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Effects of livestock grazing and habitat characteristics on small mammal communities in the Knersvlakte, South Africa

Britta M. Bösing [a,1], Daniela H. Haarmeyer [a], Jürgen Dengler [a,b,2], Jörg U. Ganzhorn [c], Ute Schmiedel [a,*]

[a] Biodiversity, Evolution and Ecology of Plants (BEE), Biocentre Klein Flottbek and Botanical Garden, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany
[b] Synthesis Centre (sDiv), German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[c] Animal Ecology, Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

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ABSTRACT

We studied the influence of different livestock grazing intensities and habitat types on small mammals in the Knersvlakte, South Africa. The Knersvlakte belongs to the Succulent Karoo Biome, a biodiversity hotspot. We placed a total of 22 plots in areas of two grazing intensities (moderate and intensive) and two major habitat types (quartz fields and loamy soils). On these plots, we carried out small-mammal live trapping (90 traps during four nights) and estimated the cover of different vegetation layers. In total, 140 small mammal individuals from ten species were caught during 7920 trap nights. All species occurred on loamy soils, but only four in quartz fields. The small-mammal community on intensively-grazed plots was a subset of that on moderately-grazed plots. The most abundant species on loamy soils were *Macroscelides proboscideus* and *Rhabdomys pumilio* and in quartz fields *M. proboscideus* and *Gerbillurus paeba*. Generalised linear models revealed that habitat type had the strongest influence on abundance and diversity of small mammals. Vegetation cover mainly had indirect influences, via the habitat type, on abundance, diversity and the body condition of small mammals. Overall, the intensities of livestock grazing showed no effect on abundance and diversity.

1. Introduction

Transformation or destruction of habitats due to unsustainable land use is one of the major threats to biodiversity (Hannah et al., 1994; Sala et al., 2000). Land-use change is perceived as a key driver of future biodiversity loss (Pereira et al., 2010). Particularly arid areas such as the southern African Succulent Karoo Biome, a biodiversity hotspot (Myers et al., 2000), are vulnerable to land degradation. This can have long-lasting negative effects on productivity and diversity, and such degradation may risk becoming irreversible (Milton et al., 1994). Fence-line studies in the western Succulent Karoo (Desmet, 2007) revealed that high grazing intensity alters plant species composition with an increase of annual, geophyte, and unpalatable shrub species, and decrease of perennial, palatable leaf-succulent shrub species, compared to the moderate grazing intensity of recommended stocking rates (Todd and Hoffman, 1999, 2009). These changes in vegetation structure had several knock-on effects on critical ecosystem functions (e.g. providing shelter and food for wild animals), resulting in changes in species composition and richness of invertebrates (Mayer et al., 2006; Seymour and Dean, 1999) and small mammal communities (Blaum et al., 2007; Eccard et al., 2000; Joubert and Ryan, 1999; O'Farrell et al., 2008).

Growing awareness of the high levels of diversity and endemism and unique vegetation structure in Namaqualand prompted the extension of protected areas (Hoffman and Rohde, 2007). Reduction or even the complete exclusion of land-use activities is typically perceived as a necessary step to conserve endangered habitats and their biodiversity (Cowling et al., 1999; but see Hendricks et al., 2005 about the Richtersveld National Park). However, livestock (mainly sheep and goats) have now partly replaced the ecosystem

Abbreviations: ANOVA, analysis of variance; BMI, body-mass index; GLM, generalised linear model; SD, standard deviation; SSU, small stock unit.

* Corresponding author. Tel.: + 49 40 42816548; fax: + 49 40 42816539.
E-mail addresses: boesing@aninut.uni-kiel.de (B.M. Bösing), daniela.haarmeyer@hotmail.com (D.H. Haarmeyer), juergen.dengler@uni-bayreuth.de (J. Dengler), joerg.ganzhorn@uni-hamburg.de (J.U. Ganzhorn), ute.schmiedel@uni-hamburg.de (U. Schmiedel).
[1] Present address: Animal Nutrition and Physiology, Christian-Albrechts University Kiel, Hermann-Rodewald-Str. 9, 24118 Kiel, Germany.
[2] Present address: Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany.

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functions of wild ungulates that originally roamed in the area, for example browsing (Farmer and Milton, 2006) and seed dispersal (Haarmeyer et al., 2010a). Thus, the question arises: what roles do livestock play in the ecosystems of the Knersvlakte? Also, what are the implications for conservation and rangeland management?

One of the largest protected areas in Namaqualand is the Knersvlakte Conservation Area. The Knersvlakte (13,500 km^2) is the southern-most bioregion of the Namaqualand (Desmet, 2007) and is an acknowledged centre of species diversity and endemism (Cowling and Hilton-Taylor, 1994; van Wyk and Smith, 2001), mainly due to phytogeographical patterns (Hilton-Taylor, 1994; Nordenstam, 1969). By contrast, the endemic fauna of the Knersvlakte is not well understood due to the lack of animal distribution data (Kuhlmann, 2009; but see Pitzalis and Bologna, 2010 for some Coleoptera species restricted to the Knersvlakte). A unique feature of the Knersvlakte is its quartz gravel plains, which are inhabited by a specific vegetation of compact leaf-succulents (Schmiedel and Jürgens, 1999). With their extreme edaphic conditions, the quartz fields support many of the endemic plant species of the Knersvlakte. Indeed, recognition of the unique flora and vegetation of this habitat was responsible for the recently establishment of the Knersvlakte Conservation Area, which was included into the study area.

The small mammal communities of South Africa are species-rich and represent a wide array of life history traits with a large number of dietary guilds such as omnivores, insectivores, granivores and herbivores (Skinner and Chimimba, 2005). Small mammals have been shown to play a crucial role within the arid ecosystems of southern Africa. The few studies to date showed that small mammals reduce interspecific competition of plants and positively influence plant diversity (Keller and Schradin, 2008; Kerley, 1992). They contribute to seed dispersal and predation (Kerley, 1992; Kerley et al., 1990) and even act as pollinators for certain plant species (Johnson et al., 2011; Kleizen et al., 2008). Small mammals respond to natural and anthropogenic impacts and, over a larger temporal scale, their community composition can be affected (Hoffmann and Zeller, 2005; Hoffmann et al., 2010). On a smaller temporal scale, changes to habitat suitability are reflected in the animals' body mass or body mass index (Blaum et al., 2007; Eccard et al., 2000; Hoffmann et al., 2010; Kok et al., 2012).

To inform future conservation and rangeland management, we investigated the effects of different intensities of small-stock farming in the Knersvlakte on small mammal species composition, taking into account the quartz fields and surrounding habitats. We addressed the following questions: How do livestock grazing intensity, habitat type, and vegetation cover influence diversity of small mammals? What is the effect on body mass and body mass index (BMI) of two common species from the major dietary guilds (i.e. insectivores and omnivores)? We discuss our findings in the context of two other studies in the same area in which we investigated the impact of different grazing intensities on plants (Haarmeyer et al., 2010c) and endozoochorous seed dispersal by livestock (Haarmeyer et al., 2010a). As studies on small mammals in the Knersvlakte are scarce, our investigation not only addresses the above specific questions, but also contributes to the body of knowledge about small mammal diversity in the area and the natural history of these species.

2. Material and methods

2.1. Knersvlakte

The Knersvlakte is a peneplain, situated in southern Namaqualand, Western Cape Province, South Africa (Fig. 1). It belongs to the units SKk 1–6 (Northern Knersvlakte Vygieveld, Central Knersvlakte Vygieveld, Knersvlakte Quartz Vygieveld, Knersvlakte Shale Vygieveld, Vanrhynsdorp Gannabosveld, Knersvlakte Dolomite Vygieveld) of the Succulent Karoo Biome (Mucina et al., 2006). The natural vegetation is generally dominated by dwarf shrubs of the families Aizoaceae and Asteraceae. During the spring-time growing season, annuals (mainly Asteraceae and Scrophulariaceae) and monocotyledonous geophytes become abundant. On predominantly sandy-loamy soils (further referred to as "loam fields"), fruticose, leaf-succulent growth forms dominate. Within this matrix vegetation, so-called quartz fields occur as a specific habitat type, characterised by gravel-like quartz stones that cover the soil surface (Schmiedel and Jürgens, 1999). The quartz gravel cover on the quartz fields ranges between 80% and 100% and shows abrupt boundaries to the loam fields where quartz gravel cover is absent. These quartz fields have very sparse and low vegetation, consisting of compact leaf-succulents, among them many Knersvlakte endemics (e.g. Haarmeyer et al., 2010c; Schmiedel, 2002; Schmiedel and Jürgens, 1999). Nowadays, indigenous large mammals are relatively rare, while small mammals are common.

The Knersvlakte is a winter-rainfall region (May to September), with a mean annual precipitation of 116 mm. Water supply is occasionally supplemented by fog and dew. Mean temperatures range from 5–10 °C in winter to 30–35 °C in summer (Haarmeyer et al., 2010b; Mucina et al., 2006).

Until the 18th century, the Knersvlakte was inhabited by the indigenous Khoikhoi people, who lived as herders and hunters (Rohde et al., 2007). For the past 200 years, the Knersvlakte has been used for commercial small stock farming (sheep and goats) by farmers of European origin. However, the land has a very low grazing capacity and agricultural potential (Desmet, 2007), with a recommended stocking rate between 8 and 12 ha per small stock unit (ha SSU^{-1}) (pers. comm., Department of Agriculture, Vredendal Office).

2.2. Investigated farms

We selected four farms in the Knersvlakte (Table 1) that have a high frequency of quartz fields and that are subject to different grazing intensities by domestic mammals. These farms are located next to the national road N7, approximately 20–60 km north-west of Vanrhynsdorp and approximately 60–80 km east of the Atlantic Ocean (31° 24′ S, 18° 30′ E, Fig. 1). Two of the farms are classified as moderately grazed (i.e. well below recommended stocking rate) and two as intensively grazed (i.e. at recommended stocking rate) by livestock and other large mammals (Table 1).

2.3. Small mammal live trapping

Trapping was performed in 22 plots of 2.025 ha (135 m × 150 m) size, each within homogenous vegetation (for spatial distribution of plots, see Fig. 1). Ten plots were positioned in quartz fields and 12 in loam fields. In both cases, half of the plots were moderately grazed and the other half intensively grazed. In every plot, 90 Sherman® live traps were placed 15 m apart from each other, arranged in ten lines of nine traps. We alternately put up small traps (15 cm long × 4.5 cm wide × 5 cm high) and large traps (25 cm × 8 cm × 9 cm) in order to catch a wide range of species.

Each trap contained cut straw for thermal insulation and was baited with a mixture of peanut butter and oat flakes plus a small piece of fresh apple to avoid dehydration of the captured animals (Krug, 2002; Patric, 1970).

In each plot, the traps were installed for four consecutive nights. The traps were opened at 6 pm and emptied and closed at 7 am the next morning. By selecting this period, we were able to trap both diurnal and nocturnal species while at the same time reduce mortality risk resulting from dehydration or overheating during the

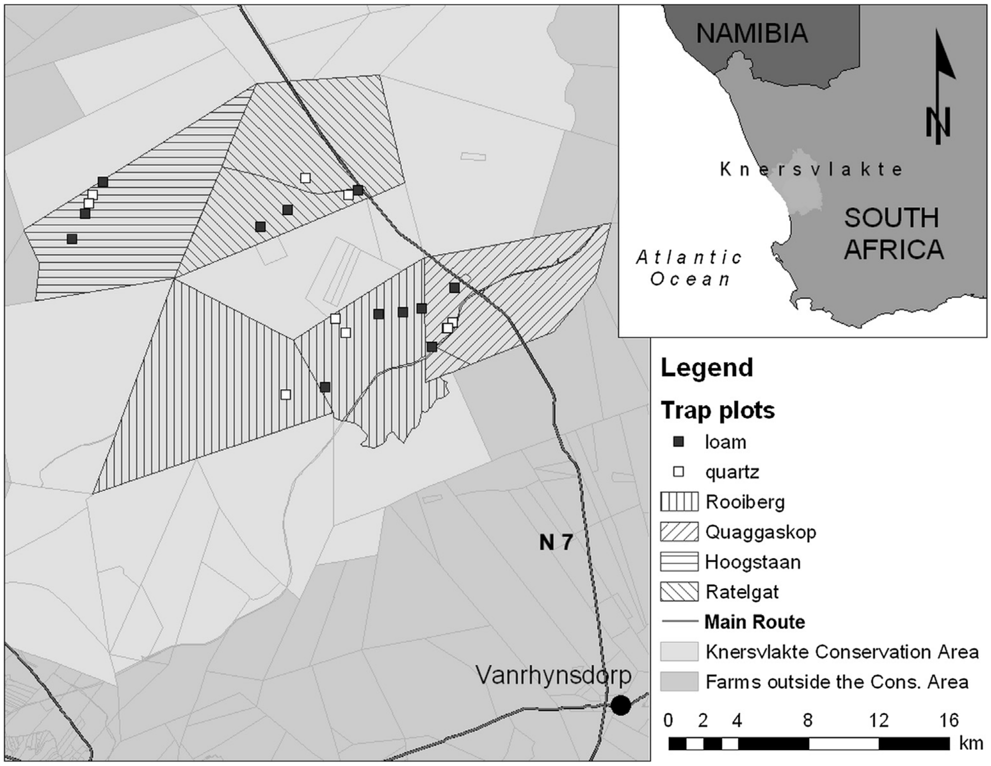

Fig. 1. Location of the Knersvlakte in the western part of South Africa. The Knersvlakte Conservation Area and the investigated farms and trap plots are shown in detail. Different farms are indicated by different textures. For land tenure and land use intensity per farm see Table 1.

day. The total trapping period covered 88 nights from August to November 2007. Straw and bait were removed and replaced after every trapping night to reduce potential odour-induced biases occurring in subsequent sessions (Drickamer, 1995).

For each animal, the following were recorded: sex, body mass (measured with a Pesola spring balance), body length (measured with a ruler) and tarsus length (measured with callipers). To ensure recognition of recaptures, a piece of fur was cut from the neck of the captured animals before release. The physical condition of adult animals (defined as those of body mass > 32 g; definition according to Apps et al., 2000) of two selected species (those with the highest number of individuals) was expressed by a body-mass index (BMI) calculated as body mass [g] divided by tarsus length [mm] (Krug, 2002).

We did not calculate estimates for population size based on mark-recapture methods as sample size is far too small for any meaningful estimate. Calculating population size would suggest information that is not available.

As a measure of vegetation structure, the horizontal vegetation cover surrounding the traps was estimated to the nearest 10% at three different height classes (<15 cm; 15–30 cm; >30 cm) within a 1 m × 1 m square centred on each trap. The cover values of the three layers were summed in order to approximate the total vegetation cover.

2.4. Statistical analyses

All statistical analyses were based on the combined or averaged measures per plot. Species abundances were quantified as total number of individuals captured per species and plot (without recaptures). Trapping success was calculated as the number of captured individuals per 100 trap nights.

To test for differences in the means of parameters between the two habitat types or the two grazing intensities, we used the permutation test (with 100,000 permutations) implemented in the statistical freeware PAST (Hammer et al., 2001). This approach does not require distributional assumptions to be met.

Generalised linear models (GLMs) were calculated to assess the effects of vegetation cover on small mammal abundance and species richness at plot level. As both dependent variables are count data, we specified a quasi-Poisson error distribution (allowing for overdispersion) and log-link function. Simple linear regressions

Table 1
Names and salient characteristics of the investigated farms. Grazing intensity assessments based on Esler et al. (2006).

Farm name	Size (ha)	Grazing intensity	Ownership	Comments
Hoogstaan	6000	Intensive (10 ha/SSU)	Private	Intensive grazing for the past c. 50 years, interrupted by a 10 year-period of light grazing (1982–1992: 26 ha/SSU)
Rooiberg	11,500	Intensive (12 ha/SSU)	State land	Past 20 years: use of only about 7000 ha of the farmland by several informal settlers. 1984–1987: use of the farm for military training causing a high level of degradation.
Ratelgat	7000	Moderate (17 ha/SSU)	Private	Moderate grazing since 2000. Before that, only sporadic use for farming.
Quaggaskop	5000	Moderate (no livestock, only some wildlife)	Private	Studied section (1500 ha) with no grazing by livestock for the past 40 years.

were applied to study the effect of vegetation cover on the performance (weight, BMI) of two selected small mammal species. Both types of regressions were calculated with the program STATISTICA 8.0 (StatSoft, Inc., 2007).

To assess whether certain mammal species are diagnostic for one of the two habitat types or grazing intensities, we applied phi-values in combination with Fisher's exact test. This approach (Chytrý et al., 2002) is now widely used for the determination of diagnostic species in plant communities (e.g. Chytrý, 2007), while we are not aware of a previous application to animal communities. Phi-values, which can take values from −1 to +1, quantify the degree to which a certain species is diagnostic for a community, with negative values indicating avoidance and positive values fidelity. Species with phi-values >0.25 are usually seen as diagnostic for a community (Chytrý, 2007). We applied Fisher's exact test (calculated using an on-line calculator: http://www.langsrud.com/fisher.htm) to check whether detected patterns of concentration or avoidance were statistically significant.

For all statistical analyses, we report means ± standard deviation (SD) and, where appropriate, also ranges or medians. We applied a statistical significance level of $\alpha = 0.05$ throughout.

3. Results

3.1. Habitat features

The mean vegetation cover of the trapping plots was generally lower than 18%. Vegetation cover in all three height classes, as well as the classes combined, was about two times higher on loam than on quartz; in both habitats it decreased in the upper vegetation strata (Table 2). Within the two habitat types, vegetation cover did not differ significantly in relation to grazing intensity.

3.2. Characterisation of the small mammal communities

Overall, ten small mammal species were identified (Tables 3 and 4). One individual escaped prior to determination. During 7920 trap nights (90 traps × 88 nights), 140 small mammal individuals were caught (detailed data are available in Bösing, 2009). This corresponds to a trapping success of 1.77%. The recapture rate was 24% (45 individuals).

All ten species occurred on loam, but only four on quartz (Table 4). The highest total number of individuals was trapped in the loamy, intensively-grazed plots, whereas the highest total species richness occurred in the loamy, moderately-grazed plots. The lowest total numbers both of individuals and species were caught on intensively-grazed quartz plots.

At plot level, mean small mammal abundance was much higher on loam (10.0 ± 13.4 individuals; range 0–41; median 3) than on quartz (2.0 ± 2.8 individuals; range 0–8; median 1), though due to the large variance this difference was non-significant ($p = 0.072$). Mean species richness was higher on loam (2.5 ± 2.2 species) than on quartz (0.9 ± 0.9 species; $p = 0.049$). The effect of grazing intensity was not significant (small mammal abundance under high and moderate grazing intensity: 7.9 ± 13.9 vs. 4.8 ± 6.4; $p = 0.523$, mean species richness 1.4 ± 1.5 vs. 2.2 ± 2.3; $p = 0.392$).

Table 2
Comparison of the mean cover for different vegetation layers (±SD) [%] on the 1-m^2 areas centred on the traps in the two habitat types. Values are means ± standard deviations. The *p*-values for differences are based on permutation tests.

Height class	Loam ($n = 12$)	Quartz ($n = 10$)	p
<15 cm	8.5 ± 3.3	5.4 ± 2.9	0.031
15–30 cm	5.8 ± 1.5	3.2 ± 2.5	0.008
>30 cm	3.1 ± 2.4	1.3 ± 1.0	0.038
All layers	17.4 ± 3.7	9.9 ± 5.9	0.003

Three species were diagnostic for the loam habitat and accordingly avoided quartz areas. However, this pattern was only significant for *Desmodillus auricularis*, which was caught in 42% of the loamy plots but in none of the quartz plots (Table 5). *Desmodillus auricularis* and *Gerbillurus paeba* generally avoided intensively-grazed plots, though this pattern was not significant (Table 4). Considering the combinations of habitat and grazing intensity, moderately-grazed loam plots were most positively characterised (five diagnostic species), while intensively-grazed quartz plots were most negatively characterised (three avoiding species) (not shown). These patterns were only significant, however, in the case of the association of *Desmodillus auriculus* with moderately-grazed loamy sites and the disassociation of *Gerbillurus paeba* with the intensively-grazed quartz patches.

Vegetation cover significantly influenced the number of individuals, but not the species richness. On loam, the vegetation cover of the lowest stratum (<15 cm) had a significant negative effect on species abundance ($b = -0.3$, $p = 0.014$), while that of the highest stratum (>30 cm) significantly increased abundance ($b = 0.43$, $p = 0.001$). On quartz, the vegetation cover had no significant influence on the number of individuals or species richness.

3.3. Detailed study of the two most abundant species

The analyses of individual condition in relation to habitat types were carried out only for the two most abundant species. These are *Macroscelides proboscideus* (round-eared elephant shrew, an insectivore) and *Rhabdomys pumilio* (four-striped grass mouse, an omnivore), representing the two guilds.

3.3.1. Abundance

None of the two species showed a significant preference for quartz or loam fields (*M. proboscideus*: 2.4 ± 4.0, range 0–13 vs. 1.1 ± 2.2, range 0–7 individuals, $p = 0.372$; *R. pumilio*: 3.3 ± 6.8, range 0–22, vs. 0.2 ± 0.4, range 0–1 individuals, $p = 0.189$). They were also no significant preferences for intensively- or moderately-grazed plots (*M. proboscideus*: 2.6 ± 4.1, range 0–13 vs. 1.0 ± 2.1, range 0–7 individuals, $p = 0.245$; *R. pumilio*: 3.2 ± 7.2, range 0–22 vs. 0.6 ± 1.0, range 0–3 individuals, $p = 0.409$).

3.3.2. Physical condition

In the following analyses only adults are considered (>32 g; see Methods). BMI of the two species did not differ significantly between loam and quartz (*M. proboscideus*: 1.26 vs. 1.13, $p = 0.198$; *R. pumilio*: 1.90 vs. 1.79, no test possible since there was only one catch on quartz). For *M. proboscideus*, BMI was higher on moderately grazed than on intensively grazed plots (1.40 vs. 1.16; $p = 0.015$), while grazing intensity had no effect on the BMI of *R. pumilio* (1.91 vs. 1.84; $p = 0.760$). Body mass and BMI did not differ between sexes of *M. proboscideus* ($p = 0.419$ and $p = 0.955$, respectively) nor those of *R. pumilio* ($p = 0.850$ and $p = 0.746$, respectively).

None of the vegetation cover values for the separate height classes had significant effects on either BMI or weight of the two study species in the linear regression analyses (not shown). By contrast, total vegetation cover positively influenced the BMI ($R^2 = 0.14$; $p = 0.017$) and weight ($R^2 = 0.17$, $p = 0.008$) of *M. proboscideus*. For *R. pumilio*, there was a very weak relationship between total vegetation cover and body weight ($R^2 = 0.09$; $p = 0.045$) and no effect on BMI ($R^2 = 0.05$, $p = 0.132$).

Table 3
Taxonomy and life history traits of the 10 trapped species based on published sources. Abbreviations for orders: M = *Macroscelidea*, R = *Rodentia*, E = *Eulipotyphla*. Range of distribution according to the IUCN Red List of Threatened species (IUCN, 2013).

Species	English name	Family	Order	Mean weight	Distribution and habitat	Feeding behaviour	Activity	References
Aethomys namaquensis (A. Smith 1834)	Namaqua rock-rat	Muridae	R	55 g	Southern Africa	Herbivore	Nocturnal	Chimimba et al. (1999)
Crocidura cyanea (Duvernoy 1838)	Reddish-grey musk shrew	Soricidae	E	9 g	Southern Africa	Insectivore	Diurnal and nocturnal	Skinner and Smithers (1990)
Desmodillus auricularis (A. Smith 1834)	Cape short-eared gerbil	Muridae	R	50 g	Southern Africa, south west arid zone, prefers open habitats with grass or karroid bushes as cover	Granivore	Nocturnal	Skinner and Smithers (1990), Downs and Perrin (1994)
Gerbillurus paeba (A. Smith 1836)	Hairy-footed gerbil	Muridae	R	25 g	Southern Africa, arid and semi-arid areas of southern Africa, prefers open habitats with low shrub cover	Omnivore	Nocturnal	White et al. (1997), Skinner and Chimimba (2005)
Macroscelides proboscideus (Shaw 1800)	Round-eared elephant shrew	Macroscelididae	M	31–47 g	Southern Africa	Insectivore	Diurnal and nocturnal	Stuart and Stuart (2000)
Malacothrix typica (A. Smith 1834)	Gerbil mouse	Nesomyidae	R	16 g	Southern Africa	Omnivore	Nocturnal	Skinner and Smithers (1990)
Mus minutoides (A. Smith 1834)	Pygmy mouse	Muridae	R	6–8 g	Southern, Central and Eastern Africa	Omnivore	Nocturnal	Skinner and Smithers (1990)
Myomyscus verreauxii (A. Smith 1834)	Verreaux's mouse	Muridae	R	44 g	Endemic to South Africa (Eastern and Western Cape Province)	Omnivore	Nocturnal	Skinner and Smithers (1990)
Otomys unisulcatus (F. Cuvier 1829)	Karoo bush rat	Muridae	R	70–135 g	Southern Africa, semi-arid Karoo region of the south west arid zone	Herbivore	Diurnal and nocturnal	Brown and Willan (1991), Pillay (2000)
Rhabdomys pumilio (Sparman 1784)	Four-striped grass mouse	Muridae	R	18–21 g	Southern, Central and Eastern Africa	Omnivore	Diurnal	Schradin and Pillay (2006), Schradin (pers. comm.)

4. Discussion

4.1. Effects of habitat type and different grazing intensities on vegetation cover

Whilst vegetation cover was generally low, it was lowest of all in quartz fields, showing that habitat type has a significant influence. The sparse vegetation is also of short stature, with the majority of plants having a height below 30 cm. The characteristics are due to a low precipitation and high average temperatures in the semi-arid study area (Mucina et al., 2006). Compared to loamy soils, quartz fields show an increased edaphic aridity due to higher stone content, shallowness (and consequently lower water storage capacity) and/or higher salinity of the soils (Schmiedel and Jürgens, 1999).

We did not find a measurable influence of grazing intensity on the vegetation cover in either of the habitat types. This suggests that in the Knersvlakte, habitat conditions influence the vegetation cover more than grazing intensity. Our results were unexpected, as other studies for the Succulent Karoo showed that selective grazing and high stocking rates of domestic animals alter the competitive relationships between plants, with consequences for plant coverage, reproduction and mortality, as well as community composition and abundance (Eccard et al., 2000; Hendricks et al., 2005; Todd and Hoffman, 1999). In addition, excessive grazing has often been referred to as an important cause of degradation and biodiversity loss in arid and semi-arid rangelands (Cowling and Hilton-Taylor, 1994; Hilton-Taylor, 1994). The reason why our results do not show this effect is that we only estimated the total vegetation cover, disregarding any differences in plant species composition. Haarmeyer et al. (2010c), however, who investigated plant species composition under different grazing intensities on the same farms and in the same year, concluded that intensive grazing indeed changes plant species composition but has a lesser effect on vegetation cover.

4.2. Effects of habitat type and different grazing intensities on small mammals

4.2.1. Trapping success

The mean capture rate across both habitat types was 1.77%. This trapping success was rather low compared with other studies in arid areas. Hoffmann and Zeller (2005) recorded a mean monthly trapping success of 3.75% on intensively-grazed plots in the Nama Karoo (arid dwarf shrub savanna) and 7.05% on plots with low-intensity grazing. A study by Decher and Bahian (1999) in the savanna of the Accra Plains of Ghana achieved a mean trapping success of 2.23%. Our low trapping success may be due to the exclusive use of all-enclosed Sherman live traps; capture rate can depend on characteristics of the traps – including type (e.g. open wire) and size – as well as the nature of their deployment (number, spacing, length and number of sessions) (Haveron, 2008; O'Farrell et al., 1994; Slade et al., 1993).

4.2.2. Habitat type

We trapped significantly more individuals and species in loam fields than in quartz fields and conclude from this that there is a higher abundance and activity of small mammals in this habitat. This could be due to the fact that living conditions in quartz fields are not only less favourable for plants, but also for animals. Even though the vegetation cover alone did not show a significant effect on small mammal diversity, there was a significantly lower vegetation cover in quartz fields and a strong effect of habitat on small mammal abundance and species richness. The combination of both results reveals that the vegetation cover is not exclusively responsible for the variation in activity and diversity between the habitat types but that the combination of vegetation and soil factors are responsible for the observed differences. The sparser vegetation cover in quartz fields provides little opportunities for small mammals to hide. It is often noted that a lower vegetation cover offers

Table 4
Overview of species composition and abundance (i.e. individuals trapped without recaptures) compiled for all plots of the two habitat types and two grazing intensities. Points indicate no captures.

Species	Total number of individuals	Habitat type/Grazing intensity			
		Loam ($n = 12$)		Quartz ($n = 10$)	
		Moderate ($n = 6$)	Intensive ($n = 6$)	Moderate ($n = 5$)	Intensive ($n = 5$)
Aethomys namaquensi	3	2	.	.	1
Crocidura cyanea	1	1	.	.	.
Desmodillus auriculari	9	7	2	.	.
Gerbillurus paeba	32	9	17	6	.
Macroscelides proboscideus	40	9	20	2	9
Malacothrix typica	1	1	.	.	.
Mus minutoides	6	5	1	.	.
Myomyscus verreauxii	3	3	.	.	.
Otomys unisulcatus	2	.	2	.	.
Rhabdomys pumilio	42	5	35	2	.
Undetermined (escaped)	1	1	.	.	.
Species richness	≥10	≥9	6	3	2
Number of individuals	140	43	77	10	10

the small mammals less protection from predation and heat (Cassini and Galanthe, 1992; Morse, 1980; Parmenter and MacMahon, 1983), as well as less food in terms of plant matter, or insects living on and off the plants (Blaum, 2004; Hoffmann and Zeller, 2005; Seymour and Dean, 1999). The resource availability hypothesis suggests that the abundance of small mammals is mainly determined by food availability (Blaum, 2004; Hoffmann and Zeller, 2005; Seymour and Dean, 1999). Moreover, the gravel cover of soil surface in quartz fields is highly uneven due to the quartz gravel, which may make it more difficult for small mammals to move about. The animals are in this way disadvantaged, as the search for food consumes more energy and it is more difficult to hide or escape from predators. Blaum and Rossmanith (2010) showed the importance of shrubs for the presence of reproduction burrows of yellow mongoose (*Cynictis penicillata*) in the Kalahari. Moreover, it is likely that burrowing is more difficult in quartz fields, and burrows here mainly occur on the scattered island-like termitaria (heuweltjies; unpublished observation U.S.). Small mammals need to be able to hide in underground nestings, particularly in order to avoid extremes in external temperature (Prakash, 1981). According to Wada et al. (1995), the burrowing limitation restricts the abundance of small mammals.

Significant effects of vegetation cover on the number of trapped individuals were found only on loamy soils. Cover of the lower vegetation height class (up to 15 cm) negatively influenced captures, while cover in the higher height class (above 30 cm) had a positive influence. A vegetation cover below 15 cm in height is probably rather unfavourable for the small mammals. The short plants affect the range of vision, create barriers to running, and are unsuitable as protection from the sun or predators due to their low height. The taller vegetation is probably advantageous for the abundance of the small mammals, as it protects from the sun – and therefore from high temperatures – and may provide a place to hide from predators. According to Hughes et al. (1994), the plant cover provides an important refuge for rodents evading predators.

Habitat type not only affected the number of individuals and species, but also the species composition. In quartz fields, only a fraction of the species occurring on loamy soils can be found, but there were no additional species. On loam, the most frequently found species were *Macroscelides proboscideus* and *R. pumilio* and on quartz *Macroscelides proboscideus* and *Gerbillurus paeba.*

All of the species that were frequently trapped display a social behaviour. Being social therefore seems to be a good survival strategy under these generally extreme environmental conditions. Mutual help strategies ensure survival, especially in times of drought and aridity, better than individualised solitary strategies. Schradin and Pillay (2005), who worked with *R. pumilio,* suggest that group-living in the Succulent Karoo is in response to habitat saturation and the benefits of philopatry.

As *M. proboscideus* and *R. pumilio* were the most frequent species occurring in the plots, we examined these two species with regard to their physical condition in the different habitat types and under different grazing intensities. According to Jakob et al. (1996), the physical condition of an animal indicates its nutritional status and general fitness. The results of our analysis show that the habitat had no significant influence on the BMI of *M. proboscideus* and *R. pumilio,* but did affect the weight of *M. proboscideus.* As the habitats are very small and patchy, the animals may move beyond habitat boundaries and may not be limited to one habitat type. As the BMI is similar for both habitat types, we conclude that small mammals are of a comparable physical condition in both habitat types. The lower body weight of small mammals caught in the quartz fields can be explained by the source-sink population dynamic (Pulliam, 1988) where the younger animals move from the loam fields (source) into the less preferable quartz fields (sink).

Total vegetation cover had a positive effect on the BMI and the weight of *M. proboscideus* as well as the weight of *R. pumilio*. Vegetation cover probably exerts this influence on the physical condition of these species through its functions of protection and food availability.

Consequently, insectivorous and omnivorous species differ between the two habitat types in terms of their distribution, but are not clearly influenced by habitat types and vegetation cover with regard to their physical condition.

Table 5
Constancies (% plots occupied) and diagnostic values of the species in the two habitat types and the two grazing intensities. Diagnostic values are indicated with + (concentration) and − (avoidance) if |phi| > 0.25. Double symbols indicate significance according to Fisher's exact test.

Habitat type	Loam	Quartz	All	All
Grazing intensity	All	All	Moderate	Intensive
Number of plots	12	10	11	11
Aethomys namaquensis	8	10	9	9
Crocidura cyanea	8	.	9	.
Desmodillus auricularis	42^{++}	$.^{--}$	36^{+}	9^{-}
Gerbillurus paeba	58^{+}	20^{-}	55^{+}	27^{-}
Macroscelides proboscideus	42	40	36	45
Malacothrix typica	8	.	9	.
Mus minutoides	17^{+}	$.^{-}$	9	9
Myomyscus verreauxii	8	.	9	.
Otomys unisulcatus	8	.	.	9
Rhabdomys pumilio	42	20	36	27

4.2.3. Grazing intensity

Neither number of trapped individuals nor the diversity of the small mammals was significantly influenced by the grazing intensity. This is in contrast to other studies in southern African arid lands where intensive grazing led to lower trapping success, number of individuals, and species richness compared to less intensive or absent grazing (Heske and Campbell, 1991; Hoffmann and Zeller, 2005; Hoffmann et al., 2010; Joubert and Ryan, 1999). However, the studies by Hoffmann and Zeller (2005), Hoffmann et al. (2010) as well as Joubert and Ryan (1999) compare heavily overstocked communal areas in arid South Africa or Namibia, respectively, with moderately grazed neighbouring farms. For their study site in the South Africa for instance, Joubert and Ryan (1999) claim that the stocking rates in the communal area have been at least twice as high as in the surrounding commercial rangelands. In contrast to that, the stocking rates on the farms of our study did not exceed the recommendations. Our study therefore suggests that grazing intensity at recommended stocking rate in the Knersvlakte does not seem to have any negative effect on the small mammal diversity and abundance on the farms. However, another parallel study at the same study site showed that the grazing had an effect on the plant species composition (Haarmeyer et al., 2010c), thus indicating that small mammals are only indirectly impacted by livestock grazing and may only respond if vegetation change significantly alters the quality of habitats.

5. Conclusions and implications for conservation

The results of this study reveal that the influences of livestock and vegetation cover on small mammals in the Succulent Karoo are complex. We found that abundances, species richness, species composition and the activity of small mammals in the central Knersvlakte mainly depend on habitat type whereas grazing intensity merely led to either concentration or avoidance by some of the species. As these results are not in line with other published studies (e.g. Hoffmann and Zeller, 2005; Joubert and Ryan, 1999) that found a much stronger impact of heavy livestock grazing on these parameters, we assume that the intensive grazing pressure in our study area, which does not exceed the recommended stocking rate, did not exceed the threshold for overgrazing and therefore did not have a negative impact on the small mammal communities. The tendency of most small mammal species in our study area to prefer moderately-grazed over intensively-grazed plots and one key species, *Macroscelides proboscideus*, showed better physical condition under less intensive grazing suggest that a reduction in grazing intensity might be positive in general. However, some species seem to profit from more intensive livestock grazing probably due to reduced competition, which suggests that the presence of domestic ungulates may also be favourable in some cases, particularly since the density of wild ungulates is currently much lower than it was in the past. In accordance with Haarmeyer et al. (2010c) we suggest a well-balanced arrangement of different grazing intensities in order to support the conservation of a full complement of small mammal species in the Knersvlakte.

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