muridae:Rodentia) in a subtropical grassland in Swaziland. South African Journal of Zoology 33:172-177

Monadjem A, Perrin MR (1996) The effects of additional food on the demography of rodents in a subtropical grassland in Swaziland. Mammalia 60:785-789

Monadjem A, Perrin MR (1997) Population dynamics of Lemniscomys rosalia (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. South African Journal of Zoology 32:129-135

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)

Norrdahl K, Korpimaeki E (1998) Does mobility or sex of voles affect predation risk by mammalian predators? Ecology 79:226-232

Norton-Griffiths M (1979) The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Serengeti: Dynamics of an Ecosystem (eds A.R.E Sinclair and Norton-Griffiths), Chicago university Press, Chicago, IL, 310-352 pp

Olff H, Ritchie M, Prins HHT (2002) Global environmental control of diversity in large herbivores. Nature 415:901-904

Ostfeld RS (1985) Limited resources and territoriality in microtine rodents. American Naturalist 126:1-15

Ostfeld RS (1990) The ecology of territoriality in small mammals. Trends in Ecology & Evolution 5:411-415

Ostfeld RS, Canham CD (1993) Effects of meadow vole population density on tree seedling survival in old fields. Ecology 74:1792-1801

Owen-Smith, N (1988) Megaherbivores. The influence of very large body size on Ecology. Cambridge University Press, Cambridge

Pacala SW, Crawley MJ (1992) Herbivores and plant diversity. American Naturalist 140:243-260

Peles JD, Barrett GW (1996) Effects of vegetation cover on the population dynamics of meadow voles. Journal of Mammalogy 77:857-869

Pellew RA (1983) The impact of elephant, giraffe and fire upon the Acacia tortilis woodlands of the Serengeti, African Journal of Ecology 21:41-74

Pfeiffer KE, Hartnett DC (1995) Bison Selectivity and Grazing Response of Little Bluestem in Tall grass Prairie. Journal of Range Management 48:26-31

Phillipson J (1992) Rainfall, primary production and ‘carrying capacity’ of Tsavo National Park, Kenya. East African Wildlife Journal 13:171-201

Power ME (1992) Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746

Prins HHT, Douglas-Hamilton I (1990) Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83:392-400

Prins HHT, van der Jeugd HP (1993) Herbivore population crashes and woodland structure in East Africa. Journal of Ecology 81:305-314

Prins HHT, Olff H (1997) Species richness of African grazer assemblages: towards a functional explanation. in: Dynamics of tropical communities. (ed. by D Newbery, HHT Prins, ND Brown). Blackwell, Oxford, 448 – 490 pp

Putman RJ (1986) Competition and coexistence in a multispecies grazing system. Acta Theriol 31:271-291

Rietkerk M, Boerlijst M, van Langevelde F, HilleRisLambers R, van de Koppel J, Kumar L, Prins HHT, de Roos AM (2002) Self-organization of vegetation in arid ecosystems. American Naturalist 160:524-530

Roques KG, O’Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

Rowe-Rowe DT, Mester J (1982) Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. South African Journal of Zoology 17:202-209

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591-596

Shaw MT, Keesing F, Ostfeld RS (2002) Herbivory on Acacia seedlings in an East African savanna. Oikos 98:385-392

Sinclair ARE (1977) The African buffalo. University of Chicago Press, Chicago, 355 p

Sinclair ARE, Norton-Griffiths M (1979) Serengeti. Dynamics of an ecosystem. Chicago University Press, Chicago, Illinois

Sinclair ARE, Dublin H, Borner M (1985) Population regulation of Serengeti Wildebeest: A test of the food hypothesis. Oecologia 65:266-268

Sinclair ARE, Arcese P (1995) Serengeti II: Dynamics, management and conservation of an ecosystem; Serengeti Research Institute Workshop, Seronera, Tanzania, December 7-11, 1991. In: Sinclair ARE, Arcese P (eds) Serengeti II: Dynamics, management, and conservation of an ecosystem. University of Chicago Press, University of Chicago Press {b}, 5801 Ellis Ave., Chicago, Illinois 60637 ; {b} London, England, p xii+665

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

Slobodkin LB, Smith FE, Hairston NG (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. American Naturalist 101:109-124

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 155:119-127

Smith LM, Kadlec JA (1985) Fire and herbivory in a great salt lake march. Ecology 66:259-265

Sparks JC, Masters RE (1996) Fire seasonality effects on vegetation in mixed-, tall- and south-eastern pine grassland communities: A review. In: KG Wadsworth, RE McCabe (eds). Transactions of the 61st North American Wildlife and Natural Resources Conf, 246-255 pp

Stein SJ, Price PW, Abrahamson WG, Sacchi CF (1992) The effects of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. Oikos 65:190-196

Taitt MJ (1981) The effect of extra food on small populations. 1 Deer mice (*Peromyscus maniculatus).* Journal of Animal Ecology 50:111-1124

Taylor P (1998) The smaller mammals of KwaZulu-Natal, University of Natal Press, Pietermaritzburg

Trollope WSW, Trollope LA, Hartnett DC (2002) Fire behaviour a key factor in the fire ecology of African grasslands and savannas. In: Viegas X (ed) Forest Fire Reseach and Wildland Fire Safety. Millpress, Rotterdam

van de Koppel J, Prins HHT (1989) The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. Journal of Tropical Ecology14:565-576

Van de Vijver CADM (1999) Fire and life in Tarangire. Effects of burning and herbivory on an East African savanna system. PhD thesis. Wageningen University, Wageningen, the Netherlands

Van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore A, Hearne J, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337-350

Van Soest PJ (1982) Nutritional ecology of the ruminant: Ruminant metabolism, nutritional strategies, the cellulolytic fermentation and the chemistry of forages and plant fibres. O and B Books, Corvallis

van Vegten JA (1983) Thornbush invasion in a savanna ecosystem in eastern Botswana. Vegetatio 56:3-7

Vesey-FitzGerald DF (1969) Utilization of the habitat of the buffalo in Lake Manyara National Park. East African Wildlife Journal 7:131-145

Vesey-FitzGerald DF (1972) Fire and animal impact on vegetation in Tanzania National Parks. Proceedings Tall Timb Fire Ecology Conference 11:297-317

Walker BH, Ludwig D, Holling CS, Peterman RM (1981) Stability of semi-arid savanna grazing systems. Journal of Ecology 69:473-498

Walker BH, Langridge JL (1997) Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): A case study from Australia. Journal of Biogeography 24:813-825

Watson RM (1972) Results of aerial livestock surveys of Kaputei division, Samburu district and Noth-eastern Province. Statistics division, Min. of Finance and Planning, Republic of Kenya, 111 pp

Werger MJA (1983) Tropical grasslands, savannas, woodlands: natural and man-made. In: W Holzner, MJA Werger, I Ikusima (eds). Man’s impact on vegetation. Dr. W Junk Publ, The Hague, The Netherlands, 107-137 pp

Wilmshurst JF, Fryxell JM, Bergmann CM (2000) The allometry of patch selection in ruminants. Proceedings to the Royal Society of London 267:345-349

Wilsey BJ (1996) Variation in use of green flushes following burns among African ungulate species: The importance of body size. African Journal of Ecology 34:32-38

Zubaid A, Gorman ML (1993) The effect of supplementary feeding upon the sizes of the home ranges of wood mice *Apodemus sylvaticus* living on a system of maritime sand dunes. J Zool, London 231:233-237

Summary

Humans have transformed large areas of the earth’s surface over the past centuries and fragmented once continuous natural habitats, thus reducing the mobility of organisms by creating dispersal barriers. Consequently, the increasing restriction of species to smaller areas of poorer quality leads to rapid losses of biodiversity. African savannas are natural biodiversity hotspots, hosting a high density and diversity of different-sized herbivores, and are therefore important ecosystems for the conservation of biodiversity on earth. In order to protect and restore African savannas it is necessary to understand the principal determinants of their species diversity and community interactions. There is a growing recognition that differences in herbivore body size may be a key factor in the functioning of these ecosystems, regulating species facilitation and competition interactions. Furthermore, in the fenced and relatively small parks in South Africa spatial heterogeneity seems to be important for the coexistence of the different herbivore species. Studies on community interactions in African savannas have focussed almost exclusively on larger herbivores, interactions of murid rodents with larger herbivore species are comparatively poorly known. Furthermore, in spite of the consequences for their interaction with larger species, information on the diet of murid rodents is very limited. In this thesis the interplay between murid rodents and large herbivore communities was investigated and the ecological consequence of these interactions for the maintenance of the savanna ecosystem was explored. The fieldwork for this study was performed in the Hluhluwe-iMfolozi Park (HIP), which is a 90,000 ha fenced protected area in KwaZulu-Natal, South Africa. The vegetation in HIP consists mainly of open grasslands to closed Acacia and broad-leaved riparian woodlands. Fire is an important management tool in the park, controlling bush encroachment and alien plants but also improving herbivore food resources. HIP harbours a high diversity and biomass of indigenous herbivores, from very large species such as elephant (*Loxodonta africana*) to smaller species such as warthog (*Phacochoerus aethiopicus*), and a whole set of mammalian carnivores.

After a general introduction (*chapter 1*) the thesis starts with the effects of large herbivores on the savanna vegetation structure and plant species composition and how this in turn influences the quantity and quality of food resources available to murid rodents and the predation risk they experience in this ecosystem (*chapter 2*). Intense grazing by large herbivores could improve the vegetation structure and food quality for murid rodents by creating vegetation mosaics that consist of high quality plant species. However, selective larger herbivore species could also decrease the abundance of high quality plant species available to smaller species. Furthermore, trampling and grazing of larger species reduces the vegetation cover, restricting the habitat of smaller species by increasing their predation risk. Different-sized large herbivores were excluded from plots of vegetation to asses the effects of large herbivores on murid rodents. Rodent trapping was conducted inside the herbivore exclosures and vegetation changes in absence of large herbivores were recorded at four study sites, located in either a high or a low rainfall area. Both plant species composition and vegetation structure changed after the exclusion of large herbivores. Rodent abundance increased with decreasing large herbivore numbers and

increasing vegetation height. However, large herbivores had no effect on rodent body weight or on the distances they moved. Furthermore, no impact of large herbivores was found on the grass species composition in the diet of the most frequently captured rodent species, *Lemniscomys rosalia spinalis*. The rodent species composition appeared to be influenced by a rainfall gradient rather than by large herbivores. The results show that different-sized large herbivores and murid rodents interact in that South African savanna. Rodent abundance may be mainly affected by large herbivores through the reduction of the vegetation cover and their subsequent increased exposure to predators. Furthermore, the results may provide evidence that rainfall differences can have an effect on murid rodent communities and their interaction with larger herbivores.

Chapter 3 examines the response of herbivore species greatly varying in sizes to short- and long-term fire succession patterns on small and landscape scales and the resulting community interactions between them. Small scale fire patterns may influence the seasonal dynamics of herbivore landscape use in the short-term as herbivores preferentially forage on young regrowth. However, the length of time it takes herbivores to respond to a burn might depend on their body size. Middle-sized herbivore species such as warthog, nyala and impala were expected to be the pioneer species on burnt vegetation patches as they selectively feed on high quality food resources and can cope with the low food quantities shortly after the fire. On the other hand, larger species such as white rhino, buffalo, zebra and wildebeest can survive on lower food quality but need high food quantities and may therefore only re-occur on the burnt patches several months after the fire. Furthermore, small species, such as murid rodents, may be influenced by their larger counterparts when they recolonise burnt areas as large herbivores affect both rodent food resource availability and predation risk. However, fires together with herbivores may also create large-scale landscape mosaics in the long-term and grazing in most recently burnt areas may maintain fire-caused habitat changes for several years. To assess the effect of fire succession on the different herbivore species small-scale experiments and observational studies on landscape scales were conducted and the herbivore response on short-term and long-term succession patterns was investigated. Rodent numbers were affected by the presence of larger herbivores rather than by seasonal patterns and increased in their absence and increasing vegetation height. Both middle-sized and large herbivore species responded to short-term post-fire patterns with large species being the pioneer species on burnt patches. However, buffalo was the only species that also responded to long-term post-fire patterns. The results indicate that savanna rodents may be influenced by larger herbivores and fire due to an increase and prolongation of the predation risk they experience in these habitats. Furthermore, the presence of grazers and the amount of rainfall may be two interacting factors that prolong fire patterns in the landscape.

The habitat utilisation patterns of murid rodents as well as habitat characteristics influencing their spatial distribution were explored in *chapter 4*. Herbivorous rodents selectively feed on high quality food resources and may therefore mainly utilise vegetation patches with an abundance of high quality grass species. On the other hand, rodents may be restricted to patches with good vegetation cover that they use as an anti-predation refuge. Capture-mark-release methods and radio-tracking were

used to investigate murid rodent spatial movement and habitat utilisation patterns. Furthermore, in order to explore ecological factors potentially influencing murid rodent distribution habitat characteristics were recorded. Overall, grass height was higher and high quality food resources were more abundant within rodent home ranges than in the surrounding areas, but females and males had different priorities. Furthermore, males and females showed differences in both the distances they moved and in their home range sizes. The results suggest that local vegetation cover is the most important factor determining the habitat selection of rodents in the South African savanna but food resource availability also plays an important role in rodent habitat use.

In *chapter 5* the interacting effects of herbivory and vegetation height on the establishment of the encroaching woody species *Dichrostachys cinerea* were studied. Seed and seedling predation by rodents may inhibit the recruitment of encroaching woody species that invade previously open savanna grasslands. This could then negatively affect larger herbivores that depend on an abundance of grass for their food supply. In addition, larger herbivores and fire can affect seed germination and seedling establishment and drive vegetation dynamics in savannas. Seeds and seedlings of the encroaching shrub *Dichrostachys cinerea* were planted in clipped and unclipped grass plots, with and without large herbivores present. Seed germination and seedling survival were both promoted by clipping the grass and the absence of large herbivores. In the presence of large herbivores seedling survival was positively affected by taller grass. Furthermore, higher rainfall appeared to promote seed germination and seedling survival. Seedlings were predominantly consumed by invertebrates but also by rodents. In conclusion, the recruitment of *D. cinerea* is strongly influenced by the interplay of grass height and herbivory. The subsequently reduced competition from grasses outweighs the higher risk of being trampled on or of being desiccated.

Finally, *chapter 6* is a synthesis of the findings reported in this thesis. The findings of this thesis suggest that in South African savannas there is a potential interaction between different-sized herbivore communities, ranging from the very small (murid rodents) to the very large (elephant). In this ecosystem, large herbivores mainly influence murid rodents by changing their predation risk (top-down, by modifying the vegetation structure) rather than competitive or facilitative interactions for food (bottom-up). Additionally, by modifying the vegetation structure large herbivores may have an impact on the tree recruitment, but to what extent this imposes a feedback on them needs to be further explored. Furthermore, some evidence that supports the hypothesis that environmental forces, such as precipitation and fire, in a strong interaction with herbivory modify African savanna ecosystems was found. It can be concluded that the recruitment of woody species is mostly limited by seed predators and browsers under low rainfall conditions, while under high rainfall conditions fire plays a bigger role.

The interaction between the different herbivore communities in South African savannas may have an ecological importance in maintaining the high biodiversity of these complex ecosystems. It is therefore of major importance to gain an insight into the principal determinants of the functioning of the savanna ecosystem in order to provide authorities with appropriate strategies for its conservation. Although it is possible to directly influence the abundance and species diversity of larger herbivore

species through e.g., reintroduction or culling, it appears to be much more difficult to conserve smaller species as they can only be influenced indirectly. Fire therefore seems to be one possible management tool in maintaining the spatial heterogeneity of savannas in order to sustain opportunities for the coexistence of different-sized herbivores. However, an appropriate fire regime is of crucial importance for the balance of the positive and negative effects of fire desired by managers.

Samenvatting

Mensen hebben grote gebieden op aarde veranderd over de afgelopen eeuwen waardoor veel van oorsprong aaneengesloten habitats sterk gefragmenteerd zijn. Door deze habitatfragmentatie ontstonden vele barrières die de mobiliteit van organismen sterk hebben gereduceerd. Deze beperking veroordeelde de bestaande populaties tot het leven in restgebieden met een lagere habitatkwaliteit, met als gevolg een versnelde afname in biodiversiteit. De Afrikaanse savannes zijn van nature erg soortenrijk (biodiversiteit ‘hotspots’) en herbergen een hoge dichtheid en diversiteit van dieren, inclusief de planteneters of herbivoren. Als zodanig spelen de Afrikaanse savannes een grote rol in de instandhouding en bescherming van biodiversiteit. Om Afrikaanse savannes optimaal te kunnen beschermen en behouden is het noodzakelijk de primaire factoren die de soortenrijkdom te bepalen en de interacties tussen verschillende gemeenschappen te begrijpen. Voor het functioneren van deze ecosystemen worden de verschillen in lichaamsgrootte van herbivoren steeds meer als een sleutelfactor gezien voor de facilitatie, competitie en interactie tussen soorten. Verder blijkt de ruimtelijke heterogeniteit binnen de omheinde, relatief kleine parken in Zuid Afrika van belang te zijn voor de coëxistentie van verschillende soorten planteneters. Tot nu toe beperkten de onderzoeken naar de interacties tussen soorten in Afrikaanse savannes zich hoofdzakelijk tot grote herbivoren. Dit in tegenstelling tot de interacties van kleine herbivoren (knaagdieren) met grote(re) herbivoren waarvan nog weinig bekend is. Informatie over het dieet van kleine knaagdieren is ook dun bezaaid, dit ondanks de consequenties die dit heeft op het dieet van de grotere soorten.

In dit proefschrift is gekeken naar de wisselwerking tussen kleine knaagdieren en de gemeenschappen van grote(re) herbivoren, om de ecologische betekenis van deze interacties voor de instandhouding van savanne ecosystemen te onderzoeken. Het veldwerk voor dit onderzoek heeft plaatsgevonden in het Hluhluwe-iMfolozi Park (HiP), een 90,000 ha groot, omheind natuurreservaat in KwaZulu-Natal, Zuid Afrika. De vegetatie van het park bestaat grotendeels uit open graslanden, dichte Acacia bebossingen en breedbladige vegetatietypes geassocieerd met rivieren. Binnen het park wordt het branden van vegetatie als een beheersmaatregel gebruikt om het indringen van struiken en uitheemse invasieve planten te voorkomen, en om de het voedselaanbod en de kwaliteit te verbeteren. Het HiP huisvest een grote diversiteit (en biomassa) van inheemse herbivoren; van grote soorten zoals de Olifant (*Loxodanta africana*) tot kleinere soorten zoals het Wrattenzwijn (*Phacochoerus aethiopicus*).

In dit proefschrift wordt, na een algemene inleiding (*hoofdstuk 1*), in *hoofdstuk 2* behandeld hoe de effecten van grote herbivoren op de vegetatiestructuur en plantensoortensamenstelling in savannes invloed hebben op de voedselkwaliteit, voedselkwantiteit en predatierisico van kleine knaagdieren. Sterke begrazing door grote herbivoren kan de vegetatiestructuur verbeteren omdat het kan leiden tot een mozaïekstructuur van plantensoorten van een hoge kwaliteit voor de knaagdieren, maar anderzijds kunnen selectieve grotere herbivoren ook de dichtheid limiteren. Verder kan vertrapping en begrazing van grote herbivoren leiden tot lagere bedekkingsgraad, wat weer de habitat van kleinere herbivoren kan limiteren door een verhoging van het predatierisico. De effecten van herbivoren van verschillende grootte op kleine knaagdieren zijn onderzocht door uitrasteren (exclosures); per raster wordt op basis van lichaamsgrote de herbivoren van groot (olifant) naar klein (konijnen) uitgesloten. In vier onderzoeksgebieden (twee in gebieden met veel neerslag en twee in gebieden met weinig neerslag) werden binnen en buiten de rasterhekken knaagdieren gevangen en vegetatie veranderingen bestudeerd. Na onderzoek bleek dat de plantensamenstelling en vegetatiestructuur in afwezigheid van grote herbivoren veranderde. De dichtheid van kleine knaagdieren nam toe met een afname in grotere herbivoren dichtheden en met een toename van vegetatie hoogte. Het bleek echter dat grote herbivoren geen effect hadden op het lichaamsgewicht of op loopafstanden van de kleine knaagdieren. Meer in detail gekeken, bleek dat grote herbivoren geen invloed hadden op de grassoortensamenstelling in het dieet van het meest frequent gevangen knaagdier *Lemniscomys rosalia spinalis*. Verder bleek de soortensamenstelling van de knaagdieren meer te zijn beïnvloed door regenval dan door de aanwezigheid van grote herbivoren, alsmede de verschillen in regenval een effect hadden op de interacties met grote herbivoren. Verder werden knaagdierdichtheden waarschijnlijk vooral bepaald door de reductie van de vegetatiebedekking als gevolg van begrazing door grote herbivoren, waardoor een verhoogd predatierisico kon ontstaan. Concluderend kan gezegd worden dat in het onderzocht gebied de kleine knaagdieren wel degelijk interactie vertonen met de aanwezige grotere herbivoren.

In *hoofdstuk 3* was de respons van verschillende grote herbivoren op het branden van vegetatie (brandhistorie) onderzocht. Door het branden op korte en lange termijn zijn successiepatronen (brandpatronen) ontstaan welke op verschillende schalen (o.a. habitatschaal, landschapschaal) zijn onderzocht, alsmede de resulterende interacties tussen herbivoorgemeenschappen. Kleinschalige brandpatronen kunnen de seizoensdynamiek van herbivoren op korte termijn veranderen door hun een preferentie voor het foerageren op jong gras. Wanneer herbivoren weer gaan foerageren op een gebrand stuk, was afhankelijk van hun lichaamsgewicht. Verwacht was dat middelgrote herbivoren soorten (Wrattenzwijn, Nyala, Impala) als eerste op de meest recent gebrande gebieden zouden gaan foerageren. Deze dieren hebben een voorkeur voor voedsel van hoge kwaliteit, maar kunnen ook omgaan met de lage voedsel kwantiteit kort na een brand. Anderzijds, grotere soorten zoals Witte neushoorn, Buffel, Zebra en Wildebeest, kunnen overleven met voedsel van lage kwaliteit maar hebben juist een hoge kwantiteit nodig. Hierdoor foerageerden deze herbivoren pas vaak maanden later in de gebrande gebieden. De duur van deze periode was weer van invloed op het voedselaanbod en het predatierisico van de kleinere herbivoren (knaagdieren).

Branden in combinatie met grazen bleek op de lange termijn te kunnen resulteren in een grootschalige landschapsmozaïek, vooral het grazen in recent gebrande gebied kan jarenlang de door brand veroorzaakte habitat veranderingen instandhouden.

Om de effecten van branden op herbivoren op habitat- en landschapschaal te kunnen onderzoeken, werd de respons van herbivoren op korte en lange termijn successiepatronen ontstaan door brand getest. Het bleek dat dichtheden van knaagdieren meer door de aanwezigheid van grote herbivoren werd beïnvloed dan door seizoensgebonden patronen. Daarnaast nam de knaagdierdichtheid toe in de afwezigheid van grote herbivoren, alsmede bij een toename van de vegetatiehoogte.

Uit observaties bleek dat middelgrote en grote herbivoren beide reageerde op korte termijn successiepatronen. De grote herbivoren waren de eerste grazers op de net gebrande gebieden, maar alleen de Buffel reageerde ook op de lange termijn successiepatronen van het branden. De resultaten indiceren dat savanne knaagdieren beïnvloed kunnen worden door grotere herbivoren en het branden van vegetatie door een verhoogd predatierisico en het prolongeren van de predatieperiode. Daarnaast waren de factoren aanwezigheid van herbivoren en regenval verantwoordelijk voor het verlengen van brandpatronen in het landschap.

De habitatpatronen waarvan kleine knaagdieren gebruik maken en de habitatkarakteristiek welke hun ruimtelijke verspreiding beïnvloeden werden in *hoofdstuk 4* onderzocht. Grasetende knaagdieren foerageren selectief op voedsel van hoge kwaliteit en werden daarom verwacht een voorkeur te hebben voor vegetatievlakken waar veel grassoorten van hoge kwaliteit groeien. Anderzijds zijn knaagdieren misschien beperkt tot vegetatievlakken met voldoende bedekking die als toevluchtsoord kunnen dienen. Om te onderzoeken wat de ruimtelijke beweging en het gebruik van de habitat van de knaagdieren was, werden de dieren gevangen en voorzien van radiozenders. Verder werden habitatkarakteristieken genoteerd om te onderzoeken welke ecologische factoren hun verspreiding beïnvloeden. Uit de resultaten bleek dat binnen het leefgebied (home range) van de knaagdieren de vegetatiehoogte en het aantal grassoorten van hogere kwaliteit groter was vergeleken met de omgeving. Ook bleek dat mannelijke knaagdieren langere afstanden liepen en hadden daardoor een groter leefgebieden vergeleken met vrouwelijke knaagdieren. De lokale vegetatiebedekking leek de belangrijkste factor voor habitatselectie bij knaagdieren in het onderzochte gebied, maar de beschikbaarheid van voedsel speelde ook een belangrijke rol in het ruimtelijke gebruik van de habitat.

De interactie-effecten van begrazing en vegetatiehoogte op de vestiging van *Dichrostachys cinerea* was onderzocht in *hoofdstuk 5*. Dit is één van de belangrijke houtige gewassen welke de open savannegraslanden binnendringt. De zaad- en zaalingpredatie van knaagdieren kan de vestiging van de soort in open savannegraslanden sterk tegengaan, wat weer een negatief effect kan hebben op het voedsel aanbod van de grotere herbivoren. Grote herbivoren en het branden van de vegetatie kunnen daarnaast de vegetatiedynamica beïnvloeden door hun effect op het kiemen van zaad en het vestigen van zaailingen. Om dit effect te testen werden zaden en zaailingen van *D. cinerea* geplant in experimentele vlakken met geknipt en ongeknipt gras in gebieden met en zonder grote herbivoren. Het bleek dat kieming en overleving beter was in de geknipte vlakken bij de afwezigheid van grote herbivoren. In aanwezigheid van grote herbivoren was de overleving van de zaailingen ook beter in het hoge gras. Verder bleek dat een hoge regenval een positief effect had op kieming en zaailingoverleving. Hieruit kan geconcludeerd worden dat de toename van *D. cinerea* sterk beïnvloed werd door de wisselwerking tussen grashoogte en begrazing en dat de effecten van een lager concurrentie met gras het hogere risico van vertrappen en uitdroging goedmaken.

In de synthese in *hoofdstuk 6* zijn de resultaten gepresenteerd in dit proefschrift besproken. Algemeen kan geconcludeerd worden dat herbivoorgemeenschappen van heel klein (kleine knaagdieren) tot en met heel groot (Olifant) interactie vertonen in het onderzoeksgebied. Grote herbivoren beïnvloeden de kleine knaagdieren vooral door het veranderen van het predatierisico (verandering van de vegetatiestructuur), meer dan door voedselcompetitie of facilitatie. Door het veranderen van de vegetatiestructuur hebben de groet herbivoren ook invloed op de aangroei van bomen, maar in hoeverre dit weer een effect heeft op de herbivoren moet nog verder worden onderzocht. Abiotische factoren zoals regenval en het branden van de vegetatie hadden een sterke interactie met herbivoren en kunnen daardoor het onderzochte savanne ecosystemen beïnvloeden. Daarnaast is gevonden dat de aanwas van *D. cinerea* grotendeels gelimiteerd werd door zaad- en zaailingpredatoren onder droge condities, terwijl het branden van de vegetatie een grotere rol speelt onder nattere condities.

De wisselwerking van verschillende herbivoorgemeenschappen in Zuid-Afrikaanse savannes kun belangrijk zijn voor de instandhouding van de hoge soortenrijkdom in deze complexe ecosystemen. Het was daarom van groot belang inzicht te krijgen in de factoren die van invloed zijn op het functioneren van het savanne ecosysteem om autoriteiten passende beheersstrategieën voor instandhouding van de savannes te geven. Alhoewel het mogelijk is de dichtheid en diversiteit van grote herbivoren soorten direct te beïnvloeden door, bijvoorbeeld afschot (‘culling’) of herintroductie, bleek het moeilijker de kleinere soorten te behouden omdat deze alleen indirect beïnvloed worden. Het branden van vegetatie bleek daarom een mogelijke beheersmaatregel voor de instandhouding van de ruimtelijke heterogeniteit van savannes om de coëxistentie mogelijkheden voor verschillende herbivoren te bewaren, maar een passend brandregime is cruciaal voor de balans in de effecten (positief en negatief) welke gewenst zijn door de beheerders.

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Curriculum vitae

Nicole Hagenah was born on December 6th 1973 in Osterholz-Scharmbeck (Germany). In 1995 she obtained her university entrance qualification from the grammar school for economics, Osterholz-Scharmbeck, Germany. In the same year she started to study Biology, firstly at the Georg-August University Goettingen and continued later at the University of Hannover. During her undergraduate studies she specialised in tropical ecology and animal behaviour. She did practical training and courses in tropical ecology in Ecuador and Costa Rica and conducted behavioural and vocal studies on a variety of primate species at the Hannover Zoological Garden, Germany.

For her masters degree she studied the ecology and intrasexual competition of the golden-brown mouse lemur (*Microcebus ravelobensis*) in a dry deciduous forest in Madagascar. Her study provided the first data on the spatial behaviour, social network and mating system of the nocturnal primate species, whose ecology was at that time hardly known. Next to her masters she was employed for seven months as a research assistant at the School of Veterinary Medicine Hannover, Germany where she assisted with the handling, morphometric measurements and care of mouse lemurs in the laboratory. In April 2001 she graduated as qualified biologist (Diplom-Biologin).

In August 2001 she received a fellowship of the Robert Bosch Foundation, Germany, and started a position as a PhD-student with the Resource Ecology Group (formerly called Tropical Nature Conservation and Vertebrate Ecology Group) at Wageningen University, the Netherlands. The aim of the study was to investigate the interplay between small mammals with large herbivores in a South African savanna. For this study fieldwork was conducted over a period of 1.5 years in the Hluhluwe-iMfolozi Park, South Africa, the results of which are presented in this thesis. Next to her PhD-project she was the teamcoordinator of the WWF volunteer-team in Groningen, the Netherlands (2004-2005).

In March 2006 she was awarded a prestigious two-year Post-Doctoral fellowship with the University of Pretoria, South Africa, to study the effects of subterranean rodents on their environment within the research group of Prof. N.C. Bennett.

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PE&RC PhD Education Statement Form

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities)

Review of Literature (4 credits)

- Department/group where study is conducted and/or presentation is given: Resource Ecology/Community and Conservation Ecology (2002-2005)

Writing of Project Proposal (2 credits)

- The interplay of small and large herbivores in southern African savannas: Aspects of functional diversity in a natural production and conservation system (2002)

Post-Graduate Courses (5 credits)

- GIS-application in land resource and land use studies (2004)
- Learning ArcGIS 8, Part I + II (2004)
- Spatial and temporal aspects in resource ecology (2005)
- Survival analysis (2005)

Deficiency, Refresh, Brush-up and General Courses (4.6 credits)

- Basic statistics (2001)
- English course for PhD’s (2001)
- Code Nederlands 1 + 2
- Scientific writing course (2002)
- Scientific publishing (2004)
- Media training (2005)

PhD Discussion Groups (5 credits)

- PhD discussion group: ‘Plant-animal interactions’ (2003-2005)
- PhD discussion group: ‘Biocomplexity’ (2004-2005)
- Research and literature colloquium on ‘Community and Conservation Ecology’(2003-2005)
- PhD discussion group: ‘Current themes – Allometry’ (2004)

PE&RC Annual Meetings, Seminars and Introduction Days (1 credit)

- PE&RC annual meeting: “Food Insecurity” (2001)

- PE&RC symposium: ‘Agriculture and Nature’(2001)
- PE&RC symposium: ‘Spatial Ecology’(2002)
- PE&RC annual meeting: ‘Global Climate Change & Biodiversity’ (2003)
- PE&RC annual meeting: ‘Biological Disasters’(2004)

International Symposia, Workshops and Conferences (5 credits)

- XXVII. International Ethological Conference. Tuebingen University, Germany (2001)
- The Kruger symposium – Ecology and Management of Savanna Heterogeneity. Kruger National Park, South Africa (2002)
- Savanna Management Symposium. Pietermaritzburg, South Africa (2002)
- 2nd International Conference on Rodent Biology and Management. Canberra, Australia (2003)
- 10th Benelux Congress of Zoology. Leiden, Netherlands (2003)
- 5th International Symposium on ‘Physiology, Behaviour and Wildlife Conservation. Berlin, Germany (2004)
- CEES Symposium ‘Biodiversity – Adaptation vs. chance’. Groningen, Netherlands (2004)

Laboratory Training and Working Visits (3 credits)

- License to perform experiments on animals. School for Veterinary Medicine Hannover, Germany (1998)
- License for animal distance narcosis. School for Veterinary Medicine Hannover, Germany (2000)
- Non-invasive monitoring of hormones. Institute for Zoo and Wildlife Research. Berlin, Germany (2004)