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# Land use affects rodent communities in Kalahari savannah rangelands

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## Abstract

Shrub encroachment caused by overgrazing has led to dramatic changes of savannah landscapes and is considered one of the most threatening forms of rangeland degradation leading to habitat fragmentation. Although changes to plant assemblages are becoming better known, however, our understanding of how shrub encroachment affects rodent communities is low. In this study, we investigated relative abundance of five rodent species in sixteen southern Kalahari rangelands where shrub cover ranged from low (<5%) to high (>25%). Rodent abundance was determined on three trapping grids (40 × 100 m) for each site. Our results show that increasing shrub cover affected rodent species differently. The relative abundance of hairy-footed gerbil, short-tailed gerbil and bushveld gerbil declined with increasing shrub cover, whereas highveld gerbil and striped mouse exhibited hump-shaped relationships with shrub cover. Overall, species richness decreased with increasing shrub cover and a negative impact of high shrub cover above 15% on rodent abundance was congruent for all species. We conclude that our results support the hypothesis that long-term heavy grazing that results in area wide shrub encroachment, threatens the diversity of arid environments.

*Key words:* rangeland degradation, shrub encroachment, species diversity, species richness, structural diversity

## Résumé

L'envahissement de buissons dû au surpâturage a conduit à des changements spectaculaires des paysages de savane et on le considère comme une des menaces les plus dangereuses pour la dégradation des pâturages menant à

la fragmentation de l'habitat. Bien que l'on connaisse mieux les changements qui touchent les associations de plantes, on comprend moins bien comment l'envahissement des buissons affecte les communautés de rongeurs. Ici, nous avons étudié l'abondance relative de cinq espèces de rongeurs dans seize prairies du sud du Kalahari où le couvert de broussailles allait de faible (<5%) à élevé (>25%). L'abondance des rongeurs était déterminée sur trois grilles-pièges (40 m × 100 m) pour chaque site. Nos résultats montrent que l'augmentation de la couverture des buissons affecte les espèces de rongeurs différemment. L'abondance relative de trois espèces de gerbilles (*Hairy-footed gerbil*, *short-tailed gerbil* et *bushveld gerbil*) diminuait avec l'augmentation du couvert buissonneux, alors que la *highveld gerbil* et la souris striée présentaient une relation <<en courbe>> avec le couvert buissonneux. Partout, la richesse en espèces diminuait avec l'augmentation du couvert des broussailles et l'impact négatif d'une forte couverture de broussailles, au-delà de 15%, sur l'abondance des rongeurs était comparable chez toutes les espèces. Nous concluons que nos résultats soutiennent l'hypothèse selon laquelle un pâturage intense de longue durée aboutit à un large envahissement de buissons et menace la diversité des environnements arides.

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## Introduction

Overgrazing by livestock leading to shrub encroachment, i.e. the increase of woody vegetation at the cost of herbaceous vegetation is a widespread phenomenon in arid and semiarid savannas throughout the world (Archer, Schimel & Holland, 1995; Roques, O'Connor & Watkinson, 2001; Cabral *et al.*, 2003; Sankaran *et al.*, 2005). This form of structural landscape change is considered one of the most serious forms of rangeland degradation (Scholes & Walker, 1993; Jeltsch *et al.*, 1997). From a rangeland perspective, shrub encroachment reduces grazing capacity and thus

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the land user's profit (Higgings, Shackleton & Robinson, 1999; Tainton, 1999). Additionally, shrub encroachment may lead to habitat loss and habitat fragmentation for plants and animals (Milton & Dean, 1995; Weber & Jeltsch, 2000), which is thought to reduce species diversity. However, shrubs or shrub patches have the potential to provide nesting sites and effective shelter to, for example, ground-dwelling mammals from avian predators (Tews, Blaum & Jeltsch, 2004; Blaum *et al.*, 2007). Nevertheless, an increase of shrubs leads to changes in the composition and spatial distribution of vegetation structures (Skarpe, 1986; Jeltsch *et al.*, 1997), which are accompanied by changes in both availability and accessibility of resources (e.g. foraging sites or predation cover). Small mammals, such as rodents, play an important role in arid and semiarid savannahs for seed dispersal and predation (Price & Jenkins, 1986; Kerley, Knight & Erasmus, 1990; Wada & Uemura, 1994). Therefore, rodents may affect not only plant abundance but also the structure and dynamics of the vegetation (Brown *et al.*, 1986).

However, for semiarid savannahs of southern Africa such as the Kalahari, our understanding of how long-term effects of shrub encroachment affect rodent assemblages is poor. Changes in shrub cover of Kalahari savannah rangelands will also affect food availability of rodents. Despite the omnivorous diet (green plant leaves, seeds and arthropods) of Kalahari rodents (Kerley *et al.*, 1990; Skinner & Chimimba, 2005), food availability is low where shrub cover is high (Blaum, 2004).

According to the resource availability hypothesis, rodent abundance will be related to primary productivity (e.g. Ernest, Brown & Parmenter, 2000; Whitford, 2002). Consequently, as shrub encroachment reduces primary productivity of above ground biomass in arid and semiarid savannahs (Scholes & Walker, 1993), rodent abundance will be negatively related to shrub cover. On the other hand, the microhabitat selection hypothesis suggests shrub encroachment to have positive effects by increasing the availability of important habitat structures, such as nesting sites or predation cover (Rosenzweig & Winakur, 1969; Price, 1978; Parmenter & Macmahon, 1983).

Both, the resource availability hypothesis and the microhabitat selection hypothesis may explain rodent abundance, but would lead to different predictions. Given this contrast, we investigated the effects of long-term shrub encroachment on the abundance of the rodent community in sixteen different Kalahari rangeland habitats where shrub cover ranged from low (<5%) to high (>25%).

Owing to the described contrary effects of increasing shrub cover, we predict a balance between positive (increase of habitat structures) and negative effects (decrease of food availability) of long-term shrub encroachment, resulting in hump-shaped responses of rodent species' abundance.

## Material and methods

### Study sites

We investigated rodent communities in Kalahari rangelands south of the Kgalagadi Transfrontier Park in the Northern Cape Province, South Africa. The savannah vegetation is described as the western form of the Kalahari Thornveld, which typically consists of trees (*Acacia erioloba*, E.Mey., *A. haematoxylon*, Willd. and *Boscia albitrunca*, Gilg & Benedict) and shrubs (*Rhigozum trichotomum*, Burch. and *A. mellifera*, Benth.) sparsely scattered in a grassy matrix (*Stipagrostis* spp., *Eragrostis* spp. and *Schmidtia kalahariensis*, Stent) (Leistner, 1967; Van Rooyen, Bredenkamp & Theron, 1991).

We established sixteen study sites of 250 ha (1 × 2.5 km), each with different degrees of shrub encroachment, in the rangeland area between Twee Rivieren and Askham (26°15'S, 20°35'E). The sites differed in their historic and present grazing impact and current stocking rates (during the last 10 years), which ranged from two livestock units/100 ha on nonshrub encroached sites to six livestock units/100 ha on heavily encroached sites (1 livestock unit = 420 kg body mass; Dean & McDonald 1994). Study sites were preselected to represent a gradient of shrub cover ranging from low cover (<5%) to high cover (>25%) by visual detection of shrub patches on a 2001 IKONOS satellite image (spatial resolution: 1 pixel = 1 m × 1 m, panchromatic). Detected shrub patches were measured using the Spatial Analyst extension of ArcView 3.2 (ESRI, Redlands, CA, USA) to determine shrub cover. Minimum distance between study sites was 2.8 km and maximum distance was 40 km. There was no relationship between shrub cover of the sites and their geographical position. Soil type of each study site was typical for the Kalahari duneveld in this rangeland area with deep and soft reddish sand (Van Rooyen *et al.*, 1991). Minimum distance of study sites to riverbeds or pans was 3.4 km, where soils differ in colour and hardness. Despite the different grazing impact, all study plots are typical for the Kalahari Thornveld. Mean annual rainfall is 174 mm, occurring predominantly from January to April

(Van Rooyen *et al.*, 1991). Extreme temperatures range from winter lows of  $-10.3^{\circ}\text{C}$  to summer highs of up to  $45.4^{\circ}\text{C}$  (Van Rooyen *et al.*, 1991).

#### Rodent surveys

We measured the relative abundance of rodents on three randomly selected trapping grids ( $40 \times 100$  m) per study site. We used the 'random number' generator in MS Excel to generate the Global Positioning System-position for the south-western corner of each sample plot. From this random point, we selected the next position in a northward direction, subsequently eastwards and finally southwards. Minimum distance between trapping grids within sites was 473 m and maximum distance 1384 m. Each study site was sampled from March to May (during the rainy season) and from August to October (during the dry season) in 2001 and 2002 (four sampling periods  $\times$  sixteen study sites  $\times$  three grids). Forty Sherman live traps were set up 10 m apart within a grid. Traps were inspected on three consecutive days at sunrise, noon and sunset and rebaited daily with a mixture of peanut butter and oats. Trapped rodents were identified to species level, marked with a fur cut and released immediately. For each sampling period and study site, abundance was estimated for each species according to the Schnabel-Schuhmacher method and calculated with the program Ecological Methodology, Mark-Recapture (Krebs, 1999).

#### Vegetation surveys

For each study site, we mapped vegetation cover on each of the three rodent trapping grids ( $40 \times 100$  m) and additionally on five randomly selected 1-ha sample plots ( $100 \times 100$  m) according to the random selection of rodent trapping grids. Overall, vegetation surveys totalled 128 sample plots among all study sites (sixteen sites  $\times$  eight plots). Vegetation was classified according to three vegetation categories: (i) grasses, (ii) herbs and (iii) shrubs. Shrub cover was determined by mapping all shrubs within this area. Shrubs were identified to species level and circumferences of individuals recorded to calculate the proportion of shrub cover per plot. At each plot, grass and herb cover was determined on six random subplots ( $5 \times 5$  m). On each subplot, the area covered by herbs and annual and perennial grass tussocks was measured with a tape measure. Afterwards, the proportion of grass- and herb cover was extrapolated to the 1-ha scale.

#### Statistical analysis

Data on vegetation cover, abundance and species richness of rodents were pooled as mean values over the four sampling periods, because we were interested in the long-term effects of shrub cover. By pooling the data, we explicitly excluded inter- and intra-annual effects. First, relationships of shrub cover with rodent abundance and with species richness were analysed by regression models with linear ( $y = b_0 + b_1x$ ) and quadratic ( $y = b_0 + b_1x + b_2x^2$ ) fits. Secondly, we used a stepwise polynomial curve fitting to test whether the addition of the quadratic term significantly improved the model (Zar, 1998). In the results we present only the higher degree model, i.e. we favoured the quadratic model over the linear model if the  $P$ -value of the polynomial curve fitting was  $P < 0.05$ . All analyses were performed on SPSS (Version 11.0.1; SPSS Inc., Chicago, IL, 2001).

#### Results

Between 2001 and 2002 we recorded 1222 captures of the diurnal striped mouse (*Rhabdomys punilio*) and four nocturnal species, short-tailed gerbil (*Desmodillus auricularis*), hairy-footed gerbil (*Gerbillurus paeba*), bushveld gerbil (*Tatera leucogaster*) and highveld gerbil (*Tatera brantsii*). Overall, the hairy-footed gerbil dominated the rodent community of most study sites (Table 1).

An increasing proportion of shrub cover affected rodent species differently (Table 1, Fig. 1). The relative abundance of hairy-footed gerbils ( $R^2 = 0.30$ ,  $P = 0.028$ ), short-tailed gerbils ( $R^2 = 0.45$ ,  $P = 0.005$ ) and bushveld gerbils ( $R^2 = 0.31$ ,  $P = 0.025$ ) had a negative relationship with shrub cover (Fig. 1b,d,e). In contrast, we found hump-shaped relationships with shrub cover for the striped mouse ( $R^2 = 0.47$ ,  $P = 0.017$ ) and the highveld gerbil ( $R^2 = 0.410$ ,  $P = 0.034$ ), with maximum number of individuals in areas where shrub cover was between 10% and 15% (Fig. 1a,c).

While rodent species richness decreased with shrub cover ( $R^2 = 0.74$ ,  $P < 0.001$ ), total rodent abundance showed a hump-shaped relationship ( $R^2 = 0.68$ ,  $P < 0.001$ ) with increasing shrub cover (Fig. 1f,g).

#### Discussion

During our 2-year study, we found differences in relative densities, species richness and composition of rodent

**Table 1** Number of individuals caught for five rodent species in sixteen Kalahari rangelands. Number of captures and vegetation cover was pooled as mean values over the four sampling periods and are given as mean  $\pm$  SE

Site no.	Shrub cover (%)	Level of shrub encroachment	Grass cover (%)	Herb cover (%)	<i>Desmodillus auricularis</i>	<i>Gerbillurus paeba</i>	<i>Rhabdomys pumilio</i>	<i>Tatera brantsii</i>	<i>Tatera leucogaster</i>	Total captures
1	5 $\pm$ 1	Low	51 $\pm$ 6	–	3.0 $\pm$ 0.4	18.0 $\pm$ 2.8	6.0 $\pm$ 1.3	9.0 $\pm$ 1.9	4.0 $\pm$ 1.5	40.0 $\pm$ 5.1
2	7 $\pm$ 2		44 $\pm$ 2	3 $\pm$ 1	1.5 $\pm$ 0.7	14.5 $\pm$ 2.4	7.0 $\pm$ 1.2	8.5 $\pm$ 1.7	4.0 $\pm$ 1.2	35.5 $\pm$ 2.5
3	7 $\pm$ 1		38 $\pm$ 3	3 $\pm$ 1	5.5 $\pm$ 1.3	22.5 $\pm$ 1.9	3.0 $\pm$ 0.4	3.0 $\pm$ 0.4	1.5 $\pm$ 0.9	35.5 $\pm$ 5.1
4	8 $\pm$ 1	Intermediate	33 $\pm$ 5	5 $\pm$ 1	6.0 $\pm$ 0.9	13.5 $\pm$ 1.5	6.0 $\pm$ 1.3	–	4.5 $\pm$ 0.9	30.0 $\pm$ 4.3
5	8 $\pm$ 2		33 $\pm$ 5	5 $\pm$ 1	3.0 $\pm$ 0.4	22.5 $\pm$ 3.0	7.5 $\pm$ 1.6	7.5 $\pm$ 0.7	–	40.5 $\pm$ 5.1
6	9 $\pm$ 2		31 $\pm$ 2	4 $\pm$ 1	1.5 $\pm$ 0.6	31.5 $\pm$ 1.5	6.0 $\pm$ 1.3	3.0 $\pm$ 1.3	–	42.0 $\pm$ 4.4
7	10 $\pm$ 2		31 $\pm$ 6	1 $\pm$ 1	1.5 $\pm$ 0.4	33.0 $\pm$ 2.0	19.5 $\pm$ 2.3	9.0 $\pm$ 1.9	–	63.0 $\pm$ 5.9
8	11 $\pm$ 3		28 $\pm$ 2	1 $\pm$ 1	–	39.0 $\pm$ 4.8	16.5 $\pm$ 2.0	6.0 $\pm$ 0.9	–	61.5 $\pm$ 5.6
9	13 $\pm$ 1		21 $\pm$ 4	2 $\pm$ 1	–	7.5 $\pm$ 1.6	25.5 $\pm$ 3.4	15.0 $\pm$ 2.4	–	48.0 $\pm$ 5.0
10	15 $\pm$ 2	High	20 $\pm$ 3	1 $\pm$ 1	–	9.0 $\pm$ 1.9	16.5 $\pm$ 2.9	13.5 $\pm$ 2.5	–	39.0 $\pm$ 5.2
11	16 $\pm$ 3		19 $\pm$ 4	1 $\pm$ 1	–	12.0 $\pm$ 1.9	13.5 $\pm$ 1.8	9.0 $\pm$ 1.7	–	34.5 $\pm$ 3.5
12	17 $\pm$ 3		19 $\pm$ 4	4 $\pm$ 1	–	16.5 $\pm$ 2.9	9.0 $\pm$ 1.9	7.5 $\pm$ 0.7	–	33.0 $\pm$ 3.8
13	21 $\pm$ 3		6 $\pm$ 3	3 $\pm$ 1	–	18.0 $\pm$ 3.3	3.0 $\pm$ 0.4	3.0 $\pm$ 1.3	–	24.0 $\pm$ 2.3
14	24 $\pm$ 3		5 $\pm$ 2	7 $\pm$ 2	–	10.5 $\pm$ 2.0	6.0 $\pm$ 1.3	–	–	16.5 $\pm$ 3.6
15	26 $\pm$ 4		5 $\pm$ 1	5 $\pm$ 1	–	10.0 $\pm$ 1.9	6.0 $\pm$ 1.3	2.0 $\pm$ 0.9	–	18.0 $\pm$ 3.2
16	26 $\pm$ 4		2 $\pm$ 1	5 $\pm$ 2	–	3.0 $\pm$ 0.4	–	–	–	03.0 $\pm$ 0.4

communities across southern Kalahari rangelands. Although the species composition was typical for this area (Nel, 1978), our results demonstrate the significant impact of shrub encroachment on rodent communities (Fig. 1).

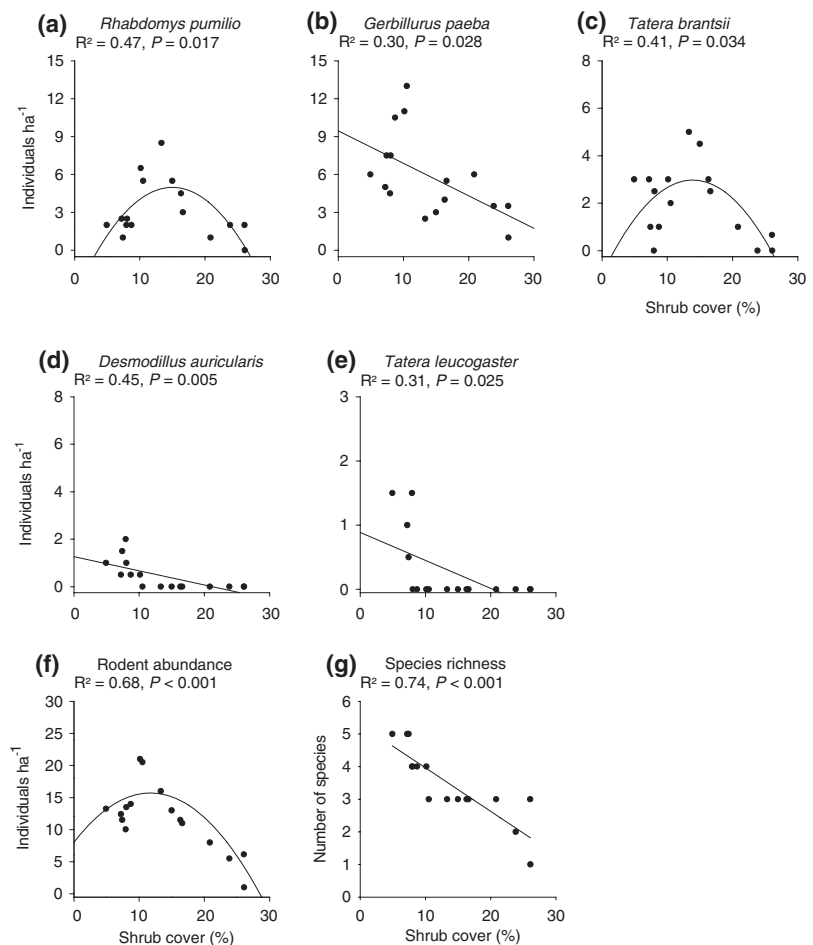
We expected rodent abundance to be determined by two opposing effects of shrubs. First (positive effects), dense shrubs offer, e.g. effective shelter against mammalian carnivores and birds of prey (e.g. Wecker, 1963; Morse, 1980; Parmenter & Macmahon, 1983) and should increase rodent abundance. Secondly (negative effects), increasing shrub cover reduces food availability (leaves, seeds and arthropods) for ground dwelling rodents (Seymour & Dean, 1999; Blaum, 2004) and should therefore reduce their abundance.

Our results show that an increase of shrub cover affected hairy-footed gerbil, short-tailed gerbil and bushveld gerbil negatively (Fig. 1b,d,e). As suggested by the resource availability hypothesis, our results indicate that the abundance of these species was mainly determined by food availability. Indeed, shrub encroachment reduces grass and herbaceous vegetation cover (Table 1) and arthropod abundance (Seymour & Dean 1999; Blaum, 2004), which is the preferred diet of hairy-footed gerbil, short-tailed gerbil and bushveld gerbil (Skinner & Chimimba, 2005). These three rodent species did not either profit by an increase of protective shrubs, or are not using shrubs as habitat structures. This is supported by their preference for

open habitats with low shrub cover (Skinner & Chimimba, 2005). In contrast, the abundance of the striped mouse and highveld gerbil increased up to a species-specific threshold in shrub cover of 10–15% (Fig. 1a,c). This can be explained by the microhabitat selection hypothesis. The striped mouse preferably uses shrubs for den sites and favours foraging under vegetation cover rather than in the open (Skinner & Chimimba, 2005). However, the impact of food availability on rodent abundance becomes more important in rangelands exceeding 15% shrub cover as the abundance of striped mouse and highveld gerbil decrease significantly.

Both, microhabitat selection hypothesis and resource availability hypothesis could partly explain variation in rodent abundance. The hump-shaped relationships between shrub cover and abundance of striped mouse and highveld gerbil clearly showed the trade-off between resource availability of food and microhabitat structures, i.e. predation cover. Our results support the resource availability hypothesis and highlight the great importance of shrubs as habitat structures for the resource availability of both food and microhabitat structures. Thus, we suggest combining these two hypotheses by classifying the amount of shrubs in a given rangeland as resource availability of microhabitat structures.

Although rodents generally depend on vegetation structures (e.g. Torre & Diaz, 2004), only few studies have



**Fig 1** The effects of shrub encroachment on rodent abundance and species richness in sixteen southern Kalahari rangelands

demonstrated that shrubby vegetation structures offer important resources and functions for animals such as nesting sites or protection against avian predators, so as to sustain species diversity in arid and semi-arid ecosystems (Thompson, 1982; Parmenter & Macmahon, 1983; Eccard, Meyer & Sundell, 2004; Blaum *et al.*, 2007). However, our results show that rodent abundance and species richness were lowest in rangelands where shrub cover exceeded 15% cover. A loss of rodents in response to shrub encroachment may have knock on effects, affecting for example the population dynamics of small mammalian carnivores (Crooks & Soule, 1999; Sinclair, Mduma & Brashares, 2003), eventually generating trophic cascades that involve rodents, carnivores and plants (Gutiérrez *et al.*, 1997; Norrdahl *et al.*, 2002). Thus, our results support the hypothesis that long-term heavy grazing which results in area wide shrub encroachment threatens the diversity of

arid environments (Scholes & Walker, 1993; Meik *et al.*, 2002; Tews *et al.*, 2004).

Understanding the relationship between species abundance at different trophic levels and shrub encroachment in arid and semi-arid rangelands is a crucial prerequisite to develop management strategies for land use practices that sustain both species diversity and the land user's profit.

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