NJE Namibian Journal of Environment

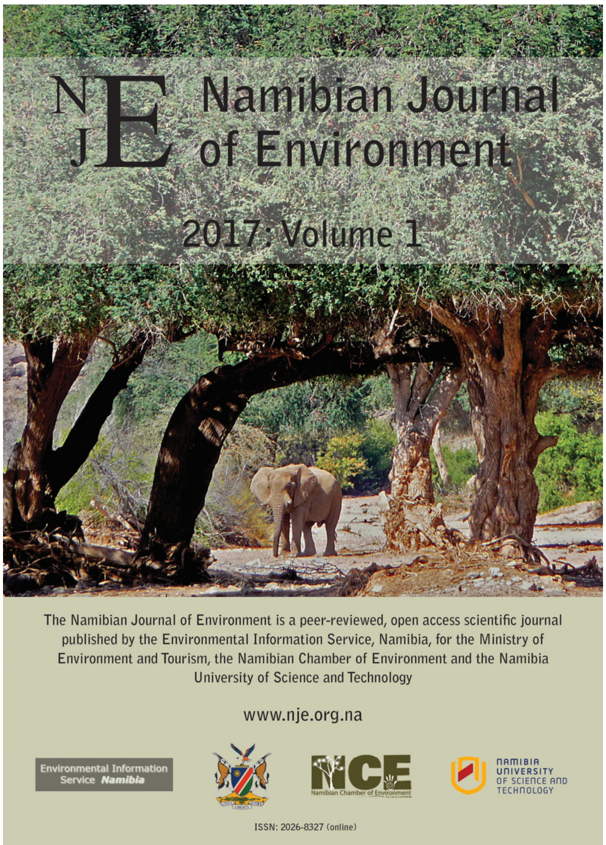
The Namibian Journal of Environment is a scientific e-journal published by the Environmental Information Service, Namibia for the Ministry of Environment and Tourism, the Namibian Chamber of Environment and the Namibia University of Science and Technology.

The *Namibian Journal of Environment* (NJE) covers broad environmental areas of ecology, agriculture, forestry, agro-forestry, social science, economics, water and energy, climate change, planning, land use, pollution, strategic and environmental assessments and related fields. The journal addresses the sustainable development agenda of the country in its broadest context. It publishes two categories of articles. **SECTION A: Peer-reviewed papers** includes primary research findings, syntheses and reviews, testing of hypotheses, in basic, applied and theoretical research. **SECTION B: Open articles** will be editor-reviewed. These include research conference abstracts, field observations, preliminary results, new ideas and exchange of opinions, book reviews.

NJE aims to create a platform for scientists, planners, developers, managers and everyone involved in promoting Namibia's sustainable development. An Editorial Committee will ensure that a high standard is maintained.

ISSN: 2026-8327 (online).

Editor: BA CURTIS



SECTION A: PEER-REVIEWED PAPERS

Recommended citation format:

Rodgers M, Bilton MC, Hauptfleisch ML (2017) Responses and feedbacks of burrowing mammals under differently managed rangelands. *Namibian Journal of Environment* 1 A: 40-51.

Responses and feedbacks of burrowing mammals under differently managed rangelands

M Rodgers[1], MC Bilton[2], ML Hauptfleisch[1]

URL: http://www.nje.org.na/index.php/nje/article/view/volume1-rodgers
Published online: 6th December 2017

[1] Namibia University of Science and Technology, 13 Storch Street, Windhoek, Namibia michellerdgrs@gmail.com
[2] University of Tübingen, Plant Ecology Group, Institute of Evolution and Ecology in Germany

Date received: 12th November 2017; Date accepted: 28th November 2017.

ABSTRACT

Bioturbating organisms are known for their benefits to landscapes and ecosystems. Studies have to date largely focussed on invertebrates with very little known about the role burrowing mammals potentially play, especially nocturnally active species. They are thought to be vulnerable to land degradation - such as shrub encroachment and livestock overgrazing - leading to increased negative effects on land productivity through the loss of their associated ecosystem services. In the Kalahari Desert ecosystem of Namibia's Omaheke Region this study compared the abundance and diversity of burrowing medium-sized nocturnal mammals between neighbouring livestock and wildlife land use types. It postulated that bioturbation by nocturnal mammals is an important feedback mechanism leading to improved soil conditions and therefore improved vegetation productivity. The study used nocturnal road strip counts during the growing and non-growing seasons of 2016 to quantify differences in medium-sized mammal population dynamics. Using high resolution multispectral unmanned aerial vehicle imagery, burrow size and abundance as well as vegetation productivity was estimated. The study found a higher diversity of nocturnal medium-sized mammals on the wildlife reserve. Furthermore, clear seasonal patterns were observed. Whereas total sighting number was similar in the growing season and winter on the wildlife reserve; on the livestock farm, there were significantly more mammals spotted in summer, and far fewer in winter. Notably, we revealed that some species of mammal have clear habitat preferences during the different seasons. Results showed that shrub encroachment had a negative relationship with burrow number on both sites, with the livestock farm particularly susceptible. Importantly some benefits were indicated by areas around larger burrows showing higher vegetative productivity. Overall, the study provided valuable insights into the movements, strategies and potential benefits of these mammals. Further research is needed to determine the precise mechanisms by which the burrowers may provide ecosystem functioning benefits to the land users.

Keywords: bioturbation, ecosystem engineer, ecosystem services, medium-sized mammals, nocturnal, rangeland productivity, Namibia.

INTRODUCTION

Land-use type and management are currently predicted to be one of the greatest impacts in global-change biology, particularly in dry environments (Sala et al. 2000). Poor management practices or inappropriate land-use can often lead to ecosystem degradation, such as over-grazing and shrub encroachment, leading to fragmentation and loss of biodiversity (Millennium Ecosystem Assessment 2005, Blaum et al. 2007, 2009). Compounding impacts such as loss of soil fertility, moisture and vegetation productivity are well documented (Prose et al. 1987, Belsky 1994, Fleming et al. 2014). However, a potentially important, yet under-studied aspect of ecosystems in dry regions, are the medium-sized burrowing mammals and mesocarnivores (Blaum et al. 2009), which provide important ecosystem services and are thought to be highly vulnerable to land degradation.

Mesocarnivores are small to medium-sized carnivores of less than 15 kg (Roemer et al. 2009) and medium-sized mammals are classified as mammals with burrow openings of 8-100 cm in diameter (Skinner & Smithers 1990). A potentially important role of these burrowing mammals in ecosystems is bioturbation – the manipulation and movement of soil by biota (Meysman et al. 2006, Fleming et al. 2014). Increasing demand for grassland habitats for livestock has resulted in conflict with medium-sized, herbivorous bioturbators, and global bioturbator numbers are declining (Davidson et al. 2012, Fleming et al. 2014). Although the benefits of burrowing mammals in an ecosystem have been documented (Meadows 1991, Zhang et al. 2003, Meysman et al. 2006, Davidson et al. 2012, Fleming et al. 2014), many livestock and crop farmers are not aware of their importance to rangeland productivity. Poor management therefore has the potential to provide feedback mechanisms that result in poorer and less productive rangelands.

Charles Darwin was the first researcher to observe the importance of burrowing animals by describing the impact of earthworms on landscape function (Meysman et al. 2006). The important role that bioturbation plays in landscape formation and evolution, through soil formation, erosion, soil stabilisation and soil fertility, has only been fully realised in recent years, but has been neglected in Namibia. International studies have found that bioturbating invertebrates improve soil fertility, increase water infiltration into the soil by 4-10 times, improve moisture retention and aerate soil (Edwards & Bohlen 1996, Gabet et al. 2003, Meysman et al. 2006, Bonachela et al. 2015).

There is, however, little empirical information regarding the importance of bioturbating mammals on ecosystems, and especially bioturbating medium-sized mammals and mesocarnivores, which play an important role in ecosystem functioning as ecosystem engineers (Jones et al. 1994, Gabet et al. 2003, Blaum et al. 2007, Roemer et al. 2009, Fleming et al. 2014). Burrowing mammals are defined as allogenic engineers that modify the environment by mechanically changing materials into different physical states (Jones et al. 1994). Ecosystem services provided either directly or indirectly by bioturbating mammals are present in most parts of the world but are often underestimated (De Groot et al. 2002, Roemer et al. 2009, Fleming et al. 2014). These services include habitat creation, soil formation, nutrient cycling, food provision, climate regulation, water regulation and even cultural and/or aesthetic values.

The study aimed to quantify differences in the abundance and diversity of medium-sized burrowing mammals between a wildlife reserve and a livestock farm in Namibia's Omaheke region, and possible impacts of their activity on rangeland productivity.

METHODS

Study sites

In this study, two neighbouring sites, with different management practices, were compared: Kuzikus Wildlife Reserve and Ebenhaezer livestock farm (Figure 1a). The study sites were located in the Kalahari sandveld of Namibia (23°12'S, 18°26'E). In general, the study area falls within the Southern Kalahari vegetation type in the broader Tree-and-shrub Savanna biome (Mendelsohn et al 2002). The Southern Kalahari covers about 12.4 million hectares of land in southern Africa, which includes Botswana, South Africa and south-eastern Namibia (Leistner & Werger 1973). In Namibia, the average annual rainfall in the area ranges from 200-350 mm while average evaporation ranges from 2,000-2,500 mm per year (Mendelsohn et al. 2002). The dominant soils are arenosols, which consist of more than 70% wind-blown sand. As a result of these factors, water infiltration is rapid, water retention is generally low and nutrients are readily leached out of the soil. Longitudinal, vegetated dunes and open grassland with scattered *Acacia* (*sensu lato*) trees are the characteristic vegetation types found in the area. Growing seasons fall in the summer, starting at the onset of rain, usually between October and June.

Kuzikus Wildlife Reserve

The 10,500 ha reserve is situated on the edge of the central Kalahari, 180 km southeast of Windhoek (Kuzikus Wildlife Reserve 2010) and at an altitude of 1380 m (Reinhard et al. 2009). The landscapes of the reserve include Kalahari savannah, saltpans with dwarf shrubland, thornbush encroached areas and low, vegetated dunes. The dominant woody vegetation on the reserve includes *Acacia erioloba*, *Acacia karroo*, *Grewia flava*, *Acacia mellifera* subsp. *detinens*, and the dominant grass species are *Aristida* and *Stipagrostis* species. Kuzikus supports about 3,000 grazing and browsing mammals of 20 species such as black rhino, giraffe, common eland, Burchell's zebra, oryx, blesbok, blue and black wildebeest and red hartebeest (Kuzikus Wildlife Reserve 2010). Wildlife continuously graze the reserve as there are no inner fences, which has resulted in over-grazed veld and subsequent increase in bush density in some areas (personal observation). A 2.4 m high game proof fence separates Kuzikus from the eastern neighbouring farm, Ebenhaezer (Reinhard et al. 2009), with which it was compared for this study.

Ebenhaezer Livestock Farm

Ebenhaezer is a 2,200 ha mixed livestock farm with karakul sheep, cattle and horses being farmed commercially (Vinte 2015). The vegetation type, rainfall, evaporation and soil texture and structure are identical to Kuzikus. The grass sward is however dominated by *Stipagrostis uniplumis*, which in this ecosystem indicates veld in good condition. Rotational grazing is practised by the farm management to prevent over-grazing, and predator control is practised to prevent sheep losses (PH Hugo pers. com.).

Night survey methodology

Night surveys were conducted to determine and compare species diversity and abundance of nocturnal mammals between the two land-uses. Road strip count routes (Bothma & Toit 2010) transversed both properties in the two dominant habitats (bush encroached and open grassland) (Figure 1b). A fixed, three-hour route was driven at 20 km/h for five consecutive nights. The strips were equidistant on each property and random start and end-points were chosen to eliminate temporal bias of sightings. This was done both in the growing (25-29 March 2016) and non-growing season (26-30 August 2016) of 2016. A minimum of three people was required to conduct the surveys each night: a driver and two observers/recorders (Sliwa et al. 2014). The two observers each used a spotlight of 1 million candlepower or higher and observed the road on both sides. Each medium-sized bioturbating mammal or mesocarnivore sighted was recorded, including the date and time sighted, GPS coordinates of their location, perpendicular distance estimated from vehicle and the habitat in which they were observed.

Habitat survey/response

Both sites were surveyed aerially to obtain multispectral imagery of the two land-uses (Figure 1c, d). A senseFly eBee drone was set up, using eMotion 2 software, to fly an area of 100 ha on both properties (senseFly 2015) (Figure 1c, d). Visual (red-green-blue) and near infrared (NIR) georeferenced images of 4 cm pixel resolution were produced. The images were processed using the Postflight Terra 3D software and were used to quantify the medium-sized mammal burrow density, shrub density and vegetation productivity.

Grid cells of 50 x 50 m were overlaid onto the two sites using QGIS software (Anonymous 2016a) to further analyse the different habitats. Areas of two different sizes were quantified per site. Firstly, approximately the full 100 ha area ("whole survey") per site, containing 196 cells in total; and secondly, due to extensive shrub encroachment, a subset of each area where shrubs were less abundant ("Less shrubby subset" – 48 cells per site) (Figure 1c, d).

Burrow and shrub density

The medium-sized mammal burrows were marked as points using QGIS and the diameter of each burrow on the images was measured. Burrow size-classes were determined by species use and classified as small, medium and large. Burrow diameters of 8-14 cm (striped polecat, *Ictonyx striatus*) were classified as small, 15-30 cm (springhare, *Pedetes capensis*; black-footed cat, *Felis nigripes*; African wild cat, *Felis silvestris lybica*; small-spotted genet,

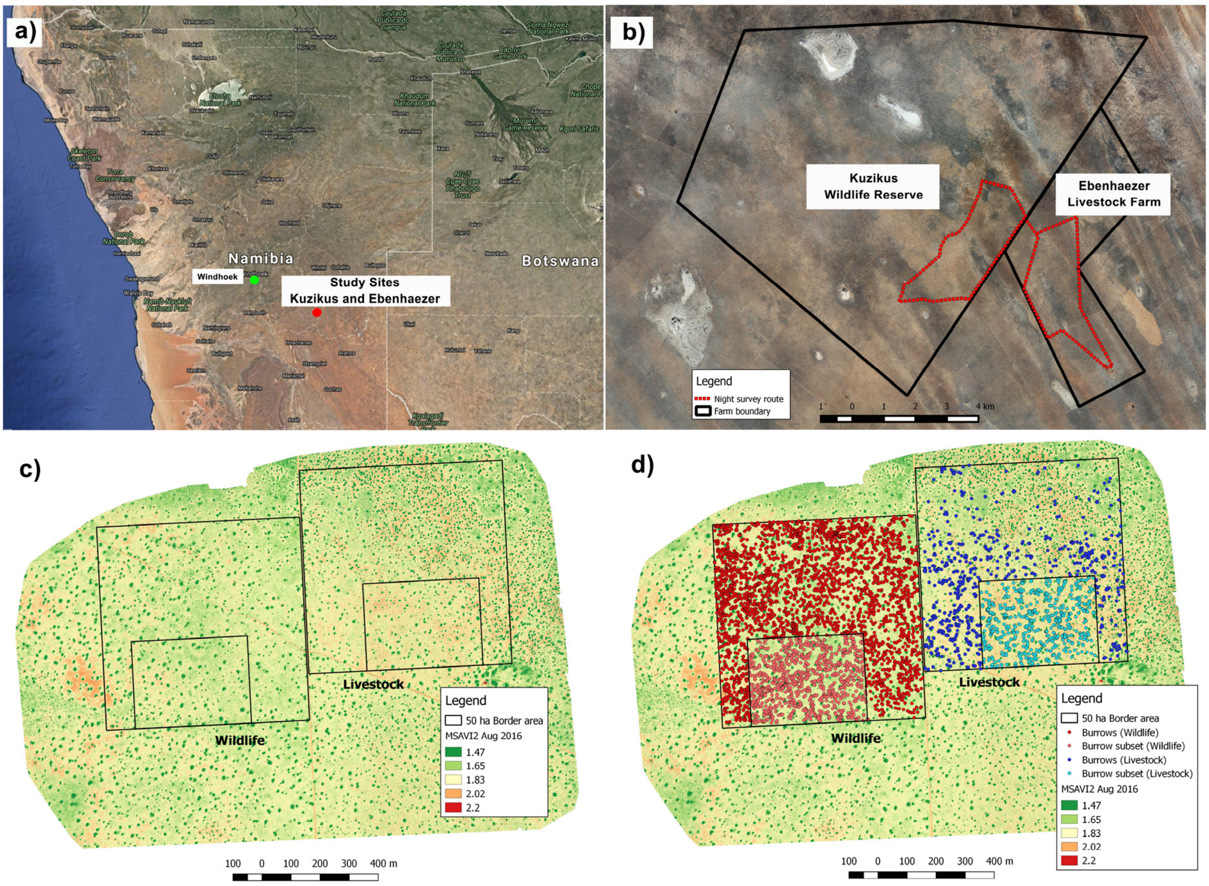


Figure 1: *Two neighbouring study sites of different management types: Kuzikus Wildlife Reserve and Ebenhaezer livestock farm. a) Location map of sites within Namibia. b) Outer borders of sites, location of fences, and night animal survey routes taken throughout growing and winter seasons. c) Defined areas for habitat survey, taken by aerial drone, including the two-sized areas: larger "whole survey" and smaller "less shrubby subset". Including productivity index MSAV12 where lower values signify greater productivity. d) Location of burrows identified on images in the two sites.*

Genetta genetta) as medium, and 31-100 cm (bat-eared fox, *Otocyon megalotis*; Cape fox, *Vulpes chama*; pangolin, *Manis temminckii*; Cape porcupine, *Hystrix africaeaustralis*; aardwolf, *Proteles cristatus*; aardvark, *Orycteropus afer*) as large (Skinner & Smithers 1990). A subset of burrows was ground-truthed to confirm size classifications (Goodchild 1994).

Similarly, shrubs were also marked on the images using QGIS software. The diameters were measured using the same protocol as for burrows, returning information for shrub number and shrub area per survey area or per cell.

Site productivity

Multispectral images taken by the eBee drone were processed and analysed using the Postflight Terra 3D software (senseFly 2015) to determine plant productivity across the two sites, as well as productivity around burrows (Bonachela et al. 2015) (Figure 1c). The Modified Soil-Adjusted Vegetation Index (MSAVI2) was used to assess productivity (Huete 1988). This is a commonly-used index that is a version of the Normalised Difference Vegetation Index (NDVI), but additionally corrects for atmospheric conditions, soil and the sun's angle. The MSAVI2 index is a ratio of the reflected visible and NIR light by vegetation (Weier & Herring 2000). Through the process of photosynthesis, visible light is strongly absorbed by chlorophyll inside green plant leaves, however NIR light is strongly reflected due to the structure of the leaves. Most of the visible light is absorbed by healthy plant biomass and, in return, a large amount of NIR light is reflected. In unhealthy or sparse plant biomass, less visible light is absorbed and, in return, less NIR light is reflected. Importantly, MSAVI2 is inversely related to productivity/green biomass. Therefore, lower values of MSAVI2 signify higher values of productivity (usually in the range of 0.5 (high productivity) to 2.5 (low productivity)).

Productivity of vegetation around burrows identified from the multispectral images was also calculated. Buffer areas (5 segments, undissolved) of five meters were created around each individual burrow identified using QGIS. A buffer polygon layer and MSAVI2 overlay was produced for each property and season. The layers were then run through the QGIS "Zonal Statistics" plugin to extract median pixel values for each burrow radius.

Statistical Analyses

All statistical analyses were performed in R version 3.2.2 (Anonymous 2016b).

The animal night-drive observation data were analysed using Generalised Linear Models (GLM) fitted to a negative binomial distribution, using R package MASS (Venables & Ripley 2002). In total, there were five nights (replications) of recordings per site per season.

Firstly, the total number of mammal observations was analysed. The response variable for this statistical model was therefore "total mammal observations", and explained with the two-level categorical explanatory variable Site (wildlife reserve or livestock farm), the two-level categorical variable Season (growing or winter), and the interaction of Site x Season.

Secondly, the single-species observational data were also analysed. In total, nine species were observed across both sites, and all are described in the tables and figures for interest (see Appendix 1 for species details). However, four of the species occurred in very small numbers, therefore, statistical analysis was only performed for a subset of the five most common species (African wild cat, aardwolf, bat-eared fox, springhare, and small-spotted genet). Similar to the total observations, the negative binomial GLM for single-species observations included the Site (wildlife reserve or livestock farm), Season (growing or winter), but additionally the five-level categorical explanatory variable Species. Also included were all three two-way interactions, and the three-way interaction Species x Site x Season.

Thirdly, as a measure of site diversity, we applied the commonly used Shannon-Wiener Diversity Index (Shannon 1948). This was modelled using linear models in the R basic stats package (Anonymous 2016b), testing the explanatory variables Site, Season and the interaction Site x Season.

For visual representation of the species observation data, log ratios were calculated to reveal the relative change in number of observations across sites in a season. Log ratios were calculated as the natural logarithm (+0.2) of the mean observations per survey in the wildlife reserve minus the log (+0.2) observations in the livestock farm. Positive values therefore signified relatively greater presence on the wildlife reserve, and negative values greater presence on the livestock farm.

For the habitat survey, many of the aerial outputs were calculated at a site level, and were therefore simply reported descriptively and not statistically analysed. However, using linear models in the R basic stats package (Anonymous 2016b), differences in productivity (median MSAVI2) around the three size categories of burrows (small, medium or large) were tested. This was performed on the whole survey and the less-shrubby subset. Replication for each site and each size area was dependent on the number of burrows observed.

Additionally, using 50 x 50 m cells per surveyed area, relationships between productivity (median MSAVI2 as response variable) and number or area of burrows per cell (log-transformed continuous explanatory variables) were tested. Finally, linear models were used to test for relationships between number or area of burrows and the number and area of shrubs.

RESULTS

Animal foraging/observations

The total number of night-time medium-sized mammal sightings was highly dependent on season. The main effect of season was statistically significant (deviance=18.86; p<0.001) with more mammal sightings in the growing season than winter (Figure 2a). However, this growing-season increase was only evident on the livestock farm, as indicated by a statistically significant interaction in the GLM of site by season (deviance=33.30; p<0.001; Figure 2a). On the wildlife reserve, sightings of mammals were similar in both seasons. Furthermore, while the overall number of sightings was similar at both sites, the sightings of mammals was higher on the livestock farm in the growing season, and higher on the wildlife reserve during winter (Figure 2).

Season also played a large role in determining the number and locality of observations of each single species (Figure 3, Table 1 and Table 2). The statistics and figures reveal that total species richness was higher on the wildlife reserve compared to the livestock farm (5 versus 2 in the growing season and 5 versus 1 in the winter).

Springhare was a key species in the interaction terms of both the single species (Table 2) comparison and total sightings (Figure 2). It switched seasonally in terms of where it was observed more frequently (Site x Season effect: deviance=29.29; p<0.001). Overall it was observed marginally more frequently on the livestock farm (Table 1), where it was seen in greater numbers during the growing season (Figure 3) but less frequently in the non-growing season.

In a similar seasonal effect, African wild cat was more abundant on the wildlife reserve during winter compared to growing season (Table 1), whereas on the livestock farm it was only observed in the growing season (Table 1) (note that this is not possible to see in Figure 3). Bat-eared fox was the only species to be seen more frequently on the livestock farm both in the growing season and in the winter (Table 1; Figure 3).

The Shannon-Wiener Diversity Index (SWDI) indicated that diversity was higher on the wildlife reserve (mean SWDI=1.02) than the livestock farm (mean SWDI=0.53) (Figure 1b; Site effect: F=20.29 p<0.01) when seasons were combined. However, there was statistically no significant difference in diversity related to season (F=3.69 p=0.08) or the interaction between Site and Season (F=0.95 p=0.34).

Habitat response/observations

The analysis of the aerial imagery revealed some important differences between the two sites in terms of number of burrows, shrubs and productivity (Tables 3, 4; Figure 1c, d). Burrows were more abundant on the wildlife reserve over the fully surveyed area and the less shrub-encroached patch (Table 3). Interestingly, the distribution of burrow sizes varied greatly between sites (Table 4) with small burrows being more abundant while medium- and large-sized burrows were much more similar in number at the two sites.

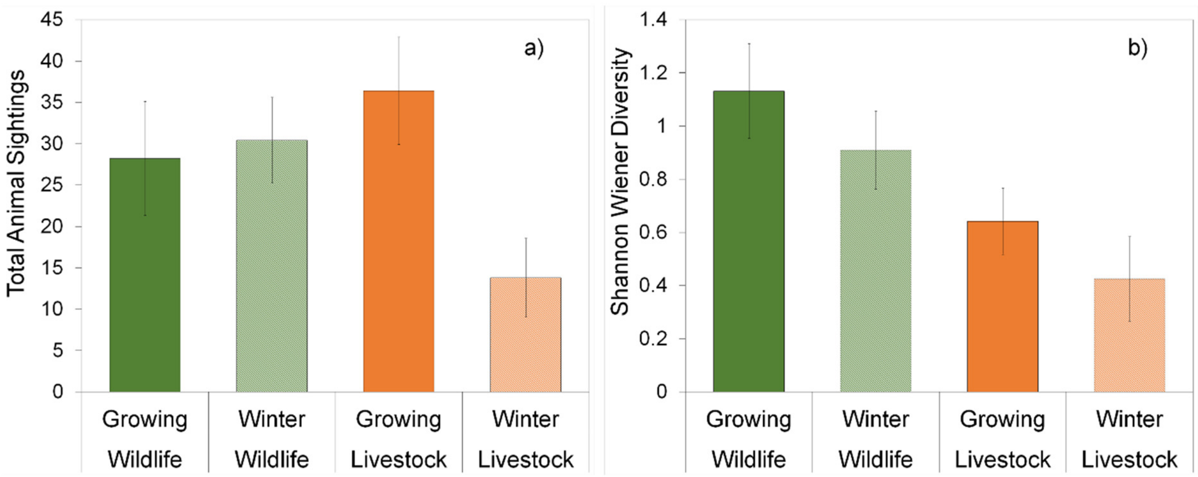


Figure 2: *a) Mean number of total medium-sized mammal sightings (per night) and b) Mean Shannon Wiener Diversity Index, surveyed during night-time drives. Five night-time drives were conducted at each site of different management type (Wildlife reserve or Livestock farm) during the growing season and winter season. Bars indicate standard errors on the normal scale.*

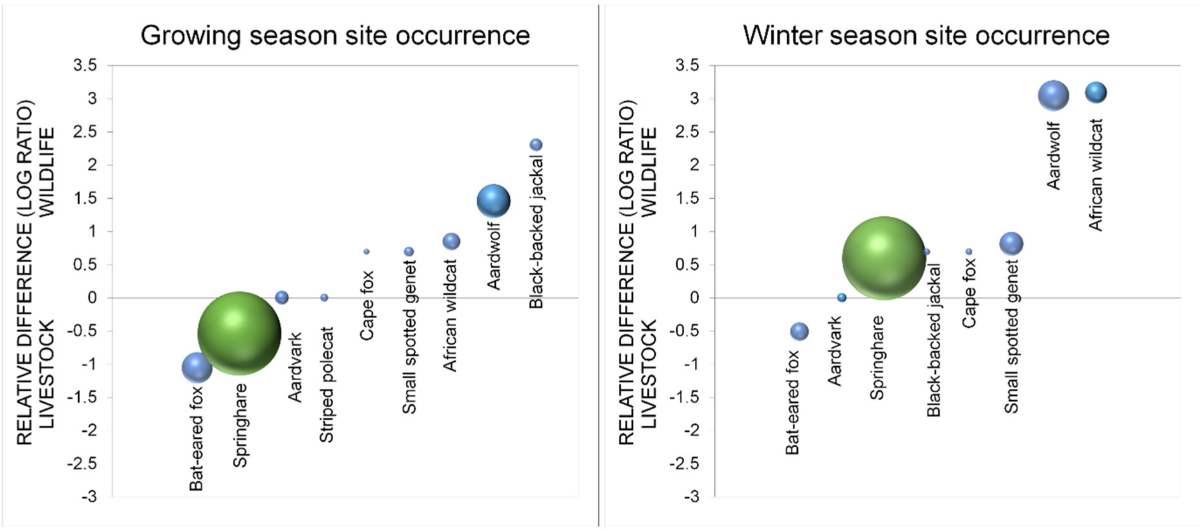


Figure 3: *Relative frequency of single species sightings during night-time drives. Y-axis gives the log ratio of mammal sightings during the growing season (left) or winter (right) at the two sites of different management types (Wildlife reserve or Livestock farm). Positive values indicate greater frequency of sightings during a season on the wildlife reserve, negative values indicate greater frequency of sightings during a season on the livestock farm. Species are ranked along each separate x-axis by strength of log ratio. Bubble sizes are related to overall frequency of sightings of a given species.*

Table 1: *Mean frequency of medium-sized mammal sightings during five night-time drives per site (Wildlife reserve, Livestock farm) per season (growing season, winter season). Values in italic font indicate standard deviations.*

	Wildlife Reserve				Livestock Farm			
Species	Growing		Winter		Growing		Winter	
African wild cat	1.4	*0.89*	2.2	*1.79*	0.6	*0.89*	0.0	*0.00*
Aardvark	0.6	*0.55*	0.2	*0.45*	0.6	*0.89*	0.2	*0.45*
Aardwolf	6.0	*4.00*	4.2	*4.97*	1.4	*0.89*	0.2	*0.45*
Bat-eared fox	1.6	*2.07*	0.6	*0.89*	4.6	*3.78*	1.0	*1.00*
Black-backed jackal	1.0	*0.71*	0.2	*0.45*	0.0	*0.00*	0.0	*0.00*
Cape fox	0.2	*0.45*	0.2	*0.45*	0.0	*0.00*	0.0	*0.00*
Small-spotted genet	0.4	*0.55*	1.8	*1.10*	0.2	*0.45*	0.8	*1.30*
Springhare	16.8	*1.10*	21.0	*2.35*	28.8	*4.97*	11.6	*3.72*
Striped polecat	0.2	*0.45*	0.0	*0.00*	0.2	*0.45*	0.0	*0.00*

Table 2: *ANOVA table for single-species sighting data during night-time drive survey. Data were analysed using a negative binomial Generalised Linear Model testing for the effect of Species (5 most common species – see text), Site (Wildlife reserve or Livestock farm), Season (Growing or Winter), and all two- and three- way interactions.*

**** indicates p<0.001; NS indicates not significant.*

Variable	DF	Deviance	p
Species	4	752.80	***
Site	1	2.20	NS
Season	1	16.17	***
Species x Site	4	53.08	***
Species x Season	4	19.81	***
Site x Season	1	33.97	***
Species x Season x Site	4	3.52	NS

The livestock farm had many more shrubs than the wildlife reserve. There were approximately 3.5 times more shrubs on the livestock farm when viewing the whole surveyed areas, and although much fewer in terms of number, there were still 2.3 times more shrubs on the livestock farm on the less shrubby subset (Table 3). Within both sites, when analysing within cell patterns, burrow area had a negative relationship with shrub area (Figure 4; Wildlife $F=12.62$ $p<0.001$; Livestock $F=71.15$ $p<0.001$; DF=194).

The wildlife area was more productive in terms of vegetation growth (lower MSAVI2) than the livestock farm (Table 3). Vegetation productivity also varied around burrows of different sizes (Table 4, Figure 5). Across the entire study site and “less shrubby subset” area on both the wildlife reserve and the livestock farm, MSAVI2 was significantly lower – and therefore had higher productivity – around large burrows compared to small burrows (Table 4; Figure 5). However, when analysing values within

Table 3: *Habitat properties of two neighbouring sites of different management type (Wildlife reserve and Livestock farm) extracted from aerial drone images. Shown are details for burrows and shrubs for both total number and total area (m²), and mean number and mean area (m²) per 50 x 50 m cells. Additionally, the productivity index (MSAVI2 median) for the surveyed areas are presented, whereby lower values indicate higher productivity. All values shown are for two sizes of survey area: larger "Whole survey" (196 cells) and "Less shrubby subset" (48 cells).*

		Whole survey		Less Shrubby Subset	
		Wildlife	Livestock	Wildlife	Livestock
Burrows	Number	4425	1340	1033	683
	Area	160.42	93.91	33.89	40.13
Burrows per cell	Number	22.58	6.84	21.52	14.23
	Area	0.82	0.48	0.71	0.84
Shrubs	Number	653	2283	130	294
	Area	2,395.65	15,893.49	385.21	1,508.79
Shrubs per cell	Number	3.33	11.65	2.71	6.13
	Area	12.22	81.09	8.03	31.43
MSAVI2 (med.)	Growing	1.7714	1.8176	1.7708	1.8435
	Winter	1.9699	1.9644	1.9619	1.9847

Table 4: *Number and characteristics of burrows identified from aerial drone images. Burrows from two sites (Wildlife reserve and Livestock farm) and two sizes of survey area (Whole survey and Less shrubby subset) were classified into size categories: small (8-14 cm); medium (15-30 cm); large (31-100 cm). Shown are the number per site per survey size in each category, the proportion of the total number per site per survey size in each category, and the vegetative productivity in the 5 m surrounding each burrow, measured using MSAVI2 median, whereby lower values indicate higher productivity. Letters next to productivity measures indicate values that did not differ significantly when compared using a linear model.*

		Whole Survey		Less Shrubby Subset	
	Burrow Size	Wildlife	Livestock	Wildlife	Livestock
Number of Burrows	Small	2071	144	522	88
	Medium	1865	847	405	449
	Large	489	349	106	146
Proportion of Burrows	Small	0.49	0.11	0.51	0.13
	Medium	0.40	0.63	0.39	0.66
	Large	0.10	0.26	0.10	0.21
MSAVI2 around Burrows	Small	1.772a	1.838b	1.774a	1.849b
	Medium	1.772a	1.822a	1.769ab	1.832a
	Large	1.767b	1.817a	1.761b	1.830a

cells, there was no relationship between number or area of burrows per cell and productivity in the less shrubby areas (Wildlife F=0.98 p=0.33; Livestock F=0.578 p=0.45).

DISCUSSION

By comparing two neighbouring sites of different management types, our study was able to reveal interesting seasonal and land-use dependent dynamics of the under-studied nocturnal mammals of southern Africa. Both the abundance of active nocturnal medium-sized mammals and burrowing activity was higher within the wildlife reserve compared to the neighbouring livestock farm. Importantly, the study revealed that some mammals have clear habitat preferences during different seasons.

Nocturnal activity

The observations carried out during night-time drives showed species-specific differences in frequencies of sightings related to management type, season and their interaction. In general, we would consider the movement of this mainly nocturnal group of animals to be related to their foraging behaviour. Surprisingly, the overall total number of sightings was similar on both the wildlife reserve and the livestock farm. However, this was confounded by a large seasonal shift observed on the livestock farm. Here, numbers were significantly lower in the winter when potential food stocks are low. In contrast, frequencies of sightings were more intermediate, but similar in number, in both the growing season and winter on the wildlife reserve. It seems much more likely that the herbivorous mammals would seek shelter and food in these areas during winter, and that the predators may be attracted by the increased prey presence.

In agreement with our hypothesis, we showed that species diversity was higher on the wildlife reserve than the livestock farm. Five mammals were seen more frequently on the wildlife reserve compared to the livestock farm, where there were only two more frequent in the growing season and one more frequent in winter. The only mammal to be consistently seen more frequently on the livestock farm was bat-eared fox. In contrast, aardwolf were more commonly observed on the wildlife reserve. This species had a higher foraging preference on the wildlife reserve in both the growing season and winter season, with similar seasonal proportions but lower sightings on the livestock farm (Williams et al. 1997, Blaum et al. 2009). African wild cat were mainly observed on the wildlife reserve and slightly more often during winter. This was probably due to the lack of vegetation cover on the livestock farm, where they were not observed at all in winter. Blaum et al. (2007) found that increased shrub cover affects African wild cat abundance negatively, which could explain their absence on the livestock farm, but increased foraging activity during winter could also explain the observations (Herbst & Mills 2010). Black-backed jackal were never observed on the livestock farm, probably as a result of them being persecuted for livestock losses (Blaum et al. 2009), and therefore avoiding this site. Jackal are known to be quick to learn avoidance behaviour to persecution (Brand et al. 1995, Kaunda 2000).

Springhare observations played a large role in the switching patterns revealed in the total number of observations and the species observations. During the growing season, it was seen regularly on the livestock farm, but during winter this species was seen in highest frequencies on the wildlife reserve. When considering the feeding preference of springhare for short and green grass (Augustine et al. 1995, Peinke et al. 2016), it could explain the switching patterns observed as the wildlife area showed more vegetation productivity than the livestock farm in the winter season. Springhare are also sensitive to human disturbances and increased human activities on the livestock farm (active management, hunting/chasing) could also result in a preference for the wildlife area (Butynski 1984, Yellen 1991, Peinke et al. 2016).

Overall, the general pattern seems to be that while many more species of these mammals were observed on the wildlife reserve, they were also observed to be foraging on the livestock farm, but mainly in the growing season when food and cover were more plentiful (Vinte 2015, Peinke et al. 2016).

Number and size of burrows

The aerial images produced for our study also revealed that not only were more species seen in the wildlife reserve, but more burrows were present there. Interestingly, the large burrows, classified in our study as between 31-100 cm, were in similar numbers on the two sites. These larger burrows are often home to mammals such as the bat-eared fox, Cape fox, pangolin, Cape porcupine, aardwolf, aardvark, and warthog (Skinner & Smithers 1990, Apps 2000, Stuart & Stuart 2013) and indeed this matches our sighting numbers well. While the aardwolf was much more often seen on the wildlife reserve, the bat-eared fox was seen in greater numbers on the livestock farm. This potentially suggests that the bat-eared fox has a relatively short foraging range (Mackie 1989, Pauw 2000). A rabies outbreak the previous year (2015) in the wildlife area (F. Reinhard pers. com.) also affected the bat-eared fox abundance (Maas 1993, Nel 1993). Furthermore, it indicates that the combined approach of using aerial images and night-time viewings as a tool to further our knowledge on these mammals is effective.

In contrast though, the high number of burrows recorded on the wildlife reserve were mainly those of the smaller size 8-14 cm in diameter, which provide homes to mammals such as the striped polecat, ground squirrel (*Xerus inauris*) and yellow mongoose (*Cynictis penicillata*). The striped polecat, being the only nocturnal species of the three, was observed only twice during the whole period of recording. This may be attributed to missed sightings as a result of small size, low preference for increased shrub cover (Blaum et al. 2007), or the recent rabies outbreak affecting abundances (Cumming 1982, Larivière 2002).

One possibly confounding effect to the greater presence of burrows on the wildlife reserve, was that shrub presence and area were higher on the livestock farm and in general, shrub presence was negatively related to burrow density. This relates to

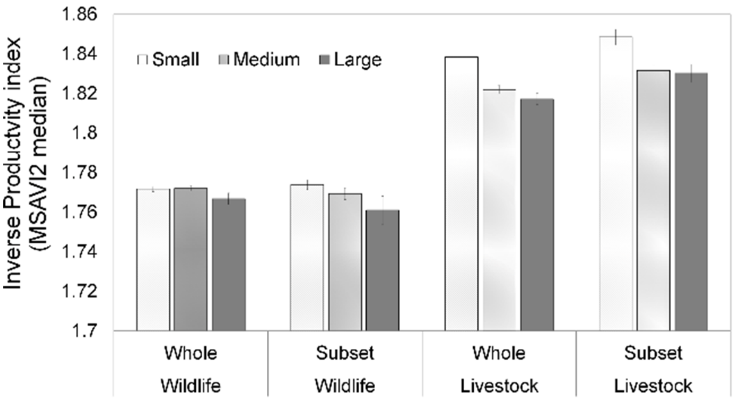


Figure 5: *Productivity (inverse) of vegetation surrounding mammal burrows of different size classifications: small (8-14 cm); medium (15-30 cm); large (31-100 cm). Data collated from aerial drone captured images, using the median MSAVI2 (productivity index) within 5 m distance from identified burrows. Lower values indicate higher productivity. Shown are values for two sites of different management type: Wildlife reserve and Livestock farm, and two sizes of survey areas "Whole survey" and "Less shrubby subset". Bars are standard errors where n equals the number of burrows per category (see Table 4).*

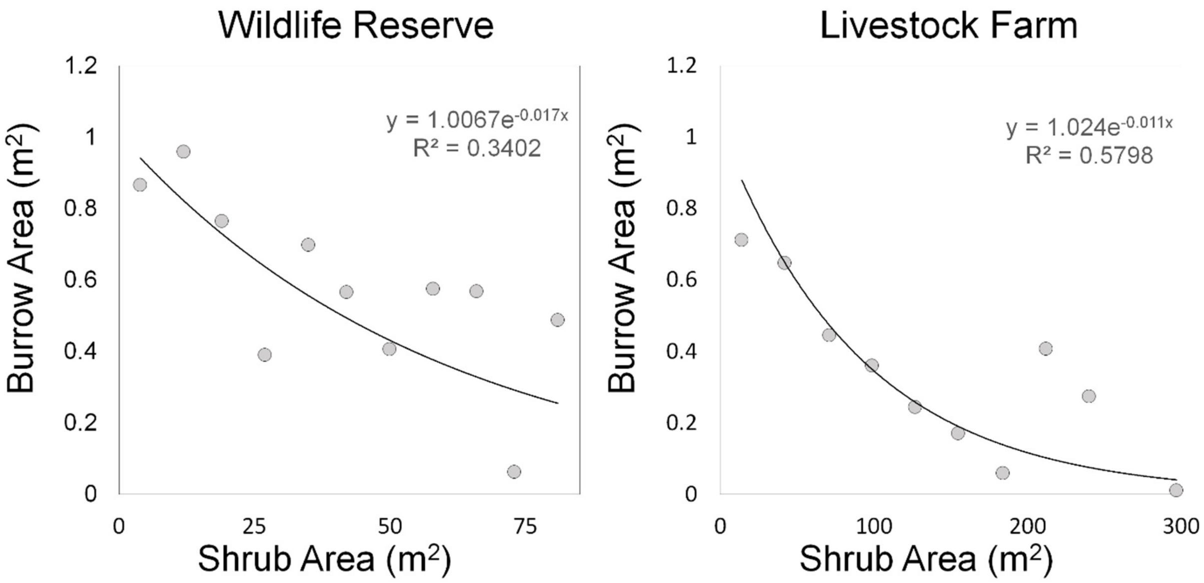


Figure 4: *Negative relationships between mean shrub area and burrow area at both sites of different management type. Data calculated from aerial drone images for "whole survey" area within superimposed cells 50m x 50m (196 cells). Note different scale on x-axis for livestock farm and wildlife reserve, with greater mean shrub area on livestock farm.*

burrowing mammals preferring short grass or open areas for their burrows (Skinner & Smithers 1990, Augustine et al. 1995, Apps 2000). However, even taking this into account, by surveying a smaller subset of less shrubby area on the livestock farm, it was still found that there were more burrows present on the wildlife reserve.

Productivity and shrubs

The aerial images revealed some important differences between the two study sites. In general, the wildlife reserve had higher vegetation productivity than the livestock farm. It is unclear whether this is a cause or consequence of the management type, whereby continual grazing by livestock in this marginal livestock farming area (Mogotsi et al. 2011) is likely to diminish quality fodder. However, grazing is not limited to the farm, and over-grazing was considered a concern on the wildlife reserve. Therefore, finding ways to keep productivity high may lie in helping to improve biodiversity in the area (Sala et al. 2000).

Potential feedbacks between medium-sized mammals and habitat

The study found that burrow size was related to vegetative productivity. In the 5 m surrounding each burrow we revealed that productivity was higher around the larger burrows (31-100 cm diameter) than the small burrows (8-14 cm in diameter). It is well known that burrowing mammals are likely to provide benefit to habitats in the same ways as do other bioturbators, such as earthworms (Meysman et al. 2006, Eldridge & James 2009, Fleming et al. 2014). It is often speculated that burrowing animals are likely to impact upon infiltration rates of water in the region (Reichman & Smith 1990, Avenant 2000), something of great importance in dry regions such as Namibia. Further turning of the soil will also cause aeration, which may help decomposition processes, and free up added nutrients (Reichman & Smith 1990, Gabet et al. 2003). Moreover, and particularly the case for the larger medium-sized mammals, defaecation close to or in the burrows will provide further nutrient sources. Therefore, provision of habitat conditions suitable for the mammals may feed back into providing more productive land.

However, despite the link between burrow size and productivity, our study did not reveal a direct link between burrows themselves and productivity. This result may be explained by the factor that burrows themselves cover an area, and cause disturbances to vegetation at their location (Butynski 1984, Augustine et al. 1995). At some intermediate point, these disturbances are likely to improve both productivity and plant species richness (Grime 1973), thereby providing great benefit to the ecosystem through the trophic levels. Further detailed analysis of the aerial images may provide more clues as to the benefit created by the mammals, by identifying and studying productivity indicators at various distances from burrows. Any findings would need to be supported by data collected at ground level, where paired localities can be compared for productivity response. Finding the mechanism for productivity increase, or the impact of the burrowing mammals, may be simpler in either a well-paired observational setting or, even more ideally, by using a controlled experimental setting, such as exclosures (Ewacha et al. 2016).

Overall, our study comparing two neighbouring sites of different management types has provided some valuable insights into the movements, strategies and potential benefits of these mammals. Further research is needed to extend these findings to other areas of Namibia, and determine the precise mechanisms by which the burrowers may provide benefits to the land. However, our study has revealed and supported evidence that these under-studied mammals have the potential to play an important role in ecosystem functioning.

ACKNOWLEDGEMENTS

Special thanks to the OPTIMASS Project and Namibia University of Science and Technology (NUST) who provided funding and support to this project. Thanks to Mr. Peter H. Hugo, owner of Ebenhaezer, and the Reinhard family, owners of Kuzikus Wildlife Reserve, for the use of their properties as study sites. Thanks to SASSCAL who provided the eBee drone. I would also like to thank Dr. Ben Strohbach for his assistance with the remote sensing data and fellow students Kaarina Shilula and Matthew Walters for their field assistance. MCB was supported by a DAAD (German Academic Exchange Service) research grant and the German research foundation (DFG-TI 338/15-1).

REFERENCES

Anonymous (2016a) *QGIS Geographic Information System*. Open Source Geospatial Foundation.

Anonymous (2016b) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Apps P (2000) *Smither's Mammals of Southern Africa*, 3rd ed. Struik Publishers, Cape Town, South Africa.

Augustine DJ, Manzon A, Klopp C, Elter J (1995) Habitat selection and group foraging of the springhare*, Pedetes capensis larvalis* Hollister, in East Africa. *African Journal of Ecology* 33: 347-357.

Avenant NL (2000) Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. *South African Journal of Wildlife Research* 30: 26-33.

Belsky AJ (1994) Influence of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.

Blaum N, Rossmanith E, Popp A, Jeltsch F (2007) Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologica* 31: 86-92.

Blaum N, Tietjen B, Rossmanith E (2009) Impact of livestock husbandry on small-and medium-sized carnivores in Kalahari savannah rangelands. *The Journal of Wildlife Management* 73: 60-67.

Bonachela JA, Pringle RM, Sheffer E, Coverdale TC, Guyton JA, Caylor KK, Levin SA, Tarnita CE (2015) Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science* 347: 651-655.

Bothma J du P, Toit JG du (eds) (2010) *Game Ranch Management*, 5th Revised edition. Van Schaik Publishers, Pretoria.

Brand DJ, Fairall N, Scott WM (1995) The influence of regular removal of black-backed jackals on the efficiency of coyote getters. *South African Journal of Wildlife Research-24-month delayed open access* 25: 44-48.

Butynski TM (1984) Nocturnal ecology of the springhare, *Pedetes capensis*, in Botswana. *African Journal of Ecology* 22: 7-22.

Cumming D (1982) *A case history of the spread of rabies in an African country*.

Davidson AD, Detling JK, Brown JH (2012) Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 10: 477-486.

De Groot RS, Wilson MA, Boumans RM (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological economics* 41: 393-408.

Edwards CA, Bohlen PJ (1996) *Biology and ecology of earthworms*. Springer Science & Business Media.

Eldridge DJ, James AI (2009) Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management & Restoration* 10: S27-S34.

Ewacha MVA, Kaapehi C, Waterman JM, Roth JD (2016) Cape ground squirrels as ecosystem engineers: modifying habitat for plants, small mammals and beetles in Namib Desert grasslands. *African Journal of Ecology* 54: 68-75.

Fleming PA, Anderson H, Prendergast AS, Bretz MR, Valentine LE, Hardy GES (2014) Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?: Loss of Australian digging mammals and ecosystem function. *Mammal Review* 44: 94-108.

Gabet EJ, Reichman OJ, Seabloom EW (2003) The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences* 31: 249-273.

Goodchild MF (1994) Integrating GIS and remote sensing for vegetation analysis and modeling: methodological issues. *Journal of Vegetation Science* 5: 615-626.

Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature, UK* 242: 344-347.

Herbst M, Mills MGL (2010) The feeding habits of the Southern African wildcat, a facultative trophic specialist, in the southern Kalahari (Kgalagadi Transfrontier Park, South Africa/Botswana). *Journal of Zoology* 280: 403-413.

Huete AR (1988) A soil-adjusted vegetation index (SAVI). *Remote sensing of environment* 25: 295-309.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373.

Kaunda SKK (2000) Activity patterns of black-backed jackals at Mokolodi Nature Reserve, Botswana. *South African Journal of Wildlife Research-24-month delayed open access* 30: 157-162.

Kuzikus Wildlife Reserve (2010) Catalogue of Kuzikus. *Kuzikus - Wildlife Reserve Namibia*.

Larivière S (2002) Ictonyx striatus. *Mammalian species*: 1-5.

Leistner OA, Werger MJA (1973) Southern Kalahari phytosociology. *Vegetatio* 28: 353-399.

Maas B (1993) Bat-eared fox behavioural ecology and the incidence of rabies in the Serengeti National Park.

Mackie JAJ (1989) Habitat selection, home range use, and group size of bat-eared foxes in the Orange Free State. *South African Journal of Wildlife Research-24-month delayed open access* 19: 135-139.

Meadows PS (1991) The environmental impact of burrows and burrowing animals—conclusions and a model. *Symposium of Zoological Society London*, 327-338.

Mendelsohn JM, Jarvis AM, Roberts CS, Robertson T (2002) *Atlas of Namibia - A Portrait of the Land and its People*. David Philip Publishers; Cape Town, South Africa.

Meysman F, Middelburg J, Heip C (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution* 21: 688-695.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: Biodiversity synthesis*. World Resources Institute, Washington, D.C.

Mogotsi K, Nyangito MM, Nyariki DM (2011) The perfect drought? Constraints limiting Kalahari agro-pastoral communities from coping and adapting. *African Journal of Environmental Science and Technology* 5: 168-177.

Nel JAJ (1993) The bat-eared fox: a prime candidate for rabies vector? *Onderstepoort Journal of Veterinary Research* 60: 395-397.

Pauw A (2000) Parental care in a polygynous group of bat-eared foxes, *Otocyon megalotis* (Carnivora: Canidae). *African Zoology* 35: 139-145.

Peinke D, Wilson B, Anderson C (2016) A conservation assessment of *Pedetes capensis*. In: Child M.F., Roxburgh L., Do Linh San E, Raimondo D., Davies-Mostert H.T. (eds) *The Red List of Mammals of South Africa, Swaziland and Lesotho*, South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Prose DV, Metzger SK, Wilshire HG (1987) Effects of substrate disturbance on secondary plant succession; Mojave Desert, California. *Journal of Applied Ecology* 24: 305-313.

Reichman OJ, Smith SC (1990) Burrows and burrowing behaviour by mammals. In: Genoways HH (ed) *Current Mammalogy*, 197-244. Plenum Press, New York and London.

Reinhard J, Brown L, Hellerich S, Marston R (2009) Distribution and abundance of large mammals in Kuzikus Wildlife Reserve. *Biological Research in Kuzikus* 1: 1-14.

Roemer GW, Gompper ME, Valkenburgh BV (2009) The ecological role of the mammalian mesocarnivore. *BioScience* 59: 165-173.

Sala OE, Chapin FS, Iii, Armesto JJ, Berlow E, Bloomfield J et al. (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770-1774.

senseFly (2015) *eBee senseFly: Extended User Manual*, 17th Revision. senseFly Ltd, Lausanne, Switzerland.

Shannon CE (1948) A mathematical theory of communication, Part I, Part II. *Bell Syst. Tech. J.* 27: 623-656.

Skinner JD, Smithers RHN (1990) *The mammals of the southern African subregion*, 2nd ed. University of Pretoria, Pretoria, South Africa.

Sliwa A, Wilson B, Kusters M, Lawrenz A, Eggers B, Herrick J, Tordiffe A, Marais P, Marais S (2014) *Report on surveying, catching and monitoring Black-footed cats (*Felis nigripes*) on Benfontein Nature Reserve, Nuwejaarsfontein and Taaiboschpoort Farms in 2014*. Black-footed Cat Working Group.

Stuart C, Stuart M (2013) *A Field Guide to the Tracks & Signs of Southern, Central & East African Wildlife*, 4th ed. Struik Nature, Cape Town, South Africa.

Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, 4th ed. Springer, New York.

Vinte M (2015) *Comparing bioturbating small mammal abundance and diversity on two different land uses in the Kalahari sand-veld, Omaheke, Namibia*. OPTIMASS annual report. University of Potsdam. Potsdam, Germany.

Weier J, Herring D (2000) Measuring Vegetation (NDVI & EVI): Feature Articles. *NASA Earth Observatory*.

Williams JB, Anderson MD, Richardson PRK (1997) Seasonal differences in field metabolism, water requirements, and foraging behavior of free-living aardwolves. *Ecology* 78: 2588-2602.

Yellen JE (1991) Small mammals: !Kung San utilization and the production of faunal assemblages. *Journal of Anthropological Archaeology* 10: 1-26.

Zhang Y, Zhang Z, Liu J (2003) Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mammal Review* 33: 284-294.

Appendix 1: *Species names and characteristics of all medium-sized mammals observed during night-time surveys on the two different habitat types: Wildlife reserve and livestock farm. Species are listed in order of frequency of sightings (Source of information: Skinner & Smithers 1990, Augustine et al. 1995, Apps 2000).*

Species	Social structure	Size of territory (foraging range)	Preferred habitat	Breeding Season	Main Diet	Predators/Hunted
Springhare (*Pedetes capensis*)	Social (2-6)	Up to 400 m from burrow	Short, open grasslands	Not seasonal	Grass seeds, stems, leaves, corms, roots & rhizomes. Seeds & seedlings of *Acacia* spp.	20 mammal species, 7 bird species, 4 reptile species, humans
Aardwolf (*Proteles cristatus*)	Solitary	Area with about 3000 termite mounds. Depends on density of termites	Nama Karoo, Succulent Karoo, grassland & savanna biomes	Mating June-July. Breeding October-December	Nasute harvester termites	Black-backed jackal greatest enemy, humans
Bat-eared fox (*Otocyon megalotis*)	Social foragers	1.5-2 km^2	Short, open grasslands	October-December	Insectivorous; harvester termites	African wild dog, hyaena, leopard, cheetah, humans and raptors
African wild cat (*Felis silvestris lybica*)	Solitary	About 4.3km^2 (territorial)	Wide habitat tolerance	September-March	Mice, rats, birds up to guinea fowl, scrub hare	Unknown
Small-spotted genet (*Genetta genetta*)	Solitary	Unknown	Open, arid habitats, woodland savanna	Summer	Insects, mice, arachnids, birds & reptiles	Unknown
Aardvark (*Orycteropus afer*)	Solitary	2.0-4.7 km^2	Open woodland, scrub and grassland	Not seasonal	Formicid ants and termites	Large predators and humans
Black-backed jackal (*Canis mesomelas*)	Solitary or in pairs	18.2 km^2	Wide habitat tolerance	May-September	Omnivorous, insects, scrub hare, springhare, small antelopes, small livestock	Large predators and humans
Cape fox (*Vulpes chama*)	Solitary	1.0-4.6 km^2	Open grassland, scattered thickets, semi-desert scrub	August-October	Rodents, invertebrates, reptiles, birds, eggs, fruit	Large predators and humans
Striped polecat (*Ictonyx striatus*)	Solitary	Unknown	Wide habitat tolerance	Summer	Insects and mice	Large predators