Among rodents and rhinos: interplay between small mammals and large herbivores in a South African savanna

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

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Abstract: Our study presents experimentally based results on how large herbivore species affect savanna vegetation and thus murid rodents in the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa. We permanently excluded groups of large herbivore guilds of various body sizes (ranging from white rhino to hares) from sixteen 40 × 40-m plots of vegetation by using different fence types. We determined grass species composition and vegetation height and collected capture–mark–recapture data on murid rodents. Nutrient concentrations of the dominant grass species and rodent diet compositions were analysed. We found that herbivore species of different body sizes had different effects on murid rodents. The exclusion of medium-sized herbivores, such as warthog, impala and nyala increased the abundance of high-quality grass species, especially *Panicum maximum*. However, the dominant rodent species *Lemniscomys rosalia* preferred the most abundant grass species, rather than high-quality grasses. The absence of large bulk feeders, such as zebra, buffalo and white rhino led to an increase in vegetation height. In response, tall vegetation promoted both rodent abundance and species diversity and altered rodent species composition. Ultimately, our results indicate that the greatest effect on murid rodents came from the reduction of vegetation cover by large bulk feeders, which likely increased rodent predation risk.

Key Words: African savanna, community interactions, herbivore exclusion, large herbivores, predation risk, savanna rodents, South Africa

INTRODUCTION

African savannas harbour a high diversity of herbivore species of different sizes. Despite the establishment of protected areas, savannas are still subject to multiple threats. Increasing human populations, changing land-use practices and the implementation of land claims in natural areas often result in ecosystem fragmentation, habitat loss and thus in species extinction (Prins & Olff 1997). To better understand the functioning of African savanna ecosystems, 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 (Olff *et al.* 2002, Owen-Smith 1988, Prins & Olff 1997). However, up to now research on community interactions in savannas has focused mostly on large ungulates, such as buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*) (Owen-Smith 1988, Prins & Douglas-Hamilton 1990). We present some of the first experimentally based results on the interplay of murid rodents with larger herbivores in African savannas. Few studies have reported the impact of large herbivore exclusion on rodent abundance and community composition (Keesing 1997, 1998a, 2000). Keesing (1998a) found that the exclusion of native ungulates and cattle resulted in an overall increase in rodent abundance, suggesting 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 way in which indigenous herbivores of different sizes affect savanna rodents has not been explored.

In the present study we experimentally excluded different size-classes of large herbivores (body sizes ranging from large: white rhino, *Ceratotherium simum*; to small: hares) from plots of savanna vegetation and monitored murid rodent abundance and species composition; and vegetation characteristics to explore their interplay. We hypothesise that the exclusion of different size-classes of herbivores has both positive and negative effects on rodents due to several possible mechanisms. For instance, intense grazing by large herbivores (e.g. white rhino, buffalo and zebra, *Equus burchelli*) improves the vegetation structure for smaller herbivores (Arsenault & Owen-Smith 2002, Farnsworth

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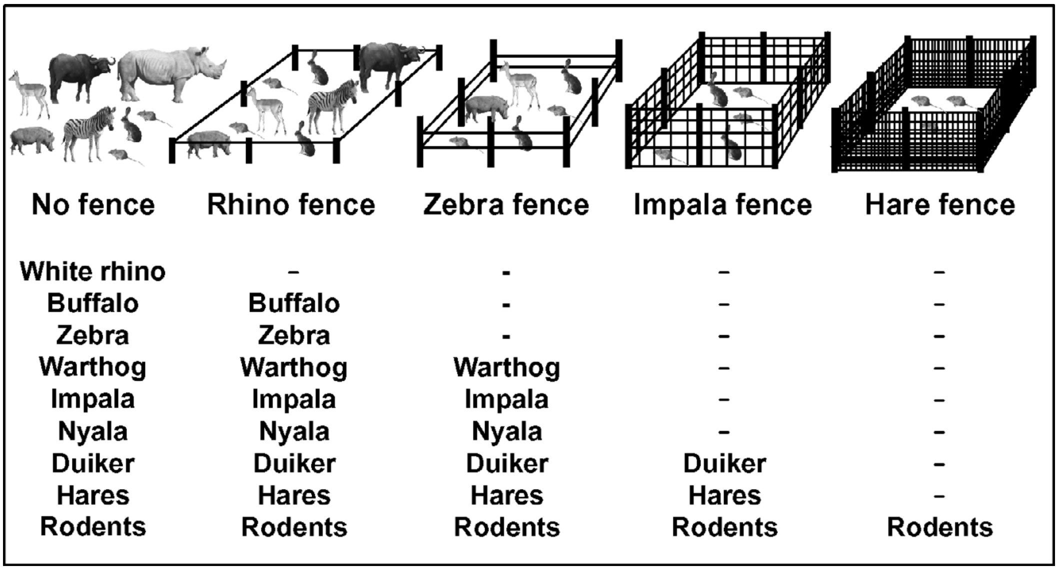

No fence	Rhino fence	Zebra fence	Impala fence	Hare fence
White rhino	-	-	-	-
Buffalo	Buffalo	-	-	-
Zebra	Zebra	-	-	-
Warthog	Warthog	Warthog	-	-
Impala	Impala	Impala	-	-
Nyala	Nyala	Nyala	-	-
Duiker	Duiker	Duiker	Duiker	-
Hares	Hares	Hares	Hares	-
Rodents	Rodents	Rodents	Rodents	Rodents

Figure 1. Design of the exclosure experiment in the Hluhluwe-iMfolozi Park, South Africa. Herbivore species of different size classes are stepwise permanently excluded from 40 m × 40-m blocks of savanna vegetation by using fences with different height and mesh width. Exclosure treatments include (from left to right) unfenced control, rhino fence, zebra fence, impala fence and hare fence. Herbivore species that are able to feed within the different exclosure treatments are listed below each. Animal pictures are copyright of O. Bonnet and A.M. Shrader.

et al. 2002, Vesey-FitzGerald 1969) as it leads to the development of patchy vegetation with short grazing lawns. The establishment of short grazing lawns has 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 medium-sized herbivores (e.g. impala, *Aepyceros melampus*) decrease the number of high-quality plant species available for smaller herbivore species and thus negatively influence rodents through competition for food (Keesing 1998a). Additionally, vegetation modifications by larger herbivores restrict the habitat available to rodents as grazing and trampling reduces the vegetation cover (Bock *et al.* 1984, Goheen *et al.* 2004, Grant *et al.* 1982, Roques *et al.* 2001). A decrease of vegetation cover leads to higher exposure of rodents to their predators and therefore increases their predation risk (Birney *et al.* 1976, Edge *et al.* 1995, Peles & Barrett 1996).

METHODS

Study area

This study was conducted between July 2002 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 vegetation types in the Park range from open grasslands to closed *Acacia* and broadleaved woodlands with a high variation in grass quality and quantity at different scales (Owen-Smith 2004). Rainfall averages 985 mm y^{-1} in the high-altitude regions (Hluhluwe) but 650 mm y^{-1} in the lower areas (iMfolozi; average 1980–2004), with a dry season from April to September. Daily maximum temperatures range from 13 °C to 35 °C. The fire management regime involves simulating natural fires in the park, where different areas are burnt with different frequencies. The park is inhabited by a large set of indigenous large herbivores and carnivores (Brooks & McDonald 1983). Important snakes and raptors in HiP potentially feeding on rodents are Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*) (Branch 1998) as well as black-shouldered kite (*Elanus caerulus*) and spotted eagle owl (*Bubo africanus*) (Maclean 1985).

Experimental design

Herbivore exclosures. Our experiment was established in early 2000 (Bond & Olff, unpubl. data). Large herbivore species of varying body sizes were permanently excluded in turn from sixteen 40 × 40-m plots of savanna vegetation by using fences with different height and mesh width (Figure 1). Two study sites were located in Hluhluwe (situated 5 km apart from each other) and two study sites were located in iMfolozi (situated 5 km apart from each other). The distance between the study sites in Hluhluwe and iMfolozi was approximately 30 km. Each of the replicates had four herbivore exclosure treatments and an unfenced control (only dominant herbivore species listed): (1) no fence: all mammalian herbivores potentially present, allowed (species list is provided as an appendix); (2) rhino fence: a thick cable slung at a height of *c.* 0.7 m above the ground (excludes both species of rhinos, elephant and giraffe but allows access to smaller grazers); (3) zebra fence: two thick cables slung at 0.7 m and 1 m height (additionally excludes animals the size of zebra and larger); (4) impala fence: a 2-m-high upside-down game fence (Bonnox) with variable mesh size, the larger holes were at ground level (allowing access to small antelope and hares but excluding impala-size antelopes and larger animals; (5) hare fence: a 2-m-high game fence with a lower strip of chicken-mesh steel-wire (chicken mesh height: 1.3 m, mesh size 1.3 cm; excludes all animals the size of a hare and larger)

The study sites in Hluhluwe included all four exclosure treatments and the unfenced control, whereas the study sites in iMfolozi contain only two exclosure treatments (rhino fence and hare fence) plus the unfenced control. The distance between the control and the exclosure treatments was not more than 10 m. Dung counts conducted in the control and the exclosure treatments indicated that the fences successfully excluded the target groups. The study sites were burned once every 2 y as part of the fire management regime in the park. During the period of this study, they were burned in August 2002 and August 2004.

Vegetation characterization. Vegetation characteristics were recorded in March 2003 in one-half of the control and each exclosure treatment in a grid with measuring points spaced 2 m apart from each other (200 points). To measure vegetation height the drop disc method (46 cm diameter, mass: 460 g) was used (Stewart *et al.* 2001). The most dominant grass species (basal area cover) was determined and the height at which the disc was resting on the vegetation was measured. To determine the quality of rodent food sources, we collected 112 samples of green leaves of the dominant grass species from all exclosures and control plots. We gathered the number of samples of each species roughly in proportion to their abundance within these plots. We analysed each sample for its N, P, Ca, Mg and Na concentration and then calculated the average concentration 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. We then calculated the average concentrations of the nutrients in the samples and classified them in two nutritional quality categories: (1) high-quality grasses and (2) low-quality grasses.

Rodent surveys. We established a permanent small-mammal trapping grid inside the control and the exclosure treatments. Each 40 × 40-m plot contained a trapping grid of twenty-five 5 × 5-m traps located approximately 7 m apart from each other. Traps were not placed closer than 3 m to a fence. We conducted nine trapping sessions of 4–5 consecutive nights each. Trapping sessions were conducted approximately every 3 months over the course of the study. PVC live-traps were placed on flat ground using one trap per station. Traps were 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 weighed, identified to species (Skinner & Chimimba 2005), and permanently individually marked with glass fibre transponders (Telinject®, ID 100, Römerberg, Germany). In July and August 2002, dung pellets of the most frequently captured rodent species were collected from the traps for micro-histological faecal analysis. Epidermis fragments of grasses in the faeces were compared to photomicrographs of epidermis fragments of the most dominant grass species occurring at the study sites on reference slides (De Jong *et al.* 1995). For the reference slides, pieces of leaf blades were cleaned in household bleach overnight, washed in water, fragments of epidermis were then stripped off and mounted in glycerol before photomicrographs were taken. The faecal samples were mixed on an individual basis; mixed samples were stored in a formalin–acetic acid–alcohol mixture (Anthony & Smith 1974) and softened by autoclaving with some water at 125 °C. Samples were then washed in a Waring Blender, strained over a 0.1-mm plankton sieve and stored in 70% ethanol. From every mixed sample, ten random samples were examined by light microscopy. At least 100 fragments of epidermis were identified by comparison with the photomicrographs and measured by using a grid of 0.01-mm^2 squares in the microscope eyepiece (De Jong *et al.* 1995). The abundance of each species was calculated as a percentage of the total area of the fragments measured (Alipayo *et al.* 1992, Cid & Brizuela 1990, Homolka & Heroldová 1992, Sparks & Malechek 1968, Stewart 1967). Because rodents were able to move between exclosures within a site, we restricted our diet analysis to differences between Hluhluwe and iMfolozi (and not exclosure treatments). Captured animals were released at their trapping location after measurements were taken.

Data analyses

The effects of large herbivores on vegetation were tested statistically in two different ways. To highlight the impact of the different herbivore size classes on the grass species composition and vegetation structure, we firstly analysed the Hluhluwe and iMfolozi areas separately. This analysis included all exclosure treatments (four in Hluhluwe vs. two in iMfolozi), plus the unfenced controls. However, to facilitate four similar replicates throughout the experiment, we also pooled the data from Hluhluwe and iMfolozi, including only the two replicated exclosure

Table 1. Leaf nutrient concentrations (mean ± SD), number of samples taken and growth-form category of each dominant grass species in the Hluhluwe-iMfolozi Park, South Africa. We found that lawn grass species had significantly higher nutrient concentrations than bunch grass species (*t*-test, $P < 0.05$). However, the nutrient concentrations in the bunch grass *Panicum maximum* were also high. *Bothriochloa insculpta* is expected to be neglected by herbivores due to its bitter taste (van Oudtshoorn 1992).

Species	Growth-form category	N	N (%)	P (%)	Ca (%)	Mg (%)	Na (mg kg^{-1})
Digitaria longiflora	lawn grass	10	1.7 ± 0.5	0.3 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	6313 ± 1213
Sporobolus nitens	lawn grass	9	2.6 ± 0.8	0.3 ± 0.1	0.4 ± 0.8	0.2 ± 0.04	5407 ± 1881
Urochloa mosambicensis	lawn grass	13	2.7 ± 0.9	0.4 ± 0.1	0.7 ± 0.2	0.4 ± 0.1	9471 ± 3888
Aristida congesta	bunch grass	5	1.9 ± 0.4	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	604 ± 349
Bothriochloa insculpta	bunch grass	11	2.2 ± 0.3	0.3 ± 0.03	0.4 ± 0.1	0.2 ± 0.1	446 ± 483
Eragrostis curvula	bunch grass	10	1.4 ± 0.3	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.03	997 ± 310
Eragrostis superba	bunch grass	13	1.9 ± 0.4	0.2 ± 0.1	0.6 ± 0.2	0.2 ± 0.1	971 ± 387
Heteropogon contortus	bunch grass	7	1.7 ± 0.3	0.2 ± 0.04	0.3 ± 0.1	0.2 ± 0.1	334 ± 162
Panicum maximum	bunch grass	16	2.5 ± 0.5	0.3 ± 0.1	0.5 ± 0.2	0.2 ± 0.1	2077 ± 968
Sporobolus africanus	bunch grass	10	1.3 ± 0.3	0.2 ± 0.1	0.3 ± 0.04	0.1 ± 0.02	383 ± 175
Themeda triandra	bunch grass	8	1.5 ± 0.2	0.2 ± 0.03	0.3 ± 0.1	0.2 ± 0.1	372 ± 210

treatments (rhino fence and hare fence), plus the unfenced control. We then used the pooled data for the remaining analyses.

We calculated the mean vegetation height (using 200 measuring points per plot) for each exclosure treatment (four in Hluhluwe vs. two in iMfolozi), plus the unfenced controls. This resulted in 10 values for Hluhluwe (four exclosure treatments + one control × two study sites) and six for iMfolozi (two exclosure treatments + one control × two study sites). We used these values to analyse the effect of large herbivores on the vegetation height in the two separate study areas with a one-way ANOVA followed by Tukey HSD tests. Then, we tested the influence of large herbivores on the mean vegetation height using a two-way ANOVA. In this analysis, exclosure treatment (hare fence, rhino fence, control) and study area (Hluhluwe, iMfolozi) were the independent factors; vegetation height was the dependent factor. We used a Pearson's Chi-square test to examine the impact of large herbivores on grass species composition in the two separate study areas (including all exclosure treatments plus control). To test for differences in both grass and rodent species composition between exclosure treatment (hare fence, rhino fence, control) and study area (Hluhluwe, iMfolozi), we used a three-way ANOVA. Seven dominant grass species were included in the analysis for the grass species composition, whereas the analysis for the rodent species composition included six different rodent species. We used a repeated-measures ANOVA followed by Tukey HSD tests to investigate the impact of large herbivores on rodent numbers and trapping success (percentage of traps that were occupied by rodents) over the course of the study. In these analyses, exclosure treatment (hare fence, rhino fence, control) and study area (Hluhluwe, iMfolozi) were the independent factors, and rodent numbers or trapping success per trapping session were the dependent factors. Relations between trapping success and vegetation height were analysed with logistic regression with rodent presence/absence as the dependent variable and vegetation height as a predictor. Due to the unbalanced number of grass species, we first tested the data on nutrient concentrations of bunch and lawn grasses for equality of sample variances. Each nutrient was then tested separately for differences between bunch and lawn grass species using a *t*-test (the sample variances for N, Mg, P and Na concentrations which were found to be unequal were estimated separately for each group). Differences in the overall diet composition of rodents and the grass components of their diet between study areas were analysed with a Pearson's Chi-square test.

RESULTS

Vegetation analysis

Grass species quality. Lawn grass species had significantly higher average N ($t_{40.4} = -2.7$, $P = 0.01$), P ($t_{42.0} = -3.5$, $P < 0.001$), Ca ($t_{110} = -3.6$, $P < 0.001$), Mg ($t_{41.5} = -4.2$, $P < 0.001$) and Na concentrations ($t_{32.6} = -11.1$, $P < 0.001$) 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 *Panicum maximum*).

Grass species composition. The stepwise exclusion of different size-classes of herbivores resulted in significant changes in the grass species composition in Hluhluwe ($\chi^2_{16} = 432$, $P < 0.001$, Figure 2a) and iMfolozi ($\chi^2_{8} = 228$, $P < 0.001$, Figure 2b). The dominant grass species in Hluhluwe were *Sporobolus africanus* and *Digitaria longiflora*, representing 67% of the recorded species. Other frequently recorded grass species included *Panicum maximum* and *Themeda triandra*. In iMfolozi, the dominant grass species were *P. maximum* and *Urochloa mosambicensis*, recorded at 49% of the measurement points. However, *Sporobolus nitens* and *T. triandra* were also recorded frequently. In both study areas, Hluhluwe

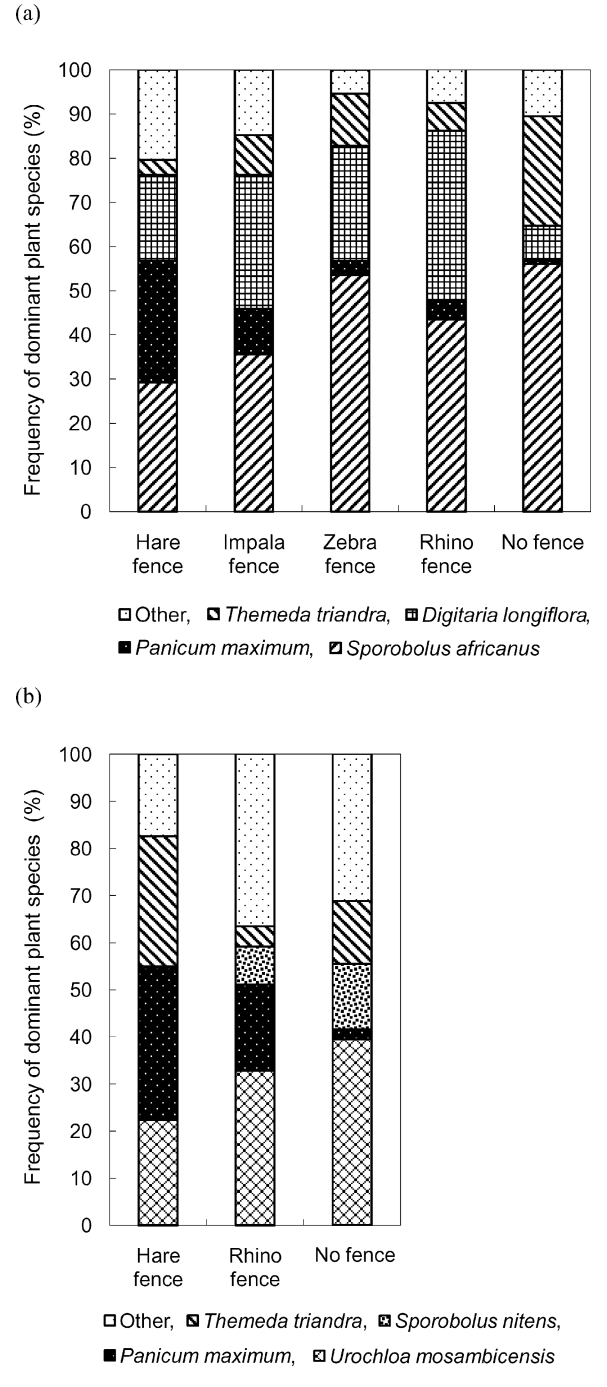

Figure 2. Frequency of occurrence of dominant grass species for the different exclosure treatments in (a) Hluhluwe and (b) iMfolozi measured in March 2003 in the Hluhluwe-iMfolozi Park, South Africa. The grass species composition was significantly different between the exclosure treatments in both Hluhluwe ($n = 200$, $\chi^2_{16} = 432$, $P < 0.001$) and iMfolozi ($n = 200$, $\chi^2_{8} = 228$, $P < 0.001$). In both study areas, Hluhluwe and iMfolozi, the abundance of the high-quality grass species *P. maximum* increased considerably in the absence of large herbivores (i.e. hare fence).

Table 2. Results of a three-way ANOVA of the effects of exclosure treatment, area and different grass species on the grass species composition in the Hluhluwe-iMfolozi Park, South Africa. 'Area' refers to the pooled data of the two study sites in each of the Hluhluwe and iMfolozi areas. The grass species composition differed significantly between Hluhluwe and iMfolozi.

Source of variation	df	MS	F	P
Exclosure treatment	2	0	0.0	1.00
Area	1	0	0.0	1.00
Grass species	6	417	0.8	0.58
Exclosure treatment × area	2	0	0.0	1.00
Exclosure treatment × grass species	12	270	0.5	0.89
Area × grass species	6	1764	3.4	0.008
Exclosure treatment × area × grass species	12	219	0.4	0.95
Error	42	521		

Table 3. Results of a two-way ANOVA of the effects of exclosure treatment and area in vegetation height in the Hluhluwe-iMfolozi Park, South Africa. 'Area' refers to the pooled data of the two study sites in each of the Hluhluwe and iMfolozi areas. The vegetation heights differed significantly between the exclosure treatments when considering only the hare fence, rhino fence and unfenced control for both study areas, Hluhluwe and iMfolozi.

Source of variation	df	MS	F	P
Exclosure treatment	2	156	18.5	0.002
Area	1	0	0.1	0.82
Exclosure treatment × area	2	16	2.0	0.22
Error	6	8		

and iMfolozi, we found a considerable increase in the abundance of the high-quality grass species *P. maximum* after the exclusion of all large herbivore species. Moreover, the grass species composition in the hare fence, rhino fence and unfenced control was significantly different between Hluhluwe and iMfolozi (Table 2).

Vegetation structure. The exclusion of all herbivore species the size of zebra and larger resulted in a stepwise increase of the vegetation height in Hluhluwe (Figure 3a). However, this increase was not significant ($F_{4,5} = 1.5$, $P = 0.31$), but followed the same trend as in iMfolozi. In iMfolozi, we found a significant increase of the vegetation height after the exclusion of white rhino ($F_{2,3} = 53.4$, $P = 0.005$; Figure 3b).

Furthermore, the vegetation heights in the hare fence, rhino fence and unfenced control were significantly different for the pooled data of Hluhluwe and iMfolozi (Table 3).

Rodent analysis

Between July 2002 and December 2004, we captured 387 murid rodents, comprising four species. The most frequently captured species was the single-striped mouse (*Lemniscomys rosalia*), a murid rodent that is common in bushveld habitats in Kwazulu-Natal (Taylor 1998). In HiP, the single-striped mouse represented about 75% of all captures. Other murid rodent species captured and identified included the Natal multimammate mouse (*Mastomys natalensis*), the pouched mouse (*Saccostomus campestris*)

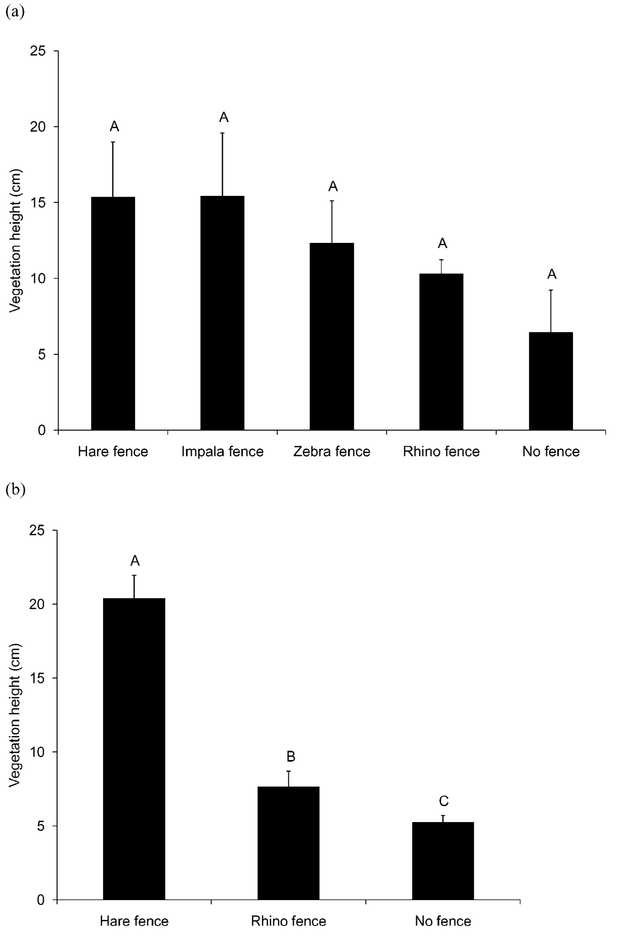

Figure 3. Mean vegetation height for the different exclosure treatments in (a) Hluhluwe and (b) iMfolozi measured in March 2003 in the Hluhluwe-iMfolozi Park, South Africa. Error bars represent 1 SE. Different upper-case letters show significant differences in vegetation height between exclosure treatments ($n = 200$, one-way ANOVA, $F_{2,\,3} = 53.4$, $P = 0.005$).

and bush-rats (*Aethomys* spp). However, several captured rodents could not be identified to species level.

From the three-way interaction, it was clear that the number of murid rodents was significantly higher in the absence of all larger herbivores throughout the course of the study (Table 4, Figure 4). The trapping success was significantly higher when all large herbivore species were absent over the course of the study (Table 5). Furthermore, the trapping success significantly increased with increasing vegetation height (Wald = 51.7, $P < 0.001$). The rodent species composition was significantly different between the three exclosure treatments (Table 6, Figure 5). Firstly, the absence of all large herbivores resulted in a higher number of rodent species. Secondly, while *Lemniscomys rosalia* and the unknown species 1 were present in all exclosure treatments, *Saccostomus campestris*, *Aethomys* spp., and the unknown species 2 were captured only in the absence of large herbivores.

Table 4. Results of a repeated-measures ANOVA of the effects of exclosure treatment, area and time on the abundance of murid rodents in the Hluhluwe-iMfolozi Park, South Africa. 'Area' refers to the pooled data of the two study sites in each of the Hluhluwe and iMfolozi areas. The three-way interaction indicates that murid rodent numbers were significantly higher in the absence of large herbivores throughout the course of the study.

Source of variation	df	MS	F	P
Exclosure treatment	2	326	3.4	0.10
Area	1	41	0.4	0.54
Exclosure treatment × area	2	104	1.1	0.40
Error	6	96		
Time	8	24	2.4	0.03
Time × exclosure treatment	16	10	1.0	0.45
Time × area	8	24	2.4	0.03
Time × exclosure treatment × area	16	20	2.1	0.03
Error	48	10		

Table 5. Results of a repeated-measures ANOVA of the effects exclosure treatment, area and time on the trapping success of murid rodents in the Hluhluwe-iMfolozi Park, South Africa. 'Area' refers to the pooled data of the two study sites in each of the Hluhluwe and iMfolozi areas. The three-way interaction shows that the absence of large herbivores significantly increased the trapping success of murid rodents over the course of the study.

Source of variation	df	MS	F	P
Exclosure treatment	2	<1	3.5	0.10
Area	1	<1	0.5	0.52
Exclosure treatment × area	2	<1	1.3	0.35
Error	6	<1		
Time	8	<1	2.9	0.01
Time × exclosure treatment	16	<1	1.5	0.13
Time × area	8	<1	3.3	0.005
Time × exclosure treatment × area	16	<1	2.6	0.005
Error	48	<1		

Table 6. Results of a three-way ANOVA of the effects of exclosure treatment, area and different rodent species on the rodent species composition in the Hluhluwe-iMfolozi Park, South Africa. 'Area' refers to the pooled data of the two study sites in each of the Hluhluwe and iMfolozi areas. The rodent species composition differed significantly between the exclosure treatments.

Source of variation	df	MS	F	P
Exclosure treatment	2	482	7.7	0.002
Area	1	62	1.0	0.324
Rodent species	5	497	8.0	0.001
Exclosure treatment × area	2	161	2.6	0.089
Exclosure treatment × rodent species	10	194	3.1	0.006
Area × rodent species	5	13	0.2	0.952
Exclosure treatment × area × rodent species	10	71	1.2	0.355
Error	36	62		

The diet of *L. rosalia* consists mainly of grass leaves and stems (65%) but also seeds (25%) and arthropods (3%), with a significantly higher grass and arthropod proportion in its diet in iMfolozi than in Hluhluwe ($\chi^2_4 = 20.7$, $P = 0.001$). Considering only the grass diet components, *L. rosalia* consumed significantly different proportions of grass species in Hluhluwe than in iMfolozi ($\chi^2_9 = 708$, $P < 0.001$). In Hluhluwe, it mostly fed on two low-quality bunch grass species, *Sporobolus africanus* (69%), and

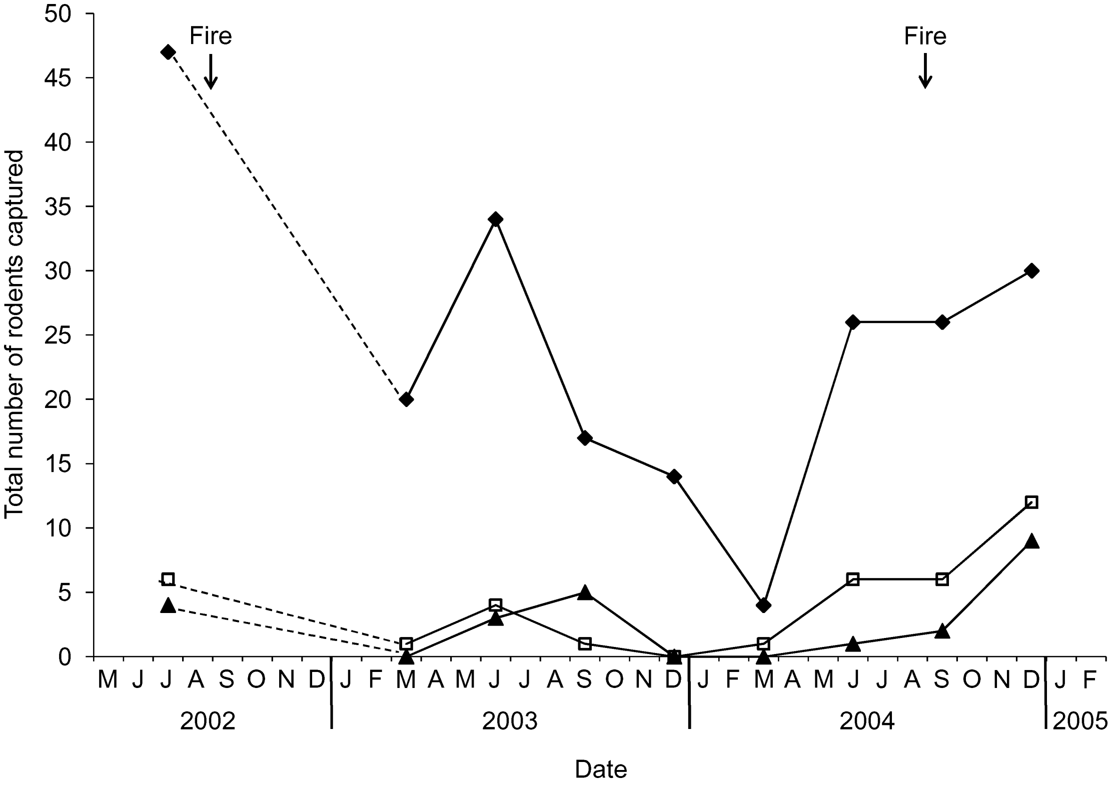

Figure 4. Total number of murid rodents captured in the different exclosure treatments from July 2002 to December 2004 in the Hluhluwe-iMfolozi Park, South Africa. The different exclosure treatments are presented as: solid diamonds = hare fence; open squares = rhino fence; solid triangles = unfenced control. The dashed lines indicate a hypothesized trend in the number of murid rodents due to a missing trapping session. Murid rodent numbers were significantly higher in the absence of all larger herbivores throughout the course of the study (n = 9, repeated-measures ANOVA, $F_{16,48} = 2.1$, $P = 0.03$).

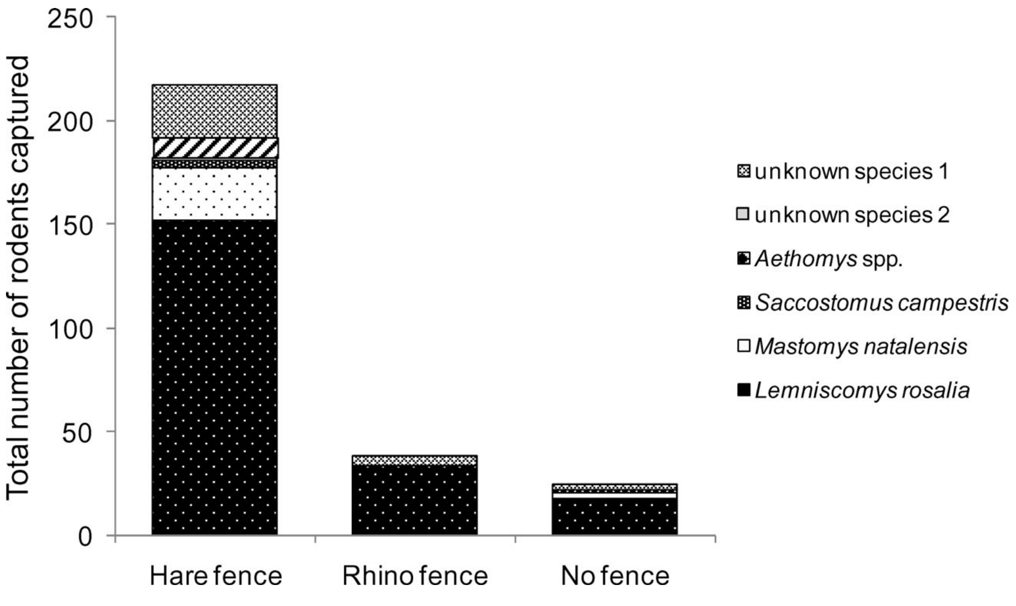

Figure 5. Total number of murid rodent species captured in the different exclosure treatments from July 2002 to December 2004 in the Hluhluwe-iMfolozi Park, South Africa. The exclusion of large herbivores resulted in a higher number of rodent species in the hare fence. In addition, the composition of the rodent species assemblage differed significantly between the exclosure treatments (n = 9, three-way ANOVA, $F_{10,36} = 3.1$, $P = 0.006$).

Eragrostis curvula (21%). In iMfolozi, it predominantly fed on the high-quality lawn grass species *U. mosambicensis* (77%); however, *T. triandra*, a lower-quality bunch grass species, was also detected in its diet (13%).

DISCUSSION

Herbivore species of different body sizes had different effects on murid rodents. Medium-sized herbivores such as warthog, impala and nyala altered mainly the abundance of high-quality grasses and thus plant species composition. Large bulk feeders such as zebra, buffalo and white rhino changed primarily the vegetation height. This in turn, had a strong impact on rodent abundance and both rodent species diversity and species composition.

Effects of large herbivores on murid rodents

Herbivore species of different body sizes select different diets due to their foraging selectivity and food quality requirements. Medium-sized herbivores (e.g. warthog, impala and nyala) can feed on individual plants or even plant parts (Ritchie & Olff 1999) and selectively feed on high-quality food resources. Large herbivore species (e.g. white rhino, buffalo and zebra), on the other hand, can only graze on multiple plants at their lowest level of selection and tolerate lower-quality food (Demment & van Soest 1985, van Soest 1994). As a consequence, herbivore species of different body sizes play various roles in creating mosaic patches of short and long vegetation (Cromsigt & Olff 2006, Vesey-FitzGerald 1969, 1972) that differ in quality and quantity.

In the present study, we hypothesized that the absence of medium-sized herbivores would lead to changes in the quantity and quality of food available to rodents. Our results showed that the exclusion of medium-sized herbivores led to changes in both food quantity and grass species composition, increasing the abundance of high-quality food resources available to rodents. Furthermore, the dominant rodent species captured in the study area, *Lemniscomys rosalia*, is mostly herbivorous and thus potentially competing with larger herbivores for food resources. However, *L. rosalia* showed a strong preference for the most abundant grass species occurring in their habitat, rather than for high-quality grass species. Moreover, the diet analysis revealed that *L. rosalia* includes arthropod components in its diet, which may be of greater importance nutritionally than the protein concentration in grass leaves. This may indicate that food is unlikely to be a limiting factor for rodents in this habitat.

We hypothesized that the absence of large herbivore species would result in increased vegetation height and thus protective cover available to rodents. Our study revealed that the exclosure of large herbivores led to a significant increase in the vegetation height. Furthermore, the abundance of rodents was strongly correlated with the vegetation height. Smit *et al.* (2001) also found taller vegetation and higher rodent density after the exclusion of large herbivores. Taller vegetation may imply a better habitat for rodents as they benefit from closed vegetation cover through a lower predation risk (Bowland & Perrin 1989, Kotler 1984, Kotler & Blaustein 1995). Several studies have shown that the amount of vegetation cover is important for protecting rodents from predators (Birney *et al.* 1976, Cook 1959, Edge *et al.* 1995, Peles & Barrett 1996). In some habitats, however, rodent numbers increase in the absence of larger herbivores despite undetectable differences in vegetation cover (Heske & Campbell 1991, Keesing 1998a, 1998b, 2000). Nevertheless, we conclude that the abundance of rodents in this habitat is most likely influenced by large-herbivore-induced changes of the vegetation cover and the subsequent increase in their exposure to predators, especially raptors, which are abundant in HiP.

Our study indicated that the absence of large herbivores results in a higher number of rodent species. We also found that some rodent species were captured regardless of the presence of large herbivores (e.g. *Lemniscomys rosalia*, *Mastomys natalensis*), whereas others were only captured in the absence of large herbivores (e.g. *Saccostomus campestris*). *Lemniscomys rosalia* is known to occupy herbivore niches, as it tends to be herbivorous (Monadjem 1997a). Its most important requirement seems to be the presence of dense ground cover of long grass (Monadjem 1997b, Taylor 1998), as it appears to breed in surface grass nests (Taylor 1998). Although *Mastomys natalensis* is known to be a pioneer species in the colonization of heavily overgrazed areas (Meester *et al.* 1979), it was also found mainly in tall vegetation. *Saccostomus campestris*, on the other hand, is a slow-moving animal that often falls prey to carnivores (Taylor 1998). It is particularly vulnerable to avian predators, which mainly use vision in hunting. Therefore, it is likely that this species prefers tall vegetation rather than areas with heavily grazed vegetation. Overall, we suggest that murid rodent abundance and both species diversity and species composition in South African savannas are driven primarily by large-herbivore-induced changes of their predation risk.

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Appendix 1. Mammalian herbivore species potentially present in the Hluhluwe-iMfolozi Park, South Africa (nomenclature follows Skinner & Chimimba 2005). Body mass represents maximum male mass.

Species	Scientific name	Body mass (kg)
African elephant	*Loxodonta africana*	6000
White rhinoceros	*Ceratotherium simum*	2300
Hippopotamus	*Hippopotamus amphibius*	1490
Giraffe	*Giraffa camelopardalis*	1190
Black rhinoceros	*Diceros bicornis*	852
African buffalo	*Syncerus caffer*	631
Burchell's zebra	*Equus burchelli*	320
Waterbuck	*Kobus ellipsiprymnus*	270
Blue wildebeest	*Connocheates taurinus*	250
Kudu	*Tragelaphus strepsiceros*	250
Nyala	*Tragelaphus angasi*	107
Warthog	*Phacochoerus aethiopicus*	80
Bushpig	*Potamochoerus porcus*	70
Reedbuck	*Redunca arundinum*	68
Impala	*Aepyceros melampus*	54
Bushbuck	*Tragephalus scriptus*	54
Mountain reedbuck	*Redunca fulvorufula*	30
Common duiker	*Sylvicapra grimmia*	18
Red duiker	*Cephalophus natalensis*	12
Porcupine	*Hystrix africaeaustralis*	11
Steenbok	*Raphicerus campestris*	11
Klipspringer	*Oreotragus oreotragus*	10
Blue duiker	*Philantomba monticola*	5
Rock dassie	*Procavia capensis*	4.5
Greater cane rat	*Thryonomys swinderianus*	4.5
Natal red hare	*Pronolagus crassicaudatus*	2.6
Scrub hare	*Lepus saxatilis*	2
Cape hare	*Lepus capensis*	1.6
Smith's red hare	*Pronolagus rupestris*	1.6
Brown rat	*Rattus norvegicus*	0.9
House rat	*Rattus rattus*	0.12
Highveld gerbil	*Tatera brantsii*	0.08
Red veld rat	*Aethomys chrysophilus*	0.08
Bushveld gerbil	*Tatera leucagastera*	0.07
Single-striped mouse	*Lemniscomys rosalia*	0.06
Natal multimammate mouse	*Mastomys natalensis*	0.06
Pouched mouse	*Saccostomus campestris*	0.05
House mouse	*Mus musculus*	0.02
Pygmy mouse	*Mus minituidis*	0.005