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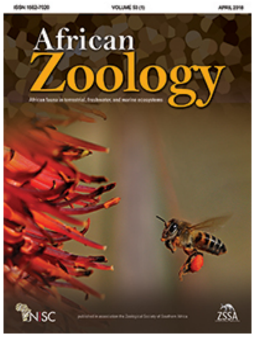

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Assessing the impacts of domesticated versus wild ungulates on terrestrial small mammal assemblages at Telperion Nature Reserve, South Africa

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Grazing by large mammals alters vegetation physiognomy, consequently changing habitat suitability for small mammal communities. We investigated the response of terrestrial small mammals to grazing by wild and domesticated ungulates at the boundary of a protected area (Telperion Nature Reserve) and surrounding cattle ranches in Mpumalanga, South Africa over two seasons. Fifteen paired grids were set on either side of the boundary fence at which small mammals were trapped in Sherman live traps placed flat on the ground. A total of 11 760 trap nights resulted in the capture of 187 animals belonging to 14 species (11 rodents, two shrews and one elephant shrew). The small mammal communities in grasslands grazed by domesticated or wild ungulates were similar in abundance, species richness, diversity and demographic parameters, likely due to the fact that vegetation structure of the two grazing systems was also similar. We used generalised linear models to show that rock and grass cover were plausible predictors of small mammal abundance in this system. Rock cover showed a positive relationship with small mammal abundance whilst grass cover showed a negative relationship. Our observations suggest that at the scale of our study and with the current stocking densities, wild and domesticated ungulates have similar impacts on the small mammal community.

Keywords: grazing, land use, terrestrial small mammals

Introduction

Through grazing and trampling of grasses, debarking of trees and browsing of shrubs both domestic and wild ungulates influence the vegetation in savanna and grassland ecosystems (O'Connor 1985; Archibald and Hempson 2016). This consequently alters habitat quality and suitability for terrestrial small mammals (Bowland and Perrin 1989; Keesing 1998; Monadjem 2001; Salvatori et al. 2001; Yarnell et al. 2007; Bueno et al. 2012). For example, excessive grazing and persistent trampling by cattle and wild ungulates can alter small mammal communities through the removal of above-ground biomass and litter (Salvatori et al. 2001; Altesor et al. 2006). The abundance and diversity of small mammals typically increase with vegetative ground cover (Monadjem 1997, 1999; Yarnell et al. 2007; Schmidt et al. 2009). For example, Monadjem (1997) observed that small mammal species diversity and biomass was higher where grass cover was greater, whilst Keesing (1998) observed a significant reduction in species diversity with increased grazing pressure by ungulates that reduced vegetation cover.

Terrestrial small mammals provide vital ecosystem functions such as soil aeration, seed dispersal, seed and insect predation, and scatter-hoarding of seeds (Avenant 2000; Singleton et al. 2007; Avenant and Cavallini 2007; Kuiper and Parker 2013; White et al. 2017), and therefore ascertaining the mechanisms that lead to changes in their populations or community structure should be of importance to ecologists. However, our understanding of how ungulates, whose populations dominate African savanna landscapes (Archibald and Hempson 2016), impact small mammal communities remains poorly understood (Yarnell et al. 2007). It is known that grazing by ungulates, particularly at high densities, may suppress terrestrial small mammal communities (Keesing 1998; Schmidt et al. 2005; Steen et al. 2005; Schmidt et al. 2009; Kuiper and Parker 2013). For example, Schmidt et al. (2009) observed significant negative effects of high-intensity livestock grazing on the abundance of the common shrew (*Sorex araneus*), and similar observations were reported for the field vole *Microtus agrestis* (Schmidt et al. 2005). Yet, the question of whether domesticated and wild ungulates have similar impacts on small mammals has not been addressed.

In southern Africa, domesticated ungulates (such as cows, goats and sheep) often graze in close proximity to wild ungulates, with the latter occurring predominantly on protected areas and the former on cattle ranches (Neke

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and du Plessis 2004). The role of ungulates in shaping the vegetation dynamics of grasslands and savannas has been well studied and reviewed by numerous authors (e.g. Werger 1977; Riginos et al. 2012; Kuiper and Parker 2013; Hempson et al. 2015). Heavy grazing pressure by domesticated livestock tends to have a negative impact on vegetation structure (by homogenisation), resulting in the suppression of wild ungulate populations (Riginos et al. 2012). However, this relationship is complicated by numerous factors, including facilitation of vegetation heterogeneity when wild ungulates graze alongside domesticated livestock (Veblen and Young 2010). Ecological interactions between ungulates and small mammals are less well known, but it appears that high grazing pressure suppresses both the diversity and abundance of the small mammal community (Keesing 1998; Eccard et al. 2000; Byrom et al. 2015). What remains untested is whether there is a differential effect of grazing by domesticated versus wild ungulates.

In this study we investigated the impact of ungulates on the terrestrial small mammal community in a protected area (with only wild ungulates), and surrounding cattle ranches (with domesticated ungulates) in the Mpumalanga province, South Africa. The objectives of the study were to (1) compare various diversity and demographic parameters of the small mammal community in grasslands grazed by domesticated and wild ungulates, (2) compare community composition of the small mammals on these two differing grazing systems, and (3) assess the relationship between vegetation variables and the small mammal community.

Methods

Field sites

The study was conducted at Telperion Nature Reserve (25°38′ S, 28°53′ E), a protected area, and surrounding cattle ranches in the Mpumalanga province of South Africa (Figure 1). Telperion was established as a protected area 41 years ago and covers an area of approximately 11 000 ha. It is bordered by a game fence, which separates it from privately owned cattle ranches to the north and south, whilst it is separated by the perennial Wilge River from eZemvelo Nature Reserve to the west. The surrounding private ranches currently farm Brahman cattle *Bos indicus*, which are the predominant ungulate in this system. The four private ranches had a total of 546 head of cattle grazing an area of 2 993 ha, giving a stocking rate of 0.18 livestock units (LSU) ha^{-1} (stocking rates on individual ranches ranged from 0.10 to 0.32 LSU ha^{-1}). In contrast, a large diversity of wild ungulates inhabit Telperion, including the following grazers: black wildebeest *Connochaetes gnou*, blue wildebeest *Connochaetes taurinus*, blesbok *Damaliscus pygargus*, red hartebeest *Alcelaphus buselaphus*, eland *Tragelaphus oryx* and plains zebra *Equus quagga* (MacFadyen 2014). The total stocking density at Telperion in 2017 was 2 161 LSU, or 0.20 LSU ha^{-1}, which is similar to the average stocking rate on the four private ranches. Meso-carnivores including black-backed jackal *Canis mesomelas*, side-striped jackal *Canis adustus*, yellow mongoose *Cynictis penicillata* and rusty-spotted genet *Genetta maculata* were observed on both the reserve and cattle ranches.

The study area experiences two distinct seasons, with a wet season from October to March and a dry season from June to August. The warmest and coolest months are January and July with daily mean temperatures of 26.1 °C and 14.6 °C, respectively. This area receives a mean annual rainfall of 674 mm (South African Weather Service 2008). The habitat at Telperion comprises an ecotone between grassland and bushveld (Grobler 1999), with the vegetation type of the sampling sites being dominated by Rand Highveld Grassland, which has undergone extensive transformation by anthropogenic activities (Low and Rebelo 1998). Currently, 35% of the grassland has been transformed by agriculture, afforestation and industrialisation and only 2.3% remains in a pristine state (Low and Rebelo 1998; Mucina and Rutherford 2006). This makes the Rand Highveld Grassland an area of high priority for conservation because it is considered an endangered vegetation unit (Reyers et al. 2001).

Capture of small mammals

This study was conducted with permission from all land owners on whose properties the work was conducted.

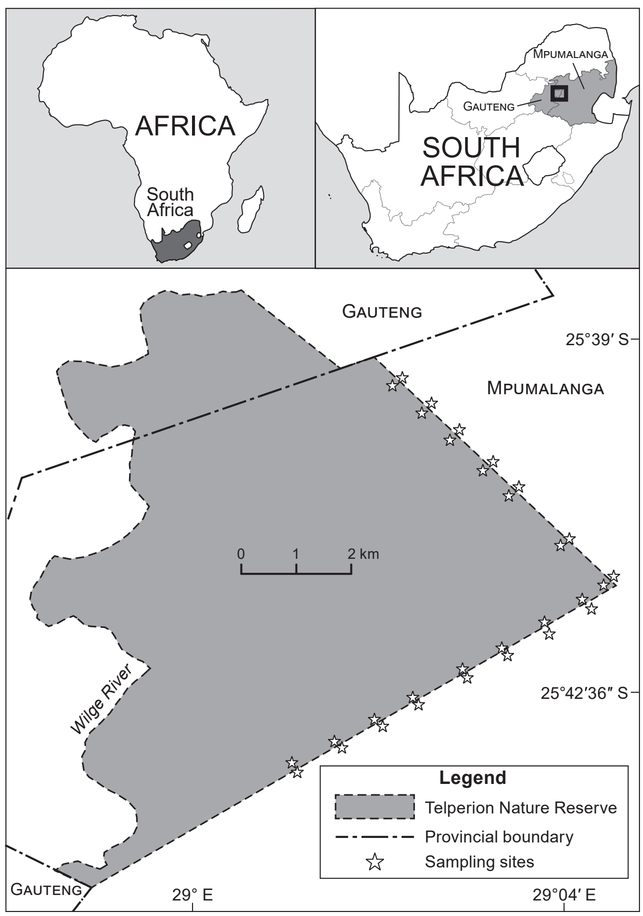

Figure 1: Location of Telperion Nature Reserve and the surrounding cattle ranches in South Africa. White stars represent the 15 paired sampling grids along the northern and the southern fenced boundary. The map shows the arrangement of two pairs of grids along the border of the two grazing systems: grey (wild ungulates) and white (domesticated ungulates)

Trapping and handling of small mammals was in accordance with the guidelines laid out by the American Mammalogist Society (Sikes 2016).

We sampled a total of 15 paired grids (15 grids in the protected area and 15 in the cattle ranches) (Figure 1) along the northern and the southern boundary of Telperion Nature Reserve. The paired grids were spaced 750 m apart and in similar habitat, while each grid was 50 m on either side of the boundary fence, resulting in a gap of 100 m between paired grids. This distance was far enough to preclude the movement of the majority of small mammal species from one paired grid to the other (Monadjem and Perrin 2003), and we did not record a single occurrence of a small mammal moving between grids in this study. We placed our grids close to the boundary fence to reduce the influence of changes in habitat determined by geology, soil or other factors outside of our control. The grids comprised 49 trapping stations, spaced 10 m apart in a 7 × 7 configuration. At each station we placed Sherman live traps, baited with a mixture of oats and peanut butter (Kok et al. 2013). We trapped over four consecutive nights per grid in the dry season (June–July 2016) and four nights per grid in the wet season (November 2016), for a total of 11 760 trap nights. Sampling of small mammals on both land uses was done simultaneously during suitable weather conditions to reduce possible influence of weather condition.

We identified captured animals to species following Skinner and Chimimba (2005), weighed them using a Pesola balance (to the nearest gram), and took standard museum measurements (head and body, tail and ear length) using a stainless-steel ruler (to the nearest millimetre) (Monadjem et al. 2015). In addition, we sexed, aged, and assessed the reproductive status of each animal; males were classified as either scrotal (testes descended) or non-scrotal (testes in abdominal cavity), whereas females were classed as either perforate (vagina open) or imperforate (vagina not open) (Monadjem and Perrin 2003; Skinner and Chimimba 2005).

Vegetation sampling

We recorded vegetation and environmental variables (grass cover, forb cover, shrub cover, rock cover and vegetation biomass) from 21 sampling stations per grid. Three sampling stations were established at 15 m intervals along each of the seven rows making up the small mammal trap grids (Simelane et al. 2018). At each station we used a 1 m × 1 m quadrat to estimate proportional cover of the four 'cover' (grass, forb, shrub and rock) variables in percentages whilst vegetation biomass was estimated using a disk-pasture meter (Bransby and Tainton 1977; Simelane et al. 2018). Finally, we recorded the dominant grass species in each quadrat and measured its average height using a 1 m ruler (van Oudtshoorn 2012). The common grasses were also classified by their potential grazing value (e.g. as an increaser or decreaser species) and successional stage (e.g. pioneer, subclimax or climax species) (van Oudtshoorn 2012).

Data analysis

We used the 'minimum number known alive' (MNA) to report all small mammal metrics, due to the low capture rate of individuals (Krebs 1999; Slade and Blair 2000; Hurst et al. 2013). We defined species richness simply as a count of the number of species, whereas species diversity was calculated using the Shannon diversity index (*H*′) (Krebs 1999). We then used these metrics as response variables in models that included grazing by wild ungulates or by cattle as predictor variables.

Our data did not fit a normal distribution (Shapiro–Wilk $W = 0.803$, $p < 0.01$). We therefore used the Mann–Whitney *U* test to test for differences in relative abundance, species richness, diversity, sex ratio and reproductive condition between the two grazing systems. These variables were tested to detect whether one system favoured a certain group, sex or cohort over the other. Furthermore, we used the Mann–Whitney *U* test to test for differences in the vegetation and environmental variables in the two grazing systems. We tested the difference in small mammal age structure between grazing by wild ungulates and cattle using the binomial test. All statistical analyses were done in the program R version 3.4.0 (R Core Team 2016).

We tested three responses of the small mammal community (species richness, diversity and abundance) to the recorded vegetation and environmental variables (e.g. grass, forb, shrub and rock cover, and vegetation biomass) using generalised linear models. These analyses were performed using the R package lme4 (Bates et al. 2015). We used the Akaike information criterion (AIC) to select the top model (Johnson and Omland 2004), which was conducted in the R package AICcmodavg (Mazerolle 2012).

We performed a non-metric multidimensional scaling (MDS) ordination and analysis of similarity (ANOSIM) in the program PRIMER (Clarke and Warwick 1994; Clarke and Gorley 2001) to test for differences in small mammal community composition between the two grazing systems.

Results

We captured a total of 187 individual small mammals of 14 species, of which 11 species were rodents (order Rodentia), two were shrews (order Eulipotyphla) and one was an elephant-shrew (order Macroscelidae) (Table 1). *Micaelamys namaquensis* and *Dendromus melanotis* were the most abundant species captured during this study. Similar numbers of species were captured in the two grazing systems (11 species in the protected area and 13 species in the cattle ranches); *Crocidura mariquensis* and *Dendromus mystacalis* were only recorded in cattle ranches, whereas all other species were recorded in both. Most of the species recorded were omnivores. Granivores and herbivores were encountered in far lower numbers on both land uses.

In both seasons, the abundance of small mammals did not differ between the two grazing systems ($U = 95.5$, $p = 0.490$). The same trend was observed in species richness ($U = 92$, $p = 0.392$) and species diversity ($U = 92$, $p = 0.395$). Furthermore, the demographic parameters of small mammals on either side of the boundary did not differ either, namely age structure ($z = 0.55$, $p = 1$), sex ratio ($U = 387$, $p = 0.934$) and reproductive condition ($U = 384$, $p = 0.\ 906$). The results of the MDS analysis indicated close similarity in species composition of small mammals between the two grazing systems indicated by the large amount of overlap in the sites (Global $R = -0.026$, $p = 0.743$) (Figure 2).

Mirroring the trend of the small mammal community, the vegetation and environmental variables did not differ on either side of the boundary fence: grass cover ($U = 67$, $p = 0.619$), grass height ($U = 92$, $p = 0.412$), shrub cover ($U = 133$, $p = 0.407$), forb cover ($U = 100$, $p = 0.618$), vegetation biomass ($U = 130$, $p = 0.486$) and rock cover ($U = 138$, $p = 0.295$).

The vegetation in both grazing systems was dominated by grasses, with less than 10% cover attributable to forbs and/or shrubs. *Eragrostis gummiflua* was the most abundant grass species in both grazing systems, which is an increaser species and associated with subclimax grasslands (Table 2). The majority of the common grasses (i.e. those that dominated sampling grids) were increaser species and associated with pioneer or subclimax grasslands (Table 2).

Only one model performed better than the null model when investigating the response of small mammal abundance to environmental variables (Table 3). The best model indicated that rock and grass cover were plausible predictors of small mammal abundance. This model indicated that rock cover (slope = 0.019) had a positive relationship whilst grass cover (slope = −0.032) showed a negative relationship with small mammal abundance. However, no candidate models performed better than the null model when investigating the responses of species richness and diversity on land-use types (results not shown).

Table 1: Terrestrial small mammals captured in Telperion Nature Reserve, which is a protected area (PA), and neighbouring cattle ranches (CR), Mpumalanga, South Africa

Order, Family, Species	PA	CR	Total	Relative abundance (%)
Rodentia	88	75	163	87.2
Muridae	58	53	111	59.4
Micaelamys namaquensis	20	23	43	23.0
Mus minutoides	8	11	19	10.2
Mastomys natalensis	13	5	18	9.6
Lemniscomys rosalia	11	2	13	7.0
Gerbilliscus leucogaster	2	8	10	5.3
Gerbilliscus brantsii	1	1	2	1.1
Aethomys ineptus	1	1	2	1.1
Otomys auratus	0	1	1	0.5
Nesomyidae	30	22	52	27.8
Dendromus melanotis	20	16	36	19.3
Steatomys pratensis	12	6	18	9.6
Dendromus mystacalis	0	1	1	0.5
Macroscelidea	8	14	22	11.8
Macroscelidae	8	14	22	11.8
Elephantulus myurus	8	14	22	11.8
Eulipotyphla	1	1	2	1.1
Soricidae	1	1	2	1.1
Crocidura mariquensis	0	1	1	0.5
Crocidura cyanea	1	0	1	0.5
Total	97	90	187	100

Discussion

Our study showed that small mammal communities did not differ in grasslands grazed by domesticated or wild ungulates, despite differences in the composition of these ungulate communities. We observed similarities in abundance, species richness, diversity and demographic parameters (age structure, sex ratio and reproductive conditions) of small mammals on either side of the boundary fence; this was mirrored in the vegetation and environmental variables that we measured. Hence, our results suggest that grazing by either domesticated or wild ungulates had an indistinguishable impact on the vegetation of the grassland ecosystem that we studied, corroborating the findings of previous studies (Bosing et al. 2014). We ascribe the similarity in small mammal communities to similar vegetation structure on either side of the boundary fence, at least at our scale of 50 m. Hence, our results suggest that the impact of grazing by domesticated or wild ungulates (at similar stocking densities) does not impact small mammal communities, unless mediated by changes in vegetation.

Our results should be accepted with several caveats. First, our sampling at a rather fine scale may have obscured impacts at larger scales (Hurst et al. 2014). Our primary objective was to show the immediate impacts of grazing; had we moved our grids further from the boundary fence, we would have introduced factors out of our control, most notably changes in habitat due to changes in soil and geology. However, it may be worth repeating this experiment on a larger scale if a suitable system can be found. Second, the grazing densities of ungulates (in both systems) were relatively low in this study. Hence, we do not know what the impacts would be at higher grazing densities, and this is again a suitable line of enquiry for future studies. Finally, other factors, such as soil type (Bosing et al. 2014) and fire regime (Valone and Kelt 1999; Yarnell et al. 2007), may play more important roles than

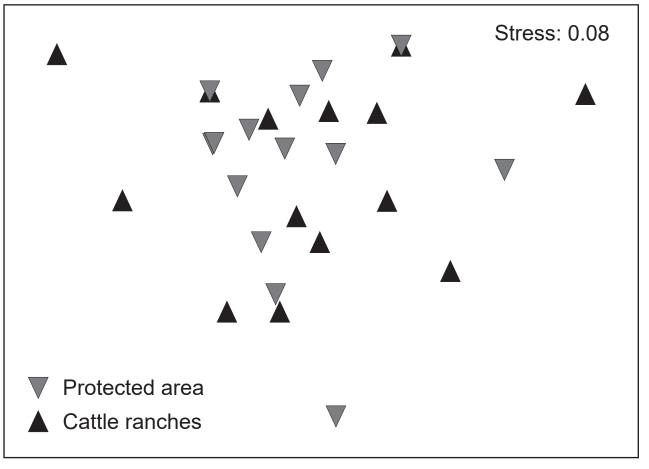

Figure 2: Non-metric multidimensional scaling plot showing small mammal species composition for the 30 grids (15 on each grazing system); grids grazed by wild ungulates are represented by grey triangles, whereas those grazed by domesticated ungulates are represented by black triangles

Table 2: Relative abundance of common grass species at Telperion Nature Reserve (protected area) and neighbouring cattle ranches, including their grazing value, ecological status and successional stage

Common grass species	Relative abundance (%)		Grass ecological value		
	Protected area	Cattle ranches	Grazing value	Succession stage	Ecological status
Eragrostis gummiflua	29	28	Low	Subclimax	Increaser
Aristida congesta	5	3	Low	Pioneer	Increaser
Cynodon dactylon	4	9	Medium	Subclimax	Increaser
Hyperthelia hirta	4	0.5	Low	Subclimax	Increaser
Aristida stipitata	2	1	Low	Subclimax	Increaser
Eragrostis curvula	2	2.5	Low	Subclimax	Increaser
Aristida transvaalensis	1	0.3	Low	Subclimax	Increaser
Themida triandra	1	1.4	High	Climax	Decreaser
Pogonathria squarossa	1	0.6	Low	Pioneer	Increaser
Eragrostis nindensis	0.1	0	Medium	Subclimax	Increaser
Panicum natalense	0.1	2.2	Low	Climax	Decreaser
Digitaria eriantha	0.1	0.1	High	Climax	Decreaser

Table 3: Summary of the plausible generalised linear models showing vegetation (and environmental) variables as predictor variables of small mammal abundance as the response variable. The Akaike information criterion (AICc) was used to select the top model. The remaining abbreviations are as follows: *K* = the number of covariates in the model; ΔAIC = the difference in AICc; AICcWt = the AIC weight; Cum.Wt = cumulative weight; and LL = the loglikelihood for each model

Predictor variables	*K*	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Grass + Rock cover	4	298.5	0.0000	0.9999	0.9999	−144.9
Grass + Shrub cover	4	316.6	18.0574	0.0001	1	−153.9
Grass + Grass height	4	324.6	26.0063	0	1	−157.9
Grass + Vegetation biomass	4	326.2	27.6927	0	1	−158.8
Grass + Forb cover	4	329.5	31.0008	0	1	−160.4
Null model	2	339.7	41.1666	0	1	−167.8

grazing *per se* in shaping the small mammal community. Given that all these factors are interrelated, experimental manipulation of the entire set of variables may be needed to better understand the system, but such ecological manipulations face serious logistical obstacles (Young et al. 1997).

We observed both dietary (*L. rosalia* and *A. ineptus*) and habitat (*G. leucogaster*, *G. brantsii* and *E. myurus*) specialist small mammal species in both grazing systems. This suggests that the disturbance by wild or domesticated ungulates was not degrading small mammal habitat (Avenant 2000; Steen et al. 2005; Yarnell and Scott 2006; Schmidt et al. 2009). Furthermore, these low levels of ecological disturbance allow for the rejuvenation of vegetation, and may generate patch heterogeneity, leading to a high diversity of small mammals (Valone and Kelt 1999), a situation that we observed at our study site with the capture of 14 terrestrial small mammal species.

Grass and rock cover were the best predictors of small mammal abundance, whilst species richness and diversity did not vary in relation to any of our measured variables. Rock cover showed a positive relationship with small mammal abundance, whereas grass cover showed a negative relationship. This partially corroborates the findings of Lancaster and Pillay (2010), MacFadyen (2014) and Fagir et al. (2014) who observed higher abundance in rocky habitats compared with that in grasslands. This suggests that in grassland systems, rocky outcrops may act as refuges for small mammals because the grasses that grow on and immediately around them are less easily grazed down by ungulates.

In conclusion, our results suggest that unlike more intensive agricultural land uses (Hurst et al. 2014), cattle ranches may not represent a hard boundary for small mammals or affect their community composition, especially at relatively low stocking rates.

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