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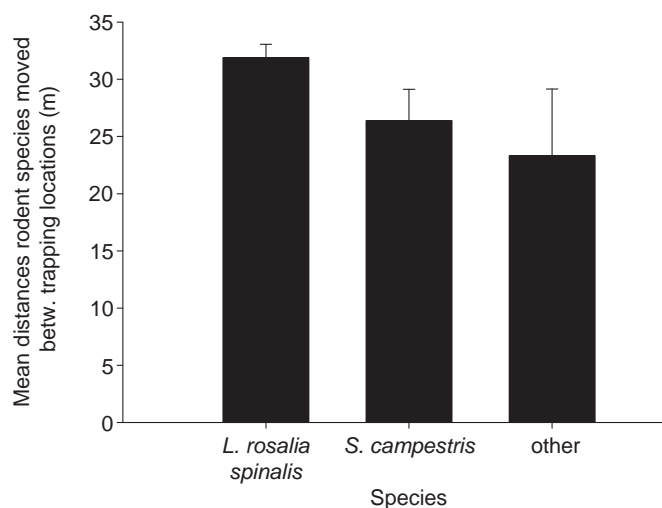
Fig 1 Mean distances rodent species moved between trapping locations over all trapping periods (± SE, n = 3). Distances species moved were not significantly different ($F_{3,42}$ = 2.11, P = 0.098).
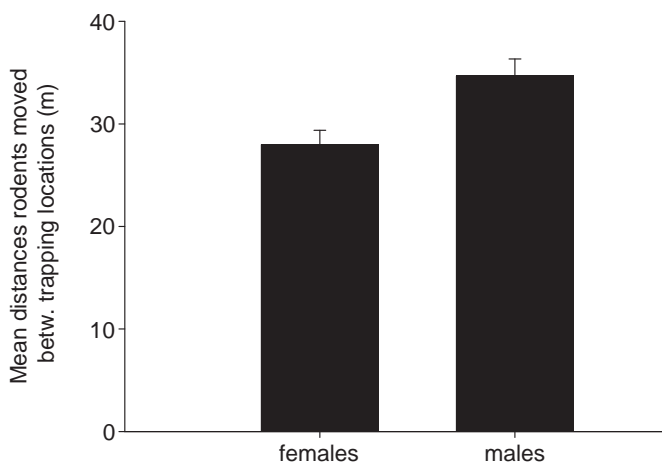

Fig 2 Mean distances female and male rodents moved between trapping locations over all trapping periods (± SE, n = 2). Distances moved were significantly different between sex ($F_{1, 38}$ = 9.34, P = 0.002).

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).
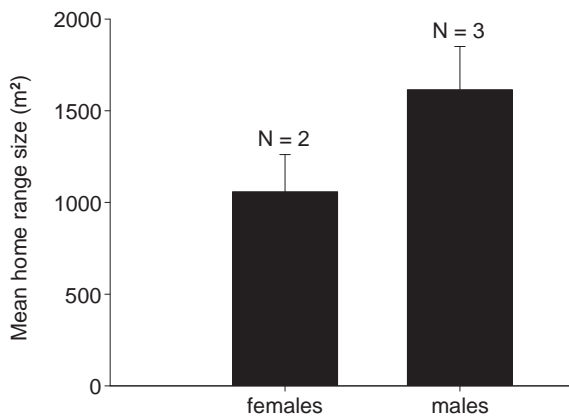
Fig 3 Mean home range sizes of female and male *L. rosalia spinalis* (± SE). Home range sizes were not significantly different between sexes ($F_{1,3} = 2.69$, $P = 0.20$).
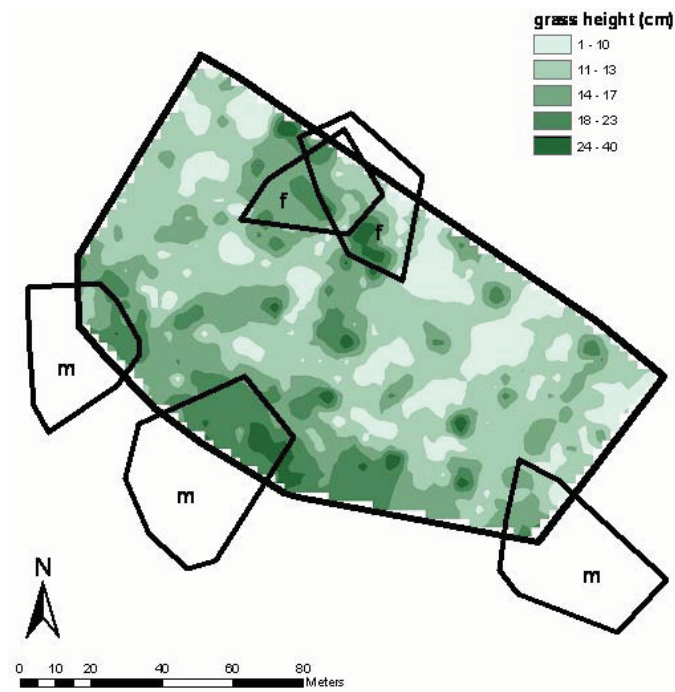
Fig 4 Distribution of female (f) and male (m) home ranges of *L. rosalia spinalis* within the trapping grid.

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).
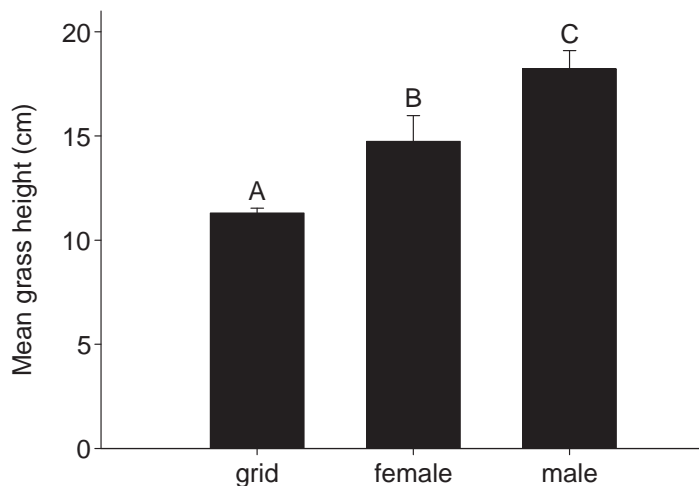
Table 1 Frequency of occurrence of dominant grass species in the trapping grid and in female and male home ranges of *L. rosalia spinalis*. The grass species composition was significantly different between the trapping grid and the home ranges of both sexes (n = 510, X^2_{20} = 83.10, P < 0.000). Quality 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
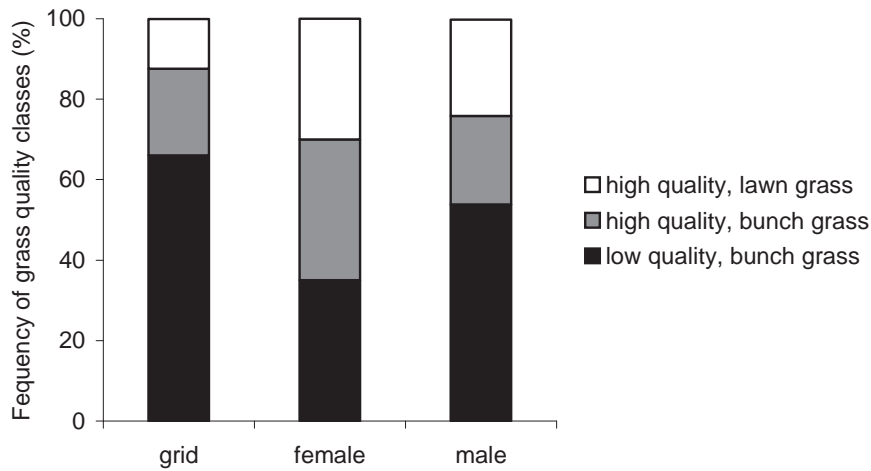
Fig 5 Frequency of occurrence of high and low quality grass species in the trapping grid and in female and male home ranges of *L. rosalia spinalis*. The composition of grass species was significantly different between the trapping grid and the home ranges of both sexes (n = 510, X^2_4 = 26.041, *P* < 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 (WaldI = 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 (WaldI = 0.954, P = 0.329).
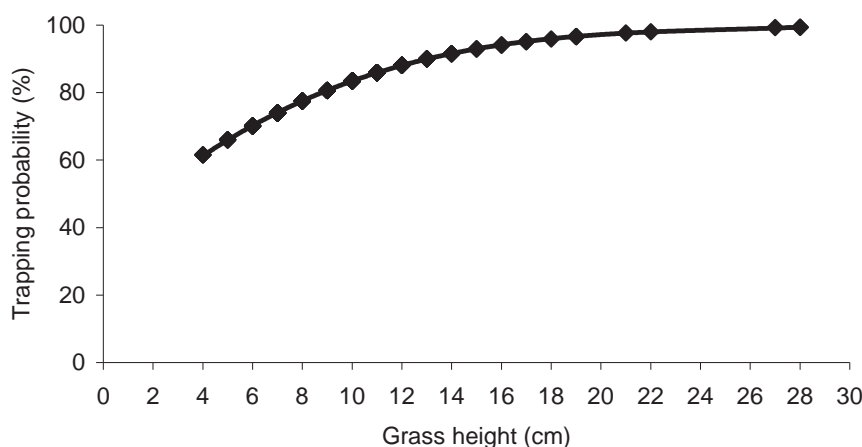
Fig 7 Trapping probability of male rodents in the different grass heights (cm). The trapping probability significantly increased with grass height (Wald = 6.506, P = 0.011).

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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