Nocturnal medium-sized bioturbators and their ecosystem services in differently managed rangelands in the Kalahari and Pro-Namib.

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Thesis submitted in partial fulfillment of the requirements for the degree of Master of Natural Resources Management (Nature Conservation) at the Namibia University of Science and Technology

NAMIBIA UNIVERSITY OF SCIENCE AND TECHNOLOGY

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Declaration

I, *Michelle Rodgers*, hereby declare that the work contained in the thesis entitled: *Nocturnal medium-sized bioturbators and their ecosystem services in differently managed rangelands and habitats, Namibia* is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

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List of Acronyms

ANOVA	Analysis of Variance
CBD	Convention on Biological Diversity
EIS	Environmental Information System
HSD	Honestly Significant Difference
MSAVI	Modified Soil-Adjusted Vegetation Index
NBSAP	National Biodiversity Strategy and Action Plan
NIR	Near infrared
NUST	Namibia University of Science and Technology
UAV	Unmanned aerial vehicle

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Dedication

This thesis is dedicated to my parents, Lynette Rodgers and Koos Rodgers, for all their love, support and patience. Thank you for giving me the motivation and support to follow through in everything that I pursue. Finally, to God Almighty for the guidance, wisdom, motivation and determination He bestowed upon me through this journey.

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 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. The abundance and diversity of burrowing medium-sized nocturnal mammals between neighbouring livestock and wildlife land use types were compared in this study in three biomes in Namibia: north Kalahari, south Kalahari, and the Pro-Namib Desert. 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 (summer) and dry (winter) seasons of 2016, 2017 and 2018 to quantify differences in medium-sized mammal population dynamics. High resolution multispectral unmanned aerial vehicle imagery was used to determine macropore abundance on the northern Kalahari sites, as well as vegetation productivity was estimated for the three study areas and years using Sentinel-2 satellite images. Rangeland productivity was investigated in the field by measuring grass biomass and moisture infiltration around burrow clusters and control sites with no burrows. On the ground burrow dimension and temperature measurements were collected to investigate the ecosystem services from bioturbation. The study found higher diversity and abundances of nocturnal medium-sized mammals and their burrows on the Kalahari wildlife reserves. Furthermore, clear seasonal patterns were observed. The Kalahari sites had more sightings during the dry season, whereas the Pro-Namib had more during the growing season. Aardwolf (*Proteles cristata*) and springhare (*Pedetes capensis*) were mostly recorded on the wildlife reserves and during the dry season, while bat-eared fox (*Otocyon megalotis*) were mostly recorded during the growing season. Scrub hare (*Lepus saxatilis*) showed no difference between seasons and land uses, although it was the species most sighted on the Pro-Namib livestock farm. Springhare were the most prolific species recorded in the Kalahari. Importantly, benefits were indicated by areas around burrow clusters showing higher vegetative productivity (more grass and higher soil moisture). This study has revealed and supported evidence that these under-studied mammals play an important role in ecosystem functioning and environmental integrity, which leads to more stable and resilient ecosystems. Further research is needed in Namibia in general, but particularly in the Pro-Namib on bioturbators and their activities.

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

Chapter 1: Introduction

It is thought that bioturbating or soil digging medium-sized mammals 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), but little is known of their effect on ecosystems in Namibia. A preliminary study found that ecosystem productivity was improved by bioturbating mammals through soil displacement, increased moisture retention and burrow microclimatic improvement (Rodgers *et al.* 2017). Furthermore, management practices on wildlife and livestock land uses may affect the abundance and diversity of bioturbating medium-sized mammals, thereby resulting in differing effects of ecosystem services as a feedback for rangeland productivity.

In Namibia, rural land is used predominantly for agriculture and wildlife conservation (Namibia Statistics Agency 2018). Many private farms are converting partially or completely from livestock to wildlife land use due to the perceived ecological and socio-economic benefits over livestock farming in semi-arid rangelands (Chardonnet *et al.* 2002, van Schalkwyk *et al.* 2010, Lindsey *et al.* 2013, Holechek and Valdez 2018). The effects of this land use conversion and subsequent intense game farming on rangelands are not well understood and needs to be fully investigated (van Schalkwyk *et al.* 2010, Lindsey *et al.* 2013, Hauptfleisch 2018). Different land uses have varying effects on the environment, however, and poor management practices lead to ecosystem degradation and loss of biodiversity (Millennium Ecosystem Assessment 2005, Blaum *et al.* 2007, 2009). Land degradation, such as overgrazing and bush encroachment, leads to fragmentation and loss of habitat to which digging mammals (Abbot *et al.* 1997, Fleming *et al.* 2014) and mesocarnivores (Woodroffe & Ginsberg, 1998, as cited in Blaum *et al.* 2008) are highly vulnerable. This in return provides a feedback mechanism which results in poorer and less productive rangeland. The role of these mammals in rangeland management of different land uses needs to be fully investigated to prevent possible loss of important ecosystem function (Fleming *et al.* 2014).

Substantial data on nocturnal and crepuscular medium mammals is lacking in Namibia, as most research focus lies with large charismatic species (Environmental Information Service 2014). Nocturnal mammals are acknowledged more from a perspective of curiosity and novelty, rather than from a perspective of their role in the ecosystem (Okonjima Nocturnal Game Drive Namibia 2019). Namibia's wildlife is an important national asset according to Vision 2030 (Government of Namibia 2004), and a sound understanding thereof is necessary in order to comply with the requirements of the Convention on Biological Diversity (CBD) (Convention on Biological Diversity 1993). In the National Biodiversity Strategy and Action Plan (NBSAP 2 of 2012) the protection of Namibia's unique biodiversity is stressed. There is however a shortage of distribution and abundance information on much of Namibia's biodiversity (mammals in particular), since the last mammal distribution and abundance study was done approximately 20 years ago (Griffin 1998). Recently the Namibian Chamber of Environment has commissioned a Red List Assessment of Carnivores in Namibia (Cheetah Conservation Fund 2017). This includes a number of small bioturbating carnivores such as mongoose, aardwolf, jackals and foxes. The assessment has highlighted the lack of information regarding these smaller species.

1.1 Bioturbation

The manipulation and movement of soil by biota is known as bioturbation (Meysman *et al.* 2006, Fleming *et al.* 2014). Charles Darwin was the first researcher to realise and investigate the importance of burrowing animals, by studying earthworm activities and their effects on the land over a 30-year period (Darwin, 1881, as cited in Meysman *et al.* 2006). He found that the small-scale bioturbation of earthworms had landscape level impacts. The important role that bioturbation plays in landscape formation and evolution, through soil formation, erosion, soil stabilisation and soil fertility, has only been fully studied in recent years, however. Studies have shown that earthworm macropores increase water infiltration into the soil by 4 – 10 times, which reduces surface runoff, and improves moisture retention and aeration in the soil (Edwards and Bohlen 1996). Earthworms also turn over and mix soil from 2 - 268 tonnes/ha depending on geographical regions and habitats, which is important for soil formation, decomposition, soil humus and soil fertility (Edwards and Bohlen 1996, Meysman *et al.* 2006). There is however little empirical information regarding the importance of bioturbating mammals on ecosystem services, and especially bioturbating medium-sized mammals and mesocarnivores that 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). Mesocarnivores are small to medium sized carnivores of less than 15 kg (Roemer *et al.* 2009) and medium mammals are classified as mammals with burrow openings of 8 - 100 cm in diameter (Skinner and Smithers 1990).

1.2 Importance of bioturbation

1.2.1 Ecosystem services

Ecosystem services are the goods and services that an ecosystem provides to humans and other biota (de Groot *et al.* 2002, Millennium Ecosystem Assessment 2005). These services are broadly classified into four groups, namely supporting, provisioning, regulating and cultural services. Bioturbating medium mammals and mesocarnivores are defined as ecological engineers by Jones et al. (1994) as they create, change and support habitats through the direct or indirect modification of resource availability to other organisms. More specifically, burrowing mammals are defined as allogenic engineers, which modify the environment by mechanically changing materials into different physical states. Ecosystem services provided, either directly or indirectly, by these bioturbating mammals are often thought to be of minor importance, but are actually present in all four of the ecosystem service groups (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 artistic values.

1.2.2 Role of bioturbating mammals

Bioturbating invertebrates, including earthworms, ants and termites, create a network of soil macropores as complicated burrows that extend deep into the ground (Gabet *et al.* 2003, Bonachela *et al.* 2015). In the process of creating these burrows ants and termites displace a large amount of soil. They also carry dead plant and animal matter deep into the soil facilitating faster decomposition and better soil fertility. Termites also modify soil into termite mounds that create areas of higher fertility (Bonachela *et al.* 2015). Mounds differ in physical and chemical composition from the surrounding soil due to improved water infiltration and decomposition by termite activities. This improves the resilience of ecosystems as vegetation can survive longer during dry spells due to increased moisture and nutrient retention. Services associated with these invertebrates are quite extensively studied.

Many arid adapted mammals are nocturnal, in order to avoid activity during high daytime temperatures (Fuller *et al.* 2014) and this is no different in the Kalahari where this study was conducted. A variety of small and medium mammals dig into the soil for shelter, to create nests or dens, and/or to forage (Reichman and Smith 1990). The burrows created have many benefits for the mammals, such as refuge from adverse temperatures and predators, and perfect sites for nests, including foraging and storage of food as fossorial mammals spend almost their entire lives underground. Burrows and burrowing do not only provide benefits for the burrower, but also provide direct and indirect benefits to other organisms and the environment (Jones *et al.* 1994, Avenant 2000, Gabet *et al.* 2003, Fleming *et al.* 2014). Avenant (2000) indicated that small mammals (mice, rats, shrews, gerbils, dormice and moles) provide ecosystem services through prey, predation, consumers, seed dispersal and bioturbation. Through bioturbation they provide better aeration for soil, increase nutrient cycling and increase water infiltration and retention (Avenant 2000, Hauptfleisch *et al.* 2017). Knowing the role that small mammals in ecosystems have, various studies have used them to monitor ecosystem health (Avenant 2000, 2011, Avenant *et al.* 2008). The role of mesocarnivores and medium mammals as possible indicators has however not been well studied.

Extensive studies have been done on Australian bioturbating mammals as a result of rapid population declines and about 50% extinctions of these species in the last 200 years. Flemming et al. (2014) indicates that the loss of bioturbating mammals has led to the loss of the important ecosystem functions mentioned above. This, in turn, affected plant productivity and resistance to disease. In recent years, the consequences of losing bioturbating mammals in Australia became evident as plant recruitment decreased considerably, increased fire intensities due to low organic matter turnover, and poor water infiltration caused severe droughts and tree mortalities.

1.3 Bioturbating mammals in Namibia

Various bioturbating medium-sized mammals occur in Namibia (Skinner and Smithers 1990, Jones *et al.* 1994). Aardvark, *Orycteropus afer*, is a strictly nocturnal species that mainly excavate three types of burrows. Two of the burrow systems are used for shelter, one shallow, temporary burrow and another longer permanent burrow that can be as long as 13 meters with various openings. The other burrows are dug when foraging for termites and can be shallow or deep, but are not used by aardvark for shelter. Burrow openings are up to 1 m in diameter and active burrows are characterised by tiny flies in the entrances (Stuart and Stuart 2013). In Botswana, species that use or depend on aardvark burrows include 17 mammals, two reptiles and one bird (Smithers, 1983, as cited in Skinner & Smithers, 1990).

One of these mammals is the aardwolf, *Proteles cristata*, which modifies and occupies abandoned aardvark, springhare or porcupine burrows (Skinner and Smithers 1990, Stuart and Stuart 2013). These linear burrow entrances are about 40 cm wide and 30 cm high, with burrows up to 5 m long. Aardwolf feed mainly on nasute harvester termites and can consume up to 300 000 termites in a night (Skinner and Smithers 1990). The pangolin, *Manis temminckii*, and Cape porcupine, *Hystrix africaeaustralis*, occupy burrows similar to aardwolf of up to 3 m in length. Another species that modify aardwolf and springhare burrows is the bat-eared fox, *Otocyon megalotis*, which excavates burrows of about 1 m deep and 3 m long. These burrows are sometimes shared with the Cape fox, *Vulpes chama*.

Elaborate burrow systems are created by springhare (*Pedetes capensis*), suricates, ground squirrels and mongooses. Springhare create burrow systems with an average of nine openings and the diameter of these openings are 12 – 25 cm. The depth can reach up to 1.22 m and the average total length of the burrow system is 42 m (Skinner and Smithers 1990, Skinner and Chimimba 2006, Peinke D *et al.* 2016). These burrow systems are occupied by one springhare and its young only. Suricates, *Suricata suricatta*, are a diurnal, colonial species that excavate numerous burrow systems for temporary shelter during the day and one permanent burrow system for sleeping at night (Skinner and Smithers 1990, Stuart and Stuart 2013). The burrow systems have many openings of 8 – 15 cm in diameter. Suricates either expel or share burrow systems with Cape ground squirrel (*Xerus inauris*) and yellow mongoose (*Cynictis penicillata*), as these species occupy similar burrows (Skinner and Chimimba 2006, Waterman and Roth 2007, Stuart and Stuart 2013).

Many other mammalian species do not necessarily dig burrows, but use abandoned burrows for shelter, including Cape hare (*Lepus capensis*), scrub hare (*Lepus saxatilis*), striped polecat (*Ictonyx striatus*), small-spotted genet (*Genetta genetta*), African wild cat (*Felis silvestris lybica*) and the rare black-footed cat (*Felis nigripes*) (Skinner and Smithers 1990, Sliwa 1993). Bioturbating medium-sized mammals are thus important microhabitat engineers for other species.

1.4 Significance of study

Substantial data on small mammals (orders Rodentia, Eulipotyphla and Macroscelidea) and particularly nocturnal and crepuscular medium mammals is lacking in Namibia, as most research focus lies with large charismatic species (Environmental Information Service 2014). Namibia's wildlife is an important national asset according to Vision 2030 (Government of Namibia 2004), and a sound understanding thereof is necessary in order to comply with the requirements of the Convention on Biological Diversity (CBD) (Convention on Biological Diversity 1993). In the National Biodiversity Strategy and Action Plan (NBSAP 2 of 2012) the protection of Namibia’s unique biodiversity is stressed. There is however a shortage of distribution and abundance information on much of Namibia's biodiversity (mammals in particular), since the last mammal distribution and abundance study was done approximately 20 years ago (Griffin 1998).

This study considers bioturbating mammals on two different land uses in Namibia, livestock and wildlife farming. They have distinctly different management, and their effect on rangelands and biodiversity are not fully understood (Hauptfleisch 2018). Private livestock farms are increasingly being converted into wildlife farming which can be seen as a positive for biodiversity (Chardonnet *et al.* 2002, Lindsey *et al.* 2013, Holechek and Valdez 2018), as global biodiversity is rapidly declining and changing due to habitat loss and climate change (Sala 2000, Millennium Ecosystem Assessment 2005). The effect of changing to intensive wildlife farming on rangeland ecosystems and biodiversity however, have not been fully investigated. There may be ecological and conservation problems associated with this conversion, which includes overstocking, herbivore diversity (browsing/grazing) in stocking ratios, increased predator persecutions, game fences influencing natural migrations, introduction of exotic species and genetic manipulation (Lindsey *et al.* 2009, van Schalkwyk *et al.* 2010, Hauptfleisch 2018).

From the literature from other geographical areas, it is already evident that bioturbating medium-sized mammals are important allogenic engineers (Jones *et al.* 1994, Fleming *et al.* 2014, Ewacha *et al.* 2016). However, many rangeland managers in southern Africa do not realise the importance of medium bioturbating mammals and often only recognise them as vermin that need to be eradicated (Blaum *et al.* 2007, Roemer *et al.* 2009). In addition to gaining a better understanding of the community composition of medium bioturbating mammals and mesocarnivores in Namibia, the ecosystem services provided by these species were explored in this study. This may lead to better awareness by land users of their benefit and the need to conserve them. The role of these mammals in Kalahari and Namib environments were investigated to fill knowledge gaps and prevent future loss of ecosystem functions. The results of this study will benefit rangeland managers in improving their management practises for a healthier and more resilient rangeland and in return help preserve the ecosystem services provided by bioturbators.

1.5 Aim and objectives of study

The aim of the study was to determine whether different land uses result in differences in the abundance and diversity of bioturbating medium mammals and mesocarnivores and whether bioturbating activity affects rangeland productivity as a measure of ecosystem services. This was achieved through the following objectives:

- Determine and compare the species diversity and abundance of nocturnal bioturbating medium-sized mammals between livestock and wildlife farming;
- Quantify medium mammal macropore density as a proxy for bioturbating effect using multispectral imagery on two land uses in different vegetation areas/zones.
- Determine and investigate rangeland productivity as a function of the effect of bioturbation and compare between land uses and vegetation areas/zone.

Chapter 2: Methods

2.1 Study area

In this study, neighbouring properties, with different management practices, were compared on three different areas in Namibia. The sites are bordering livestock and wildlife properties in three areas: north Kalahari, south Kalahari, and the Pro-Namib Desert. Qualitative informal interviews were conducted with the property management to investigate management practises that could affect bioturbators and their activities and therefore affect the data.

2.1.1 Kalahari Desert

Four of the study sites were located in the Kalahari sandveld of Namibia (23°12'S, 18°26'E). In general, two of the study areas 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 *Vachellia* (previous genus *Acacia*) and *Senegalia* (previous genus *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.

a. Northern Kalahari (23°14.126'S, 18°23.261'E)

The northern Kalahari study sites were Kuzikus Wildlife Reserve and Ebenhaezer livestock farm (Figure 1). The area is on the edge of the central Kalahari biome, 180 km southeast of Windhoek (Kuzikus Wildlife Reserve 2010) and at an altitude of 1380 m (Reinhard et al. 2009). The landscapes include Kalahari savannah, saltpans with dwarf shrubland, thornbush encroached areas and low, vegetated dunes. The dominant woody vegetation includes *Vachellia erioloba*, *Vachellia karroo*, *Grewia flava*, *Senegalia mellifera* subsp. *detinens*, and the dominant grass species are *Aristida* and *Stipagrostis species*. Average rainfall for the area is 250-300 mm (Mendelsohn *et al.* 2002). The average annual temperature is 19-20 ˚C, with the maximum temperatures 32-34 ˚C and minimum 2-4 ˚C.

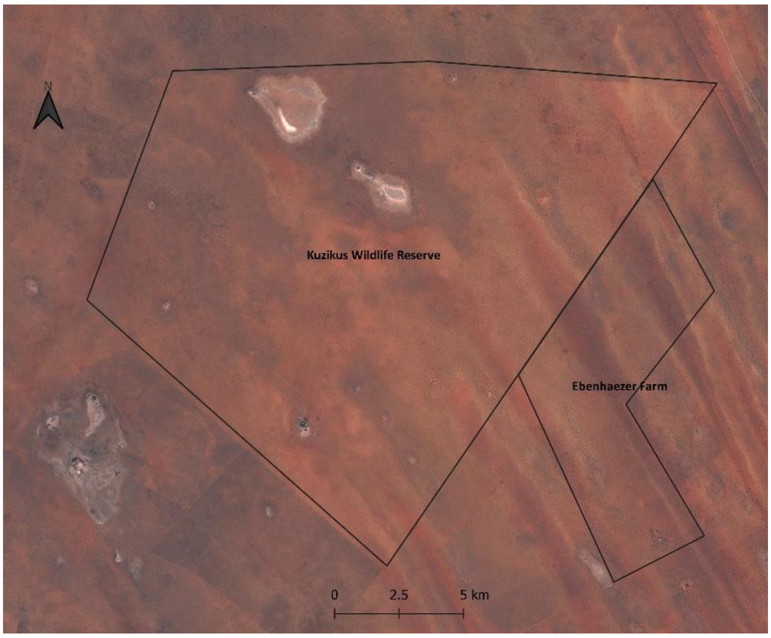


Figure 1: Bordering northern Kalahari study sites, Kuzikus Wildlife Reserve and Ebenhaezer Livestock Farm.

Kuzikus is a 10,500 ha reserve that 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 selectively over-grazed rangeland and subsequent increase in bush density in some areas (Ziegler *et al.* 2018). 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 is a 2,200 ha mixed livestock farm with karakul sheep, cattle and horses being farmed commercially (Hauptfleisch *et al.* 2017, Blaum *et al.* 2018). 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 practiced by the farm management to prevent over-grazing, and predator control is practiced to prevent sheep losses (PH Hugo, personal communication, 2016).

b. Southern Kalahari (24˚25.806'S, 18˚06.061'E)

The south Kalahari sites are the Gondwana Kalahari Anib Park and Wurm Livestock Farm (Figure 2). This area is on the edge of the Dwarf Shrub Savana in the Nama Karoo biome, 30 km north-east of Mariental. The dominant vegetation in the area include the grass species *Schmidtia kalahariensis*, *Stipagrostis uniplumis*, *Stipagrostis ciliate* (Müller 2007) and tree species *Senegalia* mellifera, *Vachellia hebeclada*, *Vachellia erioloba*, *Parkinsonia Africana*, *Tarchonanthus camphoratus*, *Rhigozum* *trichotomum* (Mannheimer and Curtis 2009) (S de Lange, personal communication, 15 November 2017). Average rainfall for the area is 200-250 mm, lower than the northern sites (Mendelsohn *et al.* 2002). The average annual temperature is 20-21 ˚C, with the maximum temperatures 34-36 ˚C and minimum 0-2 ˚C.

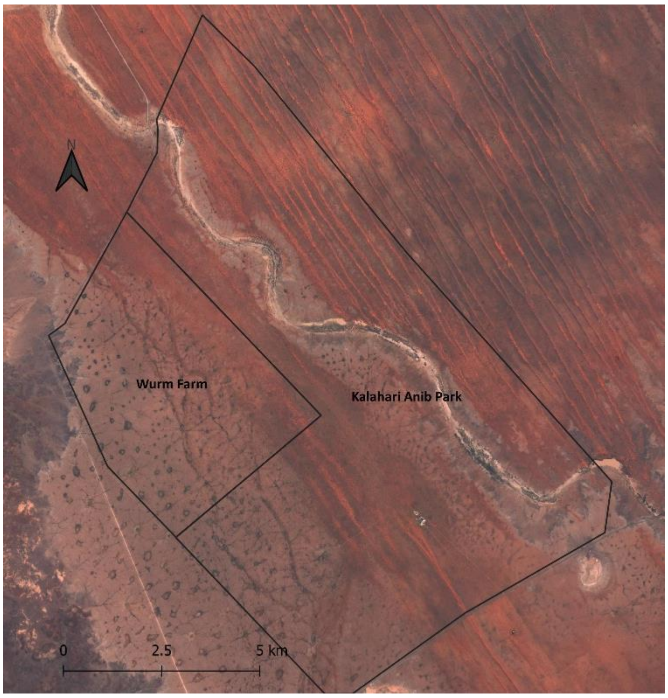


Figure 2: Bordering southern Kalahari study sites, Wurm Farm and Gondwana Kalahari Anib Park

The Gondwana Kalahari Park is a 9,800 ha reserve with a 52-room lodge, the Kalahari Anib Lodge (S de Lange, personal communication, 8 October 2019). The Park supports around 2,300 head of game of 9 main species, including oryx, eland, giraffe, plains zebra, steenbok and duiker. There are no inner fences on the property so wildlife can move and graze continuously and freely.

Wurm Livestock Farm is a 3,000 ha sheep farm. The farm has around a 1,000 sheep and about 18 cattle (S de Lange, personal communication, 17 October 2019). The farmer practices rotational grazing and active predator control. The farmer also actively hunts large burrowing mammals, such as aardvark and warthog, to prevent holes under the boundary fences where jackals and other predators can enter the farm (H Wurm, personal communication, 15 November 2017).

2.1.2 Pro-Namib Desert (23°53.314'S, 16°00.159'E)

The two remaining sites are on the edge of the Namib Desert and the Nama Karoo biomes in western Namibia (Figure 3), the habitat type is referred to as the Pro-Namib and does not include the Namib

Sand Sea (Coetzee 1970, Cowlishaw and Davies 1997, Sweet and Burke 2006, Rohde *et al.* 2019). The study sites are part of the Greater Sossusvlei-Namib Landscape conservation initiative that aims to co-manage with all the stakeholders for better landscape and biodiversity conservation and socioeconomic development (*A Strategic Collaborative Management & Development Plan for Greater Sossusvlei - Namib Landscape (2013 - 2018)* 2013). The Namib extends north-south for 2000 km, in a 200 km wide strip bounded by the great escarpment in the east, along the Atlantic coast of southern Africa (Mendelsohn *et al.* 2002, Goudie 2010). It stretches from the Carunjamba River in Angola, south through Namibia and to Olifants River in South Africa. The environment is hyper arid with 0-20 mm rainfall per annum in the central and coastal area, but increases to more than 200 mm per annum closer to the escarpment. The coastal areas can have more than 100 days of fog with precipitation of about 34 mm per annum (Lim 2017). The vegetation cover is very sparse however, 246 species of flora have been recorded in the landscape which includes a variety of *Aristida*, *Eragrostis*, *Stipagrostis*, *Vachellia*, *Senegalia, Euphorbia*, *Commiphora* and *Rhus* (Cowlishaw and Davies 1997, Mannheimer and Curtis 2009, NamibRand Nature Reserve 2013, Tree Atlas of Namibia project 2016, Rohde *et al.* 2019).

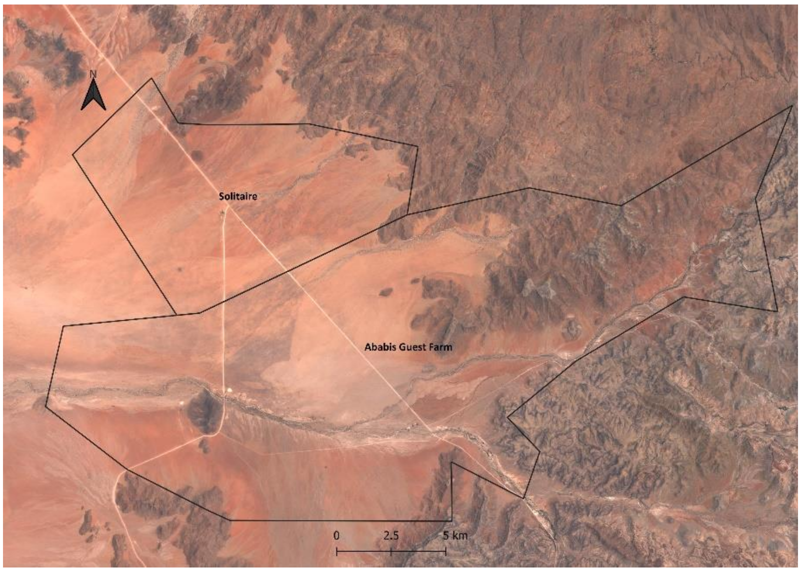


Figure 3: Bordering Pro-Namib study sites, Solitaire and Ababis Guest Farm

Solitaire Guest Farm is a 9500 ha fenceless wildlife farm that was converted from a cattle farm in the past (Solitaire Namibia – Welcoming Travellers Since 1949 2019). The study area forms part of the 18 200 ha Solitaire Land Trust that spans from the Great African Escarpment to the Namib. The management also actively remove fences to open the landscape for free wildlife movements. Wildlife in the area include oryx, springbok, kudu, mountain zebra, warthog, bat-eared fox, Cape fox, cheetah, leopard and brown hyena (Environmental Information Service 2019).

Ababis is a 32 000 ha Guest Farm where half of the farm is used for commercial cattle farming and the other half is a private nature reserve (U Schulze-Neuhoff, personal communication, 15 August 2017). Wildlife on the farm include oryx, springbok, zebra, cheetah, hyena and bat-eared fox. Active predator control, on mostly jackal and hyena problem individuals, is practiced by management on the cattle farming side of the farm.

2.2 Night road strip counts

Night surveys were conducted in the three areas in Namibia to determine and compare species diversity and abundance of nocturnal mammals between the different land-uses. Road strip count routes (Bothma & Toit 2010) transverse adjacent properties in the study areas. A fixed, three-hour route was driven at 20 km/h for five consecutive nights in each area. 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 (April-May 2018) and winter/dry season (August and November 2017) of 2017/2018. A minimum of three people were 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. Kruskal Wallis Analysis of Variance (ANOVA) for difference (non-parametric data) between species abundance, land use and season were run using the Statistica V 10 software (StatSoft Inc. 2010). Tukey's honestly significant difference (HSD) post hoc tests were run to confirm where the differences occurred between groups. The study tested for differences in abundance, species richness, study sites and seasons in means per survey.

2.3 Grass biomass

Rangeland productivity was investigated in the field by measuring grass biomass around burrow clusters and control sites with no burrows (Ewacha *et al.* 2016). A burrow cluster is defined as three or more burrow openings grouped together and these groups of burrows are separated by open areas of land without burrows (Waterman and Roth 2007, Ewacha *et al.* 2016). Six transects, two control and 4 burrow cluster sites, were set up in each area in both seasons. Transects of 20 m long were established from the edge of the burrow clusters and for the four cardinal directions (north, east, south and west). Grass clippings in a 1x1 m quadrat (Van Dyne *et al.* 1963, Ewacha *et al.* 2016) were collected every 5 meters from the edge to determine grass biomass around and away from burrow clusters. Kruskal Wallis ANOVA tests were done to analyse difference (non-parametric data) between biomass production around burrow and non-burrow sites. Tukey's honestly significant difference (HSD) post hoc tests were run to confirm where the differences occurred between groups.

2.4 Burrow characteristics

Burrow dimension (diameter and depth) and temperature measurements were collected at 90 burrows in the three study areas, in order to further investigate the ecosystem services from bioturbation (Rodgers *et al.* 2017). The burrows were measured in three size classes, small (8-14 cm diameter), medium (15-39 cm diameter) and large (40-100 cm diameter), based on the species that construct and/or occupy the burrows (Apps 2000, Skinner and Chimimba 2006, Stuart and Stuart 2013). The burrow depth was measured with measuring tape (10 m) to calculate soil volume displaced. Volume was calculated using the cylinder volume formula: $V = \pi r^2 h$, where h is burrow depth. Temperature readings were taken on the ground surface above the burrow entrance and inside the burrow cavity as an estimate of climate control service. Soil moisture levels and infiltration depth was recorded around a burrow cluster and at a control site with no burrows (2 moisture probes at the burrow cluster and 2 at the control site). Four one meter long moisture probes (Delta-T Devices 2016) were inserted vertically into the ground and left in the field for three months (February, March and April 2018).

2.5 Remote sensing

Sentinel-2 satellite imagery (10 m resolution) was downloaded from the European Space Agency's Copernicus website (https://scihub.copernicus.eu) for all three study areas of the growing and winter/dry season for 2016, 2017 and 2018 (Delwart 2015). The images were preprocessed, clipped to the study areas and processed using the "Semi-Automatic Classification Plugin" in the QGIS program (Congedo 2014). The Modified Soil-Adjusted Vegetation Index (MSAVI2) was used to assess vegetation productivity comparing the adjacent wildlife and livestock properties (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 and Herring 2000).

The northern Kalahari study site was surveyed aerially to obtain multispectral imagery of the two land uses. A senseFly eBee unmanned aerial vehicle (UAV) was set up, using eMotion 2 software, to fly an area of 100 ha on both properties (senseFly 2015). Visual (red-green-blue) and near infrared (NIR) georeferenced images of 4 cm pixel resolution were taken by the UAV. The images were processed using the Postflight Terra 3D software and were used to quantify the medium-sized mammal macropores and to determine plant productivity. The medium-sized mammal macropores were manually counted from the multispectral imagery. The macropores were marked as points using QGIS and the diameter of each burrow on the images was measured (QGIS Development Team 2016).

2.6 Assumptions and limitations

In conducting this study the following assumptions were made and limitations experienced:

- It is assumed that standing biomass has been grazed equally between sites and represents grass production.
- Due to camera malfunction, only the northern Kalahari site was successfully surveyed by the UAV and the data analysed.
- On the ground burrow temperature readings were recorded opportunistically, but mostly during the hottest part of the day (between 11h00 and 13h00), due to time restrictions during field trips.
- Only five soil moisture probes were available for this study. The expense prohibited more moisture probes from being used. While in the field, two of the probes malfunctioned due to unknown causes.
- The northern Kalahari data consisted of only winter (dry) season data due to logistical problems (no vehicle and assistants available, lack of funding) over the time period of my planned fieldwork. No grass was available to collect for biomass calculations due to severe drought conditions.

Chapter 3: Results

3.1 Nocturnal Species abundance and diversity

A total of 998 sightings of 17 nocturnal burrowing mammal species were made over 25 nights on the six study sites (Figure 4, Figure 5, and Figure 6). The Anib site had the most sightings with 337 and Ababis the least with 49 sightings. Springhare was the most sighted species on the southern Kalahari nature reserve (Anib) with a total 148 sightings, followed by bat-eared fox (58 sightings), aardwolf (51 sightings) and scrub hare (40 sightings) (Figure 4). On the adjacent livestock farm (Wurm) bat-eared fox was sighted the most with 63 sightings, followed by springhare (47 sightings). Springhare overwhelmingly dominated the dry season data of the northern Kalahari sites with an overall total of 247 sightings (138 sightings on the nature reserve and 105 sightings on the livestock farm) (Figure 6). On the Pro-Namib nature reserve (Solitaire), Cape fox and aardwolf was sighted the most with 32 and 31 sightings respectively, while scrub hare was the most sighted on the livestock farm (Ababis) (Figure 5).

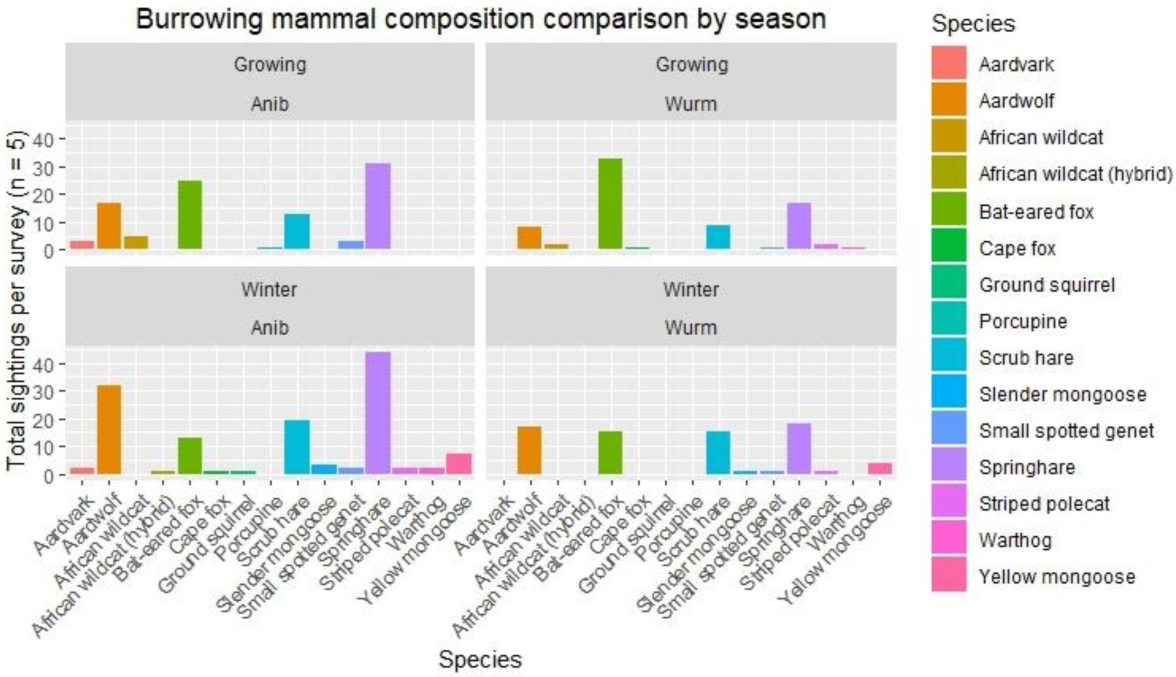


Figure 4: Burrowing mammals recorded on the southern Kalahari sites, Anib (nature reserve) and Wurm (livestock farm), and compared by season.

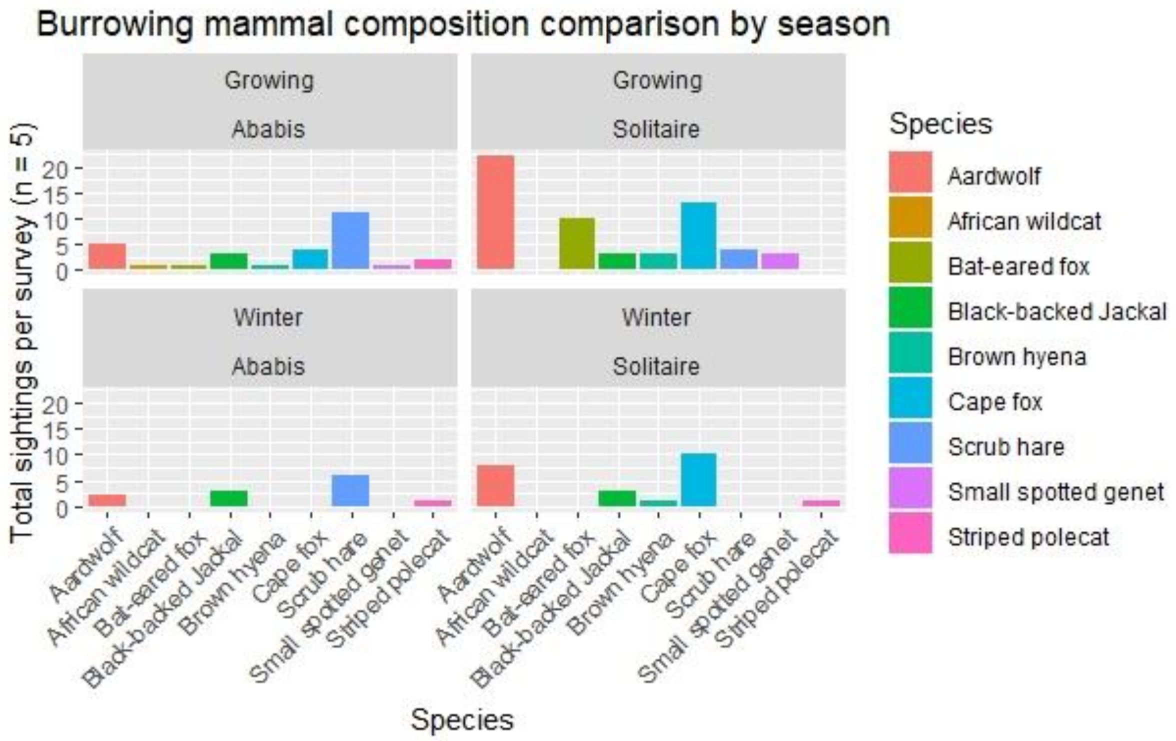


Figure 5: Burrowing mammals recorded on the Pro-Namib sites, Solitaire (nature reserve) and Ababis (livestock farm), and compared by season.

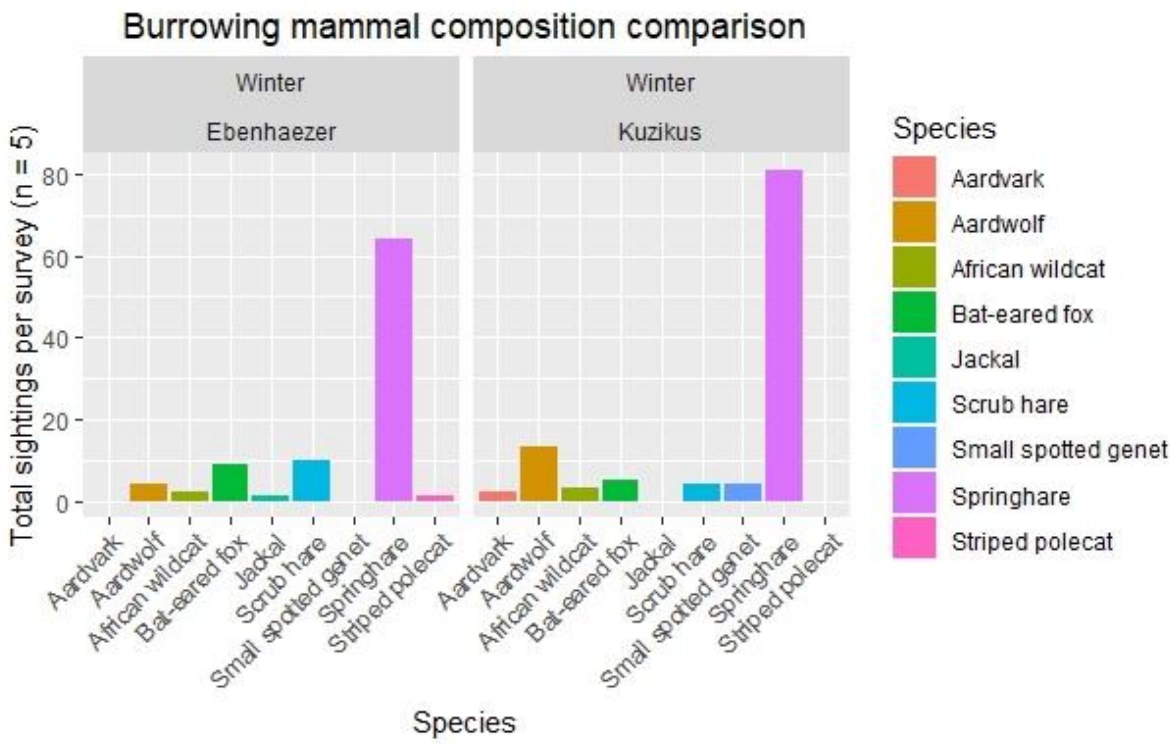


Figure 6: Burrowing mammals recorded on the northern Kalahari sites, Kuzikus (nature reserve) and Ebenhaezer (livestock farm), and compared for the dry season.

There were significant differences in the combined total sightings and sightings per survey night between the sites (Figure 7). At the Anib site (southern Kalahari) the nature reserve had significantly more sightings per survey night ($p < 0.01$) than the livestock farm. At the Pro-Namib site, no significant difference in sightings between the two land uses ($p = 0.332$). Both Kalahari sites also had significantly more sightings (Anib ~ Solitaire $p < 0.01$, Wurm ~ Ababis $p < 0.01$, Kuzikus ~ Solitaire $p < 0.01$, Ebenhaezer ~ Ababis $p < 0.01$) than the Pro-Namib sites.

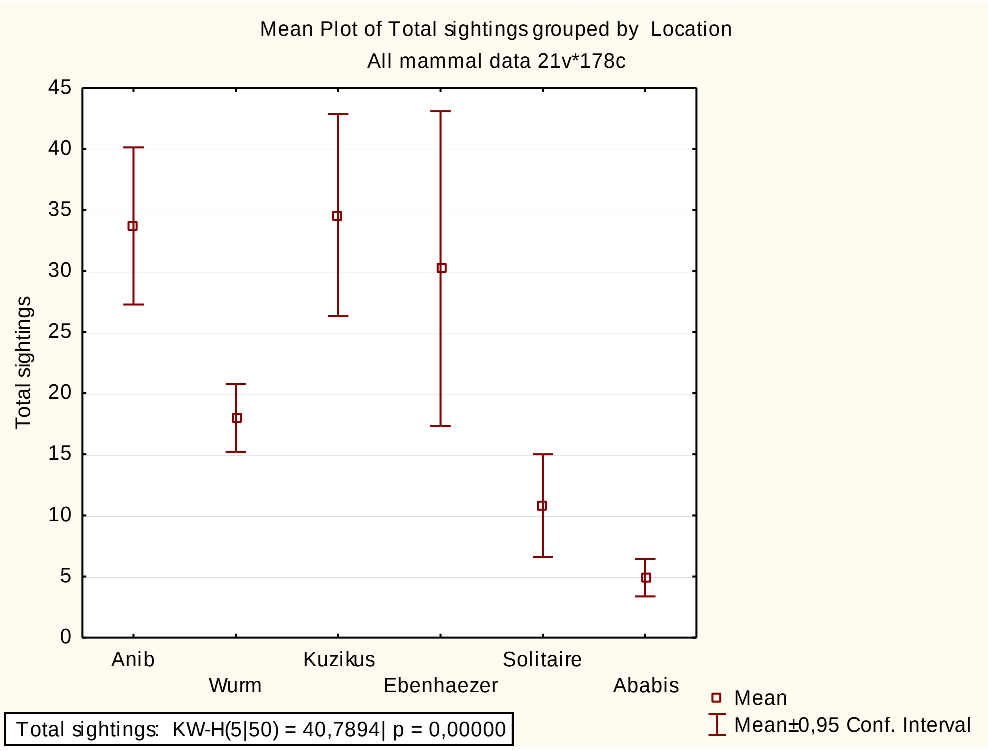


Figure 7: The total mammal sightings comparing all sites.

There were seasonal differences on the Anib nature reserve site (sightings per survey night) with more sightings during the dry season, but no significant difference observed compared to the neighbouring livestock farm (Figure 8). The opposite was observed on both the Pro-Namib sites (nature reserve: $p = 0.0465$, livestock farm: $p = 0.0135$) with significantly more nocturnal mammal sightings during the growing season.

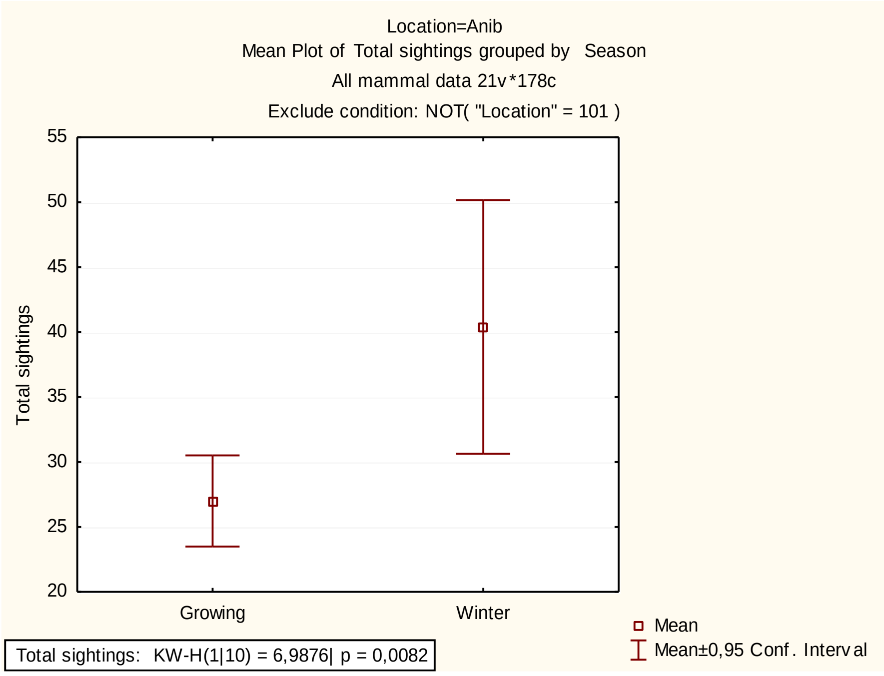


Figure 8: Total mammal sightings on the southern Kalahari reserve site, compared by season.

No significant differences in nocturnal bioturbating mammal species richness (mean number of species per survey night) were observed between the sites when combining seasons. However, there were seasonal differences on the Solitaire nature reserve (Pro-Namib) where significantly more species ($p < 0.01$) were sighted in the growing season (Figure 9). Conversely, no significant differences were observed between the seasons on Solitaire's adjacent livestock farm.

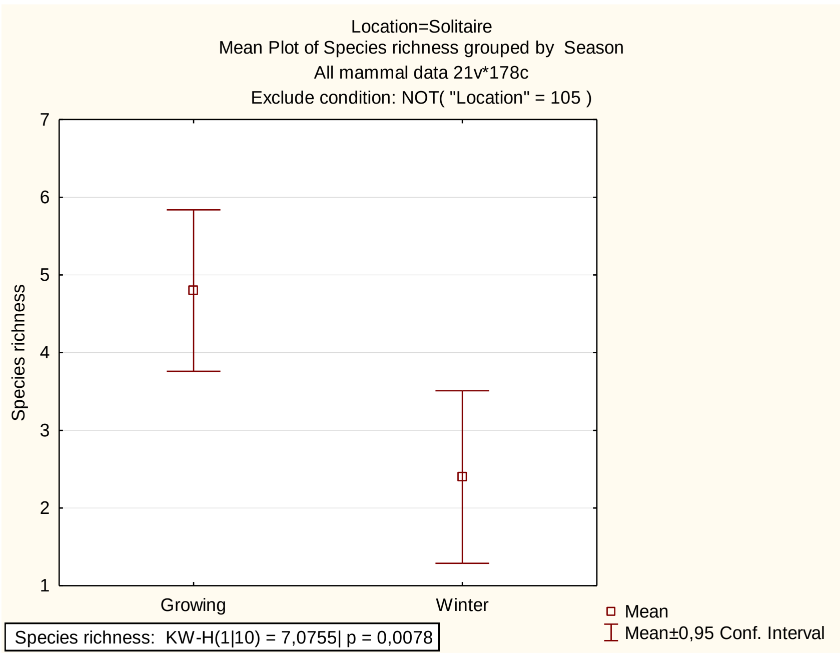


Figure 9: The total number of species on the Pro-Namib reserve site compared by seasons.

There were some interesting differences in individual species abundance between the sites and between seasons. As the most commonly observed species (Figure 4) aardwolf, bat-eared fox, springhare and scrub hare were assessed in more detail. Overall aardwolf sightings showed some significant differences between the sites when comparing all sites in all biomes, with the Anib site showing the highest number (Figure 10). It was however only significantly higher than the livestock farms Ebenhaezer ($p < 0.01$) (northern Kalahari) and Ababis ($p < 0.01$) (Pro-Namib). There were no significant differences in aardwolf sightings between seasons on all the sites, except on the Anib nature reserve (Figure 11) where sightings were higher during the winter season ($p = 0.035$).

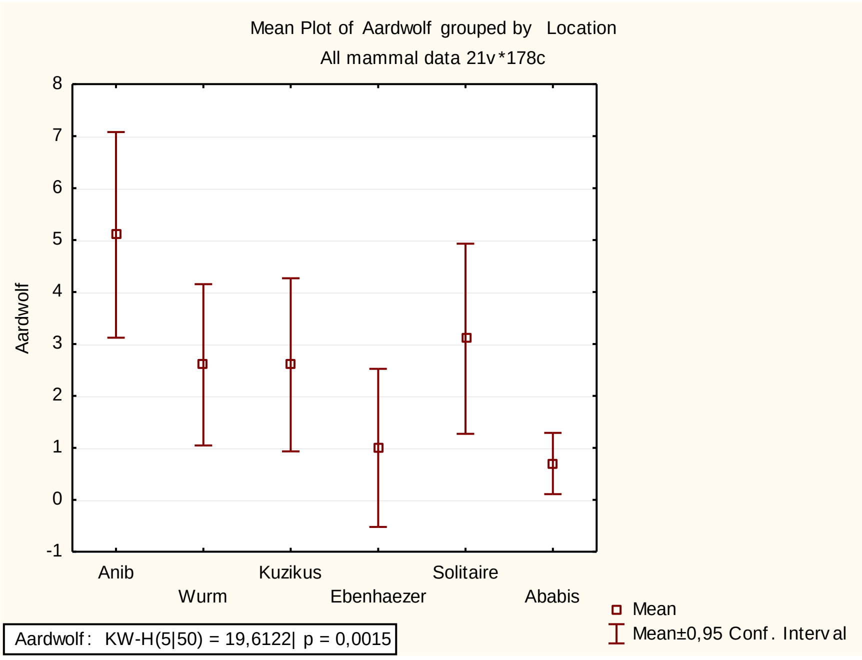


Figure 10: Overall aardwolf sightings of all sites.

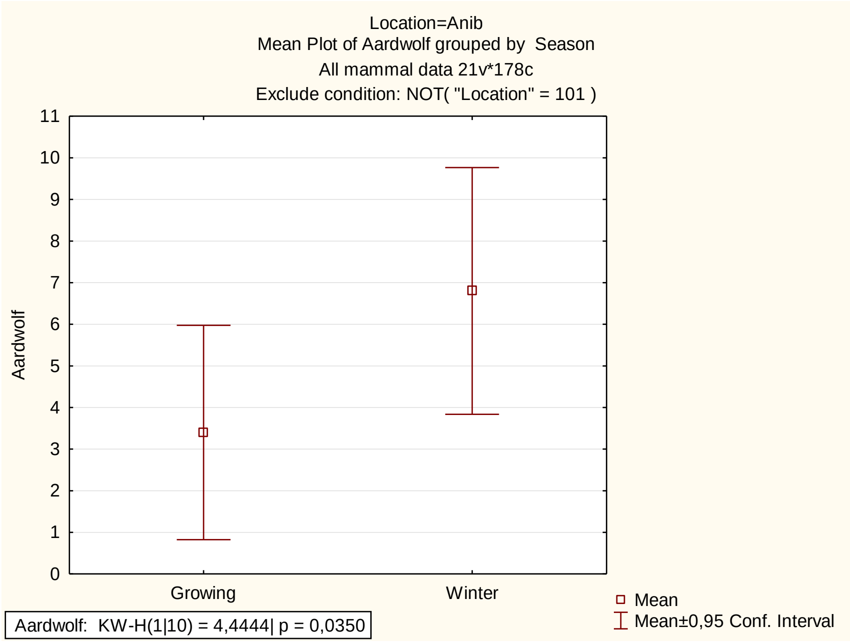


Figure 11: Aardwolf sightings compared between seasons on the southern Kalahari reserve.

Bat-eared fox numbers varied between sites (northern and southern Kalahari, Pro-Namib), but not between land uses (wildlife / livestock), except for the Pro-Namib where none were sighted on the farm (Figure 12). The southern Kalahari sites (Anib and Wurm) had the highest overall sightings and significantly higher than Kuzikus ($p < 0.05$) (northern Kalahari), Solitaire ($p < 0.05$) (Pro-Namib) and Ababis ($p < 0.01$) (Pro-Namib). Overall more bat-eared fox sightings were made during the growing season ($p = 0.0117$) (Figure 13). The southern Kalahari livestock farm (Wurm) had significantly higher sightings during the growing season ($p = 0.0119$) than the winter season, while the Pro-Namib nature reserve surveys produced no sightings during the winter season compared to 23 sightings during the growing season.

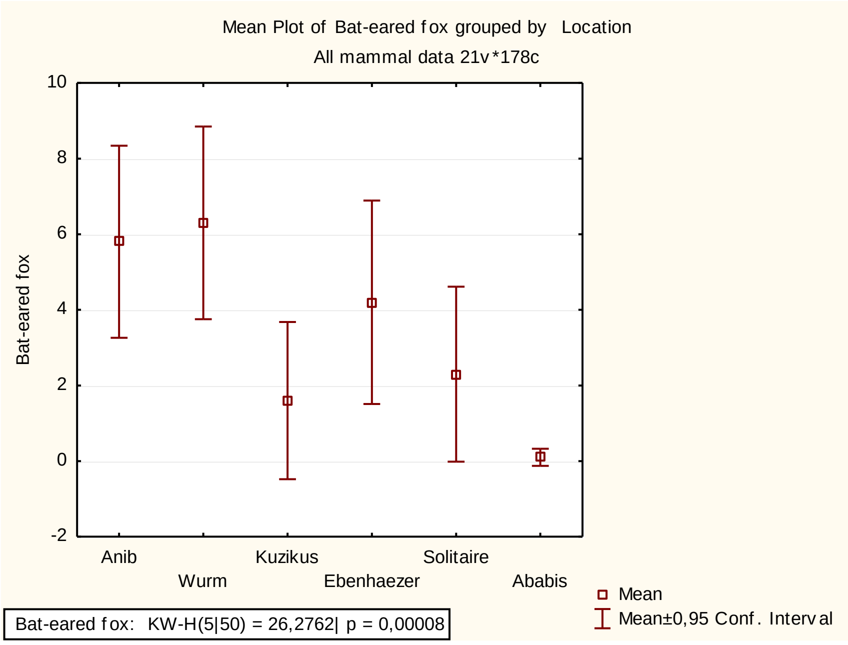


Figure 12: Overall bat-eared fox sightings of all sites.

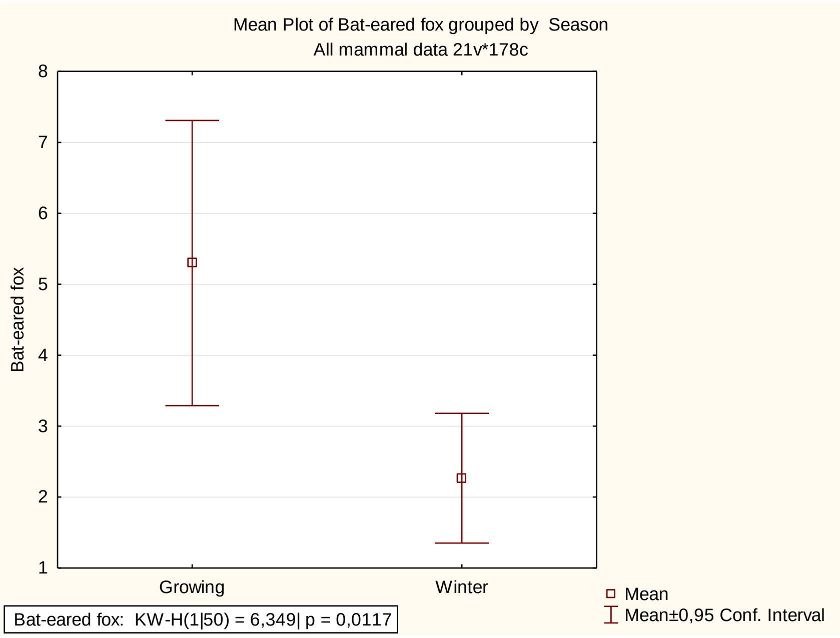


Figure 13: Overall bat-eared fox sightings compared by season.

There are some differences in scrub hare sightings between the sites (Figure 14). Anib had significantly higher overall sightings than the other two nature reserves, Kuzikus ($p < 0.01$) (only winter data) and Solitaire ($p < 0.01$), but no difference compared to the livestock farms. Scrub hare was the most recorded species on the Pro-Namib livestock farm (Ababis), with 13 and 8 sightings in the growing and dry seasons respectively (Figure 5).

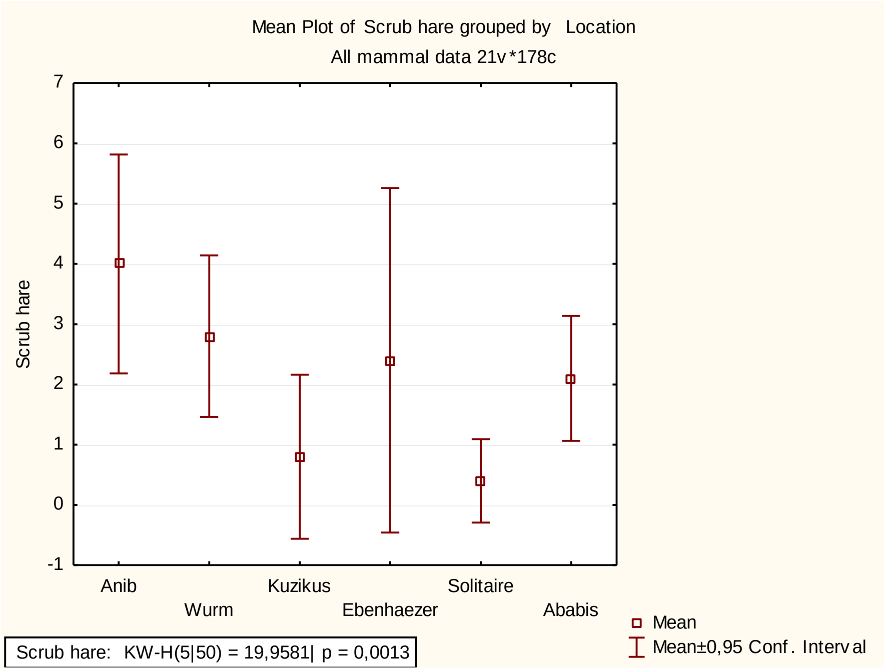


Figure 14: Overall scrub hare sightings of all sites.

Springhare was by far the most common nocturnal mammal in the Kalahari sites, while they were not observed in the Pro-Namib (Figure 15). The northern Kalahari site had significantly more sightings than the southern Kalahari site when compared by land uses (Kuzikus ~ Anib (nature reserves) $p < 0.01$, Ebenhaezer ~ Wurm (livestock farms) $p < 0.01$). Anib had significant higher springhare sightings than its adjacent livestock farm ($p < 0.01$). Most springhare were observed during the winter season when all data were pooled ($p < 0.05$) (Figure 16) and similarly on the Anib nature reserve specifically ($p < 0.01$).

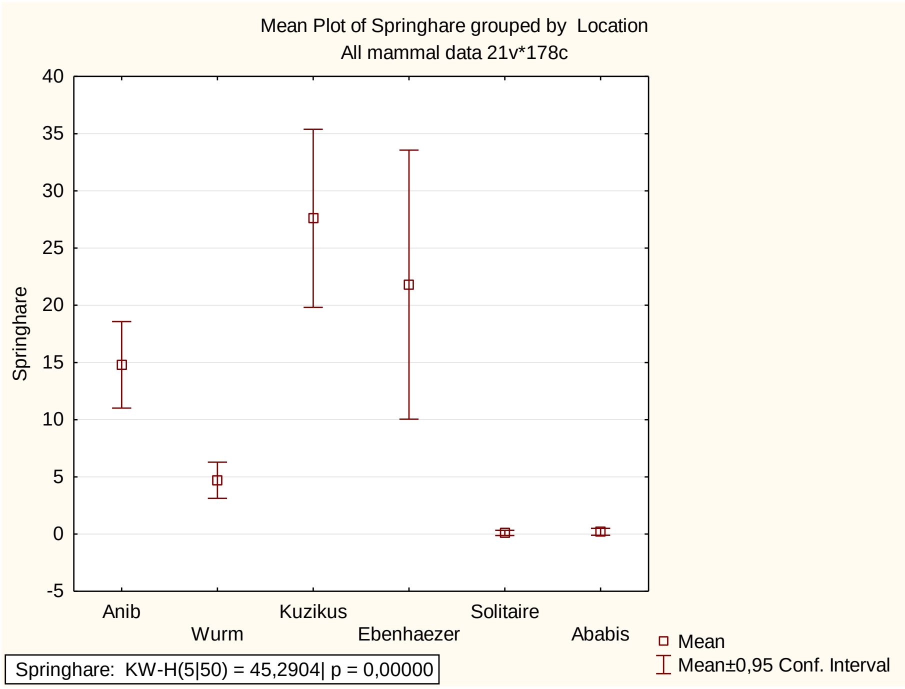


Figure 15: Overall springhare sightings of all sites.

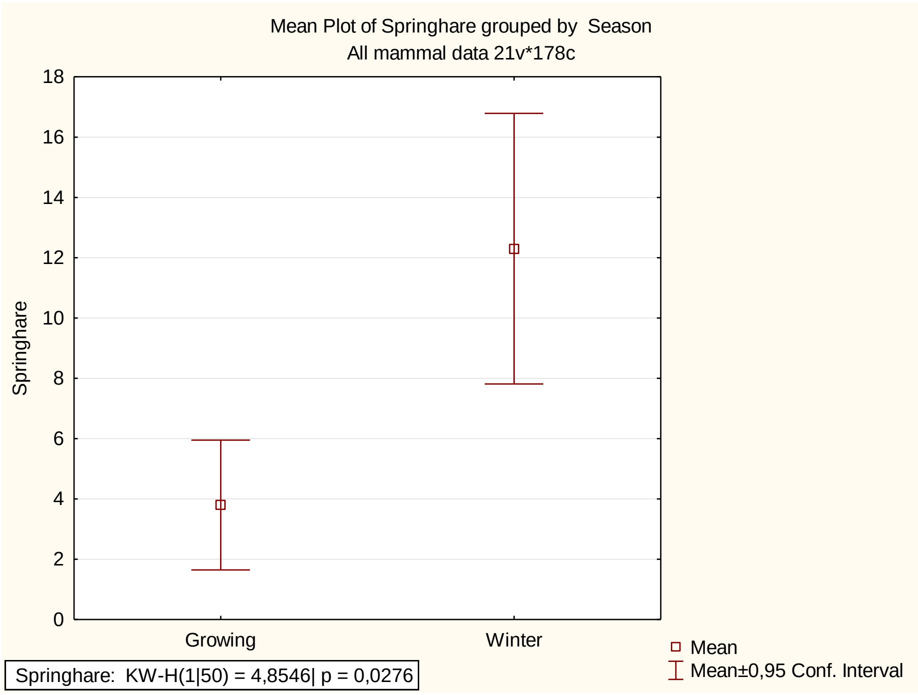


Figure 16: Overall springhare sightings compared between seasons.

3.2 Burrow characteristics

The northern Kalahari sites were the only location that was successfully surveyed by the UAV (Figure 17). A total of 5,846 burrows were counted from the imagery, of which 4,518 burrows (77.3%) were on the nature reserve and 1,328 burrows (22.7%) on the livestock farm (Rodgers *et al.* 2017). Medium sized burrows were the most abundant overall, accounting for 2,736 (46.8%) of the burrows.

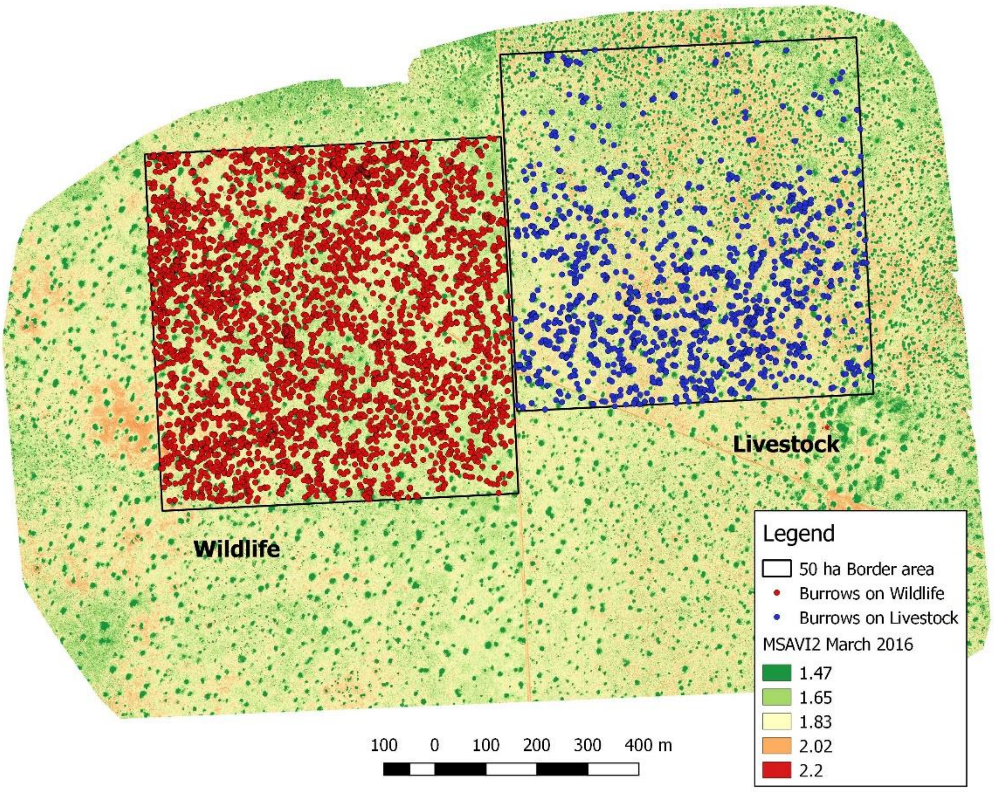


Figure 17: Cross-border habitat survey, taken by UAV, of Kuzikus Wildlife Reserve (Wildlife) and Ebenhaezer Farm (Livestock) in March 2016 (growing season) (Rodgers et al. *2017). The red and blue dots indicate the location of burrows identified on images in the two sites. MSAV12 productivity index is included where lower values signify greater productivity.*

Thirty burrows (on the ground) of the species mentioned in Section 3.1 were classified into size class (small, medium and large) at the northern Kalahari and southern Kalahari. There were no large size class burrows in the Pro-Namib, so only small and medium burrows were assessed (Table 1).

Table 1: Burrow volume data per size class for each site location.

Burrow Volume	Location	Mean Volume (m^3)	Total Volume (m^3)
Small (n=30/site)	Northern Kalahari	**0,016**	0,492
	Southern Kalahari	**0,016**	**0,495**
	Namib	0,011	0,329
Medium (n=30/site)	Northern Kalahari	0,052	1,566
	Southern Kalahari	**0,131**	**3,922**
	Namib	0,037	1,110
Large (n=30/site)	Northern Kalahari	0,336	10,083
	Southern Kalahari	**0,354**	**10,609**
	Namib	0	0
Total (n=240)		**0,954**	**28,607**

A total of 240 burrow volumes were calculated (Table 1). The overall soil displaced was 28.6 cubic meters and the average per burrow was about one cubic meter. The burrows in the southern Kalahari measured the highest soil displacement. The highest average temperature measured above ground was around 40 degree Celsius (Table 2), while the average below ground temperature was around 22 degree Celsius. This represents a 44% difference in temperature above and below ground. The lowest average burrow temperature of 21.3°C was recorded for small burrows.

Table 2: Average temperatures measured above and below ground of each burrow size class.

Burrow Temperature	Surface temp. (°C)	Burrow temp. (°C)	Difference (°C)	%
Small (8 - 14cm)	33,72	**21,27**	12,45	36,9
Medium (15 - 39cm)	34,76	**22,65**	12,11	34,8
Large (40 - 100cm)	**40,38**	22,45	**17,94**	**44,4**

3.3 Grass biomass and moisture around burrow clusters

The southern Kalahari had the highest overall grass biomass ($p < 0.01$ for all sites) collected from burrow and control sites, and thus had the biggest influence on the results. As expected the arid Pro-Namib sites produced far less grass. When comparing grass biomass in areas with burrow clusters, only the southern Kalahari grass biomass was significantly higher ($p < 0.01$) around burrow clusters (Figure 18). When all data from all sites were pooled – grass biomass was higher at burrow cluster sites but not significantly so.

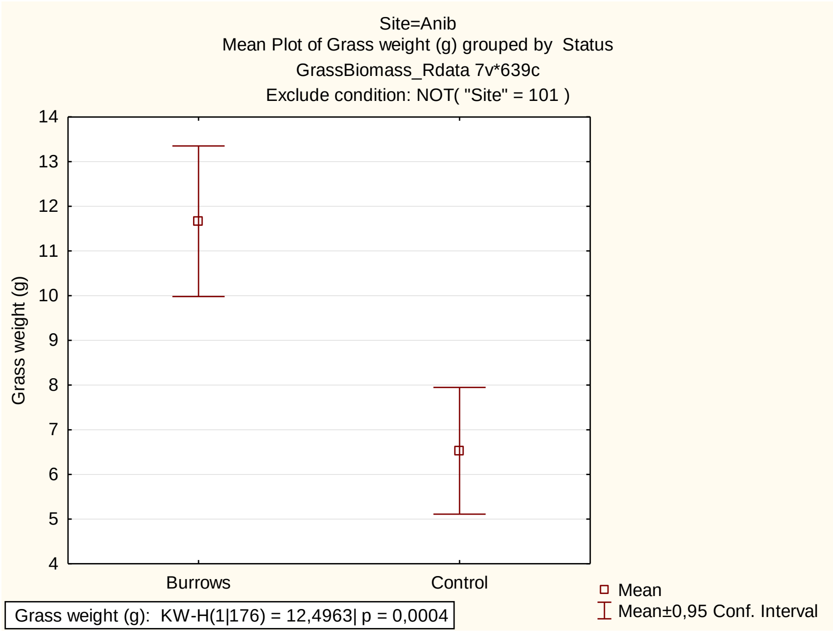
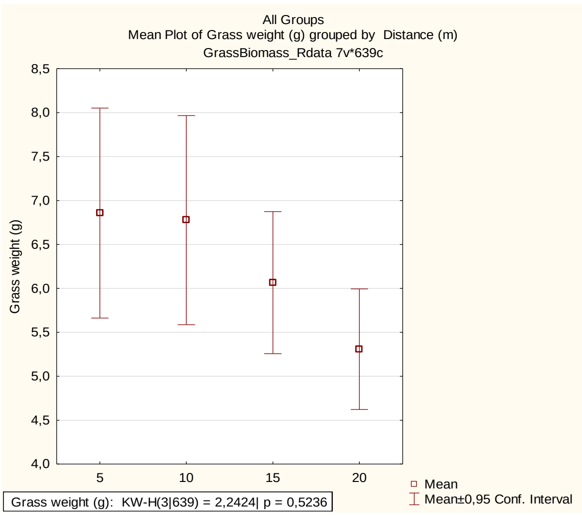


Figure 18: Grass biomass around burrow clusters and control sites in the southern Kalahari.

A decreasing trend in biomass with distance from the burrow clusters was observed, but no significant difference in the overall data (Figure 19). The decreasing trend is also present when considering the southern Kalahari in isolation, but here the hypothesis holds true with biomass being significantly higher ($p = 0.0202$) closer to the burrow cluster than twenty meters away.



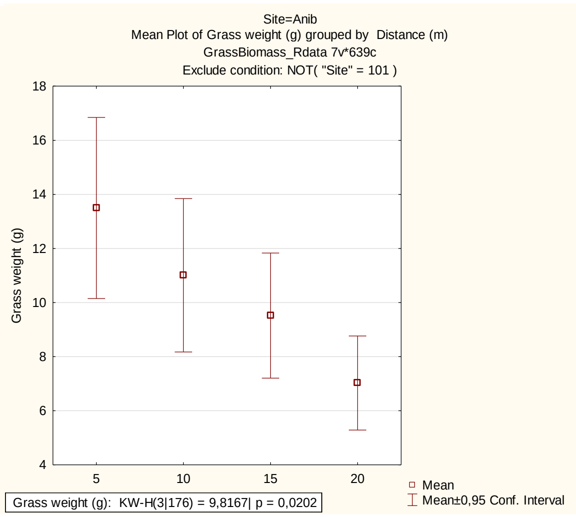


Figure 19: Grass biomass around burrow clusters from 5 to 20 meters away, for all locations (left) and only southern Kalahari (right).

Soil moisture probes set around burrow clusters also showed better water infiltration than the control site (**Error! Reference source not found.**, Figure 20). The highest average moisture percentage of 19.4% was recorded by Logger 2 in the 4th week. The control logger recorded the lowest moisture percentages with the highest average of 2.6% recorded in the 3rd week. At the 10 cm depth the control logger only recorded moisture during first week, and during the 6th week no moisture was recorded at any depth.

Table 3: Soil moisture infiltration percentages (means per week) recorded at different depths, around burrow and control sites, for six weeks.

	Week	Moisture Infiltration Depths					
		10cm (%)	20cm (%)	30cm (%)	40cm (%)	60cm (%)	100cm (%)
Logger 1	1	4,4	6,7	7,4	8,0	11,4	7,1
	2	4,6	7,0	7,4	7,9	11,6	7,2
	3	4,3	7,0	7,3	7,8	11,4	7,4
	4	3,7	6,8	7,2	7,7	11,3	7,6
	5	3,4	6,6	7,1	7,6	11,1	8,0
	6	5,0	7,0	7,5	8,0	10,9	8,8
	Avg	**4,3**	**6,8**	**7,3**	**7,8**	**11,3**	**7,7**
	Std	**0,6**	**0,2**	**0,1**	**0,2**	**0,2**	**0,6**
Logger 2	1	4,9	3,1	4,9	6,0	6,9	7,5
	2	9,7	6,1	6,5	6,4	7,2	7,8
	3	10,1	5,7	7,5	8,4	8,7	10,1
	4	10,1	6,8	9,1	10,7	11,9	19,4
	5	7,8	5,6	8,0	9,8	10,7	16,4
	6	5,9	4,1	6,2	8,0	8,5	12,0
	Avg	**8,1**	**5,2**	**7,0**	**8,2**	**9,0**	**12,2**
	Std	**2,1**	**1,3**	**1,4**	**1,7**	**1,8**	**4,4**
Control	1	0,4	1,4	1,7	1,8	1,1	1,0
	2	0,0	1,0	1,2	1,3	0,7	0,6
	3	0,0	1,6	2,4	2,6	1,5	1,6
	4	0,0	0,2	0,6	0,7	0,3	0,3
	5	0,0	0,0	0,1	0,1	0,0	0,0
	6	0,0	0,0	0,0	0,0	0,0	0,0
	Avg	**0,1**	**0,7**	**1,0**	**1,1**	**0,6**	**0,6**
	Std	**0,2**	**0,7**	**0,9**	**0,9**	**0,6**	**0,5**

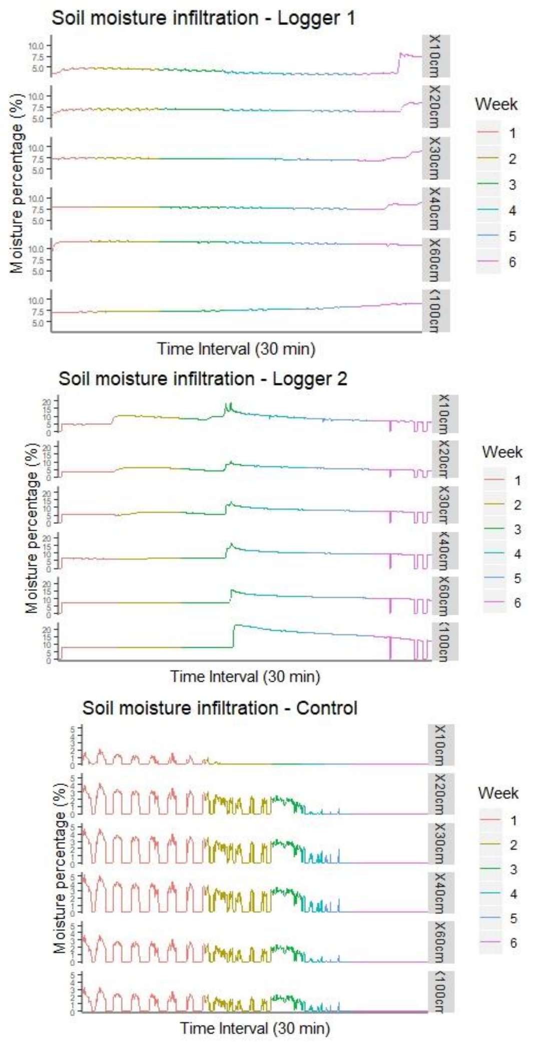


Figure 20: Soil moisture probe logger data for two burrow sites (Logger 1 and Logger 2) and a control site (Control) as moisture percentages (%), over a period of six weeks.

3.4 Remote sensing data

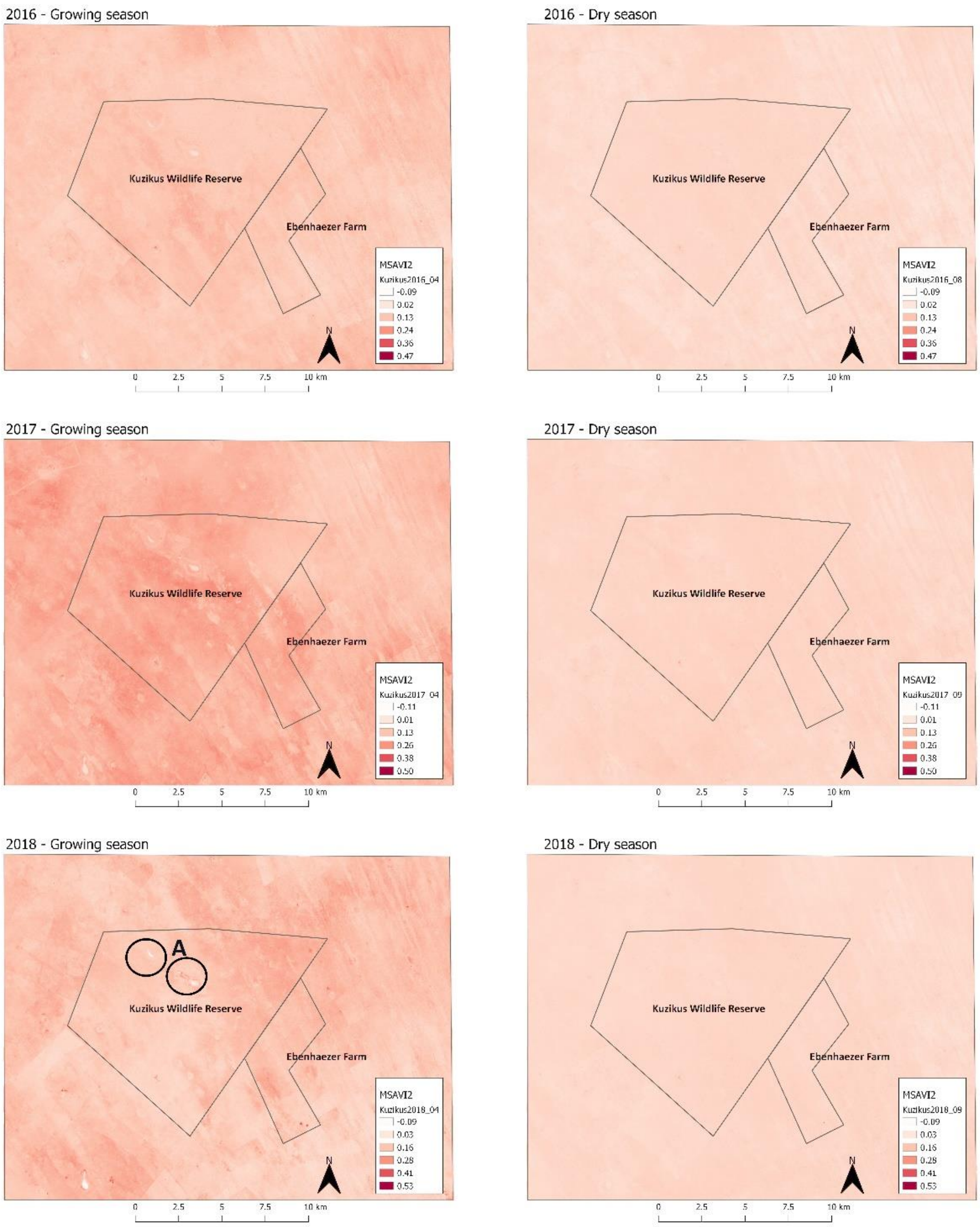


Figure 21: Sentinel images (MSAVI2) of the northern Kalahari site, comparing growing and dry seasons of three years (2016 – 2018). Higher pixel values indicate a higher MSAVI2 index as a proxy for plant productivity. A) Two salt pans on Kuzikus.

When comparing the satellite imagery of the three study sites clear differences between the seasons and subtle differences between the nature reserves and livestock farms were observed. The northern Kalahari site showed small differences between the nature reserve and the surrounding livestock farms for the 3 years observed (Figure 21). The 2016 satellite imagery of the northern Kalahari site correspond with the differences observed in Rodgers et al. (2017), where the nature reserve showed higher productivity and probable resilience than the livestock farm in the dry winter season.

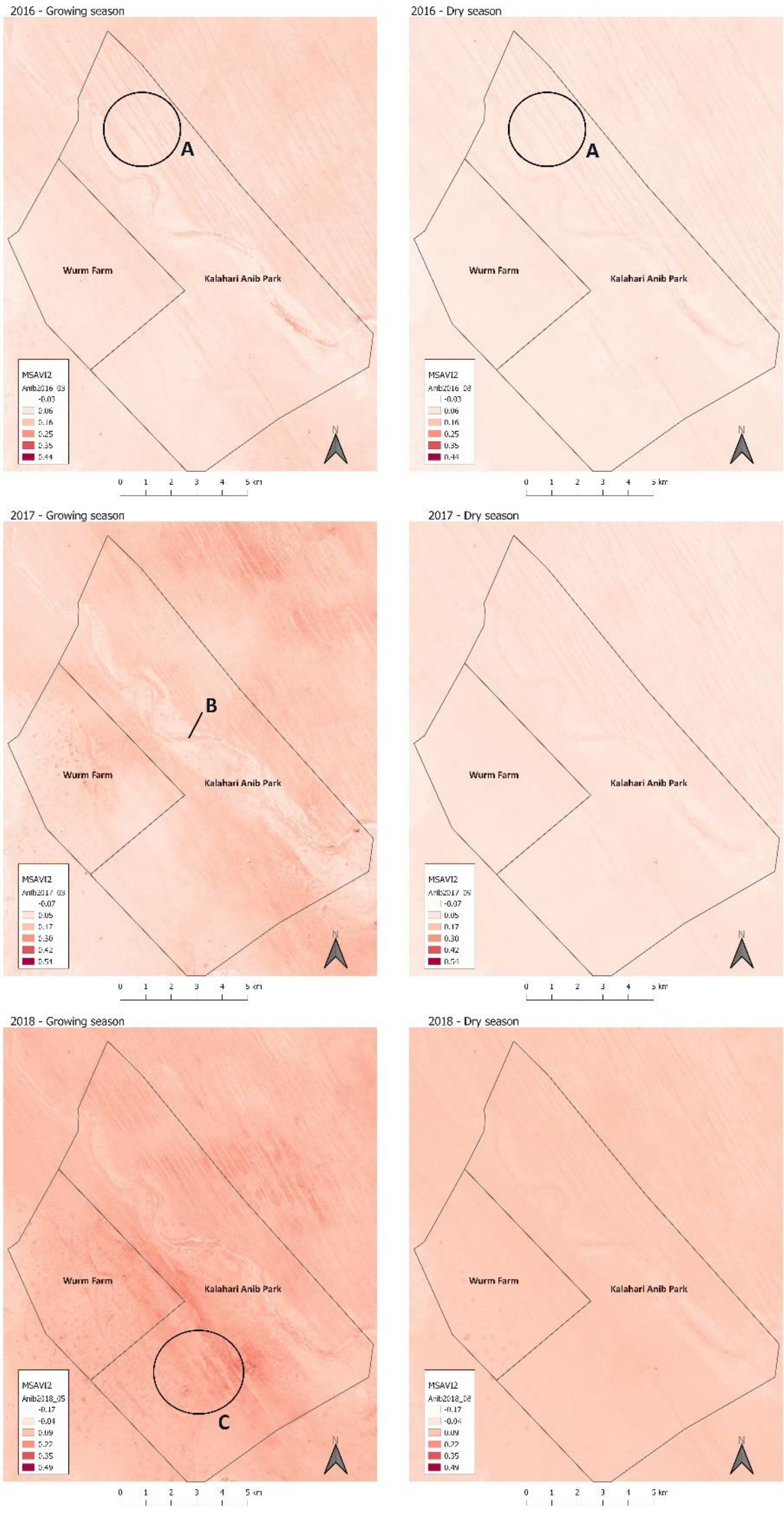


Figure 22: Sentinel images (MSAVI2) of the southern Kalahari site, comparing growing and dry seasons of three years (2016 – 2018). Higher pixel values indicate higher plant productivity. A) Vegetated linear dunes. B) Ephemeral river. C) Gradual linear dunes.

No clear distinction in vegetation productivity could be seen between the land uses in the southern Kalahari (Figure 22). Differences in vegetation/habitat diversity (Figure 22: A, B, C) between the nature reserve and livestock can be seen on the imagery, with more diversity in vegetation productivity on the nature reserve. Qualitative differences are pointed out in each analysis.

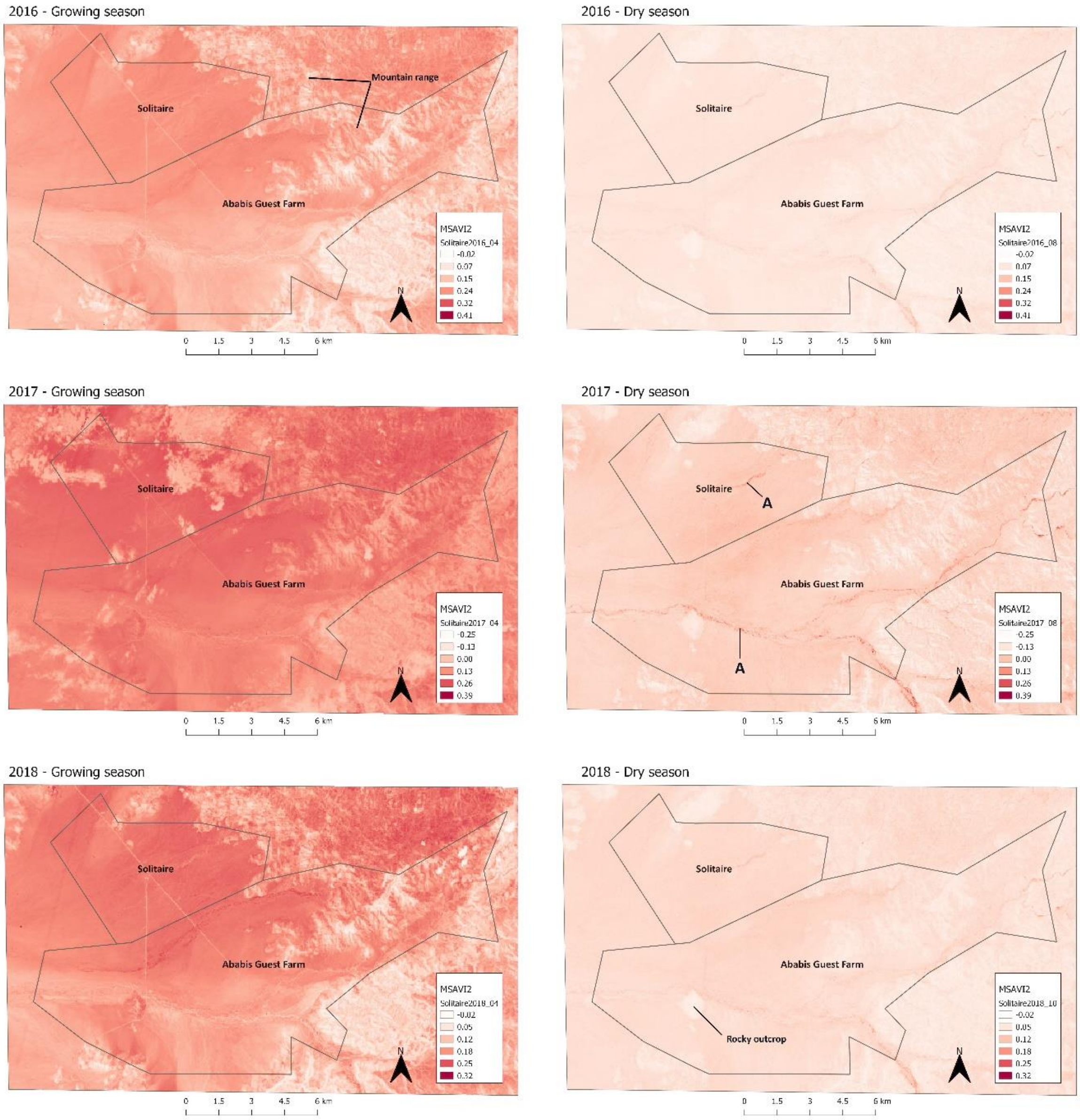


Figure 23: Sentinel images (MSAVI2) of the Pro-Namib site, comparing growing and dry seasons of three years (2016 – 2018). Higher pixel values indicate higher plant productivity. The mountain range, rivers (A) and a rocky outcrop is indicated.

Again, no clear distinction could be seen between the land uses on the Pro-Namib site during the dry season (Figure 23). In the growing season however, the nature reserve (Solitaire) shows higher vegetation productivity.

Chapter 4: Discussion

By comparing two neighbouring sites of different management types within three different habitat types, the study was able to reveal interesting seasonal and land use dependent dynamics of understudied nocturnal mammals of southern Africa.

4.1 Nocturnal bioturbator composition

In line with most known literature (Lindsey *et al.* 2013, Hempson *et al.* 2017, Rodgers *et al.* 2017, Holechek and Valdez 2018), the wildlife areas in the northern and southern Kalahari sites had the highest biodiversity and overall abundance of bioturbator species studied, while no significant differences were observed between the Namib land uses. In general, the Kalahari sites had much higher overall biodiversity and abundances than the Namib sites. This difference is greatly influenced by the different climatic and geographical characteristics of the two biomes (Mendelsohn *et al.* 2002). Importantly for this study is the lack of the keystone bioturbating Kalahari species, springhare and aardvark, which do not naturally occur in the Pro-Namib (Coetzee 1970, Skinner and Smithers 1990, Skinner and Chimimba 2006, Stuart and Stuart 2013, Peinke D *et al.* 2016) have an effect on the comparative land use differences.

Differences in soil structure between the Pro-Namib and Kalahari are also a contributor here, as the soil structure in the Pro-Namib study sites do not allow for large burrows (40 – 100 cm) to be dug (Laundré and Reynolds 1993, Mendelsohn *et al.* 2002). Attempted burrows with diameters larger than 40 cm were found in the field, but each was found collapsed and thus no active burrows of this size class could be recorded. Species that utilize large burrows, such as aardwolf, were often found in very small burrows, rock cavities or shallow holes dug by porcupines while foraging (personal observation during field work; K Prediger, personal communication, 18 October 2017). Although the Kalahari and Namib sandy soils fall within the same geological rock group, “Kalahari and Namib Sands (S)” (Mendelsohn *et al.* 2002), their soil structure seems to differ. Laundré and Reynolds (1993) suggest that in Idaho, North America, soil structures with increased percentages of silt and clay allow deer mice (*Peromyscus maniculatus*) and kangaroo rat (*Dipodomys ordii*) to dig larger, deeper and longer burrows. This could indicate that Kalahari sand has higher silt and clay content than the Pro-Namib sand, but no literature could be found on this topic. Kalahari sands are much deeper than Pro-Namib soils with bedrock often being close to the surface in the Pro-Namib (Burke 2002, Logan 2019). Reichman and Smith (1990) agrees that the distribution of many burrowing species are restricted by their soil preference. It seems that diurnal bioturbators, especially Cape ground squirrels fill this specific niche and acts as keystone species in this area (Ewacha *et al.* 2016). There is however far too little research into the impact of ecosystem engineers in the Pro-Namib ecosystem to make conclusive statements.

The pilot study revealed important information that some mammals have clear habitat preferences during different seasons and this was again observed in this study. There were no seasonal shifts in sightings observed between land uses in the southern Kalahari (as observed in northern Kalahari in the pilot study), but more overall sightings did occur during the dry season (winter) on the nature reserve (Anib) which includes aardwolf and springhare sightings. This may simply mean that visibility was better due to sparser vegetation and nocturnal activity higher due to high metabolic energy demand and lower food availability, or it could be seasonal shifts from other neighbouring properties (avoiding Wurm's livestock farm due to persecution) (Peinke and Brown 2003, Anderson 2004, Herbst and Mills 2010, Kamler *et al.* 2017).

What was interesting was that no bat-eared fox sightings were made during the dry season on the Namib sites, while 23 sightings were made during the growing season on the nature reserve. The species is generally common in this biome (NamibRand Nature Reserve 2012, Environmental Information Service 2019). The pooled data from all the sites also indicated more sightings of this species during the summer growing season. This is the opposite of what was observed with aardwolf and springhare. It is thought that bat-eared foxes change their social behaviour and movement based on seasons (Stuart and Stuart 2001, Skinner and Chimimba 2006, Kamler *et al.* 2017), causing them to form larger social groups, travel greater distances, have larger home ranges and greater home range overlap during the dry winter season compared to the summer growing season. The groups could have moved out of the study site when the data was collected. Another plausible explanation could be that the bat-eared fox population was affected by a rabies outbreak (Swanepoel *et al.* 1993, Kamler *et al.* 2017). Rabies incidences in this species peak during the dry season, reasons for this are still unknown however (Thomson and Meredith 1993, as cited in Kamler *et al.* 2017). Rabies is transmitted through physical contact so it makes sense that with greater movement and greater group sizes, higher rates of disease transmission would occur. Considering the ecological effects of burrowing mammals, the indirect impact of rabies on rangeland productivity would be an interesting ecological-epidemiology study, one not considered in literature to date.

Springhare was once again the most prolific species recorded in the Kalahari (north and south) study sites (similar springhare data to the pilot study). This species has been found to play keystone roles in Kalahari ecosystems as microhabitat engineers and as an important prey species for many species, including humans (Yellen 1991, Skinner and Chimimba 2006, Peinke D *et al.* 2016). Therefore, a healthy springhare population could indicate high environmental integrity. Springhare could be an important prey buffer species in predominantly livestock farming areas, especially for medium-sized predators such as black-backed jackal and caracal, reducing livestock losses. On the other hand, where predators are persecuted, an overpopulation of springhare could cause land degradation through overgrazing (Augustine *et al.* 1995, Peinke and Brown 2006, Peinke D *et al.* 2016). With the substantial numbers of springhare recorded on the northern Kalahari sites overpopulation could be or become a problem for rangeland managers and farmers. More research is needed to determine how an overpopulation of springhare overwrites the positive effects of bioturbation in this system.

4.2 Rangeland productivity and burrows

In the pilot phase of this study, high resolution UAV images revealed some important differences between the two study sites of the northern Kalahari. In this pilot study the wildlife reserve had a markedly higher vegetation productivity than the livestock farm (Rodgers *et al.* 2017). It was unclear whether this was a cause or consequence of the management type, whereby continual grazing by livestock in this marginal livestock farming area (Mogotsi 2011) is likely to diminish quality fodder. However, grazing was not limited to the farm, and over-grazing was considered a concern on the wildlife reserve. The wildlife farm also had a significantly higher abundance of burrows (Figure 17) than the livestock farm and this was thought to be a contributing effect to higher vegetation productivity.

UAV images were not available for the other study sites (southern Kalahari and Pro-Namib), instead 10 meter resolution Sentinel images (Delwart 2015) were used for remote sensing. Some limitations exist when applying existing remote sensing techniques to African savanna vegetation due to sparse vegetation cover (Huete *et al.* 1985, 1992, Huete 1988, Ghulam *et al.* 2007, Tsalyuk *et al.* 2017). Sparse cover results in more bare soil with high background signal and high reflectance. Bare soil and dry vegetation is also difficult to differentiate between as their spectral signals are similar due to less chlorophyll in the vegetation. The soil influences of red and yellow soils specifically, makes it difficult to detect sparse vegetation (Huete 1988). MSAVI was used to remedy this (as explained in the Methods section 2.5), but limitations remain (Qi *et al.* 1994, Tsalyuk *et al.* 2017). This could explain why there were no clear or only very subtle differences observed between the land uses during the dry season using the rougher 10 m resolution, compared to the distinct difference observed in the pilot, Rodgers *et al.* (2017), with much finer UAV image resolution (4cm). In the pilot southern Africa experienced an extreme drought year (NASA 2016) and these drought conditions continued for the two subsequent years of the current study (NASA 2019). The accumulation of environmental conditions of consecutive poor rainfall years also had an effect on the effectiveness of the remote sensing activity.

The northern Kalahari (Figure 21) and Pro-Namib (Figure 23) wildlife sites generally indicated higher vegetation productivity in the growing season, with equally poor or no productivity in the dry season. This seems to indicate higher vegetation recovery after the dry season on the wildlife sites. The predominant factor however was the lack of precipitation across the whole region, as moisture is the major driver of productivity (Sala 2000, Dirkx *et al.* 2008, O'Mara 2012). The Kalahari wildlife sites also indicated a diversity of habitats (Figure 21 and Figure 22) which contributes to the overall higher productivity and more resilient ecosystems (Sala 2000, Millennium Ecosystem Assessment 2005, Tilman *et al.* 2006). The higher vegetation productivity and recovery, although small, and more diverse habitats indicates higher environmental integrity at the wildlife sites, supporting Tilman and Downing's (1994, as cited in De Leo and Levin 1997) argument that more diverse ecosystems are generally more stable. Therefore, improving and/or conserving biodiversity contributes to maintaining or even improving productivity in rangelands.

The vegetation productivity findings were further supported by data collected at ground level, assuming that more burrows are present on the wildlife reserves as found in the pilot of Kuzikus-Ebenhaezer (Rodgers *et al.* 2017) and knowing that at least one livestock farmer actively controls digging mammals and closes up the burrows (S de Lange and H Wurm, personal communication, 15 November 2017). This is further supported by an overall decreasing trend in biomass around burrow clusters moving further away from the burrows (Results section 3.3). This further indicates a positive relationship between burrows and productivity with a higher biomass of grass growing closer to the burrows (Bonachela *et al.* 2015, Ewacha *et al.* 2016). This excludes burrowing clusters of springhare, as this species is known to clear the area of grass around their burrows for better predator detection (Butynski 1984, Skinner and Smithers 1990, Augustine *et al.* 1995, Peinke and Brown 2006).

4.3 Feedbacks between bioturbating mammals and the habitat

Burrowing mammals provide benefit to habitats in the same ways as do other bioturbators, such as earthworms (Meysman *et al.* 2006, Eldridge and James 2009, Fleming *et al.* 2014). In Section 4.2 a direct link between bioturbating activity and productivity was indicated. In the pilot study, remote sensed data of radii around burrows indicated vegetation productivity being higher closer to the burrows (10 m), which corresponds with the ground data collected in this study. Similarly, pocket gophers (*Geomys* spp.) (Reichman and Seabloom 2002), prairie dogs (*Cynomys* spp.) (Alba-Lynn and Detling 2008), kangaroo rats (*Dipodomys* spp.) (Heske *et al.* 1993) and plateau zokors (*Myospalax fontanierii*) (Zhang *et al.* 2003) were found to affect plant abundances and composition around burrow clusters, often resulting in pockets of plant communities completely different than the surroundings. No African studies could be found to compare the findings of the study with. Small (as indicated above) and medium-sized bioturbators therefore create fertile patches that feeds back into greater rangeland productivity (James *et al.* 2009, Gharajehdaghipour *et al.* 2016).

Something of great importance in dry regions such as Namibia (Sala 2000, Coetzee 2012), is the impact that bioturbation has upon soil infiltration rate of water (Reichman and Smith 1990, Jones *et al.* 1994, Avenant 2000, Fleming *et al.* 2014, Ewacha *et al.* 2016). Earthworm and arthropod (insects, scorpions, millipedes etc.) macropores are known to increase infiltration by 4 – 10 times, improving soil moisture retention and aeration, and reducing surface runoff (Edwards and Bohlen 1996, Goldbach *et al.* 2018, Marquart and Blaum 2018). Small mammal research has shown similar effects on soil infiltration (Martin 2003, Hauptfleisch *et al.* 2017, Faiz and Faiz 2018). Although the soil moisture infiltration data of this study (Results section 3.3, Table 3 and Figure 20) is limited in scientific rigour, it shows substantially higher moisture infiltration and retention around burrows compared to an area without burrows. What is interesting to note is how dry the topsoil (10 cm depth) remains at the control site. Only 0.4% moisture is retained in the topsoil in the first week and 0 % for the following five weeks, while no moisture was recorded at any depth by the sixth week. This indicates that burrows increase moisture retention in topsoil especially, which is important for seed germination, seedling growth and grass productivity (Smith and Goodman 1986, Martin 2003). This is logical as evaporation in Namibia is purported to be 3000+ mm per annum, over ten times larger than precipitation (Mendelsohn *et al.* 2002, Sweet and Burke 2006). Any mechanism that drains rainfall runoff away from the surface of the soil is therefore expected to have a positive effect on soil moisture retention.

A school of thought suggests that digging and clearing activities by bioturbators may seem destructive and degrading to landscapes (Reichman and Seabloom 2002, Zhang *et al.* 2003, Fleming *et al.* 2014). Burrows themselves cover an area, and cause disturbances to vegetation at their location (Butynski 1984, Augustine *et al.* 1995). Our study found that a total of about 70 metric tonnes (n=240) and an average of 2.2 metric tonnes of soil per burrow were displaced (Table 1). We postulate that the turning and displacement of the soil causes aeration, buries ground fodder (decomposition) and seeds (germination), and frees up added nutrients depositing it at the surface (Reichman and Smith 1990, Gabet *et al.* 2003, Martin 2003, Eldridge and James 2009). Additional turning of the soil improves soil structure and compaction, which feeds back into bioturbators being able to construct bigger, deeper and longer burrow systems (Laundré and Reynolds 1993). Therefore, at some intermediate point these disturbances improve both productivity and plant species richness (Grime 1973), thereby providing great benefit to the ecosystem through the trophic levels.

Bioturbating mammals such as springhare and aardvark are important microhabitat engineers for other species (Reichman and Smith 1990, Jones *et al.* 1994, Skinner and Chimimba 2006, Peinke D *et al.* 2016). Springhare burrows are utilised for shelter, protection from predators and foraging by at least 20 other mammal, three bird, six reptile and 22 invertebrate species (Skinner and Chimimba 2006, Peinke D *et al.* 2016). Similarly, Whittington-Jones *et al.* (2011) recorded 21 mammal, two bird, three reptile and one amphibian species utilising aardvark burrows. Burrows of medium-sized bioturbators provide important buffered microclimates against harsh semi-arid and arid environments like the Kalahari and Pro-Namib (Reichman and Smith 1990, Peinke and Brown 2003, Richardson and Anderson 2005, Burda *et al.* 2007, Whittington-Jones *et al.* 2011). In this study, differences between ground surface and below ground (burrow) temperatures were as high as 44 % with the highest average below ground temperature being 22.7 degree Celsius. The burrow temperatures indicate a stable environment with little temperature fluctuation during warm summer days (Burda *et al.* 2007). Similar results were obtained in other studies, with aardvark burrows where maximum temperatures were significantly lower below ground than outside (Whittington-Jones *et al.* 2011), and in aardwolf burrows the mean summer and winter temperatures were 27 and 12 degree Celsius respectively (Richardson and Anderson 2005). It is important to note however, that surface soil warms by absorbing direct, short-wave radiation from the sun and thus deeper burrow systems are less affected and experience less temperature fluctuations (Reichman and Smith 1990, Burda *et al.* 2007). This further stresses the importance of bioturbators being able to construct deep and extensive burrow systems. By creating microhabitats for many other species, species diversity, seed germination and habitat heterogeneity are improved/maintained feeding back into rangeland productivity and environmental integrity (Fuller *et al.* 2014).

4.4 Rangeland management

Grassland (including savanna) rangelands are the main environments used for grazing livestock and growing crops, covering about 37% of the world's landmass (Davidson *et al.* 2012, O'Mara 2012). Land degradation, in the form of overgrazing, cropland conversion and desertification, have drastically reduced suitable habitat for bioturbating mammals. Sala (2000) indicates that the largest global impact on biodiversity over all biomes will be land use change, followed by climate change as the second largest factor. When forests are converted into grasslands or grasslands converted into croplands local extinctions of plant communities and fauna that depend on it occur. Land use change also affects bioturbators most severely (Jones *et al.* 1994, Sala 2000, Davidson *et al.* 2012, Fleming *et al.* 2014). The loss of about 50% of Australian bioturbators over the last 200 years have caused detrimental effects on their ecosystems (Fleming *et al.* 2014). Aardvark as keystone species in the Kalahari savanna (Whittington-Jones *et al.* 2011, Rey *et al.* 2017) did not produce any significant sightings in both Kalahari sites (northern and southern) and the sightings that we did have revealed some very skinny individuals. Rey *et al*. (2017) has found that aardvarks are starving of drought related stress due to climate change already, possibly even related to agriculture as land use increase which degrades ecosystems. Therefore, by maintaining environmental integrity through maintained or improved biodiversity in rangelands instead of complete land use change to single species agriculture, it can potentially act as a buffer for ecosystems against climate change (Tilman *et al.* 2006, Lindsey *et al.* 2013, Hempson *et al.* 2017).

Our study indicated that higher burrowing mammal and mesocarnivore diversity and abundance has a direct and positive link on Kalahari wildlife rangeland productivity and environmental integrity. Karr and Dudley (1981, as cited in De Leo and Levin 1997) defines environmental integrity as: "the capability of supporting and maintaining a balanced, integrated, adaptive, community of organisms having species composition, diversity, and functional organization comparable to that of natural habitats of the region", and includes the capability of the system to support services that is of value to humans. This is achievable on livestock rangelands if managers are more tolerant of mesocarnivores (Blaum *et al.* 2009) which maintain or improve biodiversity. Improving biodiversity and integrity can be done through reducing overgrazing and land degradation, by reduced livestock stocking rates, including wildlife with different grazing strategies into stocking rates, better grazing regimes and applying adaptive and flexible rangeland management strategies (Barnard *et al.* 1998, Chardonnet *et al.* 2002, Odadi *et al.* 2017, Hauptfleisch 2018, Ziegler *et al.* 2018).

Benefits of bioturbation are less apparent on the Pro-Namib sites of this study. It is predicted that climate change will cause severe droughts and warming in the Namib grasslands, which will have serious impacts on biodiversity in the area (Foden et al. 2007, as cited in Ewacha *et al.* 2016). A photo matching study of 100 photos spanning from the 1940's to the present (2019) however, revealed increased vegetation in the arid Pro-Namib and hyper-arid Namib Desert in contrast of global climate change predictions (Rohde *et al.* 2019). The absence of the keystone species, springhare and aardvark, due to habitat restrictions adds to less bioturbating activity in the Pro-Namib.

Chapter 5: Conclusion and recommendations

Overall, this study comparing different management types in different biomes has provided some valuable insights into the movements, strategies and rangeland benefits of these burrowing medium-sized mammals. Further research is needed to thoroughly investigate the effects of ecosystem engineers in Namibia in general and the Pro-Namib particularly by focusing on diurnal species there. However, this study has revealed and supported evidence that these under-studied mammals play an important role in ecosystem functioning and environmental integrity, which leads to more stable and resilient ecosystems. The burrow clusters of these mammals persist in the environment for many years and create habitat for fauna and flora communities, improves habitat heterogeneity, soil fertility, soil structure and soil moisture infiltration and retention. Provision of habitat conditions suitable for bioturbating mammals will thus feed back into providing more productive land.

Recommendations:

Awareness among farmers of the role of bioturbating species needs to be raised, as many farmers continue to persecute them or dismiss their importance.

The effect of bioturbation in the drought recovery of 2020 needs to be studied, as well as further studies of these effects in the Namib.

A country-wide assessment focusing on nocturnal species are required to improve data on their distribution and abundance (Environmental Information Service 2019).

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Appendices

Appendix 1 Nocturnal mammal survey data

Appendix 2 Burrow measurement data

Appendix 3 Grass transect and biomass data