

Felicity Nonsimiso Simelane, Themb'alilahlwa A.M. Mahlaba, Julie Teresa Shapiro, Duncan MacFadyen and Ara Monadjem*

Habitat associations of small mammals in the foothills of the Drakensberg Mountains, South Africa

DOI 10.1515/mammalia-2016-0130

Received September 5, 2016; accepted March 1, 2017; previously published online June 13, 2017

Abstract: Mountains provide important habitats for many species and often have high levels of biodiversity and endemism. Habitat associations of terrestrial small mammals were investigated at Wakefield Farm at the foothills of the Drakensberg Mountains, South Africa from July 2015 to January 2016. Sherman live traps were used to capture small mammals on 35 grids in six different habitats. A total of 472 individuals, from 14 species, were recorded, comprising: 10 rodents, three shrews and one golden mole. Species diversity differed across habitats and seasons. The riparian habitat had the highest species richness, diversity and abundance of small mammals. Species composition also differed across habitats with the indigenous forest and rocky outcrops supporting the most distinct assemblages.

Keywords: Drakensberg; habitat association; small mammals.

Introduction

Mountain ranges are important for harboring diverse and endemic components of biodiversity (Kok et al. 2012) and

for the ecosystem services that they provide (Briner et al. 2013). This is true of the Drakensberg Mountains in South Africa, which exhibit high endemism of both plants and animals (Clark et al. 2009, 2011). However, this region has received only sporadic attention from small mammal biologists (Taylor 1998, Kok et al. 2012).

A total of nine species of terrestrial small mammals have been recorded from the Drakensberg range within the KwaZulu-Natal province of South Africa (Rowe-Rowe and Lowry 1982, Rowe-Rowe and Meester 1982, Bowland and Perrin 1993). A recent study from the Sneeuwberg range, to the south of the Drakensberg range but on the same South African escarpment, recorded 12 species of terrestrial small mammals (Kok et al. 2012). The Soutpansberg Mountains, representing the northern end of the South African escarpment, also reported 12 species of small mammals (Taylor et al. 2015). The Sneeuwberg study highlighted the importance of the mountain ranges along the South African escarpment and urged further research into the small mammal communities in this region (Kok et al. 2012).

Small mammals, including those of the Drakensberg Mountains, vary in their habitat requirements and the specificity of these requirements in turn affects their distribution (Haim and Tchernov 1974, Geier and Best 1980, Gebresilassie et al. 2004). Suitable habitats provide small mammals with food and shelter, and reduce the risks of predation (Kerley et al. 1990, Monadjem 1997, Monadjem and Perrin 1998, Torre 2004, Symes et al. 2013). Vegetation cover is a particularly important component of habitat because it reduces the perceived predation risk of small mammals (Monadjem 1997, Abu Baker and Brown 2010, Long et al. 2012). This is because vegetation cover reduces the probability of small mammals being detected and preyed on by aerial and ambush predators, creating a “landscape of fear” through which they move (Shrader et al. 2008, Banasiak and Shrader 2016). Therefore, vegetation cover influences small mammal movements and use of microhabitats.

Hence it is not surprising that previous studies have shown that small mammal communities respond to vegetation cover. For example, a positive relationship between

*Corresponding author: Ara Monadjem, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland; and Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa, e-mail: ara@uniswa.sz

Felicity Nonsimiso Simelane and Themb'alilahlwa A.M. Mahlaba: Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland

Julie Teresa Shapiro: School of Natural Resources and Environment, University of Florida, 103 Black Hall, Gainesville, FL 32611, USA; and Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA

Duncan MacFadyen: Department Research and Conservation, E Oppenheimer & Son, P.O. Box 61631, Marshalltown, Johannesburg 2107, South Africa

vegetation cover and small mammal species richness has been reported in southern Africa (Monadjem 1997, Yarnell et al. 2007). Furthermore, Banasiak and Shrader (2016) experimentally demonstrated that small mammals increased their foraging effort in locations with high vegetation cover, presumably because such sites were perceived to be safe. As a result, vegetation cover is considered an important factor which influences small mammal distribution, abundance and species richness (Monadjem 1997, Monadjem and Perrin 2003, Ylonen and Brown 2007, Banasiak and Shrader 2016). Hence, the objectives of this study were to: (i) compare species richness, abundance and diversity of small mammals in different habitats at the foothills of the Drakensberg Mountains and (ii) determine the relationship between vegetation cover and small mammal species composition.

Materials and methods

Study area

This study was conducted at Wakefield Farm (29°48' E; 29°89' S) between July 2015 and January 2016. Wakefield

Farm is a cattle farm located in the Umngeni Municipality, KwaZulu-Natal, South Africa (Figure 1). This area is bordered by the escarpment of the Drakensberg Mountains to the west and the Umngeni River to the east. Wakefield is predominantly an open grassland with the most common grass species being *Panicum natalense*. The grasslands extend from about 1370 m to 1780 m above sea level. There are numerous water sources on the farm with the largest river being the Umngeni River. The study area also contains indigenous forest and alien forest, the latter with planted black wattle, eucalyptus and pine trees.

Wakefield Farm is holistically managed. Holistic management is a grazing system meant to mimic the movements of wild ungulates by bringing livestock into one cohesive herd, confining a herd to a specific area for a period and moving the herd across the landscape, rather than allowing the cattle to scatter (Savory Institute 2014). In this way, livestock utilize the grazing area equally, instead of overgrazing the more desirable plants in preferred areas (Teague et al. 2013).

Wakefield has two seasons: wet (November–March) and dry (April–September). January and July were the warmest and coldest months during this study, respectively. Midday average temperatures were 25.2°C in January and 18.8°C in July.

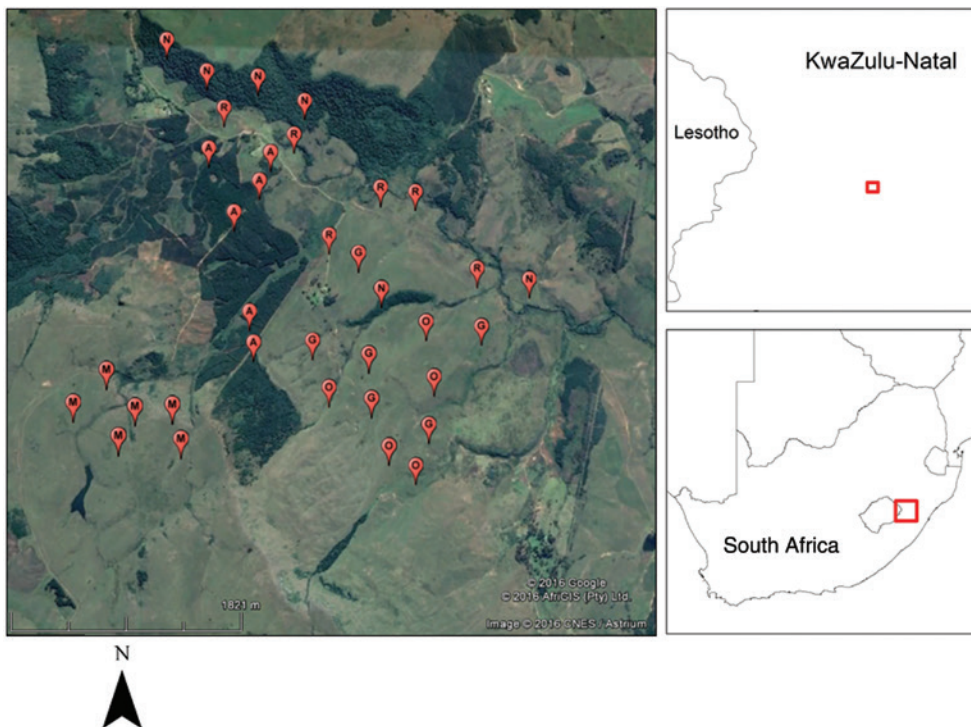


Figure 1: The six habitats sampled at Wakefield, KwaZulu-Natal, South Africa for terrestrial small mammals. Legend for habitats as follows: R, riparian; G, grassland; O, rocky outcrops; A, alien forest; N, indigenous forest; M, mountain top.

The mean annual rainfall at Wakefield typically ranges from 550 mm to 760 mm. Most of the rainfall is received during the wet season, beginning in November, with the highest monthly rainfall in January (139 mm) and the lowest monthly rainfall in June (4 mm). During the period 2015–2016 when the study was conducted, there was a drought and the rains did not start until January 2016.

Trapping

A total of 35 grids was established in the following six habitats: (1) riparian, (2) grassland, (3) rocky outcrops, (4) alien forest, (5) indigenous forest and (6) mountain top (plateau) grassland (Table 1, Figure 1). To ensure independence among sampling sites, grids were placed at least 300 m apart. Six replicate grids were set up in each habitat except for the rocky outcrops which was replicated five times due to the limited extent of this habitat. Sampling commenced during the dry season (from early July to early October) and the grids were sampled again during the wet season (from late November to late January). Each of the 35 grids was sampled once per season.

All the grids were grazed by cattle during the study and some of the grids were burnt by a run-away fire in June. Burnt grids included all those on the mountain top, two grids in the grassland and one grid in the rocky outcrops. No other grids were burnt.

Small mammal trapping

On each grid, 49 trapping stations, set 10 m apart, were laid out in a 7×7 design. Each trapping station consisted of a single Sherman live trap (7.6×9.5×30.5 cm, H.B. Sherman Live Traps Inc, Tallahassee, FL, USA) placed flat on the ground and covered with plant material to protect captured animals from extreme weather conditions. Cotton wool was placed inside each trap to protect

small mammals from the cold. Traps were baited with a mixture of oats, peanut butter and raisins. Traps were set for four consecutive nights and checked daily at dawn and rebaited in the afternoon.

Captured small mammals were identified to species, aged, sexed, measured and their reproductive condition was determined (Kunz et al. 1996, Monadjem et al. 2015). The following standard measurements were taken: body mass, head and body length, tail length and hindfoot length. The fur on the left rump of newly captured individuals was cut using a pair of scissors for the identification of recaptures.

Vegetation sampling

Vegetation structure was assessed on the 35 grids once in each of the two seasons. The following vegetation parameters were estimated or measured on 21 1 m×1 m quadrats within each grid: percentage vegetation cover, biomass, rock cover, leaf litter, woody stems and tree cover. Tree cover was determined by estimating the distance from the quadrat to the nearest tree in the four cardinal directions. The average grass height and the dominant species of grass were also recorded. A disk pasture meter was used to measure plant biomass. For each vegetation parameter on each grid, the measurements for the 21 replicates were averaged and these averages used as variables in the models described under “Data analysis”.

Data analysis

The total number of individuals captured in each grid was used as an index of abundance since small mammals were captured too infrequently for the use of mark-recapture analysis (Williams et al. 2002). Species richness was taken as the total number of small mammal species recorded, whereas species diversity was calculated using the Shannon diversity index (H') (Krebs 1989). Trap success

Table 1: Table comparing the six habitats sampled for small mammals during the study at Wakefield, KwaZulu-Natal, South Africa.

Habitat	Altitude (m)	Slope	Dominant grass species
Riparian	1373–1425	Almost flat	<i>Eragrostis curvula</i>
Grassland	1419–1449	Gentle slope	<i>Panicum natalense</i> <i>Arastida junciformis</i>
Rocky outcrops	1455–1502	Very steep	<i>Panicum natalense</i>
Alien forest	1445–1571	Fairly steep	<i>Eragrostis curvula</i>
Natural forest	1427–1478	Extremely steep	<i>Loudetia simplex</i>
Mountain top	1745–1781	Very steep	<i>Panicum ecklonii</i>

was calculated as the number of small mammals captured per 100 trap-nights where one trap-night describes a single trap set for a 24-h period.

Normality of the data was tested using the Shapiro-Wilk's W-test (Krebs 1989). Non-normally distributed data were square-root transformed. A one-way analysis of variance (ANOVA) was used to test for differences in vegetation parameters between the six habitats and across seasons (Zar 1984). ANOVA was also used to test whether abundance, diversity and species richness of small mammals differed between the six habitats and across seasons. The Tukey's pair-wise comparison (Ott and Longnecker 2010) was performed for groups with significant differences. All statistical tests were performed in the program R (R Core Team 2013).

To understand variation in small mammal species composition and patterns of dissimilarities between habitats and seasons, multi-dimensional scaling (MDS) and analysis of similarity (ANOSIM) were performed using the program PRIMER (Clarke and Gorley 2001). PRIMER's BIOENV procedure was also used to determine whether there was a correlation between small mammal communities and vegetation structure (Clarke and Ainsworth 1993).

Results

Vegetation structure differed significantly between the six sampled habitats ($F = 7.82$, $df = 5$, $p = 0.00032$) (Figure 2). The riparian habitat had the highest vegetation cover whereas the rocky outcrops had the lowest. The plant biomass was also highest in the riparian habitat, but did not differ between the remaining habitats. Rock cover was highest in the rocky outcrops and the mountain top. Leaf litter and woody stem cover were highest in the alien and indigenous forests, and these two forests had the highest tree cover. Seasonal fluctuations were observed in vegetation cover ($t = 2.9999$, $df = 1464.23$, $p = 0.00275$) and woody stem cover ($t = -2.7056$, $df = 1455.38$, $p = 0.00690$). However, leaf litter ($t = 0.06018$, $df = 1466.66$, $p = 0.54740$) and plant biomass ($t = -0.0716$, $df = 1466.08$, $p = 0.94290$) did not differ significantly between the seasons.

A total of 14 small mammal species was recorded which included 10 species of Rodentia (rodents), three Soricomorpha (shrews) and a single Afrosoricida (golden mole). Out of the 472 small mammals trapped, 342 were rodents, 129 were shrews and one was a golden mole (Table 2). The number of small mammals captured during the study varied greatly between the different species (Table 2). *Rhodomys chaka* (Wroughton, 1905) was the most abundantly trapped species contributing almost a

quarter of all captured individuals, followed by *Mastomys natalensis* (Smith, 1834) with just under a fifth of the captures. *Myosorex cafer* (Sundevall, 1846), *Mus minutoides* (Smith, 1834) and *Myosorex varius* (Smuts, 1832) contributed between 18% and 9% of captures, respectively. The remaining species contributed less than 18% of the captures. The golden mole *Amblysomus septentrionalis* (Roberts, 1913), shrew *Crocidura flavescens* (L. Geoffroy, 1827) and rodent *Gerbilliscus leucogaster* (Peters, 1852) were each captured once. There was no significant difference in the trap success between the habitats sampled ($\chi^2 = 9.9268$, $df = 5$, $p = 0.07734$) or between the dry and wet seasons ($\chi^2 = 2.7361$, $df = 5$, $p = 0.74060$).

Mastomys natalensis, *Rhodomys chaka*, *Mus minutoides* and *Myosorex varius* were recorded in most habitats, although numbers varied between habitats (Table 2). In contrast, the following species were restricted to single habitats: *Graphiurus murinus* (Desmerest, 1822), *Grammomys dolichurus* (Smuts, 1832) and *Myosorex cafer* in indigenous forest; *Crocidura flavescens* in rocky outcrops; and *Gerbilliscus leucogaster* in riparian habitat. The threatened *Mystromys albicaudatus* (A. Smith, 1834) was only recorded in rocky outcrops and on the mountain top (in rocky situations).

The abundance of small mammals differed significantly across the habitats ($F = 7.218$, $df = 5$, $p = 0.00015$) (Table 2). The highest number of small mammals was trapped in the riparian habitat and indigenous forest, with lower numbers trapped in the remaining four habitats. However, small mammal abundance did not differ significantly between seasons ($F = 2.701$, $df = 1$, $p = 0.13000$).

There was no significant difference in the species richness of small mammals across the six habitats ($F = 2.053$, $df = 5$, $p = 0.09950$). A maximum of eight species was captured in the riparian habitat and a minimum of five species in the alien forest (Table 3). Species richness differed significantly between the two seasons ($F = 10$, $df = 1$, $p = 0.01010$). During the dry season, 12 small mammal species were captured yet only nine were captured during the wet season. The following small mammals were captured only during the dry season: *Gerbilliscus leucogaster*, *Crocidura flavescens*, *Dendromus mesomelas* (Brants, 1827), *Dendromus melanotis* (Smith, 1834) and *Grammomys dolichurus*.

The same trend was observed for species diversity, with no significant difference between habitats ($F = 1.016$, $df = 5$, $p = 0.42500$) (Table 3) but differing between the dry and the wet seasons ($F = 6.099$, $df = 1$, $p = 0.03310$). The dry season had higher species diversity (1.42) than the wet season (0.94).

Multi-dimensional scaling showed some differentiation in species composition between the habitats (ANOSIM, $R = 0.404$, $p = 0.01520$), (Figure 3). The stress value of the ordination (0.14) is sufficiently robust to

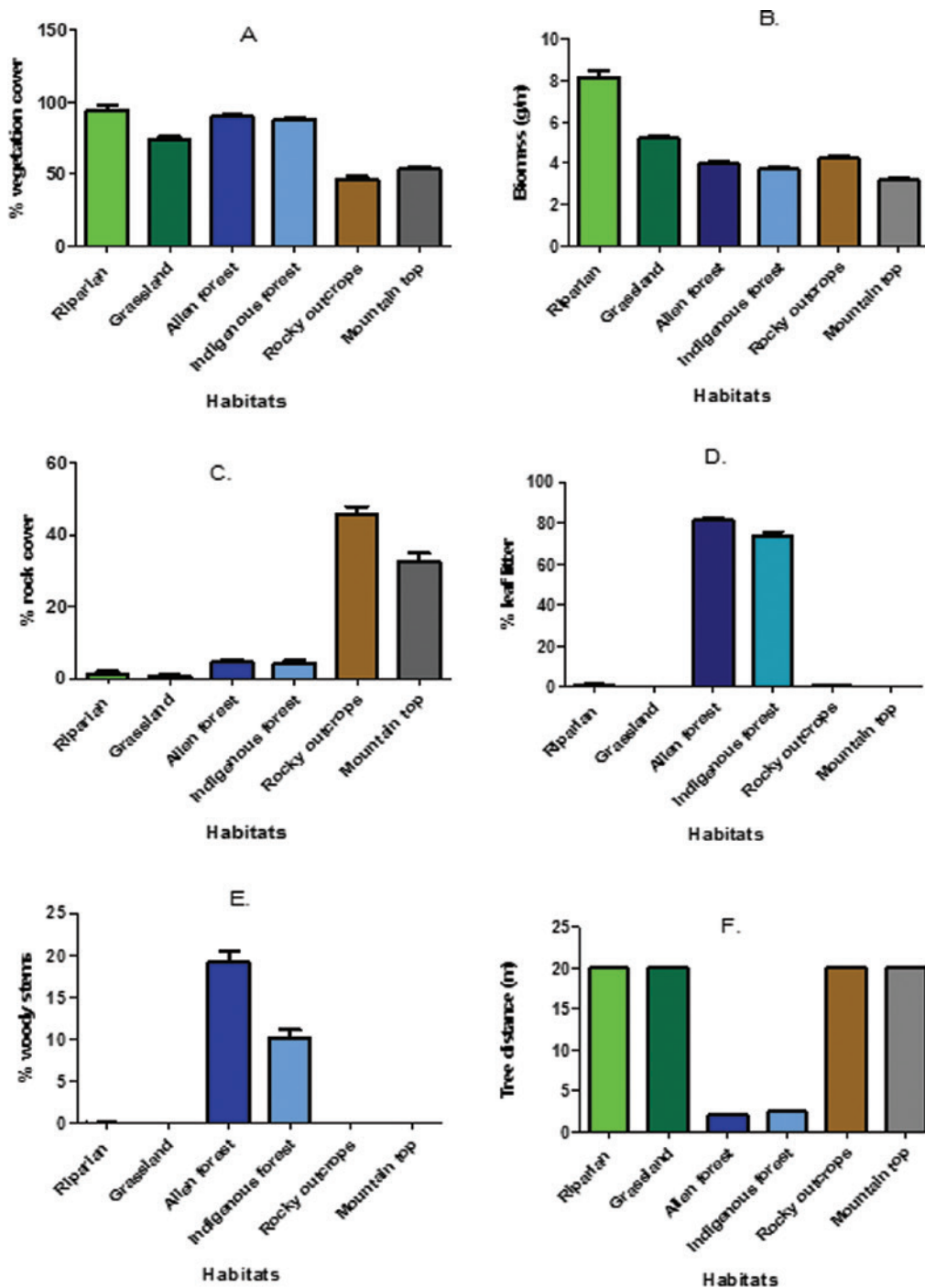


Figure 2: Figure showing the percentage vegetation cover (A), grass biomass (B), rock cover (C), leaf litter (D), woody stems (E), and tree distance (F) in the six grids sampled during the study of terrestrial small mammals at Wakefield, KwaZulu-Natal. Biomass and vegetation cover were high in the riparian habitat while leaf litter, woody stems and tree cover were high in the forest habitats. Rocky outcrops and mountain top had the highest rock cover.

provide confidence in the output (Clarke and Warwick 1994). The grids in indigenous forest were clearly separate from the rest of the sites, as were the grids in rocky outcrops. The grids in the remaining four habitats showed some overlap, indicating less differentiation of species composition between these habitats (Figure 3).

The BIOENV procedure demonstrated a weak relationship between small mammal species composition and vegetation structure. Some vegetation parameters were positively correlated with small mammal composition. Woody stems had the highest correlation coefficient of $\rho_w = 0.183$ followed by leaf litter with a correlation coefficient of

Table 2: Small mammal species captured in the six habitats at Wakefield, KwaZulu-Natal, South Africa.

Species	Rip	GL	RO	AF	IF	MT	Total	Proportion
Golden moles (Afrosoricida)							1	0.21
<i>Amblysomus septentrionalis</i>	1	0	0	0	0	0	1	0.2
Shrews (Soricomorpha)							129	27.3
<i>Crocidura flavescens</i>	0	0	1	0	0	0	1	0.2
<i>Myosorex cafer</i>	0	0	0	0	85	0	85	18.2
<i>Myosorex varius</i>	24	12	3	3	0	1	43	8.9
Rodents (Rodentia)							342	72.5
<i>Dendromus melanotis</i>	0	8	1	0	0	7	16	3.4
<i>Dendromus mesomelas</i>	1	0	0	6	1	1	9	2.1
<i>Gerbilliscus leucogaster</i>	1	0	0	0	0	0	1	0.2
<i>Grammomys dolichurus</i>	0	0	0	0	15	0	15	3.2
<i>Graphiurus murinus</i>	0	0	0	0	4	0	4	0.8
<i>Mastomys natalensis</i>	37	5	1	10	9	26	88	18.6
<i>Mus minutoides</i>	45	5	0	10	1	8	69	14.6
<i>Mystromys albicaudatus</i>	0	0	11	0	0	3	14	3.0
<i>Otomys auratus</i> (Wroughton, 1906)	17	1	0	0	3	0	21	4.5
<i>Rhodomys chaka</i>	58	19	10	6	0	12	105	22.2
Totals	184	50	27	35	118	58	472	100

Rip, riparian; GL, grassland; RO, rocky outcrops; AF, alien forest; IF, indigenous forest; MT, mountain top.

Table 3: Community indices of small mammals captured at Wakefield within the different habitats, presented as mean values (±SD).

Parameters	Riparian	Grassland	Rocky outcrops	Alien forest	Indigenous forest	Mountain top
Abundance	185 (±1.58)	49 (±0.81)	27 (±0.93)	31 (±1.05)	118 (±1.55)	58 (±0.58)
Species richness	8 (±1.37)	6 (±0.98)	6 (±1.26)	5 (±2.07)	7 (±1.03)	7 (±1.51)
Species diversity	1.09 (±0.1)	0.96 (±0.13)	0.64 (±0.20)	0.68 (±0.33)	0.67 (±0.25)	1.24 (±0.23)
Trap success	7.78 (±2.20)	2.09 (±1.14)	1.15 (±0.18)	1.53 (±1.44)	5.06 (±4.75)	2.43 (±1.99)

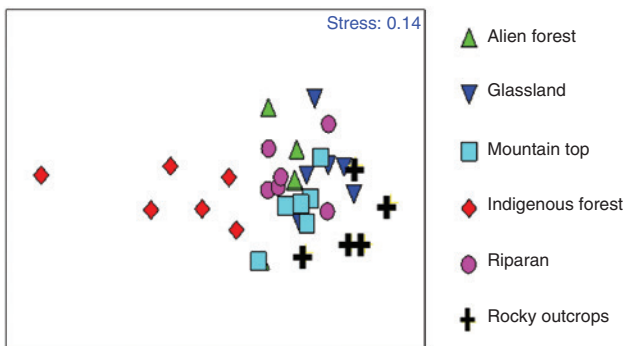


Figure 3: Non-metric multi-dimensional scaling plot of the small mammal species recorded in the six habitats sampled at Wakefield, KwaZulu-Natal, South Africa between July 2015 and January 2016. The axes represent the relative similarities in species composition between the six habitats. The closer the symbols are to each other, the more similar the species composition of those grids.

$\rho_w = 0.181$. Some parameters demonstrated a negative correlation with small mammal community structure. These included the percentage vegetation cover ($\rho_w = -0.077$),

plant biomass ($\rho_w = -0.074$) and rock cover ($\rho_w = -0.130$). Even when the different vegetation parameters were combined, there was only a weak correlation with the structure of the small mammal community. For example, the combination of leaf litter and woody stems provided a correlation coefficient of 0.183 while biomass combined with leaf litter provided a correlation coefficient of 0.114.

Discussion

We observed differences in the abundance and species composition of small mammals across the six habitats. The highest number of small mammals was recorded in riparian habitat, indigenous forest and mountain top, whereas the lowest number was in the rocky outcrops. The riparian habitat and the mountain top also supported the highest species richness and diversity of small mammals. *Rhodomys chaka*, *Mastomys natalensis* and *Mus minutoides* were both the most abundant and the most widely

distributed species during our study. Similarly, a study conducted by Banasiak and Shrader (2016) in Pietermaritzburg, KwaZulu-Natal, South Africa also showed *R. chakae* to be the most abundant species followed by *M. natalensis* and *M. minutoides*.

During this study, 14 small mammal species were recorded, which is slightly higher compared with the 12 species recorded in the Sneeuwberg mountain complex (SMC) of the Drakensberg Mountains, Eastern Cape Province, South Africa (Kok et al. 2012). More than half of the small mammal species captured during this study were also captured in the SMC with *Rhabdomys chakae* being the most abundant species in both studies.

Ecological theory suggests a relationship between habitat structure (in particular vegetation cover) and small mammals (McCarthy 1960), which has been demonstrated in various studies (Monadjem 1997, Gebresilassie et al. 2004, Avenant and Cavallini 2008). In the grasslands of KwaZulu-Natal, Banasiak and Shrader (2016) found that small mammals showed stronger preferences for habitats with greater vegetation cover. However, in our study, we were not able to link any single vegetation parameter that we measured to the composition of the small mammal community, even though we showed that the community differed significantly between the habitats. This suggests that the small mammals in our study were responding either to some other vegetation parameter that we did not measure or to a completely different set of variables such as competition (Symes et al. 2013) or predation (Banasiak and Shrader 2016).

Myosorex cafer was the most abundant insectivorous (shrew) species during the study and was captured only in the indigenous forest. Kirkland (1991) and Badgley and Fox (2000) also observed that insectivores were found in abundance in areas with high environmental moisture compared to areas with low moisture levels. These moist environments are also associated with high abundance of invertebrate prey which serves as prey for the insectivores. The high levels of moisture may therefore explain the high numbers of *M. cafer* in the indigenous forest.

Mystromys albicaudatus is a threatened species in southern Africa (Avenant et al. 2016) and the conservation of this species is important. The major threats to this species are habitat destruction and fragmentation (Coetzee and Monadjem 2008, O'Farrell et al. 2008). Therefore, the presence of *M. albicaudatus* in the Drakensberg Mountains implies that the Drakensberg Mountains provide important habitat that is relevant for the conservation of this species. During our study, the species was captured at relatively high altitudes (between 1450 m and 1750 m above sea level) in rocky situations within

grasslands, suggesting such conditions are important for its conservation (Kok et al. 2012).

Mus minutoides and *Mastomys natalensis* were the most abundant species captured in the burnt grids immediately after fire, as has been reported elsewhere (Kern 1981, Monadjem and Perrin 2003). However, as vegetation recovered, the populations of *M. natalensis* and *M. minutoides* declined. *Dendromus melanotis* showed similar patterns. *Mastomys natalensis* and *M. minutoides* are pioneer species, often closely associated with recently burnt areas (Monadjem 1997, 1999, Caro 2001), and the same may be true for *D. melanotis*.

Fire, as a disturbance, is known to have short-term impacts on small mammal communities by temporarily making the habitat suitable for pioneer species such as *Mastomys natalensis* (Monadjem and Perrin 2003). Due to the unintentional nature of the fire at Wakefield, and the fact that it burnt all the grids on the mountain top, we are unable to assess its role in this environment. Of the six grids in grasslands, two of them burnt. A comparison of species composition between these burnt and unburnt grids indicates that just a single additional species was present in the burnt grids, namely *Dendromus melanotis*. The impact of fire on small mammal communities at the foothills of the Drakensberg Mountains is a fruitful line for future research.

We captured a greater number of individuals and species of rodents than shrews. The fact that we captured a greater species richness of rodents is not surprising since there are more rodent species in this region than shrew species (Taylor 1998). However, the difference in numbers of individuals captured may be related to our trapping method (specifically the use of Sherman traps). Shrews are often overlooked or under-represented in studies where only Sherman traps are used (Nicolas and Colyn 2006, Hurst et al. 2014). However, we did capture 129 individuals (27% of all captured small mammals) of three species of shrews, which suggests that we did sample a relatively good proportion of the shrews at Wakefield. It would be interesting to compare our study with one that uses pitfall traps at Wakefield.

Species abundance, richness and diversity was lowest in the wet season compared to the dry season, mirroring the results of other studies in the region (Fuller and Perrin 2001, Monadjem and Perrin 2003, Muteka et al. 2006, Yarnell et al. 2007, Rautenbach et al. 2013). Furthermore several species (*Grammomys dolichurus*, *Dendromus mesomelas*, *Dendromus melanotis*, *Crocidura flavescens* and *Gerbilliscus leucogaster*) were only trapped in the dry season and not in the wet season demonstrating the importance of sampling in different seasons. We are not sure of the reasons for these seasonal changes, but it may be related to seasonal

fluctuations in rodent populations. Typically, in southern Africa, rodent populations reach a peak in autumn and early winter, and lowest densities in summer (Monadjem and Perrin 2003, Avenant and Cavallini 2008). Hence, we would expect to capture fewer species in summer when population densities are lowest (and fewer animals are available for entering our traps).

The diverse small mammal community and the presence of threatened species in the Drakensberg Mountains demonstrates the importance of this region in conserving this group. We repeat the call of Kok et al. (2012) that this important region requires further attention from mammalogists.

Acknowledgments: Ernest Oppenheimer and Son, Nicky and Strilli Oppenheimer are thanked for providing financial assistance and access to the property. The staff of Wakefield Farm, especially the property manager, Thulani Mnguni, is thanked for assistance in the field and for logistical support. We also thank Phumlile Simelane for assisting with fieldwork. J.T.S. received support from the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138, a National Geographic Young Explorer's Grant, and a grant from The Explorers Club Exploration Fund, Mamont Scholar's Program.

Conflict of interest statement: The authors have no conflicts of interest regarding the publication of this paper.

References

- Abu Baker, M. and T.S. Brown. 2010. Islands of fear: effects of wooded patches on habitat suitability of the striped mouse in a South African grassland. *Funct. Ecol.* 24: 1313–1322.
- Avenant, N. and P. Cavallini. 2008. Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State Province, South Africa. *Integr. Zool.* 238: 1–12.
- Avenant, N., B. Wilson, R.J. Power, G. Palmer and M.F. Child. 2016. A conservation assessment of *Mystromys albicaudatus*. In: (M.F. Child, L. Roxburgh, E. Do Linh San, D. Raimondo and H.T. Davies-Mostert, eds.) *The red list of mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Badgley, C. and D. Fox. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *J. Biogeogr.* 27: 1437–1467.
- Banasiak, N. and A.M. Shrader, 2016. Similarities in perceived predation risk prevent temporal partitioning of food by rodents in an African grassland. *J. Mammal.* 97: 483–489.
- Bowland, J.M. and M.R. Perrin. 1993. Wetlands as reservoirs of small-mammal populations in the Natal Drakensberg. *S. Afr. J. Wildl. Res.* 23: 39–43.
- Briner, S., R. Huber, P. Bebi, C. Elkin, D. R. Schmatz and A. Grêt-Regamey. 2013. Trade-offs between ecosystem services in a mountain region. *Ecol. Soc.* 18: 35.
- Caro, T. 2001. Species richness and abundance of small mammals inside and outside an African national park. *Biol. Conserv.* 98: 251–257.
- Clarke, K.R. and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.* 92: 205–219.
- Clarke, K.R. and R.M. Warwick. 1994. Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar. Biol.* 118: 167–176.
- Clarke, K.R. and R.N. Gorley. 2001. *Primer v5: use manual/tutorial*. Primer-E Ltd., Plymouth, pp. 91.
- Clark, V.R., N.P. Barker and L. Mucina. 2009. The Sneeuberg: a new centre of floristic endemism on the Great Escarpment, South Africa. *S. Afr. J. Bot.* 75: 196–238.
- Clark, V.R., N.P. Barker and L. Mucina. 2011. The great escarpment of southern Africa: a new frontier for biodiversity exploration. *Biodivers. Conserv.* 20: 2543–2561.
- Coetzee, N. and A. Monadjem. 2008. *Mystromys albicaudatus*. The IUCN Red List of Threatened Species: e.T14262A4428195. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T14262A4428195.en>.
- Fuller, J. and M. Perrin. 2001. Habitat assessment of small mammals in the Umvoti Vlei Conservancy, KwaZulu-Natal, South Africa. *S. Afr. J. Wildl. Res.* 31: 1–12.
- Gebresilassie, W., A. Bekele, G. Belay and M. Balakrishnan. 2004. Microhabitat choice and diet of rodents in Maynaguss irrigation field, Northern Ethiopia. *Afr. J. Ecol.* 422: 315–321.
- Geier, A. and L. Best. 1980. Habitat selection by small mammals of riparian communities: Evaluating effects of habitat alterations. *J. Wildl. Manag.* 44: 16–24.
- Haim, A. and E. Tchernov. 1974. The distribution of myomorph rodents in the Sanai Peninsula. *Mammalia* 38: 201–223.
- Hurst, Z., R.A. McCleery, B.A. Collier, N.J. Silvy, P.J. Taylor and A. Monadjem. 2014. Linking changes in small mammal communities to ecosystem functions in an agricultural landscape. *Mamm. Biol.* 79: 17–23.
- Kerley, G., M. Knight and T. Erasmus. 1990. Small mammal microhabitat use and diet in the southern Kalahari. *S. Afr. J. Wildl. Res.* 20: 123–126.
- Kern, N. 1981. The influence of fire on populations of small mammals of the Kruger National Park. *Koedoe* 24: 125–157.
- Kirkland, G. 1991. Competition and coexistence in shrews (Insectivora: Soricidae). In: (J.S. Findley and T.L. Yates, eds.) *The biology of Soricidae*. The Museum of Southwestern Biology, University of New Mexico, Albuquerque. pp. 15–22.
- Kok, A.D., D.M. Parker and N.P. Barker. 2012. Life on high: the diversity of small mammals at high altitude in South Africa. *Biodivers. Conserv.* 21: 2823–2843.
- Krebs, C. 1989. *Ecological methodology*. Harper Collins Publisher, New York.
- Kunz, T., C. Wemmer and V. Hayssen. 1996. *Sex, age and reproductive condition of mammals. Measuring and monitoring biological diversity: standard methods for mammals*. Smithsonian Institution Press, Washington, DC, pp. 279–290.
- Long, A., K. Barley, D. Greese, C. Tye, C. Parr, H. Lepage, K. Gelow, A. Monadjem and R. McCleery. 2012. Multiscale habitat selection

- of *Mus minutoides* in the lowveld of Swaziland. *Afr. J. Ecol.* 51: 493–500.
- McCarthy, E.J. 1960. *Basic marketing: a managerial approach*. R.D. Irwin, Homewood (Illinois).
- Monadjem, A. 1997. Habitat preferences and biomass of small mammals in Swaziland. *Afr. J. Ecol.* 35: 64–72.
- Monadjem, A. 1999. Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae: Rodentia) in a sub-tropical grassland in Swaziland. *Afr. J. Ecol.* 37: 202–210.
- Monadjem, A. and M. Perrin. 1998. The effects of supplementary food on the home range of multimammate mouse, *Matomys natalensis*. *S. Afr. J. Wildl Res.* 28: 1–3.
- Monadjem, A. and M. Perrin. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three- year period. *Afr. Zool.* 38: 127–137.
- Monadjem, A., P. Taylor, C. Denys and F. Cotterill. 2015. *Rodents of sub-Saharan Africa. A biogeographic and taxonomic synthesis*. De Gruyter, Berlin/Boston. pp. 1092.
- Muteka, S., C. Chimimba and N. Bebbett. 2006. Reproductive seasonality in *Aethomys namaquensis* (Rodentia: Muridae) from Southern Africa. *J. Mammal.* 87: 67–74.
- Nicolas, V., and M. Colyn. 2006. Relative efficiency of three types of small mammal traps in an African rainforest. *Belg. J. Zool.* 136: 107–111.
- Ott, L. and M. Longnecker. 2010. *An introduction to statistical methods and data analysis*. Duxbury Press, Pacific Grove, California, USA.
- O'Farrell, P.J., J.S. Donaldson and M.T. Hoffman. 2008. Small mammal diversity on the Bokkeveld escarpment, South Africa – implications for conservation and livestock predation. *Afr. Zool.* 43: 117–124.
- Rautenbach, A., T. Dickerson and M. Schoeman. 2013. Diversity of rodents and shrew assemblages in different vegetation types of savannah biome in South Africa: no evidence for nested subsets or competition. *Afr. J. Ecol.* 15: 17–28.
- Rowe-Rowe, D.T. and P.B. Lowry. 1982. Influence of fire on small-mammal populations in the Natal Drakensberg. *S. Afr. J. Wildl. Res.* 12: 130–139.
- Rowe-Rowe, D.T. and J. Meester. 1982. Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. *S. Afr. J. Zool.* 17: 202–209.
- Savory Institute. 2014. *Holistic Management: Portfolio of Scientific Findings*. http://www.savory_institute_2014_grazing_bibliography.pdf. (June 15, 2016).
- Shrader, A.M., J.S. Brown, G.I.H. Kerley and B.P. Kotler. 2008. Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *J. Arid Environ.* 72: 1811–1819.
- Symes, C.T., J.W. Wilson, S.M. Woodborne, Z.S. Shaikh and M. Scantlebury. 2013. [Resource partitioning of sympatric small mammals in an African forest-grassland vegetation mosaic](#). *Austral. Ecology* 38: 721–729.
- Taylor, P.J. 1998. *The smaller mammals of KwaZulu-Natal*. University of Natal Press, Pietermaritzburg.
- Taylor, P.J., A. Munyai, I. Gaigher and R. Baxter. 2015. Afromontane small mammals do not follow the hump-shaped rule: altitudinal variation in the Soutpansberg Mountains, South Africa. *J. Trop. Ecol.* 31: 37–48.
- Teague, W.R., F. Provenza, U.P. Kreuter, T. Steffens and M. Barnes. 2013. Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience? *J. Env. Man* 141: 310–322.
- Torre, I. 2004. *Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: the role of climate, vegetation structure and predation risk* (PhD Thesis).
- Williams, B.K., J.D. Nichols and M.J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, New York, pp. 817.
- Yarnell, R., D. Scott, C. Chimimba and D. Metcalfe. 2007. Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia* 154: 387–402.
- Ylonen, H. and S. Brown. 2007. Fear and the foraging, breeding and sociality of rodents. In: (J.O. Wolff and P.W. Sherman, eds.) *Rodent societies*. University of Chicago Press, Chicago, IL. pp. 352.
- Zar, J. 1984. *Biostatistical analysis*, 2nd ed. Prentice Hall, London.