

## Chapter 2

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

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## 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 assess 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 led 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 than 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 Olf 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 Olf 1997, Olf 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  $\pm 13$  °C to  $\pm 35$  °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 preying on rodents are black-shouldered kite (*Elanus caerulus*) and spotted eagle owl (*Bubo africanus*).

## *Experimental design*

### **Herbivore enclosures**

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 enclosure 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 enclosure treatments, whereas the study sites in iMfolozi contain only three enclosure treatments (control, rhino fence and hare fence). Dung counts conducted in the control and the enclosure 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 enclosure 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 enclosures 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 enclosure 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<sup>®</sup>, 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 enclosures and therefore may have fed in different enclosures 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 overall 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*).

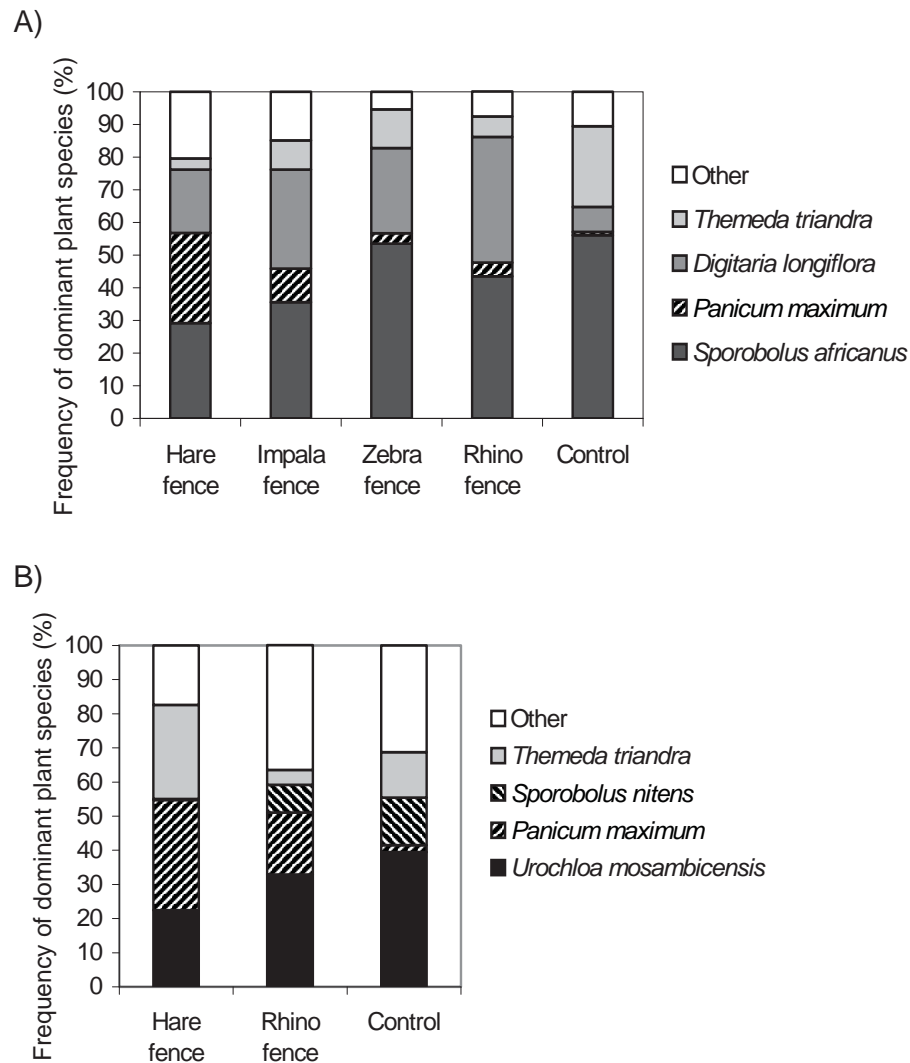
#### **Plant species composition**

The grass species most frequently dominant at the Hluhluwe sites occurring in all enclosure 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 ( $\chi^2_{12} = 377.141$ ,  $P < 0.001$ ). 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 ( $\chi^2_6 = 139.498$ ,  $P < 0.001$ ).

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

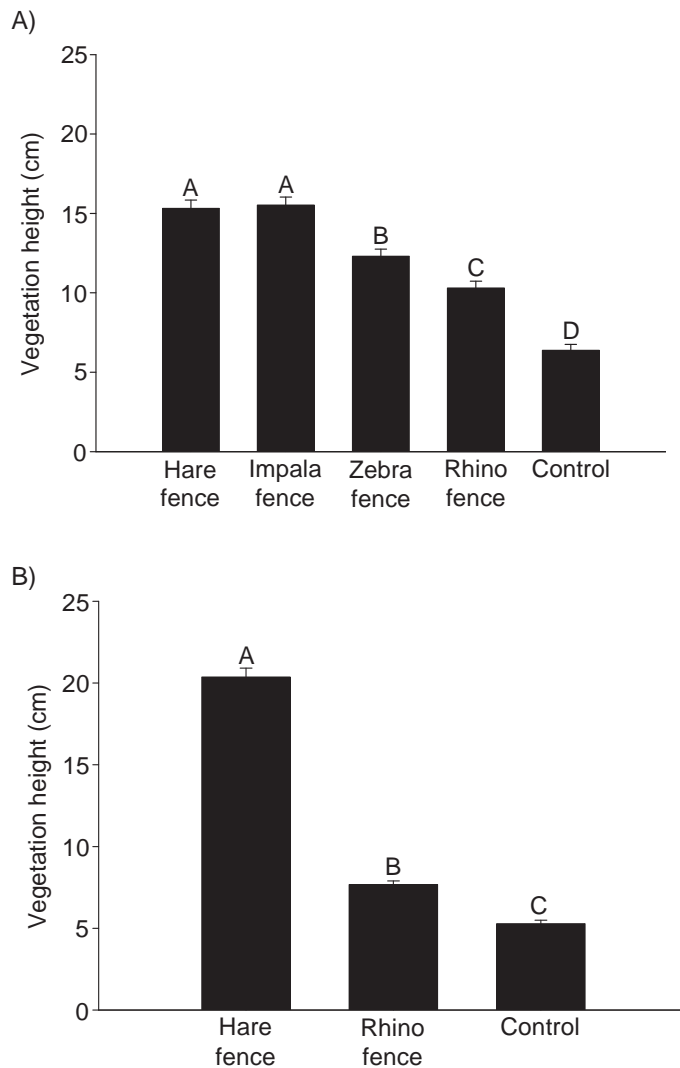




**Fig 1** Frequency of occurrence of dominant grass species for the different fence types at the Hluhluwe (A) and iMfolozi sites (B) measured in March 2003. The grass species composition was significantly different between the fencing treatments at both the Hluhluwe ( $n = 200$ ,  $X^2_{12} = 377.141$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

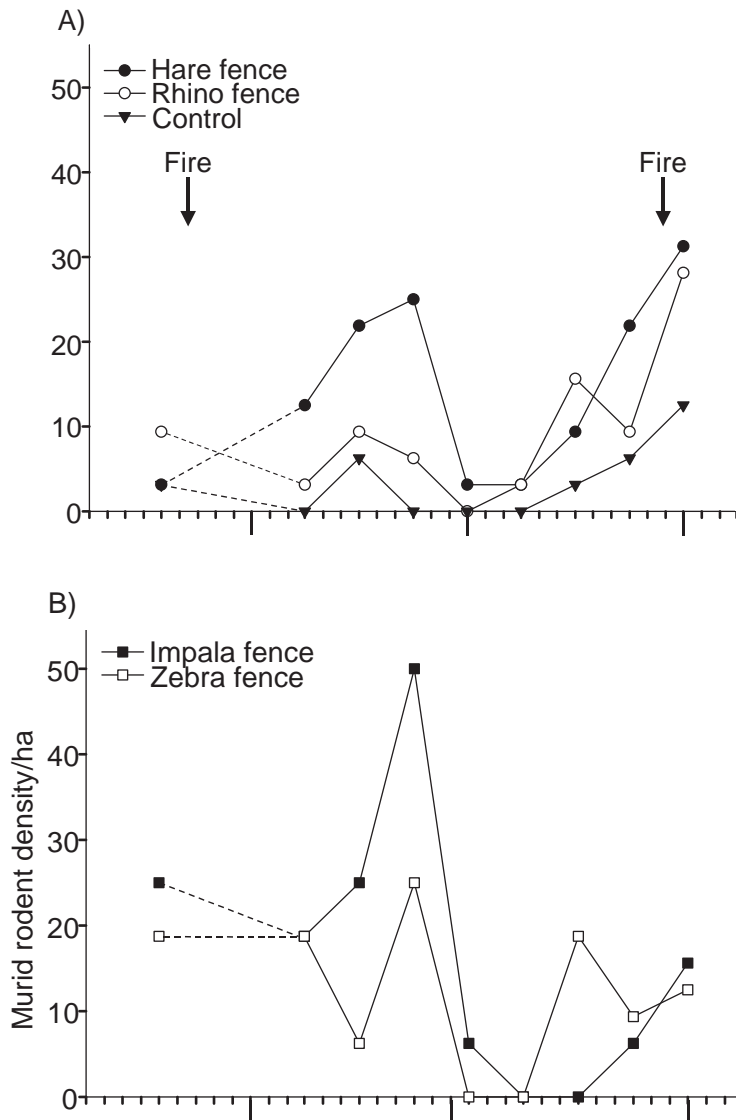


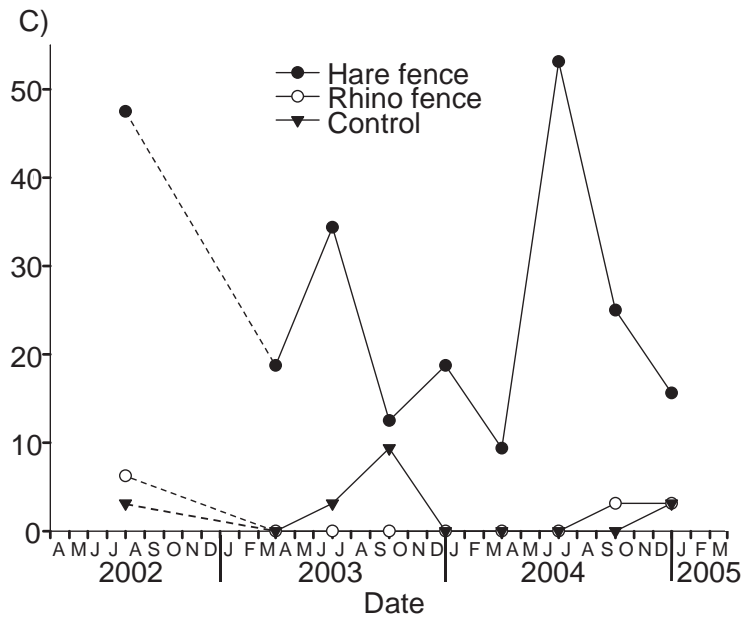
**Fig 2** Mean vegetation height for the different fence types at Hluhluwe (A) and iMfolozi sites (B;  $\pm$  SE,  $n = 200$ ) measured in March 2003. Different letters show significant differences,  $P < 0.001$ .

### *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 enclosure 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*

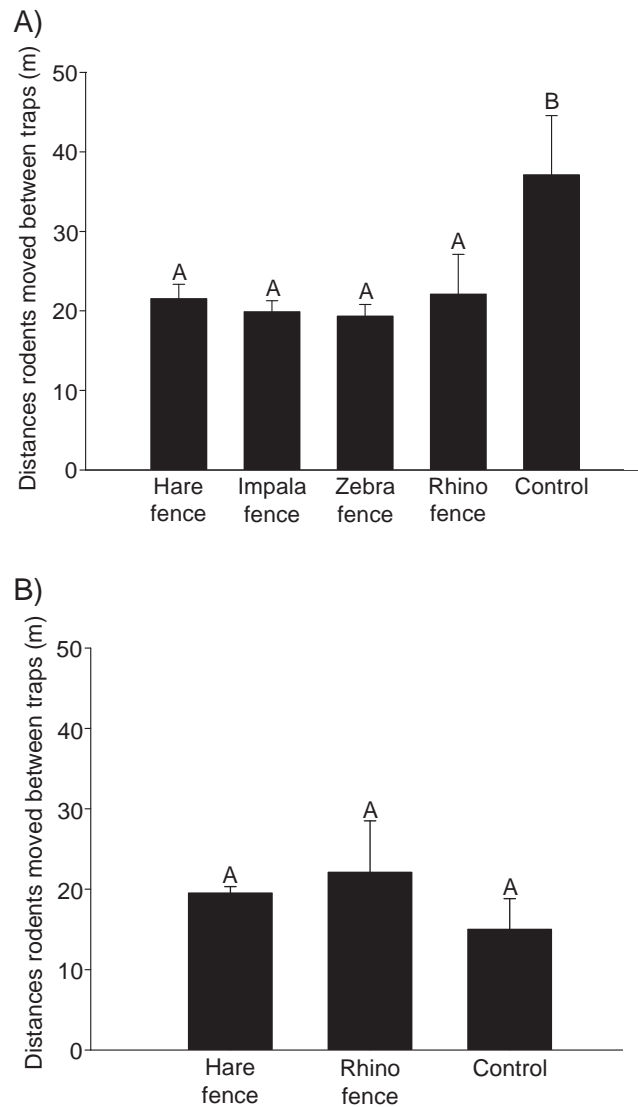
*campestris*) and bush-rats (*Aethomys* spp). However, several captured rodents could not be identified on a species level. Overall, the exclusion of different size groups of larger herbivores lead to a significant increase of total rodent numbers ( $F_{32, 32} = 1.99$ ,  $P = 0.028$ ; Figs 3A and B) 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 ( $F_{32, 32} = 1.085$ ,  $P = 0.41$ ).





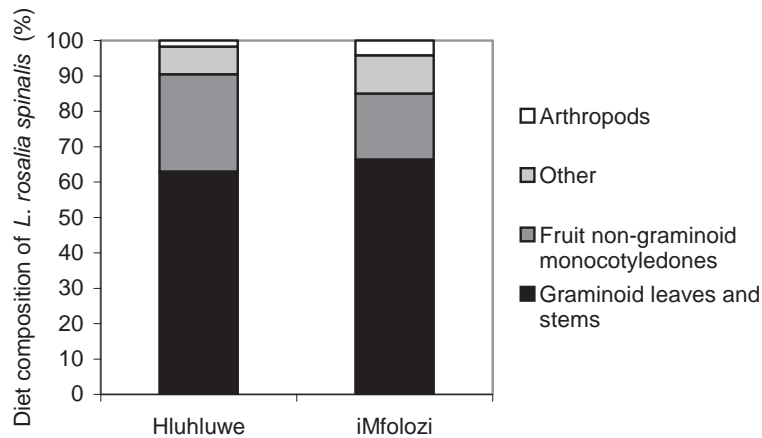
**Fig 3** Density of murid rodents (total number of individuals over all species) for the different fencing treatments at the Hluhluwe (A and B) and iMfolozi sites (C) for July 2002 to December 2004. Overall, differences in numbers between treatments are statistically significant (Repeated Measures ANOVA,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



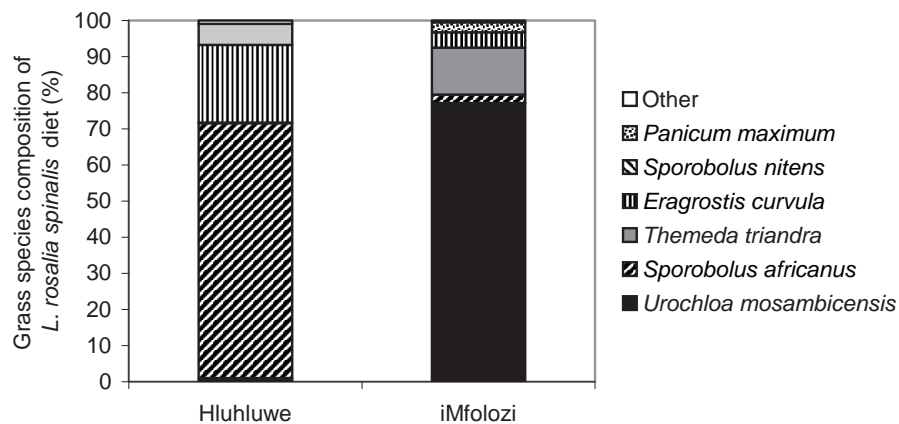
**Fig 4** Mean distances murid rodents moved between trapping locations at the Hluhluwe (A) and iMfolozi sites (B) over all trapping periods ( $\pm$  SE,  $n = 9$ ). Different letters show significant differences,  $P = 0.01$ .

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



**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 ( $n = 12$ ,  $X^2_4 = 20.708$ ,  $P = 0.001$ ).

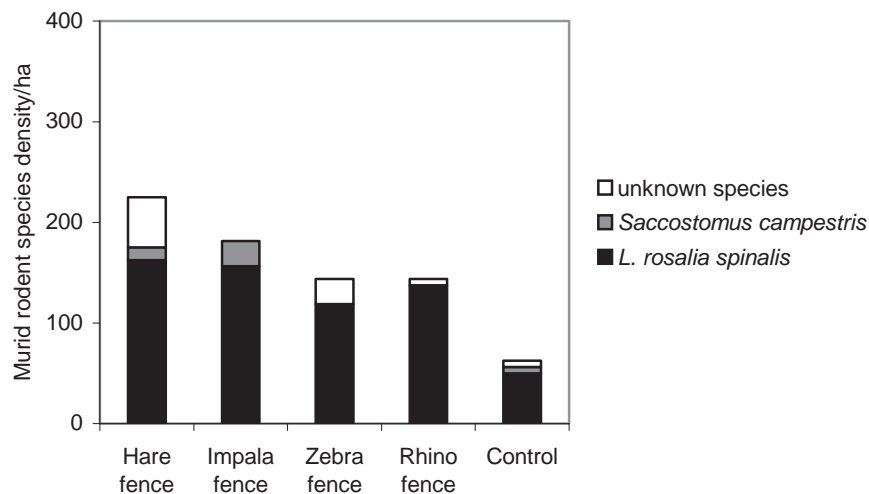
Considering only the graminoid diet components, *L. rosalia spinalis* consumed significantly different grass species at the Hluhluwe than at the iMfolozi sites ( $X^2_9 = 708.29$ ,  $P < 0.001$ ). At the Hluhluwe sites they mostly fed on two low quality bunch grass species, *S. africanus* and *E. curvula* (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 ( $F_{2, 162} = 0.257$ ,  $P = 0.77$ ).



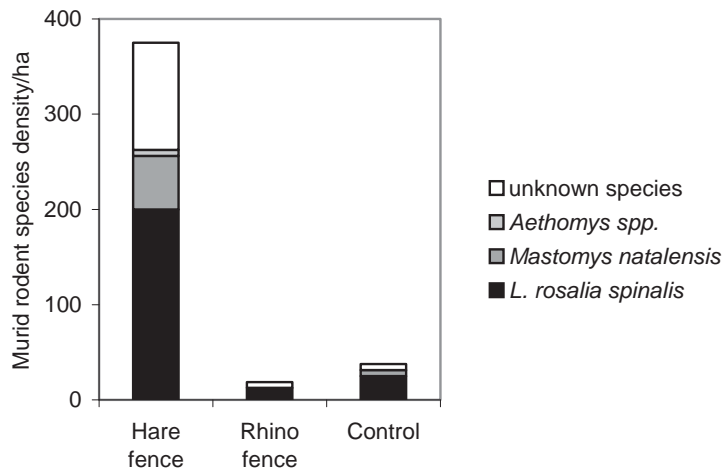
**Fig 6** Grass species composition of the *L. rosalia spinalis* diet at the Hluhluwe and iMfolozi sites in July 2002. The grass species composition was significantly different between the Hluhluwe and iMfolozi sites ( $n = 12$ ,  $X^2_9 = 708.29$ ,  $P < 0.001$ ).

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) ( $n = 9$ ,  $\chi^2_8 = 29.594$ ,  $P < 0.001$ ).

## 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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