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**SECTION A: PEER-REVIEWED PAPERS**

Recommended citation format:

Responses and feedbacks of burrowing mammals under differently managed rangelands

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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 mediumsized 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. 2003, 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).

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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 (*Ictonyx striatus*) were classified as small, 15-30 cm (*Pedetes capensis*; black-footed cat, *Felis nigripes*; African wild cat, *Felis silvestris lybica*; small-spotted genet, *Genetta vittata*).

*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 (batar-
eared fox, Otocyon megalotis; Cape fox, Vulpes
chama; pangolin, Manis temminckii; Cape porcupine,
Hystrix afer; 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)
fit 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 (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 (Table 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.
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

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**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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wildlife Reserve</th>
<th></th>
<th>Livestock Farm</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Growing</td>
<td>Winter</td>
<td>Growing</td>
<td>Winter</td>
</tr>
<tr>
<td>African wild cat</td>
<td>1.4</td>
<td>0.89</td>
<td>2.2</td>
<td>1.79</td>
</tr>
<tr>
<td>Aardvark</td>
<td>0.6</td>
<td>0.55</td>
<td>0.2</td>
<td>0.45</td>
</tr>
<tr>
<td>Aardwolf</td>
<td>6.0</td>
<td>4.00</td>
<td>4.2</td>
<td>4.97</td>
</tr>
<tr>
<td>Bat-eared fox</td>
<td>1.6</td>
<td>2.07</td>
<td>0.6</td>
<td>0.89</td>
</tr>
<tr>
<td>Black-backed jackal</td>
<td>1.0</td>
<td>0.71</td>
<td>0.2</td>
<td>0.45</td>
</tr>
<tr>
<td>Cape fox</td>
<td>0.2</td>
<td>0.45</td>
<td>0.2</td>
<td>0.45</td>
</tr>
<tr>
<td>Small-spotted genet</td>
<td>0.4</td>
<td>0.35</td>
<td>1.8</td>
<td>1.10</td>
</tr>
<tr>
<td>Springhare</td>
<td>16.8</td>
<td>1.10</td>
<td>21.0</td>
<td>2.35</td>
</tr>
<tr>
<td>Striped polecat</td>
<td>0.2</td>
<td>0.45</td>
<td>0.0</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**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.
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 seasonal trend 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

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**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).

<table>
<thead>
<tr>
<th></th>
<th>Whole survey</th>
<th>Less Shrubby Subset</th>
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<tr>
<td>Area</td>
<td>160.42</td>
<td>93.91</td>
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<tr>
<td>Burrows per cell</td>
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<td></td>
</tr>
<tr>
<td>Number</td>
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</tr>
<tr>
<td>Area</td>
<td>0.82</td>
<td>0.48</td>
</tr>
<tr>
<td>Shrubbs</td>
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<td></td>
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<tr>
<td>Number</td>
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<tr>
<td>Area</td>
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<tr>
<td>Shrubbs per cell</td>
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<td></td>
</tr>
<tr>
<td>Number</td>
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</tr>
<tr>
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<tr>
<td>MSAV2 (med.)</td>
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<td>Growing</td>
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</tr>
<tr>
<td>Winter</td>
<td>1.9699</td>
<td>1.9644</td>
</tr>
</tbody>
</table>

**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 MSAV2 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.

<table>
<thead>
<tr>
<th>Burrow Size</th>
<th>Whole Survey</th>
<th>Less Shrubby Subset</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>2071</td>
<td>144</td>
</tr>
<tr>
<td>Medium</td>
<td>1865</td>
<td>847</td>
</tr>
<tr>
<td>Large</td>
<td>489</td>
<td>349</td>
</tr>
<tr>
<td>Proportion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>0.49</td>
<td>0.11</td>
</tr>
<tr>
<td>Medium</td>
<td>0.40</td>
<td>0.63</td>
</tr>
<tr>
<td>Large</td>
<td>0.10</td>
<td>0.26</td>
</tr>
<tr>
<td>MSAV2 around Burrows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>1.772a</td>
<td>1.838b</td>
</tr>
<tr>
<td>Medium</td>
<td>1.772a</td>
<td>1.822a</td>
</tr>
<tr>
<td>Large</td>
<td>1.767b</td>
<td>1.817a</td>
</tr>
</tbody>
</table>

---
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 wart hog (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).]
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

![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.](image)
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

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REFERENCES


**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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Social structure</th>
<th>Size of territory (foraging range)</th>
<th>Preferred habitat</th>
<th>Breeding Season</th>
<th>Main Diet</th>
<th>Predators/Hunted</th>
</tr>
</thead>
<tbody>
<tr>
<td>Springhare <em>Pedetes capensis</em></td>
<td>Social (2-6)</td>
<td>Up to 400 m from burrow</td>
<td>Short, open grasslands</td>
<td>Not seasonal</td>
<td>Grass seeds, stems, leaves, corms, roots &amp; rhizomes. Seeds &amp; seedlings of <em>Acacia</em> spp.</td>
<td>20 mammal species, 7 bird species, 4 reptile species, humans</td>
</tr>
<tr>
<td>Bat-eared fox <em>Otocyon megalotis</em></td>
<td>Social foragers</td>
<td>1.5-2 km²</td>
<td>Short, open grasslands</td>
<td>October-December</td>
<td>Insectivorous; harvester termites</td>
<td>African wild dog, hyaena, leopard, cheetah, humans and raptors</td>
</tr>
<tr>
<td>African wild cat <em>Felis silvestris lybica</em></td>
<td>Solitary</td>
<td>About 4.3km² (territorial)</td>
<td>Wide habitat tolerance</td>
<td>September-March</td>
<td>Mice, rats, birds up to guinea fowl, scrub hare</td>
<td>Unknown</td>
</tr>
<tr>
<td>Small-spotted genet <em>Genetta genetta</em></td>
<td>Solitary</td>
<td>Unknown</td>
<td>Open, arid habitats, woodland savanna</td>
<td>Summer</td>
<td>Insects, mice, arachnids, birds &amp; reptiles</td>
<td>Unknown</td>
</tr>
<tr>
<td>Aardvark <em>Orycteropus afer</em></td>
<td>Solitary</td>
<td>2.0-4.7 km²</td>
<td>Open woodland, scrub and grassland</td>
<td>Not seasonal</td>
<td>Formicid ants and termites</td>
<td>Large predators and humans</td>
</tr>
<tr>
<td>Black-backed jackal <em>Canis mesomelas</em></td>
<td>Solitary or in pairs</td>
<td>18.2 km²</td>
<td>Wide habitat tolerance</td>
<td>May-September</td>
<td>Omnivorous, insects, scrub hare, springhare, small antelopes, small livestock</td>
<td>Large predators and humans</td>
</tr>
<tr>
<td>Cape fox <em>Vulpes chama</em></td>
<td>Solitary</td>
<td>1.0-4.6 km²</td>
<td>Open grassland, scattered thickets, semi-desert scrub</td>
<td>August-October</td>
<td>Rodents, invertebrates, reptiles, birds, eggs, fruit</td>
<td>Large predators and humans</td>
</tr>
<tr>
<td>Striped polecat <em>Ictonyx striatus</em></td>
<td>Solitary</td>
<td>Unknown</td>
<td>Wide habitat tolerance</td>
<td>Summer</td>
<td>Insects and mice</td>
<td>Large predators</td>
</tr>
</tbody>
</table>
