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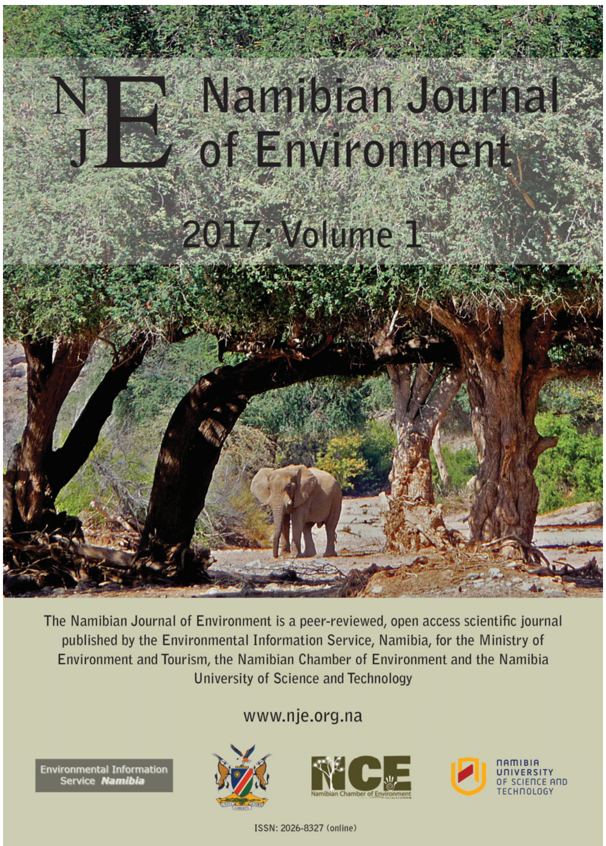

SECTION A: PEER-REVIEWED PAPERS

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A comparison of the community dynamics of bioturbating small mammals between livestock and wildlife farming areas in the Kalahari, Namibia

ML Hauptfleisch[1], MP Vinte[1], N Blaum[2]

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[1] Namibia University of Science and Technology, 13 Storch Street, Windhoek, Namibia. mhauptfleisch@nust.na
[2] Potsdam University, Am Mühlenberg 3, Potsdam, Germany.

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ABSTRACT

The study compared abundance and diversity of small mammals between a commercial livestock and neighbouring game farm in the Kalahari Thornveld of Namibia's Omaheke region. Sherman traps baited with standard small-mammal attractants were set out in grids in similar habitats on each land use for four trap-nights during the growing season and the non-growing season of 2015. In total, 174 individuals of five species of small mammals were trapped, 118 on the livestock farm, and 56 on the game farm. Species richness totalled five species of the order Rodentia of which the bioturbating species *Gerbillurus paeba* represented 79.9% (n=139). All five species were trapped on the livestock farm, and only three on the game farm. With similar stocking rates but different grazing management strategies, it is expected that rangeland condition and perennial grass cover differences influenced the densities and species richness of small mammals. This suggests that ecosystem services associated with these mammal species would be more effective on the livestock farm, leading to better soil moisture infiltration and retention, as well as more effective soil nutrient cycling and seed dispersal.

Keywords: abundance, bioturbator, diversity, ecosystem services, Kalahari, land use, Namibia, nutrient cycle, rodentia, seed dispersal, small mammals, soil moisture, community dynamics

INTRODUCTION

Small mammals play a vital role in ecosystem functioning through the dispersal of seeds, seed predation, nutrient cycling through ground bioturbation, specialist and primary consumption, predation and as prey for animals on a higher trophic level (Avenant 2000). This study concentrated on the impacts of livestock and game farming on the abundance and diversity of subterranean-living small mammals, known as bioturbators. Bioturbation is the tilling and mixing of soils by living organisms, usually resulting in heterogeneity of soil structure and aeration (Gabet et al. 2003). This disturbance of soils by burrowing small mammals can positively improve the status of degraded land by supporting key geo-biosphere feedbacks (Eldridge & Leys 2003). In particular, their burrow systems increase the surface macro-pores, which can accelerate water infiltration back into the ground and improve plant-available soil water (Eldridge & James 2009). Borchard and Eldrich (2011) found that foraging small mammals turn over between 1,000 to 3,000 kg of soil per year. This process can aid the germination and penetration of seedlings from soils surfaces considered to be crusted and impermeable.

Overgrazing of rangelands and its consequences for vegetation cover in the Namibian savannas are well documented (Seely & Jacobson 1994). The introduction of wildlife to arid parts of the Namibian savanna has resulted in particular challenges such as selective grazing and shortage of drought reserve grazing (Bothma & du Toit 2010). Farms with excessive numbers of ungulates (both livestock and wildlife) sustain extensive damage to vegetation from trampling and grazing pressure. These land-use induced changes in vegetation cover and composition influence soil temperature and structure (Joubert & Ryan 1999) and consequently affect the habitat assemblage of small mammals (Giere & Zeller 2005). Indirectly, this is likely to feed back to plants as lower aeration and moisture content of soil. Bush thickening, a major form of savanna rangeland degradation, may be a double-edged sword for small mammals (Blaum et al. 2007b). Bush thickets in the midst of open savannas provide important functions for biodiversity (Blaum et al. 2007b) and probably improve soil productivity. They do, however, lower overall rangeland productivity (Tainton 1999) and can lead to fragmentation and a loss of species diversity (Blaum et al. 2007a, 2007b, 2009, 2012).

This study investigated differences in the abundance and diversity of small mammals in two major land uses in the Namibian Kalahari, namely livestock (cattle, horse and sheep) and wildlife (hunting and tourism). It explored the reasons for, and consequences of, the differences. The study selected small mammals as model organisms since they rapidly respond to sudden changes in their environment (Avenant & Cavallini 2007) and have been successfully used in ecosystem service assessments (Avenant 2000, Avenant et al. 2008). The study further identified key ecosystem services likely to be impacted by the differences in density and diversity of small mammals.

METHODS

Study site

The study was carried out in the south-eastern Kalahari Sandveld of Namibia's Omaheke Region at two adjacent farms namely, Kuzikus (23˚14.214'S, 18˚23.435'E) and Ebenhaezer (23˚13.127'S, 18˚26.769'E). Kuzikus is a wildlife sanctuary with consumptive and non-consumptive tourism activities. Dominant wildlife species are eland *(Tragelaphus oryx*), oryx (*Oryx gazella gazella*), kudu (*Tragelaphus strepsiceros*) springbok (*Antidorcas marsupialis),* blesbok (*Damaliscus albifrons*), red hartebeest (*Alcelaphus buselaphus*), Burchell's zebra *(Equus quagga burchellii*), giraffe (*Giraffa giraffa angolensis*), black rhinoceros *(Diceros bicornis bicornis)* and ostrich (*Struthio camelus*). Dominant grasses include *Aristida congesta, Aristida stipitata* and *Schmidtia kalahariensis,* indicating poor rangeland condition (van Oudtshoorn 2002).

Ebenhaezer is a livestock farm, sustaining herds of cattle, karakul sheep and horses. The farm practices rotational grazing as a management tool to avoid overgrazing (PH Hugo pers. com.). Dominant grasses include *Stipagrostis uniplumis* and *Stipagrostis ciliate,* indicating a veld in good condition (van Oudtshoorn 2002), although *S. kalahariensis, A. congesta* and *A. stipitata* also occur.

Trapping of small mammals

To determine species diversity, richness and abundance of small mammals, four grids (two grids in each farm) consisting of 40 collapsible Sherman aluminium live-traps (23 x 8 x 9 cm) were set concurrently on both farms. Traps were set at 10 m spacing interval (Leirs et al. 1995, Avenant 2000, Avenant & Cavallini 2007). Grid sites were selected with similar soil, vegetation and topographical characteristics, and equidistant from water-points. Trapping was done over four consecutive nights per session during the months of March (growing season), and June (non-growing season) in 2015. These months were chosen because populations of small mammals are most likely to be at their highest during the growing season (Blaum et al. 2007a), and decrease in winter (June), therefore the rate of population decline could be determined. According to Giere and Zeller (2005) a trap-night signifies one trap set out for 24 hours, hence 160 traps used in the study yielded 640 trap-nights per trapping session. Bait consisted of a mixture of peanut butter, rolled oats, Bovril™ (for insectivores) and sunflower oil. Traps were inspected every morning at 06h00, emptied and then left closed. They were re-baited every afternoon at 17h00 and left open, consequently sampling only nocturnal and crepuscular species. The study excluded diurnal trapping because the extreme maximum temperatures of the Kalahari, which reach up to 45˚C in summer (Mendelsohn 2010), would have resulted in unnecessary mortalities of trapped small mammals.

The possible impact of small-mammal burrowing activity on soil moisture infiltration was tested by simulating a 20 mm/hour rainfall event for 1 hour on a 1 m^2 site with burrow activity and on a similar site without burrows. Water was stained with bromothymol blue to record the depth of infiltration. The result of this experiment is descriptive only, as replication was not possible within the short study period.

Data analysis

Trapped individuals were identified to species level, weighed, and sexed by visual dimorphism. Other morphometric measurements such as right hind-foot length (RHFL) were taken. Hind-foot/mass ratio was tested as a possible indicator of fitness (Krebs & Singleton 1993). Capture-mark-recapture was used, and retrapped individuals were removed from the abundance and fitness analyses. Normality of data was determined by the Shapiro Wilks W test. For non-parametric (all) comparisons between seasons and land uses the Kruskal Wallis Anova test was used. Statistica for Windows version 10 (StatSoftInc. 2011) was used for statistical analysis. A 95% level of confidence was regarded as significant.

RESULTS

In total, over both seasons, 174 individuals of five small mammal species were trapped. Of these, 56 (32.18%) individuals were trapped on the wildlife sanctuary (Kuzikus) and 118 (67.82%) on the livestock farm (Ebenhaezer). The livestock land use produced a total species richness of five rodents whereas only three species were trapped at the wildlife sanctuary (Table 1). Overall, *Gerbillurus paeba* represented 79.89% (n=139) and this species was trapped on both farms. Also captured on both properties were *Gerbilliscus brantsii* 13% (n=23), *Mus indutus* 3% (n=6). *Saccostomus campestris* 2% (n=4) and *Gerbilliscus leucogaster* 1% (n=2) were only trapped on the livestock farm (Table 1) and were absent in the wildlife sanctuary. Abundance of small mammals (mean per grid per trap-night) was significantly higher in the livestock farm, in both the growing season (Fig. 1a) ($H_{1,12}$=4.41, $p<0.05$) and the non-growing season (Fig. 1b) ($H_{1,12}$=16.00, $p<0.01$).

The fitness of *G. paeba* individuals (mass / right hind foot ratio) was higher on the livestock farm, and marginally lower in winter. These differences were, however, not statistically significant. Low numbers of trapped individuals from other species precluded any statistical comparison of fitness.

A single soil moisture infiltration experiment (20mm/ hour rainfall event) provided a preliminary indication that rainfall infiltrates deeper in soils with burrows than without. Figure 3 illustrates water infiltration up to a depth of 300 mm in an area without burrowing activity, and 400 mm in an area with small-mammal burrowing.

Species richness (mean per trap-night) was significantly higher on the livestock farm (Ebenhaezer) in both the growing season (Fig. 2a) ($H_{1,12}$=4.41 $p<0.05$) and the non-growing season (Fig. 2b) ($H_{1.2}$=5.75 $p<0.01$).

DISCUSSION

Significantly higher abundance and species richness of small mammals were found on the livestock farm in both the growing and non-growing season of 2015. This corresponds with earlier work by Caro (2001) and Muck and Zeller (2006) who showed that abundance and diversity of small mammals were higher in areas adjacent to protected areas as opposed to inside. Though the cause of this phenomenon is unclear, Caro (2001) speculated that inter-specific competition between continually grazing ungulates and small mammals as well as reduced cover by mega-herbivore grazing could be one of the reasons.

Our study also complements the findings of a study at Namibian airports which showed that abundance of small mammals was higher in un-mowed area than in mowed areas (Hauptfleisch 2014). This Namibian study suggested that mowing the airport properties and areas adjacent to the runways could reduce the density and diversity of small mammals (Hauptfleisch & Avenant 2015).

Wild ungulate grazing on enclosed farms such as Kuzikus results in continuous and selective grazing (Trollope 1990) leading to consistently reduced cover, as well as reduced rangeland productivity and sustainability (McGranahan 2008). This results in reduced overall vegetation cover, known to be unfavourable for small mammals (Muck & Zeller 2006, Hauptfleisch & Avenant 2015). This is evident on Kuzikus, the wildlife farm used in this study (BR Reinhardt pers. com.). Conversely, the livestock farmer is able to regulate grazing pressure through rotational grazing and drought reserve planning (PH Hugo pers. com.). Furthermore, the grazing

Table 1: *Small mammals trapped at Kuzikus and Ebenhaezer during the growing and non-growing seasons of 2015 (Numbers of retrapped individuals are indicated in parentheses).*

		Ebenhaezer (livestock)			Kuzikus (wildlife)		
Season	**Species**	**Grid A**	**Grid B**	**Total**	**Grid A**	**Grid B**	**Total**
Summer	*Gerbilliscus leucogaster* (Bushveld gerbil)	0 (0)	2 (2)	2	0 (0)	0 (0)	0
Winter		0 (0)	0 (0)	0	0 (0)	0 (0)	0
Summer	*Gerbilliscus brantsii* (Highveld gerbil)	12 (5)	9 (2)	21	1 (1)	1 (0)	2
Winter		0 (0)	0 (0)	0	0 (0)	0 (0)	0
Summer	*Gerbillurus paeba* (Hairy-footed gerbil)	23 (9)	19 (2)	42	23 (2)	7 (1)	30
Winter		26 (25)	19 (13)	45	7 (6)	15 (11)	22
Summer	*Mus indutus* (Desert pygmy mouse)	1 (1)	2 (2)	3	0 (0)	2 (0)	2
Winter		1 (1)	0 (0)	1	0 (0)	0 (0)	0
Summer	*Saccostomys campestris* (African pouched mouse)	1 (1)	3 (3)	4	0 (0)	0 (0)	0
Winter		0 (0)	0 (0)	0	0 (0)	0 (0)	0
Summary							
Overall	Total captured	64	54	118	31	25	56
Summer	Total captured	37	35	72	24	10	34
Winter	Total captured	27	19	46	7	15	22
Summer	Species Richness	4	5		2	3	
Winter	Species Richness	2	1		1	1	
Overall	Species Richness	4	5		2	3	
Summer	Shannon Diversity	0.86	1.2		0.17	0.8	
Winter	Shannon Diversity	0.16	0.2		-	-	
Overall	Shannon Diversity	0.69	0.95		0.14	0.44	

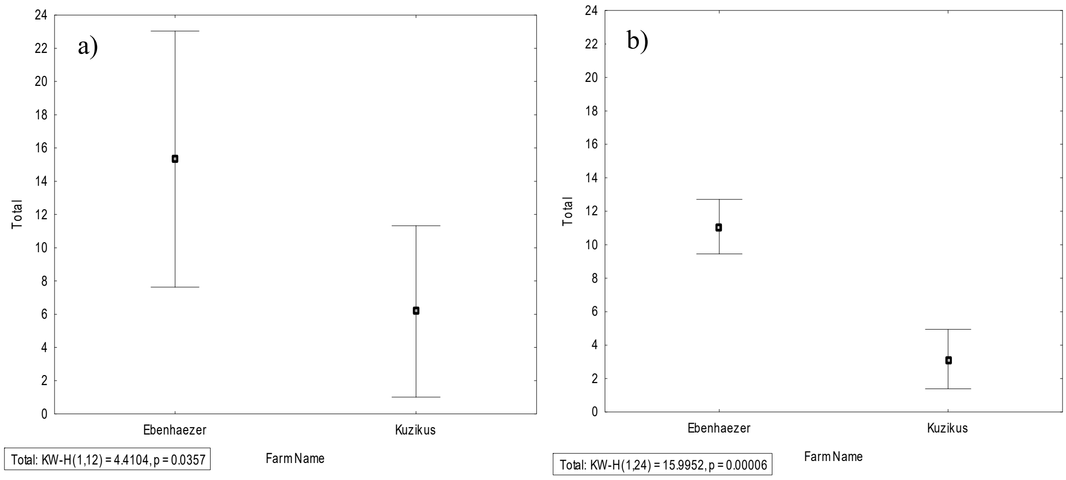

Figure 1: *Abundance of small mammals (mean per trap-night) in the growing (a) and non-growing season (b) of 2015.*

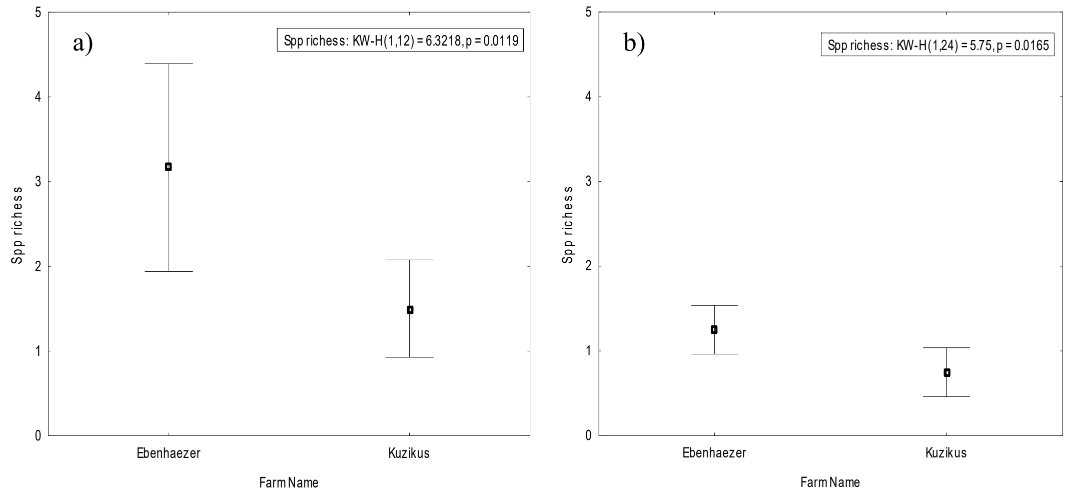

Figure 2: *Species richness of small mammals (mean per trap-night) in the growing (a) and non-growing season (b) of 2015.*

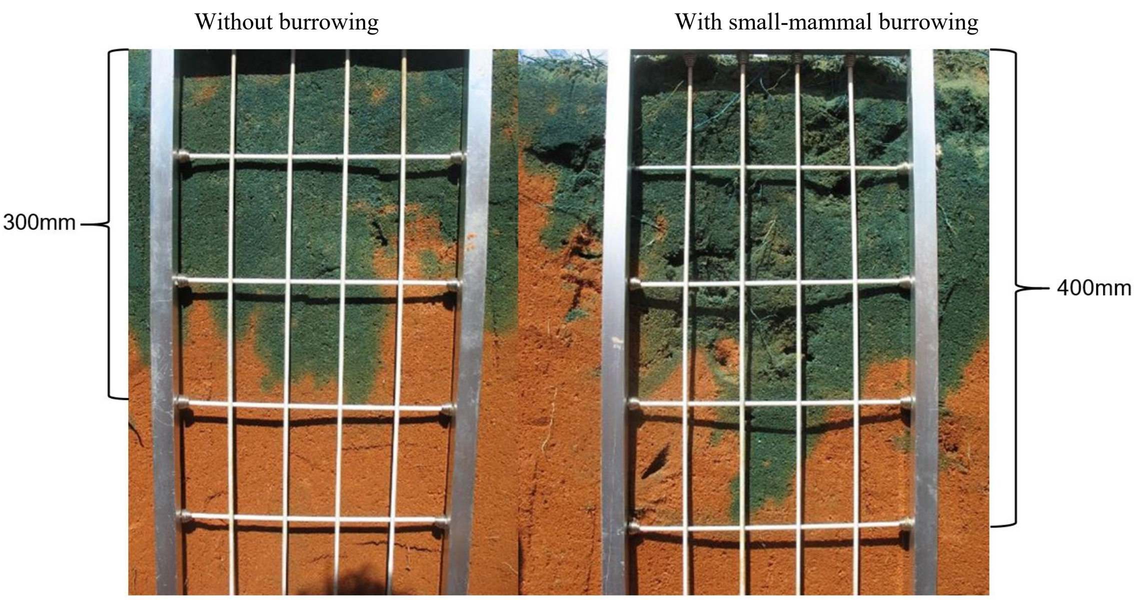

Figure 3: *Soil moisture infiltration following a simulated one-hour rainfall event of 20 mm.*

technique of cattle, feeding on central tillers of tall perennial grass, is known to create corridors for small mammals to move among collapsed outer tillers (Mentis 1981), reducing the risk of predation to small mammals.

Secondly, active meso-carnivore control is practiced on the livestock farm (PH Hugo pers. com.). This includes species such as black-backed jackal (*Canis mesomelas*) and African wildcat (*Felis silvestris lybica*), both important rodent predators (Chimimba 2005). This provides sanctuary for populations of small mammals, a phenomenon also found at Namibian airports surrounded by livestock farming (Hauptfleisch 2014, Hauptfleisch & Avenant 2015).

In recent years more livestock farmers are converting to wildlife ranching as a better option of land use, largely because such practices are perceived to be less costly, more resilient to climate change and more natural for the maintenance of healthier ecosystems and biodiversity (Cloete et al. 2007). However, findings of this study indicate that this may not always be the case, and that wildlife farming with limited grazing management options could be detrimental to biodiversity.

Small mammals have a crucial role in dispersal of seeds and diet for higher predators within the Kalahari (Blaum et al. 2007a). These ecosystem services are likely to be less effective as a result of reduced abundance and species richness of small mammals in the wildlife land use. The loss of bioturbation may reduce soil moisture infiltration (Figure 3) and retention, and important pedological characteristic affecting the performance of arid rangelands.

Dynamic densities and diversity of small mammals found in this study, seemingly perpetuated by the land use practiced on the neighbouring farms, emphasises the value of small mammals as indicators of ecosystem integrity and rangeland condition, supporting other southern African findings (Muck & Zeller 2006, Avenant 2011). Although there are many ways to measure land degradation, the role of small mammals as biological indicators (Avenant & Cavallini 2007, Avenant 2011) could be assimilated in rangeland management practices for savanna ecosystems in Namibia.

While the data collection period of this study was of short duration (one summer and one winter only), the comparative nature of the study provides useful insights. Soil moisture infiltration experiments need to be repeated and key soil and vegetation condition properties should be quantified in order to be able to assess the impacts of the activity of small mammals on soil and vegetation productivity.

CONCLUSION

The study found significantly higher abundance and diversity of small mammals on a livestock farm compared to its neighbouring wildlife farm. This difference occurred in the growing and non-growing seasons of 2015. No significant differences in the fitness of the small mammals could be determined however. The burrowing hairy-footed gerbil, *G. paeba,* was found to be the dominant species on both land uses, with two other gerbils, *G. leucogaster* and *G. brantsii,* occurring on both land uses. The mice *S. campestris* and *M. indutus* were trapped only on the livestock farm. Our results suggest that continuous and selective grazing on the wildlife farm resulted in consistently lower vegetation cover than on the rotationally-grazed livestock farm, thereby reducing cover for small mammals to thrive. The removal of meso-carnivores from the livestock farm further reduced predation of small mammals. The reduction of numbers of small mammals on the wildlife farm is expected to result in the loss of important ecosystem services such as soil moisture infiltration and retention, soil aeration and seed dispersal. With very little trapping of small mammals currently being conducted in southern Namibia, the survey provides current records for updating knowledge on the distribution of nocturnal small mammals in Namibia.

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