AN ASSESSMENT OF TRENDS IN POPULATION ABUNDANCE AND SPATIAL DISTRIBUTION OF ROAN ANTELOPE (*Hippotragus equinus*) AND SABLE ANTELOPE (*Hippotragus niger*) IN THE GREATER WATERBERG PLATEAU COMPLEX, NORTH-CENTRAL, NAMIBIA.

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ABSTRACT

Understanding factors affecting the demographic status and spatial distribution of large mammals is of major relevance in wildlife conservation and management. This is particularly the case for the roan (*Hippotragus equinus*) and the sable (*Hippotragus niger*) populations in the Waterberg Plateau Park (WPP) whose growth appears to have been suppressed since 1994, after being introduced in 1975 and 1980, respectively. The lack of scientific assessments on potential factors influencing their growth and spatial distribution has been a major challenge confronting their management in the WPP, which is the aim of this study. The study used the Generalized Additive Modelling and State Space Models to assess trends in the abundance of roan and sable between 1975 and 2019 in the WPP based on historical aerial count data. Additionally, occupancy modelling and detection probability was conducted to assess the influence of site and detection covariates on their spatial distribution in the Waterberg Plateau Farm based on the camera trapping data collected during the wet and dry seasons. The study estimated with uncertainty a negative population growth for roan (r = - 0.02 ± 0.06, CI95 = -0.13 – 0.09) and a zero-population growth for the sable (r = 0.00 ± 0.08, CI95 = -0.14 – 0.16). These growth trajectories tend to be positively influenced by annual rainfall, and the occasional auctioning, and the introduction of individuals. Contrary, it was insignificantly but negatively influenced by the low-lagged rainfall and the increase of the buffalo population. Occupancy modelling showed that roan distribution is significantly influenced by the co-occurrence of sable both during the wet and the dry seasons. Sable distribution was positively influenced by forage and the presence/absence of leopard during the wet season while positively influenced by the presence/absence of waterhole during the dry season. The cumulative effect of these variables is likely to have resulted in the reduction of the survival and reproduction rate as these antelopes are unable to escape the semi-closed isolated study areas. Future interventions involving the introduction of these species outside their native ranges should be careful thought, and must consider the potential impacts of climate change to improve the success of this management strategy.

Keywords: Aerial counts, camera trapping, population abundance, population dynamics, occupancy, spatial distribution, generalized additive model, and state space model

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ACRONYMS

AIC Akaike’s Information Criterion

CI Confident Interval

GAM Generalized Additive Model

GLM Generalized Linear Model

IS Instantaneous Sampling

IUCN International Union for the Conservation of Nature and Natural Resources

KNP Kruger National Park

MEFT Ministry of Environment, Forestry and Tourism

NDVI Normalized Vegetation Index

REM Random Encounter Model

SD Standard Deviation

SSC Species Survival Commission

SSM State-Space Models

STE Space to Event

TTE Time to Event

WH Waterhole

WPF Waterberg Plateau Farm

WPP Waterberg Plateau Park

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DECLARATIONS

I, **Martha Alfeus** hereby declare that this study is my own work and is a true reflection of my research and that this work or any part thereof has not been submitted for a degree at any other institution.

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CHAPTER 1

1. INTRODUCTION

1.1 Background of the study

A thorough understanding of population dynamics and factors affecting the demographic status and spatial distribution of large antelopes has been a concern across conservation areas in Africa (Gasaway, Gasaway, & Berry, 1996; MacKenzie, Nichols, Royle, Pollock, Bailey & Hines, 2006; Owen-Smith & Mills, 2006; Marshal, Rankin, Nel, & Parrini, 2016). Importantly, assessments of the determinants of animal distributions naturally focus on range boundaries and the biotic and abiotic factors responsible for their locations. For example, the loss of iconic species such as the black rhinoceros (*Diceros bicornis*), has occurred across much of their historic range, and currently, the species is on the verge of extinction despite extensive conservation investment (Crosmary, Chamaillé-Jammes, Mtare, Fritz, & Côté, 2015). Consequently, the long-term survival of wildlife depends largely on the careful protection of natural habitats. Hence, conservation is particularly relevant to protected areas e.g. national parks and reserves, in preventing small populations from declining further. Still, population numbers have declined drastically over the past few decades in national parks (Ogutu & Owen-Smith, 2005; Crosmary, et al., 2015). Thus, this decline raises serious concerns about the effectiveness of protected areas in ensuring long-term conservation of the species.

In turn, among the species exhibiting long-term declines in abundance are roan (*Hippotragus equinus*) and sable (*Hippotragus niger*). These antelope species have demonstrated recent declines in many protected areas such as the sable antelope in

Kgaswane Mountain Reserve (Marshal, Rankin, Nel, & Parrini, 2016) and roan antelope in Kruger National Park (Harrington, Owen-Smith, Viljoen, Biggs, Mason, Funston, 1999; Kroger & Rogers, 2005). According to Wilson and Hirst (1977), these species appear to be strongly influenced by the nature of the terrain, the vegetation, the availability of water, and their breeding population size and density. Unsurprisingly, potential factors leading to the population dynamics are confounded and several different factors may in fact interact. Owen-Smith and Mills (2006) specified that identifying the causes of population dynamics can be difficult because of interacting factors whose influences cannot always be isolated such as interspecific and intraspecific competition, predation, rainfall, disease, lack of food resources, and human activities. But mostly, the dynamics of animal populations and fluctuations in abundance can be influenced by climatic variation, prevailing resources, population density, predation, and through the delayed effects of trophic interactions and abiotic effects on habitat conditions (Owen-Smith & Mills, 2006). For instance, based on Gasaway, Gasaway, and Berry's (1996) study, predation appeared largely responsible for the decline of several ungulate populations in the Etosha National Park in Namibia while in South Africa's Kruger National Park, variability in annual rainfall controlled the population dynamics of kudu through its effects on food resources, but affected several other ungulate species by changing their susceptibility to predation risk (Owen-Smith & Mills, 2006). The concept of the "landscape of fear" has recently become central to describing this spatial variation in risk, perception, and response (Bleicher, 2017; Gaynor, Brown, Middleton, Power, & Brashares, 2019).

According to Georgiadis, Hack, and Turpin (2003), savannah herbivores are fundamentally resource-limited. Several studies of wild ungulates have identified rainfall as a key limiting factor (Georgiadis, Hack, & Turpin, 2003; Owen-Smith & Mills, 2006) and others have implicated predation or disease (Gasaway, Gasaway, & Berry, 1996) and illegal hunting and competition. In addition, Duncan, Chauvenet, McRae, and Pettorelli (2012) suggest that certain life-history traits can be expected to make species more susceptible to animal behaviour, such as strong dependence on permanent water sources, obligate grazing or mixed feeding, and or sedentary behaviour. In this context, active management is required, preferably based on some understanding of the ecological processes regulating populations.

Consequently, due to the rarity and threat of most of these large antelopes in Africa, the Ministry of Environment, Forestry and Tourism (MEFT), has reintroduced a number of game species throughout Namibia as part of a program aimed at protecting the game species and to establish protected breeding populations. This was the case of the roan and sable antelopes which were introduced to the Waterberg Plateau Park in 1975 and 1980, respectively (Martin, 2003). Since their reintroduction, MEFT has monitored these species through aerial transect counts. These counts indicated that populations increased from 1975 to 1990, but slumped after 1994 (Martin, 2003). Because of this concern, the park management decided to translocate the two antelopes to the nearby farm, Waterberg Plateau Farm (WPF) while assessing factors that may be suppressing their population growth, the focus of this paper. In this study, we are proposing to undertake a contemporary and retrospective assessment of the population trends, current occupancy, and the factors that have influenced roan and sable antelope demographics since 1994 in the Waterberg Plateau Park. Ultimately, this project will significantly contribute to biodiversity conservation by identifying the key factors shaping these antelopes' distribution and population dynamics within the Waterberg Plateau Park, hence providing sound empirical grounds to design effective and locally adapted conservation plans.

1.2 Problem statement

The lack of scientific assessments of factors affecting wildlife populations' demographic and spatial distribution status has been and continues to be a major challenge confronting their management and conservation. Due to escalation in the spectra of environmental dynamics and climate change, many wildlife species may struggle to adapt to new environmental conditions. Such changes can deem the ecosystem vulnerable to perturbations and therefore may lead to profound changes in its structure, resulting in the reduction or even permanent loss of biological diversity (Willig, 2003; Marshal, Rankin, Nel, & Parrini, 2016). Thus, new environmental changes impose threats to many of the wildlife population dynamics. For example, on Waterberg Plateau "island", species population growth can only be achieved through intrinsic growth (i.e. higher rates of fecundity and survival than mortality) or new restocking as immigration is not an option. This is because on one side the periphery of the plateau forms almost vertical cliffs, up to 300 m high, and on the other side the area is fenced, so immigration and emigration cannot occur.

On that note, factors causing reintroduced roan and sable antelope populations' slump in the Waterberg Plateau Park (WPP) have been and continues to be a major challenge confronting their management and conservation. This is because roan and sable antelope populations in WPP have not grown for the past two decades (Figure 1). Yet, the potential ecological and environmental factors causing roan and sable population's slump have not been sufficiently scientifically assessed. Equally the driving factors influencing these species spatial distribution patterns are unknown. Therefore, this study aims to assess factors potentially related to the suppression of these antelopes' populations and the regulation of their distribution. The ultimate goal of this research is to contribute with sound knowledge useful for the definition of appropriate management actions aimed at preventing these species from local extinction and also to propose sustainable ecological habitat types.

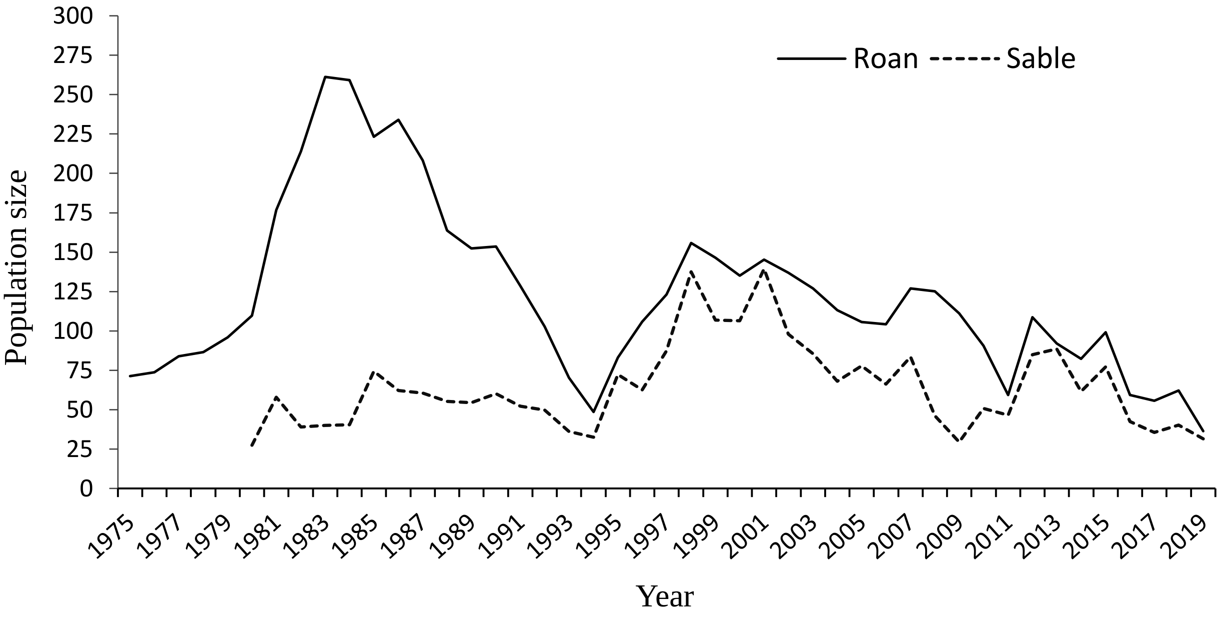

Figure 1 Demographic dynamics of the roan and sable population in Waterberg Plateau Park from 1975 to 2019.

1.3 Aim

This study aimed at improving our understanding of the factors influencing the population trends and spatial distribution of roan and sable antelope populations in the WPP and WPF.

1.4 Specific Objectives

Specific objectives were **to determine**:

1. Trends in the abundance of roan and sable in WPP from 1975 to 2019,
2. The relative abundance and spoor frequency of roan and sable in the WPF, and
3. The area occupied and the effect of site covariates potentially influencing roan and sable populations' occupancy and detection probability in the WPF.

1.5 Significance of the study

The findings of this study contribute critical yet lacking information on factors related to change in population size and occupancy of roan and sable antelope and provide recommendations towards their existing management or conservation plans. In addition, it is expected that the implementation of its findings will halt further sable and roan antelope decline. Ultimately, the study findings inform with recommendations the current introduction strategies for these highly economic and valuable species.

1.6 Study limitations and delimitations

The main limitation of this study was an inadequate number of remote camera traps. To circumvent this, a single camera was placed at each sampling site. However, this should not have affected the study findings, as individual identification was not a requirement in this study. Moreover, a drawback of using aerial counts is that it does not account for imperfect detection whereby false positive and positive negatives are possible (Pollock & Kendall, 1987; Schlossberg, Chase, and Griffin (2016). This could lead to counts being underestimated or overestimated by an unknown amount (Pollock & Kendall, 1987). To overcome this error the study made use of the models that explicitly allow the estimation of the variance for both the observation (i.e. counts) and process (i.e. trend in abundance) error associated with measurement of data and uncertainty on population dynamics, resulting in a more robust assessment of trends in the abundance of a population.

The only delimitation is that the expected findings may only be applicable to populations of roan and sable antelope confined to a study area with potentially similar ecological communities.

CHAPTER 2

2. LITERATURE REVIEW

2.1 Taxonomy, conservation status, and geographic distribution of roan and sable antelope

Roan antelope *Hippotragus equinus* and sable antelope *Hippotragus niger* belong to the family Bovidae and the genus *Hippotragus* (Furstenburg, 2011). These species are endemic to Africa and share many historic characteristics (Matthee & Robinson, 1999). For example, they are among the rarest and most symbolic largest African antelopes with the highest economical value than all other antelopes in the ecotourism and hunting industries (Adeyeye & Aye, 2013). The species appear to be strongly influenced by the nature of the terrain, the vegetation structure, the availability of water, and their breeding population size and density (Wilson & Hirst (1977). Furthermore, historically these antelopes were widely distributed across the savanna woodlands and grasslands of sub-Saharan Africa (IUCN o Antelope Specialist Group, 2017). However, they have disappeared from most parts of their former range, including for example in Eritrea and Burundi and they are on the verge of going extinct in Mauritania (Figure 2) (East, 1999). Their present distribution is discontinuous, with a 'patchy' distribution at a finer scale, a factor that can increase the risk of local extinction. Besides the contraction in their geographic range, their numbers have drastically decreased over the past decade from the 1970s (East, 1999). This reduction in abundance and the isolation of meta-populations has resulted in countries creating breeding populations by introducing the species within protected areas and develop conservation plans. Confronted by this optimistic scenario, these species are classified as "Least Concern" by the IUCN (IUCN SSC Antelope Specialist Group, 2017) and as a protected game of conservation concern in Namibia (Nature Conservation Ordinance, 1975). The IUCN SSC Antelope Specialist Group (2017) highlighted that the species status may be elevated to 'Threatened' if the present negative trends continue. The following sections provide a general overview of each species' biology and ecology.

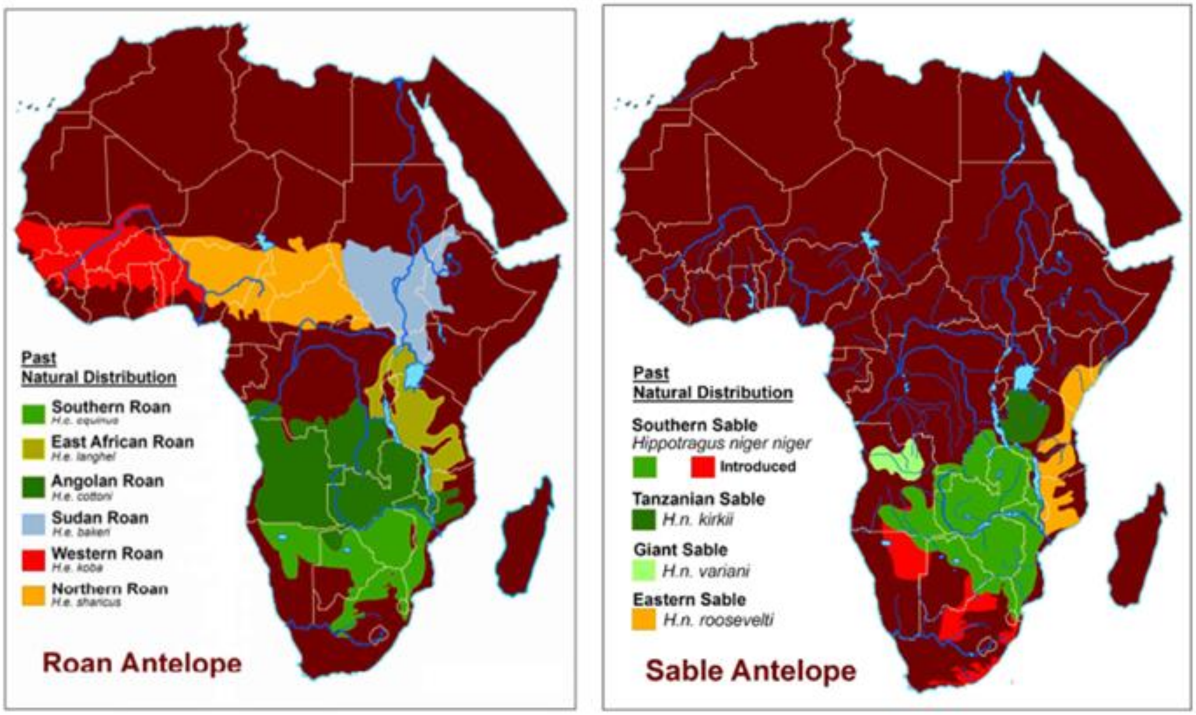

Figure 2 The geographical distribution of roan and sable antelope in Africa with subspecies delineations. *Source:* Furstenburg (2011, 2016, p. 3, 4)

2.2 Biology structure and ecology of roan antelope

The roan antelope is the largest member of Hippotragini and Africa's second-largest antelope species with a male and female weighing between 242-300 kg and 223-280 kg, respectively, and a shoulder height of 130- 145 cm (Adeyeye & Aye, 2013). Six subspecies: *H. equinus, H. cottoni, H. langheldi, H. bakeri, H. charicus, and H. koba* are recognized based on genetic (Matthee & Robinson, 1999; Alpers, Van Vuuren, Arctander, & Robinson, 2004) and morphological (Ansell, 1971) studies. Subspecies are spread across 31 countries with two main strongholds located in West and Southern Africa (Figure 1). A significant genetic structure based on microsatellites and mitochondrial DNA markers was detected across 18 roan antelope populations (Matthee and Robison 2003; Alpers et al., 2004). From the six subspecies, two are found in Namibia: the Southern roan antelope *H. equines equinus* and the Angolan roan antelope *H. equines cottoni* (Ansell, 1971; Furstenburg, 2011). In Namibia, these two subspecies occur naturally in the northeast (Bwabwata National Park, Mangetti National Park, Khaudum National Park, and Mamili National Park) and northwest (Kaokoland). In addition to these populations, two populations occur in the north-central (WPP and Etosha National Park), which were established through the introduction of animals from the Bwabwata National Park in the north-eastern Kavango region. Consequently, these two populations are outside the species' natural range and are the only roan antelope populations occurring in areas with an average rainfall below the 400mm isohyet (Martin, 2003).

The species' natural habitat preferences include open savannah bushveld or broken woodland with continual access to surface water and a thick, tall grass layer of predominantly sweet or intermediate palatable grass species (Taolo, 1995; Furstenburg, 2011; Kruger, Parrini, Koen, Collins, Nel; Child, 2016). Furthermore, the species occurs on rocky outcrops (MET, 2008). This preference corresponds well with that of a typical tropical savanna tree, *Burkea africana* (Erb, 1993). Roan antelope are predominantly intermediate grazers feeding only on grass such as the red grass *Themeda triandra*, spear grass *Heteropogon contortus*, wool finger grass *Digitaria pentzii*, and white buffalo grass *Panicum coloratum* (Taolo, 1995). In WPP roan antelope were observed exclusively feeding on *Digitaria seriata* during the wet season, but because this grass dries out very quickly, it is then rejected in favour of species such as the *Panicum sp, Eragrostis jeffreysii,* and *Aristida stipitata* (Erb, 1993). However, during the dry season when grass forage palatability drops below threshold levels, individuals can readily browse on available broad leaves (Wilson & Hirst, 1977; Furstenburg, 2011).

The roan antelope is primarily diurnal and partially gregarious with a breeding herd of 5 to 25 individuals dominated by one breeding bull (Furstenburg, 2011). The number of herds and herd sizes change with seasonal variation (Erb, 1993; Kimanzi, 2011; Kasiringua, Procheş, & Kopij, 2019). Kimanzi (2011) recorded group sizes of 2 - 14 individuals in Ruma NP, Kenya. In WPP, roan antelope herds were observed comprising 3 to 12 animals (Erb, 1993; Kasiringua, Procheş, & Kopij, 2019). This indicates that they are within the species herd threshold (Havemann, Retief, Tosh, & Bruyn, 2016), a threshold that once crossed exacerbates the acceleration in the declining rate, thus an increase in population extinction probability (Owen and Mills 1996). This is in agreement with the extinction vortex theory (Brook, Sodhi, & Bradshaw, 2008) which describes the process a declining species will experience under the mutual reinforcement of biotic and abiotic factors that pull the population downwards to extinction.

A breeding herd is comprised mostly of cows and young (Furstenburg, 2011; Kimanzi, 2011). Adult cows within the herd sustain a hierarchy of dominance that is related to physical strength and age, with the most dominant cow being the group leader

(Furstenburg, 2011). The young males form small bachelor herds which eventually give way to solitary, older, territorial bulls. The dominant bull becomes a permanent solitary nomad after losing its dominance. A breeding herd home range size varies from 2 to 100 km^2 (Martin, 2003; Kruger, et al., 2016) whereas the territory size of one male is estimated to be around 12 km^2 (Erb, 1993). Conversely, Furstenburg (2011) found that dominant breeding bulls do not establish static territories, but sustain an individual territorial zone of approximately 300-500m wide surrounding the periphery of the breeding herd.

Roan antelope are capable of reproducing throughout the year (MET, 2008). The calving season often starts as early as August when the veld is still dry. This synchronizes with the period after the initial rains in September and October when sprouting green grass provides lactating cows with the necessary dietary protein (Martin, 2003). Thus, there appears to be a relationship between early-season rainfall and calving success (Martin 2003).

2.3 Biological structure and ecology of sable

Sable antelope are slightly smaller than roan antelope with a body mass that rarely exceeds 225kg and a shoulder height of 135 cm (Wilson & Hirst, 1977). These antelope comprise of four subspecies namely the eastern (*Hippotragus n. roosevelti*), Zambian (*H.s n. kirkii*), common or southern (*H. n. niger*), and giant or Angolan (*H. n. variani*) sable (Matthee & Robinson, 1999; Ansell, 1971). These subspecies are spread across 10 countries mainly located in East and Southern Africa with an isolated population of Giant Sable antelope in central Angola (Figure 2). Even so, Matthee and Robinson (1999) observed a disruption in gene flow between the sable populations from East

Africa and those occurring in Southern Africa. This disruption was attributed to zoogeographical barriers between the subpopulations (*Ibid*). Of the four subspecies, only the southern sable antelope *H. niger niger* occurs in Namibia. Here, the species' natural range includes the tree savanna and Kalahari woodland. However, although sable experienced range reduction in the past, they have been reintroduced to many parts of their former range and also introduced to areas where they have never naturally occurred including Waterberg Plateau Park and Etosha National Park in Namibia (Martin, 2003). Outside Namibia, healthy roan antelope populations are found in protected areas in Botswana, Zambia, Tanzania, and Malawi (Ansell, 1971; Hensman, Owen-Smith, Parrini, & Bonyongo, 2013). By contrast, populations exhibiting long-term declines occur in the Kgaswane Mountain Reserve (South Africa) (Marshal, Rankin, Nel, & Parrini, 2016), Kruger National Park (South Africa) (Owen-Smith & Mills, 2006); Malilangwe Wildlife Reserve(Zimbabwe) (Capon, 2011), Greater Hwange National Park (Zimbabwe) (Crosmary, et al., 2015) and Waterberg Plateau Park (Namibia) (Martin, 2003).

Sable antelope occur in a variety of habitat types in the savanna biome. The species is an "edge" species that prefers woodland/grassland ecotone over open areas and open woodlands with veils of grassland (Nowak, 1991; Parrini, Koen, Dalton, & Eksteen, 2016)). Unlike roan antelope, this species avoids areas with high tree density and short grass (Parrini, Koen, Dalton, & Eksteen, 2016). Within this woodland grassland ecotone, like roan antelope, sable antelope are selective feeders with a preference for freshly grown grasses (40–140 mm high) with *Panicum maximum* and *Themeda triandra* as key ingredients (Grobler, 1981; Roux, 2010). However, they have a general dietary acceptance for other grass species such as *Brachiaria nigropedata, Heteropogon contortus*, *Digitaria spp.* and *Eragrostis spp.* (Parrini, Koen, Dalton, & Eksteen, 2016; Roux, 2010). Sable antelope are known to browse more than any other species of Hippotragini ((Parrini, Koen, Dalton, & Eksteen, 2016)). Browsing is a mechanism used to avoid competition with the roan antelope where they occur sympatrically (Nowak, 1991). Additionally, they are reported to be a water-dependent species (MET, 2008) drinking every 3 to 4 days and staying at least 1km away from the water source (Grobler, 1981).

Socially, the sable antelope is a gregarious species characterized essentially by a matrilocal organization. Within the matrilocality, the alpha female plays a leading role in initiating group activities such as feeding, drinking, moving, and flight (Furstenburg, 2016). Unlike roan antelope, sable antelope bulls appear to be strictly territorial and are never attached to a mobile group of females (Martin, 2003). The optimal habitat range with an annual rainfall of 400-500 mm, is five sable per $10km^2$ (Furstenburg, 2016). The species breeds seasonally with variation in the timing depending on the geographical location of populations (Wilson and Hirst 1977). For example, in Kafue National Park, Zambia, the calving period is in September, while in the Kruger National Park, South Africa it is in February and March, and in northern Botswana, it is in January and February. In the WPP, sable antelope calve between January and March (MET, 2008; Erb, 1993). This period coincides with the season when rainfall conditions are favourable thus increasing survival probability and breeding performance (Erb, 1993).

2.4 Population trends, dynamic and spatial distribution

Population dynamics can simply be defined by reproduction, mortality, and movement in and out of the geographic area (McCullough, 2010). This determines the change in abundance, age, and sex structure of a species based on the biotic and abiotic environmental factors. However, these simple factors can seldom be defined or even accurately measured in wildlife populations (McCullough, 2010). Because of the difficulty in determining the importance of specific processes, many recent studies have attempted to infer mechanisms indirectly by the analysis of population time series (Willig, 2003; Olexa & Gogan, 2007; Boyd, et al., 2018; Owen-Smith & Mason, 2005) and spatial distribution (Blom, Zalinge, Heitkönig, & Prins, 2005; Peterman, Crawford, & Kuhns, 2013; Anderson, et al., 2016). While spatial distribution is defined as the presence of individuals across an area, the spatial structuring of populations or communities is an important driver of their functioning and influence ecosystems. Therefore, implementation of the plan under the adaptive management paradigm requires an understanding of the spatial and temporal structure of the population and factors influencing the demographic status.

In turn, population dynamics and factors affecting the demographic status and spatial distribution of large antelopes have been a concern across conservation areas in Africa (Gasaway, Gasaway, & Berry, 1996; Owen-Smith & Mills, 2006; Marshal, Rankin, Nel, & Parrini, 2016). McNaughton, Ruess, and Seagle (1988) pointed out that early research in Africa focused on the distribution of animal species in relation to vegetation species composition and structure. They stated that although the habitat properties influence and dictate animals' distribution, wildlife also regulates those habitat properties to a significant extent. For instance, the combination of elephants killing large trees and browsers constraining the vertical growth of saplings, preventing them from becoming fire-resistant large trees can convert a closed woodland into open grassland (McNaughton et al., 1988). However, recently species occupancy modeling approaches have been used to predict species distribution and can identify critical significant habitat characteristics associated with species occurrence (MacKenzie, et al., 2006; Rich, Miller, Robinson, McNutt, & Kelly, 2016; Altwegg & Nichols, 2019).

Consequently, the African continent, once known as a harbor of both large and small mammals, is threatened with loss of biodiversity due to a range of factors arising from both environmental and anthropogenic effects. According to many studies, climate change, habitat loss, fragmentation, predation, disease, overexploitation, and human-wildlife conflict have accelerated rates of extinction, creating biodiversity crises and population dynamics across the world (Willig, 2003; Gasaway, Gasaway, & Berry, 1996; Havemann, Retief, Tosh, & Bruyn, 2016; Marshal, Rankin, Nel, & Parrini, 2016). For instance, Matandiko (2016) determined that anthropogenic activities, vegetation, and predation are the dynamic forces constraining the density of ungulates in Kafue National Park, Zambia. Anthrax and predation were the primary cause of population decline and persistent low densities of plain ungulates in Etosha National Park (Gasaway, Gasaway, & Berry, 1996). Crosmary, et al., (2015) found out that the decline of sable antelope in Hwange National Park, Zimbabwe was due to adverse rainfall conditions. In particular, Hwange National Park experienced a severe drought that resulted in the general decline of sable antelope populations in the region during the 1990s (Crosmary, et al., 2015)while Kimanzi (2018) identified poaching as the main cause of roan antelope decline in Ruma National Park, Kenya. However, even though most of the time these factors are perceived to reduce habitat ranges and species abundance, they are also increasingly responsible for range extensions. In some cases, the spread of species to areas outside the original ranges has been inadvertent. Conversely, species can be purposely relocated or reintroduced to establish breeding populations and for conservation purposes.

Correspondingly, roan and sable antelope population dynamics and distribution are influenced by a range of factors including intra-specific competition, trends in habitat quality, predation, and the lack of availability of water. These combined factors ultimately lead to population decline and local extinction. Since these antelope are highly selective feeders, this trait has been demonstrated to be detrimental under intensive competition. For instance, Harrington, et al., (1999) and Knoop and Owen-Smith (2006) identified competition with zebra (*Equus burchelli*) and wildebeest *(Connochaetes taurinus)* and predation from lions (*Panthera leo*) to be the factors causing roan antelope decline in Kruger National Park. Correspondingly, the correlation analysis by Kimanzi (2011) indicated that the abundance of roan antelope is negatively associated with the increasing abundance of reedbuck and hartebeest populations in Ruma National Park, Kenya. Dry season rainfall affected the survival of juvenile sable antelope in KNP (Owen-Smith, Mason, & Ogutu, 2005) and predation on calves and juveniles (Ginsberg & Milner-Gulland, 1994). Healthy adult roan and sable antelope are likely to be relatively invulnerable to predation, but the calves and juveniles, ill and elderly adults are taken by large predators such as lions, hyenas, leopards, and wild dogs (Kingdon, 1984 as cited in Kimanzi, 2011). Furthermore, though avoided in many cases by leopards, the apex predators in the WPP, roan and sable antelope feature on leopard and spotted hyaena prey composition (Hayward, Henschel, O'Brien, Hofmeyr, Balme, & Kerley, 2006; Hayward, 2006). Leopards and spotted hyaenas feed opportunistically on a variety of prey species and switch prey items according to their relative abundance (Hayward, et al., 2006; Hayward M. W., 2006). Harrington, et al., (1999) estimated that low rainfall which mostly results in grassland deterioration also contributed to the species decline in the park. Additionally, Havemann, Retief, Tosh and Bruyn (2016) stated that in areas where herds are subject to high levels of predation, they may be unable to recruit new members or merge with other viable herds before being predated upon themselves. This, in turn, could hasten them into an extinction vortex state (Frankham, 2005) where reintroduction may be necessary. Altogether these factors may play a role in the roan and sable antelope population demography and spatial distribution in the WPP.

2.5 Introductions and translocations

Fischer and Lindenmayer (2000) defined introduction as an attempt to establish a species outside its recorded distribution. This is often confused with "re-introduction", the attempt to establish a species in an area that was once part of its historical range, but from which it has been extirpated or gone extinct. Meanwhile, translocation is the intentional and mediated movement of wildlife from one part of their range to another (Fischer & Lindenmayer, 2000). In Namibia, the introduction and translocation of wildlife have been practiced as part of a program aimed at protecting game species and establishing protected breeding populations which include recovering species, increasing their range to boost their survival, and solving human-animal conflict (MET, 2008;

Ministry of Environment and Tourism, 2010). Namibia's PAs generate a source of wildlife for farmers, communities, and others wishing to have wildlife on their land through translocations. For example, between 1999 and 2009, more than 7 300 animals (14 species) were translocated by the MEFT to 27 communal conservancies (Ministry of Environment and Tourism, 2010). Contemporarily, due to accelerating ecological changes and increasing acute pressure on biodiversity populations, introductions and translocations are considered as conservation tools and reinforcement to restore the wildlife population. The translocation is mainly undertaken to restore, rescue, and recover the species and also to establish new, viable populations in suitable habitats within the country (Ministry of Environment and Tourism, 2010).

Nevertheless, although it is recognized that introduction and translocation are valuable conservation tools, there are potential risks associated with these conservation strategies, for example, disease transmission on endemic populations and the stress to the animal during the transition. There are also ecological and genetic impacts of introduced and translocated species. Translocated populations can hybridize with native populations of the same species or closely related species, consequently impacting the genetic purity of each species (Souty-Grosset & Grandjean, 2006). For instance, Wyk, Dalton, Kotze´, Grobler, Kropff, and Vuuren (2019) discovered that cross-hybridization has reduced and eliminated Western roan antelope alleles in the indigenous roan antelope gene pools since they were introduced on private farms in South Africa. This can have serious consequences reducing survival and growth and decreasing the ability of individuals in the population to adapt to a changing environment. Therefore, IUCN/SSC (2013) emphasized that due to multiple threats that may jeopardize the species survival rate, their associated communities, and ecosystem functions, intentional introduction and translocation of biodiversity should primarily be intended for increasing population size and genetic diversity, animal welfare, political, commercial or recreational interests or conservation objectives.

Nevertheless, translocation practices still serve as an effective conservation tool, bringing various species back from the brink of extinction through reintroduction and introduction and they can shape ecosystem dynamics. Benjamin-Fink and Reilly (2017) prove that the blooming of the keystone species, black wildebeest in South Africa serves as a positive practice of translocation after they previously experienced two population bottlenecks. Accordingly, due to the threats and decline of the roan and sable antelopes, MEFT has introduced these species to the Waterberg Plateau Park in 1975 and 1980, respectively (Martin, 2003). Since their reintroduction, MEFT has monitored these species through full moon waterhole and aerial counts. IUCN/SSC (2013) translocation guidelines strongly enforced that monitoring and continuing management must be put in place to ensure the succession of the species in the area.

Unfortunately, the introduction and translocation of most wildlife species have experienced frequent failures in recent decades. This is because many translocation projects lacked important ecological and behavioural information on the species or the release environment (Berger-Tal, Blumstein, & Swaisgood, 2019). It is a well-researched fact that the quality of the habitat into which the animals are released is one of the main predictors of translocation and introduction outcomes (Berger-Tal, Blumstein, & Swaisgood, 2019). Souty-Grosset and Grandjean (2006) added that the success of the translocations is also related to the number of animals released, stating that introducing animals less than the possible breeding population size can greatly increase the chances of failure. This is due to the lack of genetic diversity in the population, increased inbreeding depression, and also genetic drift which can result in reduced survival, population growth and can decrease the ability of individuals in the population to adapt to a changing environment (Wyk, et al., 2019; Souty-Grosset & Grandjean, 2006). Having roan and sable antelope introduced outside their natural range in WPP, we hypothesize that this could be one of the factors contributing to their population dynamic and trends.

In turn, the likelihood of the unsuccessful translocation of ungulates to protected areas is sometimes increased by the presence of anthropogenic activities (Matandiko, 2016; Lendelvo, 2018). Precisely, habitats exposed to hunting and auctioning or other human-related interactions occasionally lead to the failure of ungulates to settle or establish viable populations after introduction. This is because hunted animals are normally selected based on their exceptional phenotypic traits such as large trophies and healthy bodies. As a result, it is becoming evident that there are some negative effects of trophy hunting on the phenotypic traits and population dynamic of hunted species (Muposhi, Gandiwa, Bartels, Makuza, & Madiri, 2016). For instance, Davidson, Valeix, Loveridge, Madzikanda, and Macdonald (2011) found that trophy hunting appeared to influence the socio-spatial behaviour of the lion population, whereby their home range sizes decreased in both sexes and became more closely distributed. Quite frequently, studies focus only on the phenotypic variability of species without considering the breeding populations' genetic variability and population dynamics. Nevertheless, MET has introduced hunting and auctioning concessions as a form of incentive in Namibia to maintain and restore wildlife as a land-use type within protected areas such as WPP (Nature Conservation Ordinance, 1975). Accordingly, roan and sable antelope are some of the rarest species and are therefore highly valued in the hunting industries. For this reason, trophy hunting could be one of the factors influencing population dynamics and trends of roan and sable antelope in WPP.

2.6 Surveying techniques and monitoring of roan and sable antelope populations

Wildlife populations are in flux worldwide with some species disappearing at alarming rates (Ogutu & Owen-Smith, 2005; Wilson & Hirst, 1977; Gasaway, Gasaway, & Berry, 1996) while others are becoming overabundant or invasive (Macdonald, 2003). Ecological monitoring is essential for understanding these population dynamics and rigorous monitoring facilitates informed management. Monitoring of animals is important for both management and scientific purposes. For management, monitoring provides wildlife managers with information on abundance, spatial distribution, and spatial-temporal dynamics in these state variables (Jones, Asner, Butchart, & Karanth, 2007; Nichols & Williams, 2006; Yoccoz, Nichols, & Boulinier, 2001). In other words, information is needed on how many animals are in the area (the wildlife population), and where and when (at what time of year) they are found (e.g. Yoccoz, Nichols, & Boulinier, 2001). The end goal is thus to manage wildlife populations more effectively and efficiently. Consequently, monitoring programs are being used increasingly to assess the spatial and temporal trends of biological diversity with an emphasis on evaluating the efficiency of management policies (Yoccoz, Nichols, & Boulinier, 2001). As a result, scientists and wildlife managers employ an array of survey methods to estimate wildlife populations and distributions to develop effective management plans and policies. For example, Chamaillé-Jammes, Charbonnel, Dray, and Fritz (2016) found that the spatial distribution of herbivores at waterholes was strongly associated with the distribution of vegetation in the landscape. Thus, they have recommended that to prevent homogenization of vegetation and maintain heterogeneity spatial distribution of herbivores across Hwange National Park, Zimbabwe, managers should aim to distribute artificial waterholes in the park. Of equal importance are monitoring programs that can evaluate the effectiveness of management actions relative to stated objectives.

Recently, ecologists and conservationists have acknowledged that species distribution and population estimates are some of the most important dynamics that need to be understood for better biodiversity conservation and management. However, monitoring and collecting wildlife population data can be challenging and tedious, therefore numerous techniques to collect such data have been proposed. Multiple surveying techniques and statistical analytical models are available for monitoring herbivore species. Surveying techniques can be grouped into direct and indirect techniques. Direct techniques involve establishing direct contact with the target species (e.g. aerial, waterhole, or transect counts), while indirect counts include spoor tracking, detections of animal vocalizations, and even detections based on remote methods such as camera traps. The choice of the technique depends on the objectives of the study, the target species, study sites, and other constraints that are inherent to a given project (i.e. availability of human or financial resources). The aims of indirect surveying methods are to be as non-invasive as possible and to avoid change in the animals' behaviour while gathering all the essential information. Moreover, non-invasive methods offer the advantages of obtaining larger sample sizes of individuals and conducting population-level studies (Karanth & Nichols, 2017). These sampling methods also allow the use of models to estimate abundance while accounting for the difficulty of detecting individuals in the wild. Of equal importance, wildlife managers can measure different state variables including abundance, population density, and occupancy to monitor wildlife populations (Stokes, Johnson, & Rao, 2010).

In addition to identifying the most suitable technique for monitoring a species, proper estimation of state variables and inferences about their variation over time and space requires that sampling designs account for spatial variation and detectability (Yoccoz, Nichols, & Boulinier, 2001) which includes imperfect detection (Rowcliffe, Field, Turvey, & Carbone, 2008). From the aspect of large mammal communities, the spatial heterogeneity of African savannas is caused by spatial variation in plant and soil nutrients available, which in turn creates patchiness in the quality and quantity of vegetation used by ungulates as food (Anderson, et al., 2016). This spatial variation within ecosystems is an important factor underlying the structure of wildlife populations. Detectability denotes that even in locations that are surveyed by investigators, it is very common for animals and even entire species to be missed and go undetected (MacKenzie, et al., 2006). This detection error can be further subdivided into false positives (which occur when a species is recorded at a site that is unoccupied by that species, misidentification of animals) and false negatives which occur when individuals are not detected at occupied sites (Miller, Nichols, Mcclintock, Grant, Bailey, & Weir, 2011). A consequence of this ubiquitous source of error is that count-based inferences often tend to be negatively biased (Miller, et al., 2011). But also, techniques that rely on direct counts (which rarely allow verification of each sighting), false positives are prone to occur. Therefore, direct count estimates might be biased upwards or downwards in unpredictable ways. Equally important is the choice of study design which may impact estimates of detectability.

Different methods have been used to monitor roan and sable antelope with aerial counts being the most practiced method. Aerial count data was used to study the population dynamics of sable and roan antelope in Kgaswane Mountain Reserve, South Africa (Marshal, Rankin, Nel, & Parrini, 2016) and Kruger National Park, South Africa (Harrington, et al., 1999). Tyowua1, Orsar, & Agbelusi (2012) used line transect to describe habitat preference of roan antelope in Kainji Lake National Park, Nigeria.

2.6.1 Aerial counts

Over the past 50 years, aerial counts have been widely used to monitor wildlife populations in Africa and globally. They are useful for efficiently and effectively estimating the numbers of wildlife species in very large areas (Keeping, et al., 2018). Therefore, because of the vastness and remoteness of many wildlife areas in Africa, aerial counts continue to be an important tool for wildlife management. Similar to other countries, Namibia has implemented a remarkable aerial monitoring survey program across the country in all protected areas ((Ministry of Environment and Tourism, 2010)). Apart from fixed-wing and helicopter aerial traditional methods, advanced technology is developing extremely rapidly with various forms of aerial monitoring techniques which include drones and satellite imaging (Hodgson, et al., 2018). The most common method involves flying strip transects and counting all the detected individuals within the strip (Sutherland,2006). All strip transects should be in parallel to avoid overlap and double counting (Sutherland, 2006). While remote imaging simply includes taking a digital photograph from a plane or helicopter directly over the area and counting the individual detected in the photograph (Hodgson, et al., 2018), aerial surveys are often used to obtain abundance and density estimates but are subject to problems necessitating the consideration of novel techniques. For example, Marshal, Rankin, Nel, and Parrini (2016) and Harrington, et al., (1999) used aerial count data to study the population dynamics and trends of sable and roan antelope in Kgaswane Mountain Reserve and Kruger National Park, South Africa, respectively. Hodgson, et al., (2018) demonstrated that remotely piloted aircraft (drones) data is, on average, between 43% and 96% more accurate than the traditional ground-based data collection method.

Aerial surveys are often conducted from the air using methods that do not correct for variation in the probability of detection and often focus on temporal trends in density without directly testing what factors affect density. The main problem is the accuracy of the resulting estimates caused by the consistent undercounting bias (Pollock & Kendall, 1987). The main factors that influence bias estimation of wildlife from the air are the animals' reactions to an over-flying aircraft, dispersion, body size, colour of the animal, and habitat terrain (Jachmann, 2002). Using helicopter count methods, Schlossberg, Chase and Griffin (2016) found that elephant populations were underestimated by 13% in Botswana. Correspondingly, based on aerial count data, Lee and Bond (2016) concluded that the population of giraffe in Tanzania was negatively biased and Keeping, et al., (2018) determined that vacant grid cells in their study area (done by aerial survey) often included false absences, which does not necessarily mean the sites are unoccupied. Extensive evaluations of aerial counts throughout the latter 20th century led to the conclusion that undercounting bias is often severe and unavoidable (Pollock & Kendall, 1987). Therefore, there is a need to calibrate aerial count data or at least compare point counts among surveying techniques (Lee & Bond, 2016; Schlossberg, Chase, & Griffin, 2016).

2.6.2 Camera trapping

Camera trapping has become a powerful non-invasive standard method for monitoring a variety of species over relatively large areas (Rowcliffe, Field, Turvey, & Carbone, 2008; Niedballa, Sollmann, Mohamed, & Bender, 2015; Steenweg, et al., 2017). Rich, Miller, Robinson, McNutt, & Kelly (2016) used camera-trap surveys to provide insights into the spatial and temporal ecology of an African mammal community while, Stein, Fuller and Marker (2008) assessed species diversity and species composition of mammals and birds in WPP and the surrounding farms using camera trapping. There are multiple reasons camera trapping has increasingly become one of the most powerful non-invasive monitoring tools for collecting such data. Significantly because data derived from camera trapping allows multiple research objectives to be addressed which include, tracking trends in abundance, density, habitat use, occupancy, species identification, and behaviour and population demography (Rovero, Zimmermann, Berzi, & Meek, 2013; Nakashima, Fukasawa, & Samejima, 2017; Rovero, Martin, Rosa, Ahumada, & Spitale, 2014), colonization and extinction (Miller, et al., 2015). Additionally, remote camera trapping is a particularly suitable technique for longer-term monitoring in forest habitats (Rovero, et al., 2014). Furthermore, it is relatively cost-effective in terms of effort, its ability to collect data during day and night, its ability to detect elusive and cryptic wildlife species, and most importantly, the fact that it is a non-invasive monitoring method with low bias (Amin, Bowkett, & Wacher, 2016). Even though the use of camera traps is more time-consuming and costly, this method is evaluated as a trustworthy estimator of population sizes (Royle & Nichols, 2003; Rowcliffe, Field, Turvey, & Carbone, 2008). Furthermore, camera trapping is likely the most appropriate method to collect density data for unmarked species because it provides information such as where and when the animal was active (Rowcliffe, Field, Turvey, & Carbone, 2008; Chandler & Royle, 2013) which was the case in this study.

Consequently, the emerging studies developing models that allow estimation of density and population size for species that cannot be uniquely identified nor detected with certainty is critical. For instance, Rowcliffe, Field, Turvey, and Carbone (2008) Developed and tested the Random Encounter Model (REM), which allows estimating density estimates of known abundances without individual species identification. However, a key challenge with this model is estimating movement rates (Keeping & Pelletier, 2014). More recently, Moeller, Lukacs, and Horne (2018) developed three models namely: time to event (TTE) model to estimate abundance from trapping rate, space to event (STE) model that is not sensitive to movement rate, and instantaneous sampling (IS) estimator that applies fixed-area counts to cameras. Though promising, there is a general lack of scientific assessment on the use of camera trapping as a technique to monitor roan and sable antelope populations, which is the aim of this study. Besides estimating density and abundance, camera trapping data can be used to determine and assess drivers of population occupancy.

2.6.2.1 Occupancy modelling and density estimate

Occupancy modelling is a widely used flexible analytical approach, that provides a state metric (occupancy) (Mackenzie et al., 2006; Midlane, O’Riain, Balme, & Robinson, 2014) because it accounts for imperfect detection (i.e. the probability of detecting a sign or an individual of the species of interest is < 1), false-positive and positive negative and hypothesis testing (Bailey, MacKenzie, & Nichols, 2014; Noon, Bailey, Sisk, & Mckelvey, 2012). The latter, refers explicitly to assessing the influencing of site and survey covariates on species distributions and detection probability, respectively, while false positive means that these species signs will not be misidentified or falsely detected when absent. False-negative means that the species will not be detected in occupied sites. Furthermore, this method allows for the inclusion of the above-mentioned covariates that may influence the occupancy. Moreover, data collected over multiple seasons or years can be used to draw inferences about rates of extinction and colonization of sampling units in the presence or absence of hypothesis (Hines, Nichols, & Collazo, 2014; MacKenzie et al., 2006).

Numerous studies rely on occupancy for understanding and predicting species distribution under diverse scenarios of climatic change, land use, dynamics of fragmented populations and meta-population, and dynamics of invasive species (Rowcliffe, Field, Turvey, & Carbone, 2008; Hines, Nichols, & Collazo, 2014; Miller & Grant, 2015). MacKenzie, et al., (2006) defined occupancy as a proportion of an area occupied by a species or a fraction of a landscape unit where the species is present. The basic sampling protocol commonly used for occupancy estimation simply involves visiting sites and spending time recording the presence-absence of the species and their abundance. A key assumption of these estimates is that sampling should be random with respect to animal distribution (Rowcliffe, Kays, Carbone, & Jansen, 2013) which means that the detection of the target species at one site is independent of detecting the species at other sites. This conceptual model also includes the assumption that the occupancy status of sites does not change between surveys (i.e. closure of the site to changes in occupancy or density state) (MacKenzie, et al., 2006). Occupancy does not change at a site within the sampling season, but it can change between sampling seasons. Most importantly, heterogeneity in occupancy and detectability per site should be explained with the measured covariates.

Occupancy modelling has become a widely used approach for drawing inferences about a number of interesting ecological concerns. Hypothetically, verifying the presence of a species is simple because researchers only need to records the occurrence to know about its existence. Therefore, occupancy modelling is well suited to camera-trap survey data because detection/non-detection data can be collected more efficiently over a large number of sampling occasions than through other methods such as signs or direct sighting surveys (Amin, Bowkett, & Wacher, 2016). For example, Rich, Miller, Robinson, McNutt, & Kelly (2016) assessed the spatial ecology of an African mammal in Botswana using camera trapping and hierarchical occupancy modelling.

2.6.3 Spoor tracking

Animal footprints or spoor tracking is one of the oldest traditional non-invasive methods for identifying a mammal’s presence in an area. It involves detecting and identifying footprints in various substrates such as dust, mud, sand, or snow. The use of indirect measures such as spoor tracks that rely on the presence and detection of field signs as an index of true density became a less favourable option due to lack of repeatability and potential influence of unaccounted factors. Spoor surveys have been used extensively, mainly as a monitoring tool is mostly carnivore species including leopard, lion, and African wild dogs in Namibia (Stander, 1998), lion in Zambia (Midlane, O'Riain, Balme, & Robinson, 2014, and Houser, Somers, and Boast, (2009) estimated the true density of a known population of free-ranging wild cheetah in Botswana.

This method is cheap and non-disruptive because the observers are not present when the species are active. Moreover, because some terrestrial mammals are nocturnal, cryptic in appearance, and generally adept at avoiding being seen, which limits well-developed methods of direct observation, this trial forces ecological scientists to use indirect observation instead. However, because of higher imperfect detection, an accurate measure of abundance is difficult to obtain (Karanth & Nichols, 2017). In turn, many monitoring programs use the observed counts as a proxy for true population size (Karanth & Nichols, 2017; Keeping & Pelletier, 2014). More accurately, both track counts and camera trap rates have been utilized as indices of abundance and extended to predict density by calibration through double sampling (Torrents-Ticó, et al., 2017). Few studies have been done on estimating population density from indirect signs using the Formozov–Malyshev–Pereleshin (FMP) formula (Stephens, Zaumyslova, Miquelle, Myslenkov, & Hayward, 2006; Keeping & Pelletier, 2014). According to Keeping and Pelletier (2014), the FMP formula provides a theoretical foundation for understanding the relationship between animal track counts and the true density of species. If standard methods are employed, these counts can be used as an index of relative abundance (Sutherland, 2006).

Practically, to determine precise density estimates from indirect methods such as spoor tracking large sample sizes are required (Keeping & Pelletier, 2014). Noting that it is often difficult to avoid bias, bias in the estimates can be minimized by ensuring that the assumptions are not violated (Karanth & Nichols, 2017) because the validity of the true estimates would depend not only on the relationship between the number of animals and the number of spoor in the area but also on the effectiveness of one's searching for the signs (Karanth & Nichols, 2017). One may regulate this by walking along pre-defined transect lines and applying distance sampling to estimate the density of spoor, thus reducing one level of variation (Sutherland, 2006). In addition, it is necessary to distinguish between the tracks of various, sometimes closely related species and species with similar tracks. Misidentification of tracks could lead to under or overestimation of the true density or population abundance.

2.7 Relative abundance index (RAI) and Spoor Frequency (SF)

One of the most contentious issues among wildlife researchers is the extent to which we can rely on indices of abundance for monitoring populations and making comparisons over space and time (O'Brien, 2011). Hence, it is recommended to be used only when it is not possible to conduct proper population estimates or when a study only includes the estimation of the detection probability (O'Brien, 2011). With the application of spoor tracking and camera traps to monitoring wildlife, the relative abundance index (Liu, et al., 2013) and spoor frequency (Stander 1998) have become two of the most popular indicators of population abundance for inventories and assessment. As it is impracticable to count all individuals of each species within a community, relative abundance indices are often used to compare between species' abundance. For camera trapping, a common relative abundance index is typically calculated as the number of sightings per number of camera trap days. While SF is the number of spoors per total distance covered. RAIs and SFs are assumed to be linearly correlated to overall abundance and can be calibrated against independent counts to provide correlation coefficients between the index and population size (Palmer, Swanson, Kosmala, Arnold, & Packer, 2018). Using data from camera-trapping Jenks, et al., (2011) demonstrated how RAI can be used to monitor the wildlife population. He found out that the population decline of large mammals from 1999 to 2000 in Khao Yai National Park, Thailand was linked to the increased in human activities. Stander (1998) used spoor count as indices of carnivores population in Khaudum National Park and Tsumkwe District, Namibia.

CHAPTER 3

3. MATERIALS AND METHODS

3.1 Description of the study area

This study was carried out in the Greater Waterberg Plateau Complex which includes Waterberg Plateau Park (WPP) and the Waterberg Plateau Farm (WPF) in North-Central Namibia (Figure 3). The WPP was proclaimed as a sanctuary for rare and endangered game species in 1972. Since then WPP has played a vital role in being a breeding site of rare species and for the restocking of other national parks and conservation areas (e.g. conservancies). The management of breeding the high-value wildlife species populations also include trophy hunting, auctioning, and reintroduction. The WPP covers a total surface area of 405 km^2. In 2008, a nearby farm, WPF was purchased, which added an extra 6 449 hectares to the plateau area. These wildlife management areas are separated by an extensive 4 m high meshed wire fence that was erected to prevent the movement of wildlife from the park to the farm, as the farm was privately owned. The acquisition of the farm by MEFT was to extend the carrying capacity of the park. The plateau is approximately 1850 meters above sea level and 200 meters above the surrounding (Erb, 1993) with 50 km-long porous sandstone (Figure 3a). The park is divided into three management zones: wilderness, trophy hunting, and tourism. At the base, the plateau is surrounded by commercial game farms. The study area falls within the “Hot steppe” climatic zone characterized by mean annual temperatures above 18°C (Erb, 1993). During the wet season (Dec-May) the average daily minimum temperature ranges between 4 °C and 5 °C. While the average daily maximum temperature during the dry season (June - Nov) ranges between 31 °C to 32 °C. The Waterberg Plateau receives an annual rainfall between 300 and 500 mm of which most fall within 40 to 50 days of the rain season. Since there is no natural occurring permanent open water source found on the plateau, seven artificial waterholes were established on the park and four on the farm to supplement wildlife’s need for water (Figure 3b).

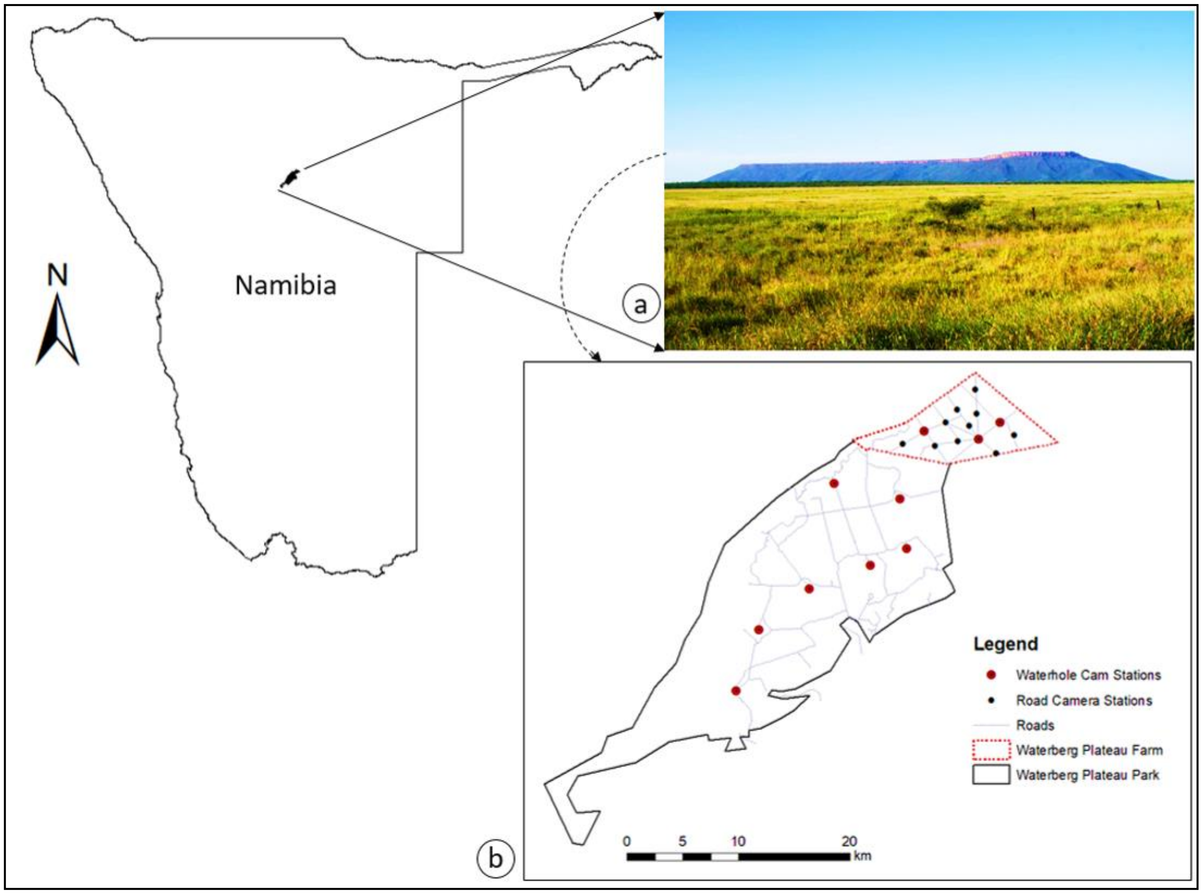

Figure 3 Map of the Waterberg Plateau Park and Waterberg Farm with an outlay of (a) 50-km-long porous sandstone and (b) zonation of the two areas, waterhole points, and camera trap stations.

The vegetation structure at the plateau falls under the tree and shrub Savannah biome (Mendelsohn, Jarvis, Roberts, & Robertson, 2002). The vegetation type includes among other species the Leadwood tree (*Combretum imberbe*), silver Terminalia (*Terminalia sericea*), kudu bush (*Combretum apiculatum*), *Ochna pulchra, Burkea Africana,* a variety of Acacias (*Acacia erioloba*, *A. erubescens*, and *A. tortilis*), *Pertiforlum africanum* and more than 100 lichen species. In terms of fauna, dinosaurs roamed on the plateau about 150 million years ago as evidenced by their tracks that are presently used as tourism attraction (Wagensommer, Latiano, Mocke, & Porchetti, 2016) Currently, the park has mammal species that naturally occur in the park such as steenbok (*Raphicerus campestris*), duiker (*Sylvicapra grimmia*), kudu (*Tragelaphus strepsiceros*), and warthog (*Phacochoerus africanus*). In addition to these naturally occurring species, the park has a number of resident populations of introduced species as part of the MEFT program aimed to establish protected species breeding populations in the country. Introduced species include the black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhino, buffalo (*Syncerus caffer*), roan and sable antelope, eland (*Taurotragus oryx*), tsessebe (*Damaliscus lunatus*), giraffe (*Giraffa angolensis*), and impala (*Aepyceros melampus*) (Martin, 2003; Ministry of Environment and Tourism, 2010). Predators naturally occurring in the park include the leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*), black-backed (*Canis mesomelas*), and side-striped jackals (*Canis adustus*). Furthermore, the park is a hot spot of more than 200 bird species recorded, including the rüppell’s parrot (*Roicephalus rueppelli*), monteiro’s hornbill (*Tockus monteiri*), and the last known breeding colony of Cape vultures (*Gyps coprotheres*) in Namibia. The mammal community between the Park and Farm are similar except for buffaloes that only occur in the Park. This is because buffalo is hypothesized to be a factor that has been suppressing the growth trajectory of sable and roan.

3.2 Data collection

To attain this project’s aim and objectives, quantitative data from three common wildlife surveying techniques were used: aerial wildlife counts, camera trapping, and spoor tracking.

3.2.1 Aerial game count surveys

The aerial game count has been the method of choice used by the MEFT to monitor the wildlife population in the WPP and other national parks in Namibia. The counts have been conducted annually from the 1960s to the present, during the dry season (i.e. June – October) when visibility conditions were best (Kilian, 2000). For surveying purposes, the Park has been divided into different blocks, a number that has varied across time. From 1970 to 1996, the Park was divided into 27 blocks, from 1997 to 2000 in eight (8) blocks (Kilian, 2000), from 2000 to 2020 in three blocks (Beytell, 2015) (Figure 4). A fourth block was added in 2015, which is currently the Waterberg Farm. Transects in blocks one and three are orientated in a north-south direction and block two and four in an east-west direction. Transect line directions are based on the gullies of the rocky terrain in each block. Transects are less than 10 km long and spaced 400 m apart (Kilian, 2000; Erb, 1993). This inter-transect distance was set to minimize the risk of double counts. Transects were generated with ArcGIS software and uploaded into two hand-held GPS units.

During surveys, a helicopter without doors with three surveyors on board, a pilot, and two observers, was flown over a transect moving approximately at the speed of 90 km/h (50 knots/h) and 80 m above the ground. Counts were conducted from 08:00 to 14:00 with the observers seated on each side of the helicopter. Upon sighting the game, the following information was recorded where possible: the species, group size, gender, age, and geographical location. In cases of gregarious species such as rhino, buffalo, roan, sable, or eland the helicopter was circled to obtain accurate counts. Additionally, photographs of some larger animal groups were taken for subsequent verification of group size (Beytell, 2015). A key assumption of this method was that surveyors assumed perfect detection in that all animals in the park that are available for detection were detected (*p* =1), where *p* is the probability of detecting the species during the survey, given it is present (detectability). However, potential bias can arise from false negatives (non-detection of existing animals), but also false positives (misidentification of animals). Often the relative importance of each of these error rates is of an unknown quantity at the time of sampling.

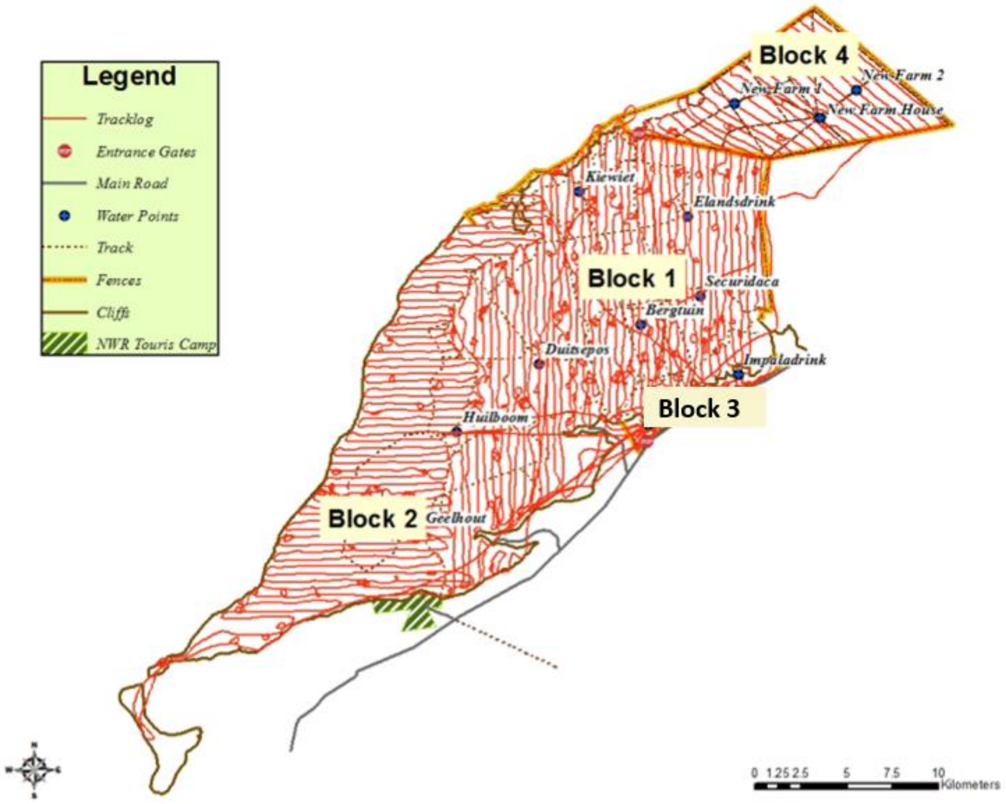

Figure 4 Layout of helicopter line transects in the Waterberg Plateau Park (block 1, 2, and 3) and Waterberg Plateau Farm (block 4). *Source*: Beytell, 2015.

3.2.2 Camera trapping

Camera trapping was conducted to determine seasonal relative abundance and occupancy of roan and sable on the Waterberg Plateau Farm (WPF) in 2018. A regular grid of 4 km^2 was superimposed over the WPF 72 km^2 that resulted in 17 grid cells (Figure 5). From these 17 cells, 13 were opportunistically sampled and four were not sampled due to an insufficient number of camera trap units. A single Hyperfire Reconyx infrared camera trap (HC600) was deployed in each of 13 grid cells during the wet (16 February-17 May) and the dry (07 July – 06 October) seasons. Cameras were active for 91 days in each season, to conform to the assumptions of a closed geographic and demographic population as well as the occupancy (Hines, Nichols, & Collazo, 2014). The assumption of closed occupancy is that occupancy does not change at a site within the sampling session, but it can change between sampling seasons. For example, a site that is occupied at the beginning of a sampling session retains that status throughout the session and vice-versa. Seasonal sampling allows for inferences about occupancy dynamics, including estimation of seasonal occupancy and the covariates that drive changes in this state variable (MacKenzie, et al., 2006; Hines, Nichols, & Collazo, 2014). A single camera was set on each of the 13 cells, 10 along roads and three near waterholes. This selection of deployment sites was because of the rarity of animal trails on the farm. Cameras were about 1 m from the edge of the road (into the bush) and less than 20 m at the edge of the waterholes (Figure 5). Cameras were mounted on a tree and/or a metal pole at the height of about 1 m above the ground. All cameras were programmed to take three photographs per trigger with a three seconds delay. Cameras stations were visited every two to three weeks to download photographs, replace batteries, and ensure that cameras were operational.

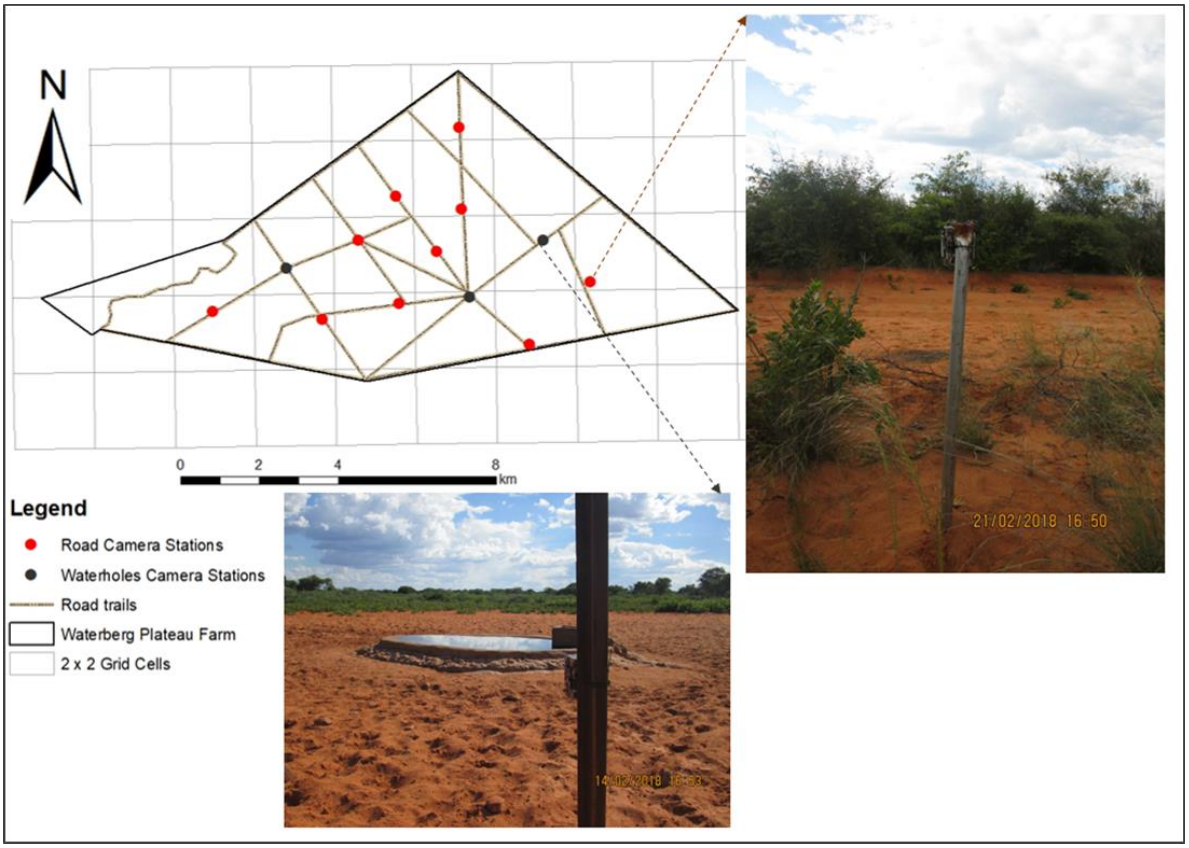

Figure 5 Location of camera trap stations in the Waterberg Farm, north-central Namibia.

3.2.3 Spoor tracking

Spoor tracking was conducted to determine the spoor frequency of roan and sable in the study area. To ensure accurate spoor identification of animals occurring in the park spoor tracking included an indigenous spoor tracking expert and a field ranger from the MEFT who can identify and distinguish the signs of sable, roan, and other species reliably and accurately. Additionally, a field guide to animal tracks of Southern Africa (Liebenberg, 1990) was used to aid with differentiation and identify all the species in the area. Spoor tracking was conducted on an approximately 1 km segment of the roads in the 17 grid cells (Figure 6). Each transect was subdivided into 10 100 m spatial replicates with the starting point randomly determined. This segmentation is because a single animal can move along the road for distances that cover multiple segments, creating dependence in detection probability and history between adjacent segments, resulting in biased estimates of occupancy (Hines, Nichols, & Collazo, 2014). (Hines, Nichols, & Collazo, 2014) suggest that such bias can be reduced by considering the probability of species presence on each segment depending on whether the previous segment was occupied (i.e. Markovian process). Due to the cell borders, one transect was divided into two cuts, the 1 km had to be continued on a different transect within the same grid cell.

Surveys were conducted on a single day from early morning to early afternoon (7:00 – 13:30) during the wet (May) and dry (August) seasons. Tracking was conducted during that time when the angle of the sun is low as it increases the probability of spoor detection (Stander, 1998). During a survey, two observers, a MEFT spoor tracking expert and the student, seated on the bonnet of a car driving at a speed of around 15 km/h scanned the transects for signs of target species. Upon encountering a spoor, the vehicle was halted, and the spoor was identified to species level. Only spoor that was deemed to be less than 24 hours was recorded to adhere to the demographic population closure and occupancy assumptions (Stander, 1998; Karanth & Nichols, 2017). Besides the spoor of the target species, surveyors also recorded spoor of other species residing in the area including the spoor of kudu, Oryx, eland, black rhino, steenbok, brown hyaena, and leopard. Surveyors recorded detection and non-detection data (e.g. 1010000011) of the identified species at every 100 m intervals and the total number of spoors in 1 km. A hand-held Garmin GPS unit was used to record the coordinates of the starting and the ending points of each transect. Upon completion of each survey, data were entered into Microsoft Excel.

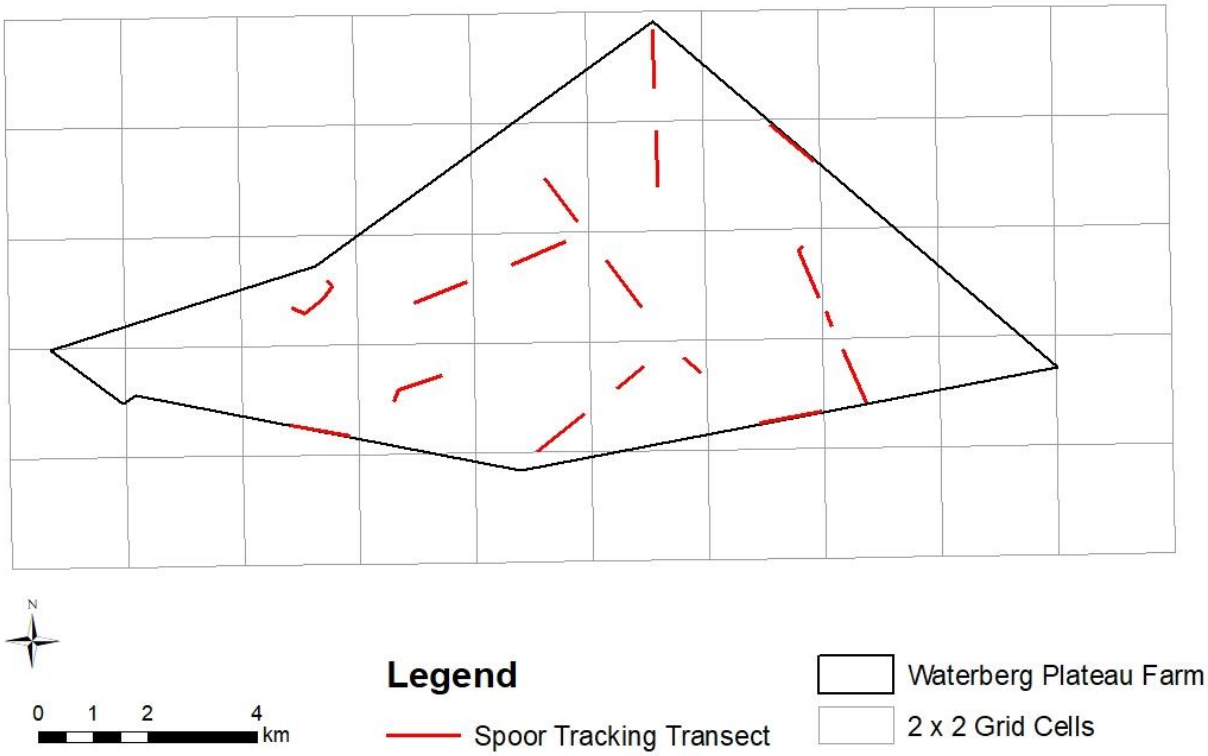

Figure 6 Spoor tracking transects (1 km long) in the Waterberg Plateau Farm, north-central Namibia.

3.2.4 Environmental covariates influencing roan and sable occupancy

To examine factors that are deemed to possibly influence the occupancy of roan and sable population in the WPF, several environmental (i.e. site) and surveying covariates were identified based on published literature. It was hypothesized that occupancy of roan and sable may be influenced by intra-specific and inter-specific competition (Harrington, et al., 1999; Hensman, Owen-Smith, Parrini, & Bonyongo, 2013), the presence of leopard (i.e. predation risk) (Lima, 1998; Schuette, Creel, & Christianson, 2016) and of waterholes (given that these species are water-dependent), and vegetation resources (Macandza, Owen-Smith, and Cain, 2012). Data for modelling the potential effect of interspecific competition between the target species and the presence of leopard was derived from camera trapping data (i.e. detection/non-detection data). For estimating the potential effect of forage, seasonal NDVI values were derived through QGIS Desktop 3.8.1 based on Sentinel-2 images for the wet (Feb - May) and the dry (Jul - Oct) season. NDVI was used as a proxy of forage availability as it measures the state of plant productivity based on the plant reflectance of light at a certain frequency (Funghi, Heim, Schuett, Griffith, & Oldeland, 2020). Sentinel-2 images were downloaded from the Global Agricultural Monitoring (https://glam1.gsfc.nasa.gov/). Sentinel-2 NDVI satellite images are recommended for monitoring phenology and plant productivity because of their high spatial and temporal resolution of 2 m up to 10 m and multi-spectral images every 10 days with 13 spectral bands (Vihervaara, et al., 2017; Funghi, et al., 2020). NDVI values were estimated using the following formula: $I = \frac{NIR-RED}{NIR+RED}$, where NIR is the reflection in the near-infrared spectrum (band 4) and RED the reflection in the red range of the spectrum (band 8). These indices values range from -1 to 1, with values close to -1 indicating bare soil and values closer to 1 indicating greenly vegetation. NDVI values displayed similar levels of variability throughout the study area with at least a 10% difference between grid cells. Significantly, NDVI varied considerably between seasons with the highest values ranging between 0.38 to 0.42 during the wet season and from 0.17 to 0.19 during the dry season throughout the study area.

3.3 Data analysis

3.3.1 Trends in abundance of roan and sable between 1975 and 2019

To examine trends in the population abundance of roan and sable over 44 years (1975 - 2019) in the WPP, two statistical frameworks were employed, the Generalized Additive Modelling (GAM) (Pedersen, Miller, Simpson, & Ross, 2019; Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000) and the State Space Models (SSM) (Buckland, Newman, Thomas, & Koesters, 2004). These models are complementary and suitable for modeling population dynamics and corresponding observations made on the population. Under the GAM framework, the trend in abundance (i.e. the process) is modeled as a smooth, nonlinear function of time (Fewster, et al., 2000). Furthermore, the GAM framework tests the statistical significance of changes in abundance that identifies periods in a time series where population sizes significantly differ from the average trend. In turn, SSM allows the estimation of the variance for both the observation (i.e. counts) and process (i.e. trend in abundance) error associated with measurement of data and uncertainty on population dynamics explicitly (Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008). Importantly, both frameworks allow the inclusion of covariates making testing of the ecological and biological predictors underpinning trends relevant.

3.3.2 Modeling trends in the population abundance through Generalized Additive Model

GAM is an extension of the Generalized Linear Model (GLM). As such, GAM comprises a collection of non-parametric and semi-parametric regression techniques for exploring relationships between response and predictor variables (Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000). The advantage of GAM is that there is no need to make any prior assumption on the functional form linking the two sets of variables, as these relationships are modelled with smooth functions (Wood, 2017). GAM produces a smooth temporal abundance trend by applying a scatterplot smoother to detect the trend from yearly fluctuations, identify periods of significant temporal change while accounting for model uncertainty (Simpson, 2018; Fewster, et al., 2000). Periods of significant change are points in the time series (e.g. a count in a particular year) when the rate of change differs significantly from the rest of the time series with the inclusion of covariates. These models enable the mean of the dependent variable (counts) to depend on an additive predictor through a nonlinear link function (Crawley, 2007). This statistical property of GAM fitting non-parametric smoothers to the data without specifying any particular mathematical model makes the model suitable to estimate directly nonlinear trends from time-series data of population numbers (Simpson, 2018). That is, the model identifies the best representation of the data without forcing it into a predefined shape. To identify periods of significant change, that is, when a count(s) differ significantly from the average trend of the time series, 95% simultaneous intervals were computed. Points were the 95% simultaneous intervals of the first derivative of the fitted trend did not include zero given the uncertainty in the estimate of the derivate were considered as periods of significant changes in a population trajectory (Simpson, 2018).

In this study, all GAM models were fitted through the function *gam* in the *mgcv* package (Wood, 2017) implemented in the statistical software R (R Core Team, 2018). First, the estimation of the smooth function $f\ (x)$, where x is the explanatory variable and specification of the degree of smoothing was obtained (Simpson, 2018). The degree of smoothness in the GAM model is determined by the degrees of freedom (*df*) (Fewster et al., 2000). The sufficient value for the rank (k) was obtained via the $gam.check$ function. This value indicates the dimension of the basis where additional nonlinearity or structure in the residuals can be explained by a further smooth of x_t (Simpson, 2018). Four basis dimensions, k of 1, 3, 6, and 9, were tested to unlock the better fitting model whilst using a similar number of effective degrees of freedom (*edf*). A k of six and nine produced the best wiggling regression on the fitted trend for sable and roan, respectively. The same *k* was used as smooth terms of the covariates to allow for nonlinear responses.

A GAM is constructed by the sum of smoothed functions of the predictor variables, which can identify the types of effects and nonlinear relationships between variables.

$$N_t = f\ (\text{year}) + f\ (\text{rainfall}) + f\ (\text{buffalo}),$$

Where N_t is the population abundance estimate of each antelope in year t and f ( ) is a spline smoothing function of the variable (i.e. buffalo and rainfall).

Second, a total of four GAM models were fitted using the Restricted Maximum Likelihood (REML) method and Poisson error distribution for each species. The REML method is recommended to compare models with different effect structures as it is less sensitive to outliers (Simpson, 2018). The Poisson distribution is suited when dealing with count data and only positive integer values as was the case in this study (Fewster et al., 2000; Pedersen, Miller, Simpson, & Ross, 2019). To assess factors that could have influenced the population trajectory of these two species average annual rainfall data and buffalo population size covering the same period were included as predictor variables.

These were included because they are reported to influence the target species distribution and abundance (Harrington, et al., 1999; Hensman, Owen-Smith, Parrini, & Bonyongo, 2013; Kimanzi & Wanyingi, 2014).

The first GAM model was fitted with all the two smoothed predictors. Second, the stepwise removal regression method was then applied to identify which covariate contributed significantly to the model. Significance was ascertained at $p < 0.05$. Moreover, the study assessed the unitary effect of trends in annual rainfall and buffalo population size on the declining abundance of roan and sable antelopes. The model with a maximum variation of deviance explained R^2 was retained. Coefficients of predictor variables and a fitted trend were deemed to be statistically significant at $p < 0.05$ (Crawley, 2007). Model selection was made based on Akaike Information Criterion (AIC) a measure of the fit of a model (Burnham & Anderson, 2002). AIC values were calculated using the function *dredge* of the package *MuMIn* (Barton, 2018). The model with the lowest AIC value was considered the model with the strongest support, and models that differed in AIC value from this model by less than two were considered equally parsimonious (MacKenzie *et al.,* 2006).

3.3.3 Modelling trends in the population abundance through State-Space Model

The second framework employed to assess temporal dynamics in the abundance of roan and sable was the State-Space Modeling (SSM). SSM is a deterministic population projection used to evaluate the dynamics of populations from disordered or incomplete datasets (Thomas, Buckland, Newman, & Harwood, 2005). SSM describes the true but unknown state of a population at successive time steps while linking this unknown state to the observation process (i.e. counts) (Thomas et al., 2005). The SSM was applied using a GLM which accounts for process and observation errors (Ahrestani, Hebblewhite, & Post, 2013). Observation error is an error from population counts (e.g. misidentification) while process errors are due to biotic or abiotic processes (Buckland, Newman, Thomas, & Koesters, 2004).

The state-space models were analysed using the Monte Carlo Markov Chain Bayesian algorithm implemented in JAGS using the rjags package of the R computing environment (R Core Team, 2018). Roan and sable population dynamics were modelled as:

$$\text{State process: } \log(N_{t+1}) = \log(N_t) + r_t + X_t$$

$$\text{Observation process: } Y_t = N_t + E_t$$

Where N_t denotes antelope abundance in year t, N_{t+1} is abundance in the subsequent year $t+1$, r_t is the population growth rate from year t to year $t+1$, and Y_t denotes the observed animal count in year t. X_t is the process error in each year t. X_t and E_t represent the process error and observation error in year t, respectively. Observation error was assume to have a normal distribution with mean zero and variance (τ^2), modelled as E_t ~ dnorm (0, τ^2) while the process error was assumed to have a normal distribution with mean zero and variance (σ^2), modelled as X_t ~ dnorm (0, σ^2). Errors were assumed to have no auto- or cross-correlations.

The expected population growth rate was calculated in the logarithmic scale as follows:

$$r_t = r_{mean} + B_1 RF + B_2 LRF + B_3 BF + B_4 Intro + B_5 Auc + X_t$$

in which $r_{mean}$is the mean population growth during the study period in the logarithmic scale, $\beta_1\mathrm{RF}$ and $\beta_2\mathrm{LRF}$ is the effect of annual rainfall and lagged rainfall, respectively, and $\beta_3\mathrm{BF}$, $\beta_4\mathrm{Intro}$, $\beta_5\mathrm{Auc}$ is the effect of buffalo population size, introductions, and auctions on the population growth of each antelope, respectively. All covariates were standardized to mean = 0 and the standard deviation (SD) = 1.

The mean population growth rate r_t represents a composite measure that accommodates the effects of survival and fecundity. The process stochasticity was assumed to be normally distributed with a mean of zero and the standard deviation was estimated. The effect of individual covariates was interpreted according to its' respective parameter posterior distributions.

To estimate the model's parameters, a Bayesian framework was adopted by using the Markov Chain Monte Carlo (MCMC) method. The MCMC Bayesian framework is recommended for analyzing time series because its two-tier modelling approach detects both observation and process error (Ahrestani, Hebblewhite, & Post, 2013). A Markov chain is a time series of random events, where the probability of the next event in the chain depends only on the current state. That is, the observed count data is what defines the probabilities of population states, and is not dependent on how the population state reached the present state. Models were fit in JAGS (Plummer, 2018) accessed via the jagsUI package (Kellner, 2016) in the R program (R Core Team, 2018). JAGS uses MCMC to simulate conditional posterior distributions for parameter estimates based on the observed counts, the model specification, initial values, and specified prior distributions. Three chains of 50,000 steps were run following an initial "burn-in" period of 20,000 steps. For population abundance (N) a vague normal distribution (0, 10 000) was used to have little effect on the resulting parameter estimates. In the state process, for the initial population size (logN) a normal distribution (dnorm) (7, 0.01) was used. For the mean growth rate (r_{mean}), dnorm (0, 0.001) was used and an uninformative distribution (dunif) (0, 1) was used for the standard deviation (SD) of the state process. For all β coefficients, dnorm (0, 0.001) was used. While dunif (0, 1) was used for SD of the observation process and dnorm (0, 1) for all β coefficients (β_t) with missing data. The model convergence was assessed from a visual inspection of chain trace plots and from the Gelman-Rubin statistic (R-hat), where values < 1.1 suggested reliable convergence (Gelman & Rubin, 1992). The significant effect of variables on population growth was assessed based on how different posterior distributions differed from zero.

3.3.4 Relative abundance index, and spoor frequency

Two population indices were determined, the relative abundance index (RAI) (Jenks, et al., 2011) and spoor frequency (SF) (Stander, 1998; Keeping, 2014). The latter was based on spoor tracking data and the RAI on camera trapping data. RAI was used because the target species are difficult to identify individually. These indices assume that species have similar detection probabilities, or that differences between detection probabilities are known and can be corrected for. In addition, it is assumed that detectability (β) is constant between two time periods, then $\beta_1 = \beta_2 = \beta$ (O'Brien, 2011). Species-specific seasonal RAI estimates were determined based on the following formula:

$$RAI = \frac{A_{\mathrm{i}}}{trap \quad nights} \text{ x } 100$$

Where A_{i} represents the total number of independent photographs of a species by all cameras, trap nights is the total number of the nights when all the cameras were active per season. Independent photographs were detection captures that were taken 30 minutes apart.

The SF is based on the observed proportion of transects P within an area that contained animal spoor (Stander, 1998). The frequency index can perform best when the habitat and substrate are relatively homogeneous (Karanth & Nichols, 2017). These conditions were met because the study area has a relatively homogeneous vegetation structure and soil type. The SF is based on the assumptions that the animals' spoor has a detection probability of one when present on the transect and that detection of spoors are independent both at the transect and grid cell level (Skalsi, Ryding, & Millspaugh, 2005).

SF was calculated as $\hat{P} = \frac{M}{K}$ (Skalsi, Ryding, & Millspaugh, 2005), where M is the total distance travelled across all grid cells (17 km) and K is the total number of spoors detected.

3.3.5 Assessing seasonal detection and occupancy probability

Photographs were sorted to species level. The *camtrapR* version 0.99.5 package (Niedballa et al., 2016) in program R version 3.2.2 (R Core Team, 2018) was used to organize and build species-specific detection/non-detection histories per camera trap per occasion for each target species. The 24 hours was considered an occasion. History consisted of a binary variable where j = 1 if the species was detected on camera trap j and 0 if otherwise. The histories accounted for camera malfunctioning periods and these were denoted as *NA.* Each trap day was treated as a repeat survey at a particular camera station resulting in 91 and 92 maximum sampling occasions per camera station during the wet and dry season, respectively. A single detection was considered even though the species may have been detected multiple times in a day by the same camera in an interval. To increase detections and reduce the volume of the presence/absence data, three sampling occasions were clumped and treated as a single occasion (Niedballa, et al., 2016). This resulted in 31 sampling occasions for each season. Similarly, data for assessing the influence of observation and site covariates on detection and occupancy (ψ) probability were extracted from camera trapping data. These included data on the co-occurrence of the target species and a binary variable indicating the presence or absence of leopard, respectively. These tested the hypothesis that species detection and occupancy were influenced by interspecific interactions and predator presence or absence (i.e. predation risk). Additionally, the influence of water on the target species distribution was assessed by including a binary variable. To ensure uniformity effect of covariates and improve convergence the continuous variable (i.e. NDVI) and presence/absence data were standardized using the formula: $xi = \frac{x_i - a}{ab}$, where x_i was an observed covariate value or a total number of occasions in cell *i*, and *a* was the average of the covariate values or observations, and *b* the standard deviation.

The roan and sable single seasonal detection probability and occupancy were modelled in the R program using the *unmarked* package (Fiske & Chandler, 2011). This package fits hierarchical models to imperfectly detected species occurrence and abundance datasets (Fiske & Chandler, 2011). The *logit link* function was used during model building to express the effects of covariates on the parameter. The use of occupancy modelling is adequate when the intent is to explore habitat associations between target species and season-specific parameters as it considers estimation of seasonal specific occupancy, and the dynamic changes in occupancy as a first-order Markov process (Mackenzie et al., 2006).

While the initial intent was to estimate and assess the influence of covariates on occupancy and detection for both target species such assessment was not possible for the roan antelope. This was because roan was detected at all sites during both seasons resulting in a naïve occupancy of 1 (James Hines, pers. obs. 2020). As such, detection probability was modelled as a function of observation covariates to ascertain drivers of the variability detection across sites. As such, in total there were two assessments of detection probability for roan one per season while for sable, similarly two assessments of detection probability and two of occupancy probability.

A two-step process was used to assess factors influencing the occupancy probability and causing variability in detection probability of roan and sable in WPF (MacKenzie, et al., 2006; Peterman, Crawford, & Kuhns, 2013). In the first step, the influence of site covariates on the detection probability (p) of roan and sable was modelled while holding occupancy constant. The structure of the base model for this step was as follow: $\Psi(.)\, p_{ij} = j(\text{predator presence} + \text{inter} - \text{specific interaction} + \text{NDVI} + \text{presence of waterhole})$.A fifth covariate was initially considered, distance from the waterhole. However, it was excluded because it was highly correlated with waterhole presence based on the Pearson correlation coefficient test (R^2 = 88%). First, the null model "$psi(.), p(.)$ was run which represents the hypothesis that the target species detection and or occupancy probabilities were not influenced by any covariate. The Akaike's Information Criterion (AIC) values were used to select model(s) that fit the data best (Burnham & Anderson, 2002). The model with the lowest AICs was a top-ranked model, and models with $\mathrm{deltaAIC} < 2$ indicated that the candidate model is as good as the best model. DeltaAIC is the relative difference in AIC values between each model and the currently top-ranked model. In the event, multiple models had similar support, model averaging was used to compute coefficient estimates. In addition, to understand the effect of each covariates untransformed beta coefficients are presented.

In the second step, the occupancy for sable was modelled using the best model for detection probability while holding the detection probability constant. The structure of the base model for this step was as follow: $p(.)\Psi_{ij} = j(\mathrm{predator\ presence} + \mathrm{interspecific\ interaction} + \mathrm{NDVI} + \mathrm{presence\ of\ waterhole})$. Similar analysis as described above concerning occupancy modeling, model selection, and averaging of coefficients were performed.

Lastly, the kernel density estimation function was used to model the temporal overlap in activity patterns of the two antelopes and their most important predator, the leopard. Kernel density estimation is a nonparametric density estimation method capable of estimating continuous probability density functions (Węglarczyk, 2018). The kernel density estimation approach offers a very flexible framework for modelling species habitat suitability from species presence-only data. This is because it uses all sample points' locations, therefore, it better reveals the information contained in the sample. Statistical analyses were implemented in the software R (R Core Team, 2018) using the *camtrapR* package (Niedballa et al., 2016). The quantification of the overlap in activity patterns was based on the overlap coefficient (Dhat1). Dhat1 is the area under the curve that is formed by taking the minimum of two density functions (Kernel density) at each point in time (Węglarczyk, 2018). It ranges from 0 (no overlapping activity patterns) to 1 (identical activity patterns).

CHAPTER 4

4. RESULTS

4.1 Trends in the Population abundance of roan and sable

4.1.1 The trend in roan population size based on the Generalized Additive Model

The trend of the fitted-based GAM with 95% confident intervals as a measure of uncertainty follows a similar pattern as that of the observed counts (Figure 7a). The roan antelope population fluctuated during this study period with having increased from 70 animals' size of the introduced population in 1975 to 275 animals in 1984. This period was followed by a drastic decline of 84% in animals counted from 275 to 45 individuals in 1994. Forty-five is the lowest population size recorded in the trajectory of this population since the introduction in 2019. From 1994 onwards, the trend became more wavering with two pre-peaks occurring in 1998 (n = 162) and 2012 (n = 132). Particularly, the population sluggishly declined from the year 2000 onward. However, the decline seems to be insignificant, based on the 95% CI overlapping with zero. This trend was found to be statistically significant ($edf = 4.856$; $F = 11.19$, $p < 0.001$). Two periods were found to be of significant changes, the period between 1979 to 1983 and 1987 to 1991, as the 95% CI at these points does not include zero (Figure 7b). During the former, period the population significantly increased above the long-term trend while significantly decreased during the latter. Outside these two periods, the population appears to have remained stable with two non-significant points of increase, the first one between 1995 and 1998 and the second from 2007 to 2013 (Figure 7b). The width of the 95% CI was narrower during the two significant periods of change in relation to the rest of the time series indicating greater certainty in the estimated trend. The wider 95% CI at both ends reflects uncertainty in the estimated trend at these points.

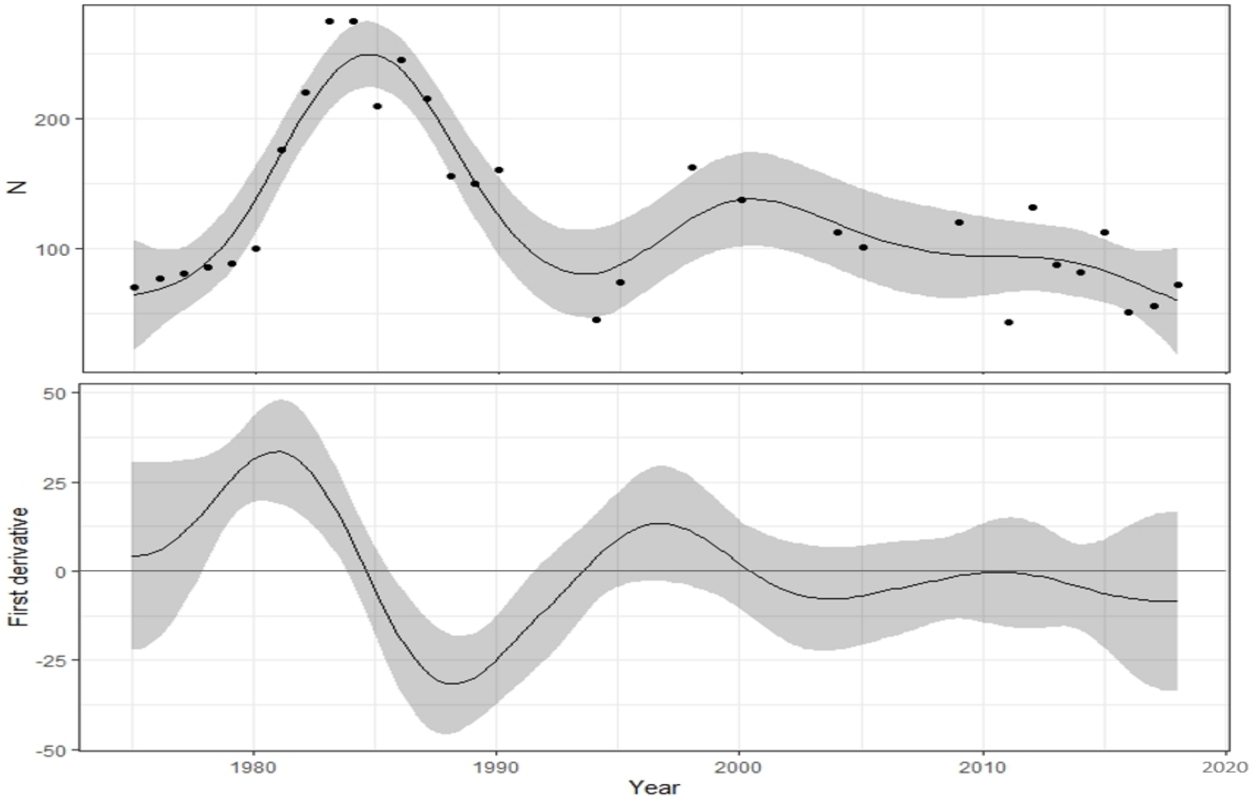

Figure 7 Annual trend in the roan antelope (a) fitted based-generalized additive models population size with shaded areas representing 95% confidence interval and (b) first derivate with reference level at zero (straight line).

The GAM model that most supported the trend in the roan population was the interactive model that included buffalo population size and annual rainfall (Table 1). This model explained 60% (R^2 = 0.462) of the deviance. The second non-competing highest-ranked model was the combination of annual rainfall and buffalo that assumed an additive effect of these predictors on roan population size. The least supported models were when both predictors were assumed to have independent effects (Table 1). Based on each variable deviance, rainfall had a significant effect on this population trend followed by the buffalo.

Table 1 Summary of Generalized Additive Model derived model deviances, Akaike's Information Criterion (AIC) values, Degree of freedom (*df*).

Model	**% deviance explained**	**AIC**	**deltaAIC**	***df***
Rain * buffalo	59.8	674.1	0	16
Rain + buffalo	60.1	682.6	8.5	15
Rain	40.5	825.7	151.6	8
Buffalo	32.5	904.6	230.5	8

4.1.2 The trend in roan population-based on State Space Model

4.1.3 The trend in sable population size based on the Generalized Additive Model

4.1.4 The trend in sable population size based on State Space Model

The overall trend in the sable population observed using state-space models showed an increasing phase during the period from 1980 to 1998, during which the population size increased from 25 to 137 animals (Figure 11). Following a peak of 137 animals in 1998, population abundance became more variable until 2019 when sable reached the lowest population number of 18 individuals. This population had three peaks in abundance that differ in magnitude. The first peak occurred around 1995 when the population reached 72 animals, the second and highest around 1998 of 137 animals and around 2001 of 139 animals, and the third around 2013 when the population reached a number of 89 animals. Two troughs in abundance were noticeable, one in 1994 and another in 2009 when the population dropped to 33 and 30, respectively. The SSM mean observation variance mean (σ_{obs}) was σ_{obs} = 0.07 ± 0.08 (CI95 = 0 - 0.3) and process variance mean (σ_{proc}) was σ_{proc}= 0.17±0.12, (CI95 = 0 - 0.45) (Appendix 1 Table 2S). The estimated abundances coincided closely with observed counts (Figure 11).

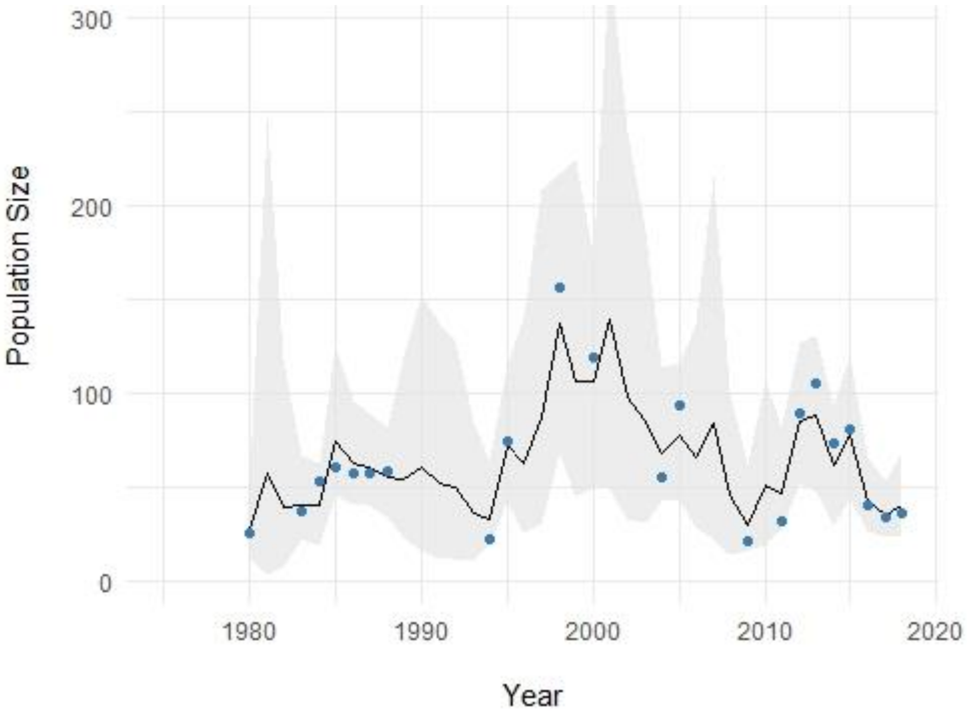

Figure 8 Population trend in the abundance of sable in Waterberg Protected Park, in north-central Namibia based on aerial count surveys (black dots) and the estimated abundance (solid black line) with 95% confidence interval (grey shading).

The SSM estimated a stationary population growth for the sable population (r = 0.00 ± 0.08, CI95 = -0.14 – 0.16) (Appendix 1 Table 2S). However, the growth was negatively influenced by lagged rainfall (β_2LRF = -0.12 ± 0.13, CI95 = -0.39-0.14) and slightly by the buffalo population size (β_3BF = -0.05 ± 0.09, CI95 = -0.24 - 0.14) (Figure 12, Appendix 1 Table 2S). In turn, annual rainfall (β_1RF = 0.15 ± 0.14, CI95 = -0.13 - 0.43) and auctions (β_5Auc = 0.15 ± 0.14, CI95 -0.13 - 0.41) tend to have positive relationship with this population growth (Appendix 1 Table 2S; figure 13). Similarly, the introduction of new individuals had a slight positive effect on the population growth (β_4Intro = 0.05 ± 0.25, CI95 = -0.45 - 0.52).

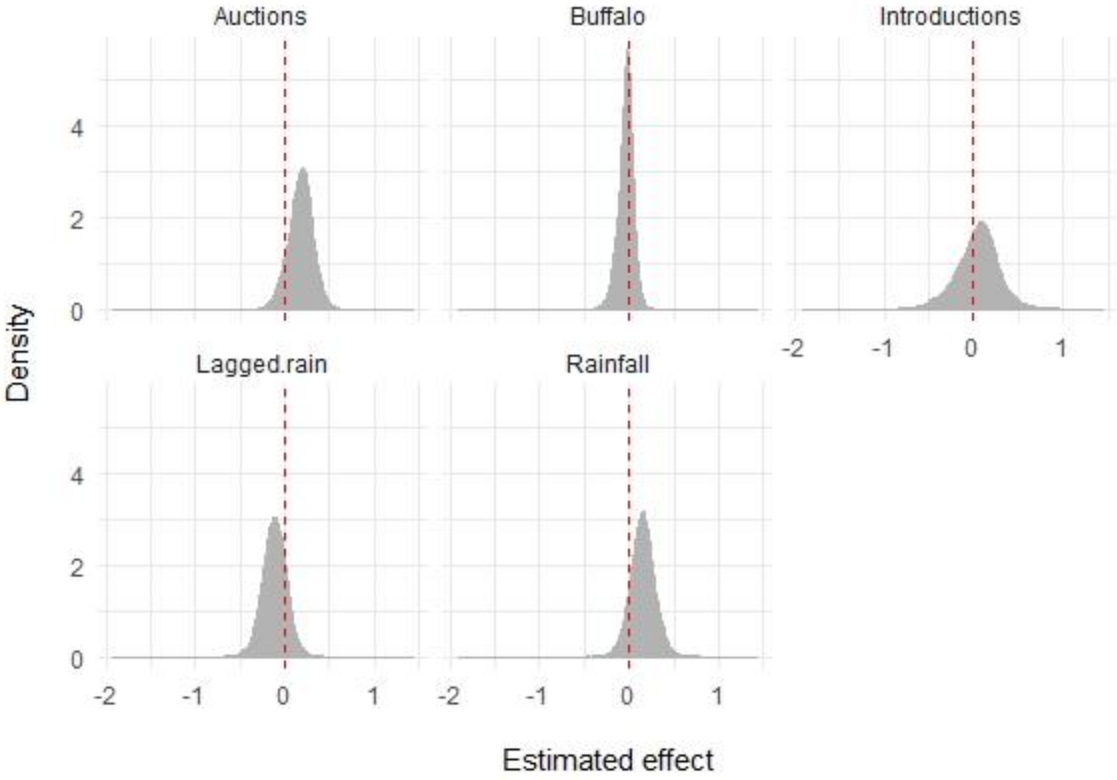

Figure 9 Posterior distributions estimated effect for model parameters on the sable population growth time-series. The dotted line is used to assess the effect of model parameters being zero.

4.2 Roan and sable seasonal relative abundance and spoor frequency index

4.2.1 Relative Abundance Index

Camera traps accumulated a total number of 938 and 934 trap days during the wet and dry seasons, respectively (Table 3). Despite similar sampling efforts roan had more independent photographs than sable in both seasons. Roan registered a total of 165 and 193 independent records during the wet and dry seasons, respectively. Based on these independent records, the relative abundance index for roan was estimated to be 20.7 during the dry season and 17.6 during the wet season (Table 3). In turn, sable had 147 and 106 independent records during the dry and the wet season, respectively. This translated to a higher RAI for the wet than the dry season (RAI_{dry} = 11.3 vs. RAI_{wet} = 15.7). Grid cells with waterholes had higher RAIs during the dry season for both species (Roan RAI_{wet} = 8.5 versus RAI_{dry} = 16.7 and Sable RAI_{wet} = 8.6 versus RAI_{dry} = 15).

Table 2 Seasonal relative abundance index (RAI), camera trap nights, and total and independent photograph records of roan and sable antelope in the Waterberg Park Farm.

Season	**Camera trap-nights**	**Total photographs**		**Independent photographs**		**RAI^a**	
		Roan	Sable	Roan	Sable	Roan	Sable
Wet	938	1,010	968	165	106	17.6	11.3
Dry	934	5,530	4,774	193	147	20.7	15.7
Total	**1,872**	**6,540**	**5,742**	**358**	**253**		

4.2.2 Spoor Frequency

A total of 16.3 km was surveyed during the wet and dry seasons each. During each season a total of 10 spoors of roan and sable were detected. This translated into a spoor frequency of 2.7 spoor/km and 4.1 spoor/km for roan and sable antelopes in both seasons, respectively (Table 4). Thus, spoor frequencies were similar between seasons for both species.

Table 3 Number of transects, total distance sampled, and roan and sable spoor detection in WPF.

Season	**No. of Transect**	**Total distance (km)**	**Independent Spoor Detections**		**Frequency**	
			Roan	Sable	Roan	Sable
Wet	17	16.3	6	4	2.7	4.1
Dry	17	16.3	6	4	2.7	4.1

4.3 The probability of detection and occupancy of roan and sable

4.3.1 The probability of detection of roan antelope

4.3.1.1 Wet season

A total of 938 night-traps were registered during the wet season that accumulated 165 independent photographs of roan across all the 13 sites during the wet season (Table 3). Using this data, a total of 16 single-species single-season detection models were fitted (

Table 4). From this suite of models, three were ranked as top models (ΔAIC < 2). That is, these were models had considerable support in terms of best describing the detection variability of roan antelope during the wet season. The cumulative weight of the candidate models was 67% representing the probability of them being the best. A fourth model, that represented a combined effect of NDVI and co-occurrence of sable, had a deltaic of two (Table 5). All covariates were represented among the top four models in different combinations suggesting that the detection probability of roan in the wet season is not influenced by any single covariate, except the co-occurrence of sable. The null model was not among the candidate set of models, suggesting that detection probability indeed varied across the grid cells. Among the candidate models, the model that most supported the variability in roan detection probability was the model with the presence and absence of sable, followed by the one with co-occurrence of sable and presence or absence of leopard (Table 5). The least supported model among all 16 models were those that included only the presence of waterhole, the NDVI values, and their combined effect. Among the four covariates, sable was the only covariate that appeared in all the top three models. Model averaged values indicate that sable had a slight significant positive effect on roan detection probability which was highest on sites where sable was absent or less detected ($\beta_i Sb = 0.49$, CI95 = 0.22 - 0.77) (Figure 13). There was a high degree of overlap (Dhat1 =0.81) in activity patterns of roan and sable (figure 14). Roan and sable were highly diurnal, primarily active from 06:00 in the morning to 18:00 afternoon (figure 14). Additionally, the presence of waterhole points had a similar positive effect (β_iWH = 0.042, CI95 = -0.53 -0.62). In turn, detection probability of roan was negatively influenced by the NDVI values (β_iNDVI = - 0.01, CI95 = -0.26 - 0.24) and the presence of leopard (β_iLp = -0.05, CI95 = -0.35 - 0.25). There was noticeable temporal segregation in peak use and activity pattern between roan antelope and leopard (Dhat1 = 0.59) as leopard were dominantly active during the early evening and the approach of dawn periods (Figure 14). The 95% CI of the waterhole, NDVI, and leopard overlapped with zero (Figure 10) indicates an insignificant effect of these predictors on the roan detection probability during the wet season.

Table 4 Summary of model selection results for roan antelope single-season detection (*p*) models for the wet season including the degree of freedom (*df*), model likelihood (logLik), Akaike's Information Criterion (AIC), relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model*	*Df*	logLik	AIC	deltaAIC	Model weight
p(Sb)Ψ(.)	3	-194.44	394.88	0.00	0.38
p(Lp+Sb)Ψ(.)	4	-194.39	396.77	1.89	0.15
p(Sb+WH)Ψ(.)	4	-194.43	396.86	1.98	0.14
p(NDVI+Sb)Ψ(.)	4	-194.44	396.88	2.00	0.14
p(Lp+Sb+WH)Ψ(.)	5	-194.37	398.75	3.86	0.06
p(Lp+Sb+WH)Ψ(.)	5	-194.38	398.75	3.87	0.05
p(NDVI+Sb+WH)Ψ(.)	5	-194.42	398.85	3.97	0.05
p(Lp+NDVI+Sb+WH)Ψ(.)	6	-194.36	400.72	5.84	0.02
p(Lp)Ψ(.)	3	-199.47	404.95	10.07	0.00
p(Lp+WH)Ψ(.)	4	-199.16	406.31	11.43	0.00
p(Lp+NDVI)Ψ(.)	4	-199.45	406.89	12.01	0.00
P(.)Ψ(.)	2	-201.69	407.38	12.50	0.00
p(Lp+NDVI+WH)Ψ(.)	5	-199.08	408.16	13.28	0.00
p(WH)Ψ(.)	3	-201.10	408.21	13.33	0.00
p(NDVI)Ψ(.)	3	-201.42	408.84	13.96	0.00

p(NDVI+WH)Ψ(.)	4	-200.72	409.45	14.56	0.00

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Sb = sable presence/absence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

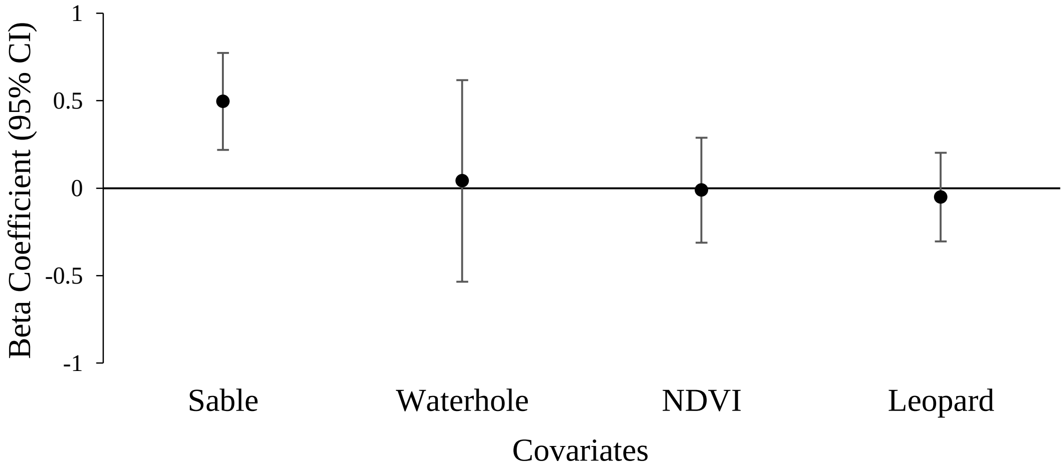

Figure 10 Mean beta coefficients of covariates influencing detection probability of roan during the wet season with the error bars denoting the 95% confidence interval (CI).

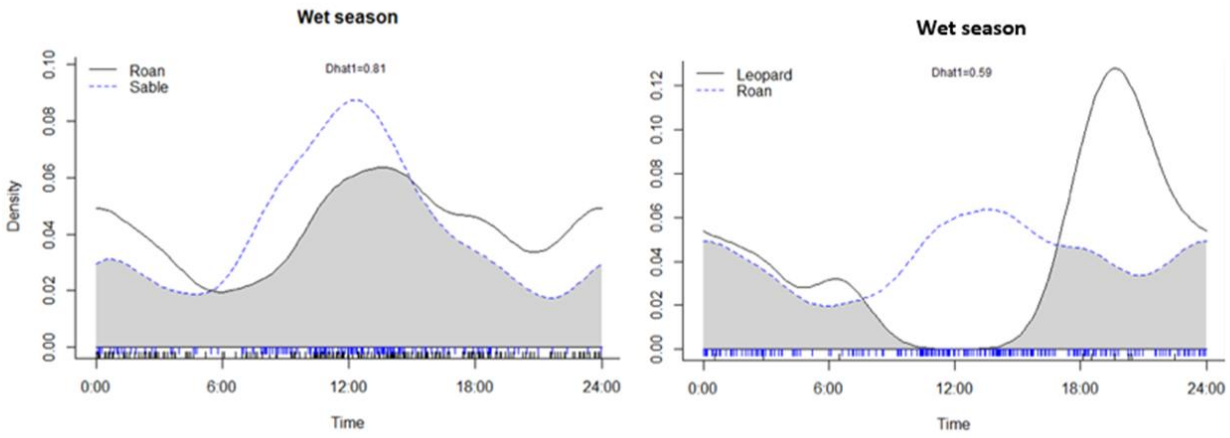

Figure 11 Daily activity patterns of roan based on detection rate in relation to sable and leopard activity patterns during the wet season in Waterberg Plateau Farm with the area

of time overlap (grey shaded) and the simulated data (rug at the bottom of the plot). Dhat1 represents the degree of overlap with 0 indicating no overlap and 1 total overlap.

4.3.1.2 Dry season

Camera traps accumulated a total of 193 independent photographs of roan during the dry season, respectively (Table 3). Roan was detected at 12 of the 13 sites during the dry season. From the 16 single-season detection probability models ran five were ranked as top models (ΔAIC < 2) (Table 6). These models included all the covariates, suggesting that the detection probability of roan in the dry season is not influenced by a single covariate, other than by the co-occurrence of sable. Similar to the wet season, the model that best describes the variability in roan detection probability was the model with the presence/absence of sable (Table 6). The second-highest ranked model was modelled the combined effect of the presence or absence of waterhole and co-occurrence of sable, followed by the one with the effect of sable combined with waterhole presence and absence, and NDVI values. The least supported models among the 16 models were those that included the combined influence of the presence of leopard and NDVI, leopard, and the null model (Table 6). Similar to the wet season results, sable was the common factor in all the top five models. Model averaged detection probability estimate of roan was highest in cells where sable was absent or less detected (β_iSb = 1.30, CI95 = 0.68 - 1.92). As daily activity patterns of roan and sable overlapped significantly (Dhat1=0.84) during the dry season with both antelopes being active diurnally from 06:00 to 18:00 (Figure 16). Contrary, this probability was negatively influenced by the presence of leopard (β_iLp = -0.09, CI95 = -0.38 - 0.20). There was a large partitioning of peak use and activity pattern between roan antelope and leopard (Dhat1 = 0.32) (Figure 16).

Moreover, the detection probability was also negatively influenced by the NDVI values (β_iNDVI = -0.22, CI95 = -0.69 - 0.24) and waterhole points (β_iWH = -0.72, CI95 = -2.12 - 0.67) (Figure 15). However, the 95% CI of these predictor variables overlapped with zero (Figure 15) indicating that their effect was not significant on the roan detection probability for the dry season.

Table 5 Summary of model selection results for roan antelope single-season detection (*p*) models for the dry season including the degree of freedom (*df*), model likelihood (logLik), model likelihood (logLik), Akaike's Information Criterion (AIC), the relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model*	*Df*	logLik	AIC	deltaAIC	Model weight
p(Sb)Ψ(.)	3	-140.04	286.08	0.00	0.29
p(Sb+WH)Ψ(.)	4	-139.75	287.50	1.42	0.14
P(NDVI+Sb+WH)Ψ(.)	5	-138.76	287.52	1.44	0.14
p(NDVI+Sb)Ψ(.)	4	-139.82	287.63	1.56	0.13
p(Lp+Sb)Ψ(.)	4	-139.84	287.68	1.60	0.13
p(Lp+Sb+WH)Ψ(.)	5	-139.45	288.90	2.82	0.07
p(Lp+NDVI+Sb+WH)Ψ(.)	6	-138.75	289.50	3.42	0.05
p(Lp+NDVI+Sb)Ψ(.)	5	-139.78	289.55	3.47	0.05
p(Lp+NDVI+WH)Ψ(.)	5	-147.84	305.68	19.60	0.00
p(NDVI+WH)Ψ(.)	4	-149.91	307.82	21.74	0.00
p(WH)Ψ(.)	3	-151.81	309.61	23.53	0.00
p(Lp+WH)Ψ(.)	4	-151.38	310.75	24.67	0.00
p(NDVI)Ψ(.)	3	-167.23	340.46	54.38	0.00
p(Lp+NDVI)Ψ(.)	4	-166.95	341.90	55.82	0.00
p(Lp)Ψ(.)	3	-172.37	350.74	64.66	0.00

P(.)Ψ(.)	2	-173.98	351.95	65.87	0.00

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Sb = sable presence/absence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

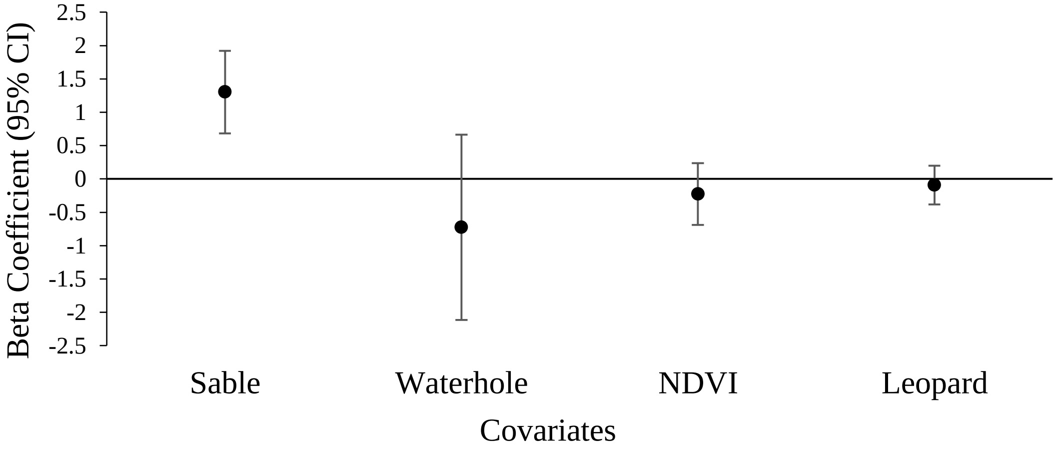

Figure 12 Mean beta coefficient for covariates influencing detection probability of roan during the dry season with the error bars denoting the 95% confidence interval (CI).

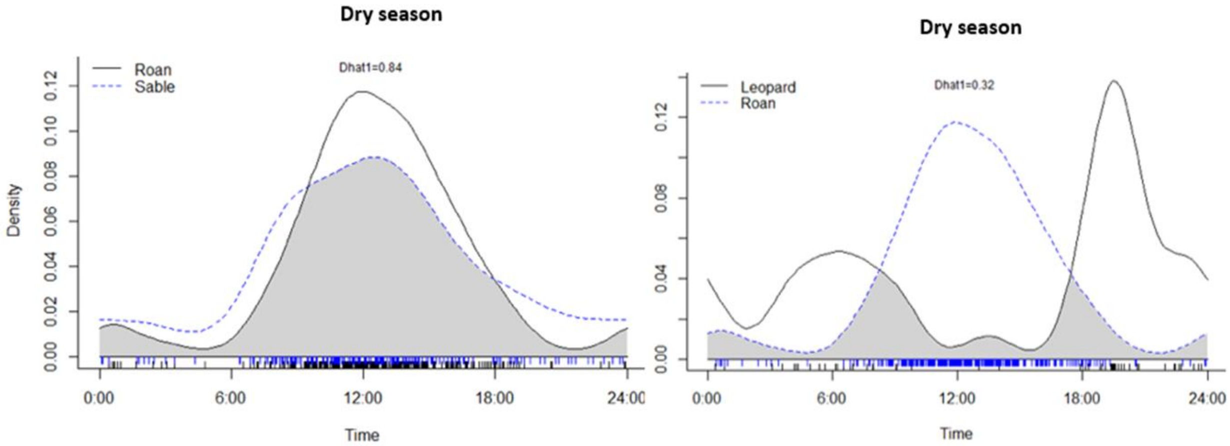

Figure 13 Daily activity patterns of roan based on detection rate in relation to sable and leopard activity patterns during the dry season in Waterberg Plateau Farm with the area

of time overlap (grey shaded) and the simulated data (rug at the bottom of the plot). Dhat1 represents the degree of overlap with 0 indicating no overlap and 1 total overlap.

4.3.2 The probability of detection and occupancy of sable antelope

4.3.2.1 Wet Season

Camera traps accumulated a total of 106 independent photographs of sable across eight sites (table 3) during the wet season. A total of 16 single-species single-season models were fitted to assess the variability in the detection probability of sable during the wet season (Table 7). Five competing models were identified as top-ranked (deltaAIC < 2) with a combination of all four different covariates. Among these candidate models, the most likely model assumed the influence of NDVI values and occurrence of leopard, followed by the one with a combination of the influence of waterhole, presence and or absence of roan and NDVI values. The least supported models among all 16 models assumed the influence from the presence or absence of leopard, constant detection, and NDVI. Detection probability of sable was highest in cells where NDVI values were higher (β_iNDVI = 1.18, CI95 = 0.50 - 1.86), where leopard was not detected (β_iLp= 1.11, CI95 = 0.54 - 1.68) (Figure 17). There was large segregation in the daily activity pattern of sable antelope and leopard (Dhat1=0.42). Sable was active during the daytime (06:00 – 18:00) while leopard was predominantly active nocturnally (18:00 – 06:00). Similarly, detection probability of sable positively influenced by the presence of waterhole points (β_iWH = 1.03, CI95 = -0.19 - 2.26) and the co-occurrence of roan (β_iRn= 0.36, CI95 = -0.18 - 0.91). Sable and roan had almost identical daily activity patterns (Dhat1=0.81) (Figure 18). However, the 95% CI of waterhole and co-occurrence of roan overlapped with zero, indicating that their effects on sable detection probability were insignificant (Figure 17).

Table 6 Summary of model selection results for sable antelope single detection probability (p) models for the wet season including the degree of freedom (*df*), model likelihood (logLik), AIC, Akaike's Information Criterion (AIC), relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model*	*Df*	logLik	AIC	deltaAIC	Model weight
p(NDVI+Lp)Ψ(.)	4	-103.26	214.52	0.00	0.22
p(Lp+NDVI+WH) Ψ(.)	5	-102.44	214.89	0.36	0.19
p(Rn+WH)Ψ(.)	4	-103.55	215.10	0.58	0.17
p(Lp+NDVI+Rn)Ψ(.)	5	-103.06	216.12	1.60	0.10
p(Lp+NDVI+Rn+WH)Ψ(.)	6	-102.31	216.63	2.10	0.08
p(Lp+WH)Ψ(.)	4	-104.43	216.87	2.34	0.07
p(NDVI+Rn+WH)Ψ(.)	5	-103.49	216.98	2.46	0.07
p(Lp+Rn+WH)Ψ(.)	5	-103.54	217.09	2.57	0.06
p(WH)Ψ(.)	3	-106.14	218.28	3.76	0.03
p(NDVI+WH)Ψ(.)	4	-105.74	219.48	4.96	0.02
p(NDVI+Rn)Ψ(.)	4	-108.35	224.70	10.17	0.00
p(Rn)Ψ(.)	3	-110.35	226.71	12.19	0.00
p(Lp+Rn)Ψ(.)	4	-110.33	228.65	14.13	0.00
p(Lp)Ψ(.)	3	-113.81	233.61	19.09	0.00
p(.)Ψ(.)	2	-118.55	241.10	26.58	0.00
p(NDVI)Ψ(.)	3	-118.26	242.52	28.00	0.00

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Rn= roan co-occurrence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

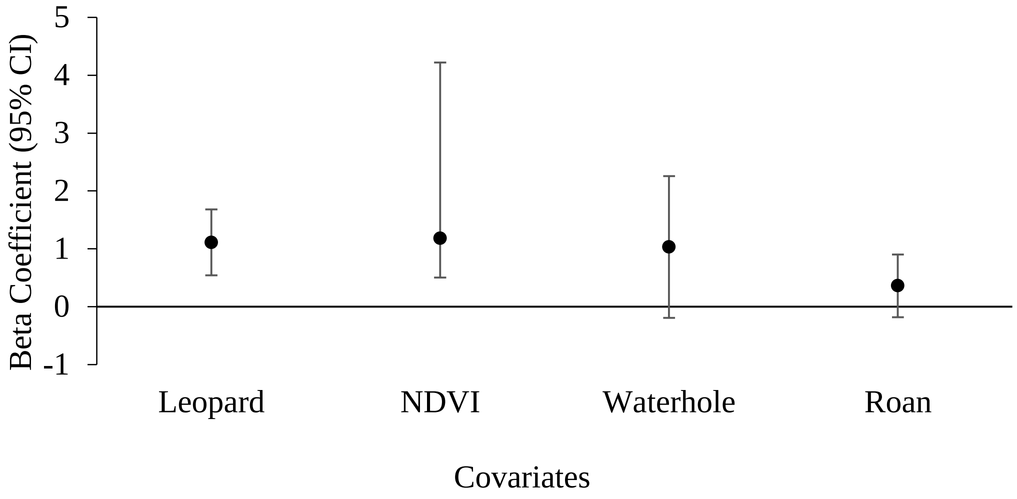

Figure 14 Mean beta coefficient for covariates influencing detection probability of sable during the wet season with the error bars denoting the 95% confidence interval (CI).

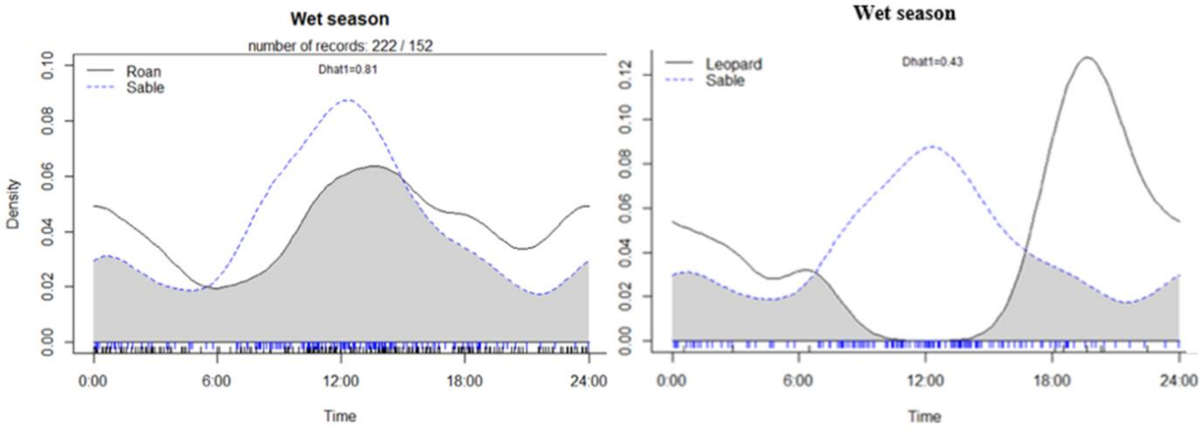

Figure 15 Daily activity patterns of sable based on detection rate in relation to roan and leopard activity patterns during the wet season in Waterberg Plateau Farm with the area of time overlap (grey shaded) and the simulated data (rug at the bottom of the plot). Dhat1 represents the degree of overlap with 0 indicating no overlap and 1 total overlap.

A total of 16 single-species single-season occupancy models were fitted (Table 8). Occupancy modeling with all covariates resulted in four competing models (AIC < 2).

Among these models, the one with the influence of NDVI values had the highest likelihood of being the best model (18%), followed by the one with the combined influence of forage and the presence of leopard and the null model. Among the 16 models, the least supported were those that included the combined influences of all covariates, the only occurrence of roan and waterhole, and lastly of the presence of the leopard, roan, and waterhole (Table 8). The NDVI predictor had occurred on four of the five top-ranked models. As a result, the occupancy probability of sable was positively influenced by the NDVI values (β_iNDVI = 1.25, CI95 = -0.32 - 2.83), and by the presence and absence of leopard (β_iLp = 0.95, CI95 = -0.72 - 2.61). Contrary, it was less influenced by co-occurrence of roan (β_iRn= 0.58, CI95 = -0.87 - 2.04) and lastly by the presence or absence of waterhole points (β_iWH = 0.133, CI95 = -2.94 - 3.21) (Figure 19). The 95% CI of these predictor variables overlap with zero (Figure 19) indicating that their effect on sable occupancy during the dry season was not significant.

Table 7 Summary of model selection results for sable antelope single-season occupancy (Ψ) models for the wet season including the degree of freedom (*df*), model likelihood (logLik), Akaike's Information Criterion (AIC), relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model*	*Df*	logLik	AIC	deltaAIC	Model weight
p(.)Ψ(NDVI)	3	-125.10	256.20	0.00	0.18
p(.)Ψ(NDVI+Lp)	4	-124.31	256.61	0.41	0.15
p(.)Ψ(.)	2	-126.56	257.13	0.93	0.12
p(.)Ψ(NDVI+Rn)	4	-124.75	257.49	1.29	0.10
p(.)Ψ(NDVI+WH)	4	-125.10	258.19	1.99	0.07

p(.)Ψ(Lp)	3	-126.28	258.56	2.36	0.06
p(.)Ψ(Lp+NDVI+Rn)	5	-124.30	258.60	2.40	0.06
p(.)Ψ(Lp+NDVI+WH)	5	-124.31	258.61	2.41	0.06
p(.)Ψ(Rn)	3	-126.42	258.84	2.65	0.05
p(.)Ψ(WH)	3	-126.54	259.09	2.89	0.04
p(.)Ψ(NDVI+Rn+WH)	5	-124.73	259.46	3.27	0.04
p(.)Ψ(Lp+WH)	4	-126.27	260.54	4.35	0.02
p(.)Ψ(Lp+Rn)	4	-126.27	260.54	4.35	0.02
p(.)Ψ(Lp+NDVI+Rn+WH)	6	-124.30	260.60	4.40	0.02
p(.)Ψ(Rn+WH)	4	-126.42	260.84	4.64	0.02
p(.)Ψ(Lp+Rn+WH)	5	-126.27	262.53	6.34	0.01

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Rn = roan co-occurrence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

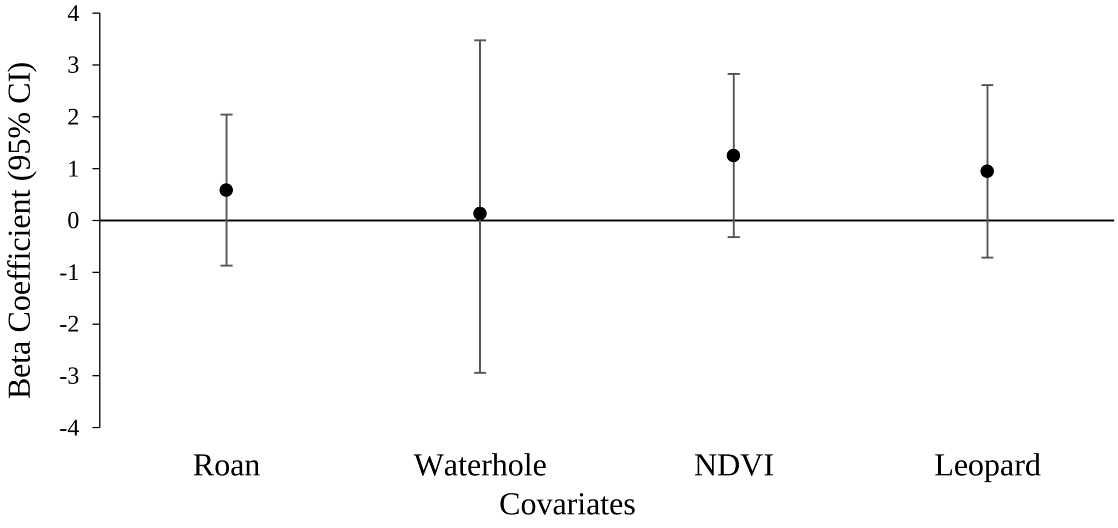

Figure 16 Mean beta coefficients for covariates influencing occupancy probability of sable during the wet season with the error bars denoting the 95% confidence interval (CI).

4.3.2.2 Dry Season

During the dry season, camera traps accumulated a total of 147 independent photographs of sable antelope. Spatially, sable was detected at seven sites. From the set of 16 single-species single models fitted to assess the variability in detection probability of sable during dry season three were ranked as top-model (deltaAIC < 2) (Table 9). All the covariates were included in this suite of candidate models. This implies that the variability in detection probability is not influenced by a single covariate, but rather a combination of different environmental covariates. The cumulative weight of these three models was 68%. Detection probability was most influenced by the interaction between the presence/absence of waterhole and of leopard followed by these former combined with the influence of roan, and the former with the influence of NDVI. The least supported models among the 16 ones, were the ones that included the combined influence of presence or absence of leopard with NDVI, constant, and only NDVI. Both leopard and waterhole were the predictor variables that occurred in the three top-ranked models during the wet season. Sable was highly detected in cells with waterhole points (β_iWH = 4.96, CI95 = 3.18 - 6.74) and where leopard were not detected (β_iLp = 0.55, CI95 = -0.05 - 1.15) (Figure 20). Alike during the wet season, there was a minimum overlap in the daily activity pattern of sable antelope and leopard (Dhat1=0.46) (Figure 21). Sable seems to be diurnal species while the leopard is predominantly nocturnal (Figure 21). In contrast, detection of sable was negatively influenced by the co-occurrence of roan (β_iRn = -0.41, CI95 = -1.74 - 0.92), and NDVI values (β_iNDVI = -0.29, CI95 = -1.30 - 0.72).There was a high degree of overlap (Dhat1= 0.84) in the activity pattern of the two antelopes during the dry season (Figure 21). Nonetheless, because the 95% CI of co-occurrence of roan, leopard, and NDVI values overlapped with zero (Figure 20), their apparent effects were not significant on target species occupancy.

Table 8 Summary of model selection results for sable antelope single detection probability (*p*) models for the dry season including the degree of freedom (*df*), model likelihood (logLik), Akaike's Information Criterion (AIC), relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model*	*df*	logLik	AIC	deltaAIC	Model weight
p(Lp+WH)Ψ(.)	4	-64.88	137.76	0.00	0.36
p(Lp+Rn+WH)Ψ(.)	5	-64.68	139.36	1.60	0.16
p(Lp+NDVI+WH) Ψ(.)	5	-64.72	139.44	1.68	0.16
p(NDVI+WH)Ψ(.)	4	-66.11	140.21	2.45	0.11
p(Lp+NDVI+Rn+WH)Ψ(.)	6	-64.57	141.13	3.37	0.07
p(WH)Ψ(.)	3	-67.75	141.50	3.74	0.06
p(Rn+WH)Ψ(.)	4	-66.92	141.84	4.08	0.05
p(NDVI+Rn+WH)Ψ(.)	5	-66.10	142.21	4.44	0.04
p(Lp+NDVI+Rn)Ψ(.)	5	-72.90	155.81	18.04	0.00
p(NDVI+Rn)Ψ(.)	4	-75.52	159.05	21.29	0.00
p(Rn)Ψ(.)	3	-84.32	174.63	36.87	0.00
p(Lp+Rn)Ψ(.)	4	-84.20	176.39	38.63	0.00
p(Lp)Ψ(.)	3	-118.24	242.48	104.72	0.00
p(Lp+NDVI)Ψ(.)	4	-117.98	243.96	106.19	0.00
p(.)Ψ(.)	2	-118.55	241.10	26.58	0.00
p(NDVI)Ψ(.)	3	-119.90	245.80	108.04	0.00

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Rn = roan presence/absence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

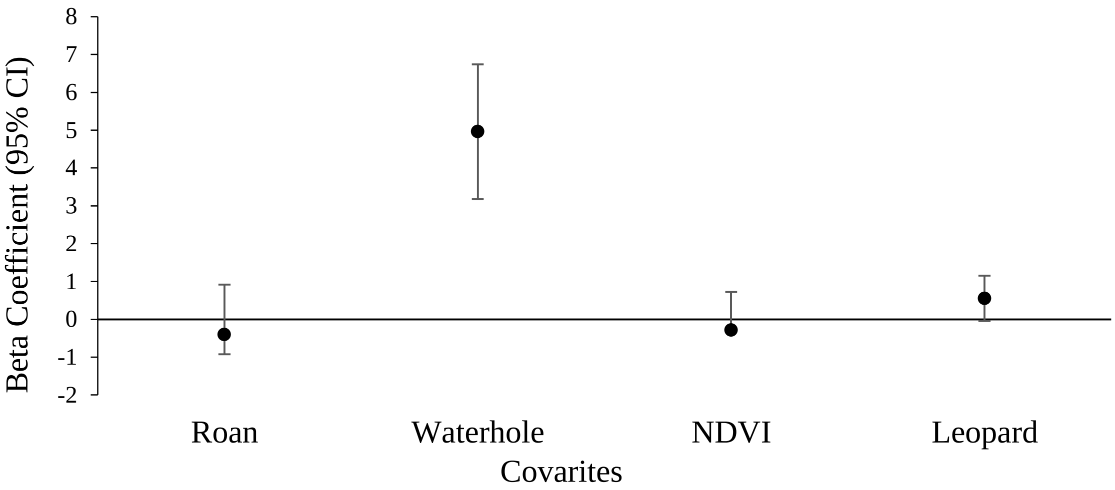

Figure 17 Mean beta estimates for covariates influencing detection probability of sable during the dry season with the error bars denoting the 95% confidence interval (CI).

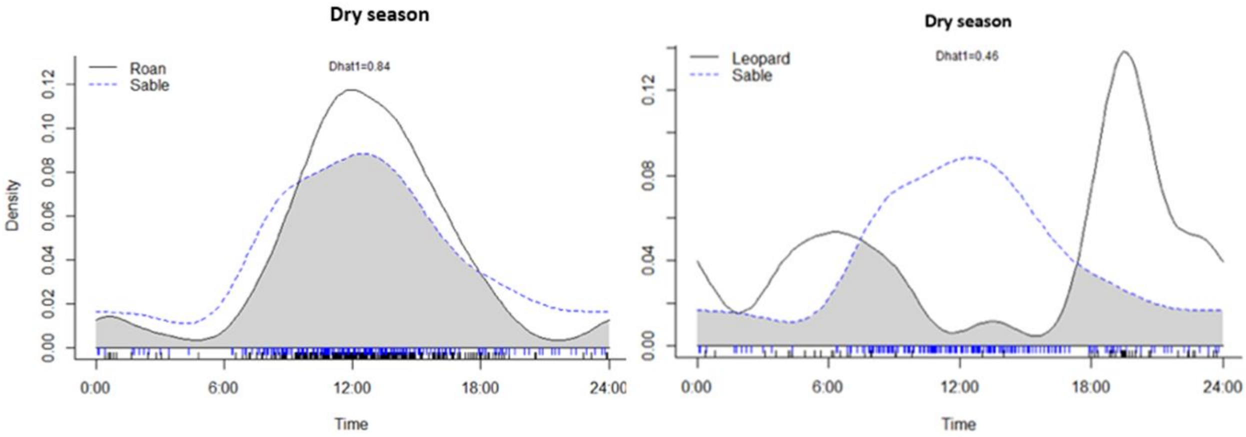

Figure 18 Daily activity patterns of sable based on detection rate in relation to roan and leopard activity patterns during the dry season in Waterberg Plateau Farm with the area of time overlap (grey shaded) and the simulated data (rug at the bottom of the plot). Dhat1 represents the degree of overlap with 0 indicating no overlap and 1 total overlap.

Second, a total of 16 single-species single-season occupancy models were fitted. From these suites of models, four top-ranked models had deltaAIC < 2 (Table 9), indicating an influence by the combination of different variables (Table 10). The model that best described the sable distribution was the model with a combined influence of the presence/absence of leopard and co-occurrence of roan. The second-highest ranked model was the one with interaction between NDVI values, the occurrence of leopard and roan. The model with the co-occurrence of roan as a single variable was the third model. The least and the last model contained the interaction effect of presence/absence of roan, NDVI values, and waterhole. The co-occurrence with roan featured on all four top-ranked models. Subsequently, the occupancy probability of sable was positively influenced by the absence of roan (β_iRn = 6.03, CI95 = -3.79 - 15.84), leopard (β_iLp = 0.042, CI95 = -2.69 - 10.48) and waterhole (β_iWH = 1.88, CI95 = -87.18 - 90.95) (Figure 22). Alike during the wet season, the occupancy probability of sable was negatively influenced by the NDVI values (β_iNDVI = -1.41, CI95 = - 6.34 - 3.51). However, the effect of all predictor variables on sable occupancy during the dry season seems to be insignificant because the 95% CI of these variables overlapped with zero (Figure 22).

Table 9 Summary of model selection results for sable antelope single-season occupancy (Ψ) models for the dry season including the degree of freedom (*df*), model likelihood (logLik), Akaike's Information Criterion (AIC), relative difference in AIC values (deltaAIC) and model weight. Best fit models (deltaAIC < 2) are grey shaded.

Model	*Df*	logLik	AIC	deltaAIC	Weight
p(.)Ψ(Lp+Rn)	4	-127.60	263.20	0.00	0.33
p(.)Ψ(Lp+NDVI+Rn)	5	-127.39	264.79	1.59	0.15
p(.)Ψ(Rn)	3	-129.58	265.15	1.96	0.13
p(.)Ψ(Lp+Rn+WH)	5	-127.60	265.19	1.99	0.12
p(.)Ψ(Lp+NDVI+Rn+WH)	6	-127.39	266.77	3.57	0.06

p(.)Ψ(NDVI+Rn)	4	-129.42	266.83	3.63	0.05
p(.)Ψ(Rn+WH)	4	-129.57	267.14	3.95	0.05
p(.)Ψ(Lp+WH)	4	-129.93	267.86	4.66	0.03
p(.)Ψ(WH)	3	-131.38	268.76	5.57	0.02
p(.)Ψ(NDVI+Rn+WH)	5	-129.41	268.82	5.63	0.02
p(.)Ψ(Lp+NDVI+WH)	5	-129.90	269.79	6.59	0.01
p(.)Ψ(NDVI+WH)	4	-131.21	270.41	7.21	0.01
p(.)Ψ(Lp)	3	-132.61	271.22	8.02	0.01
p(.)Ψ(.)	2	-133.62	271.24	8.05	0.01
p(.)Ψ(NDVI)	3	-133.38	272.76	9.56	0.00
p(.)Ψ(Lp+NDVI)	4	-132.60	273.20	10.00	0.00

*(.) = constant or null model, p = detection probability, Ψ = occupancy probability, NDVI = Normalized Vegetation Index, Rn = roan presence/absence, Lp = presence/absence of leopard and WH = presence/absence of waterhole.

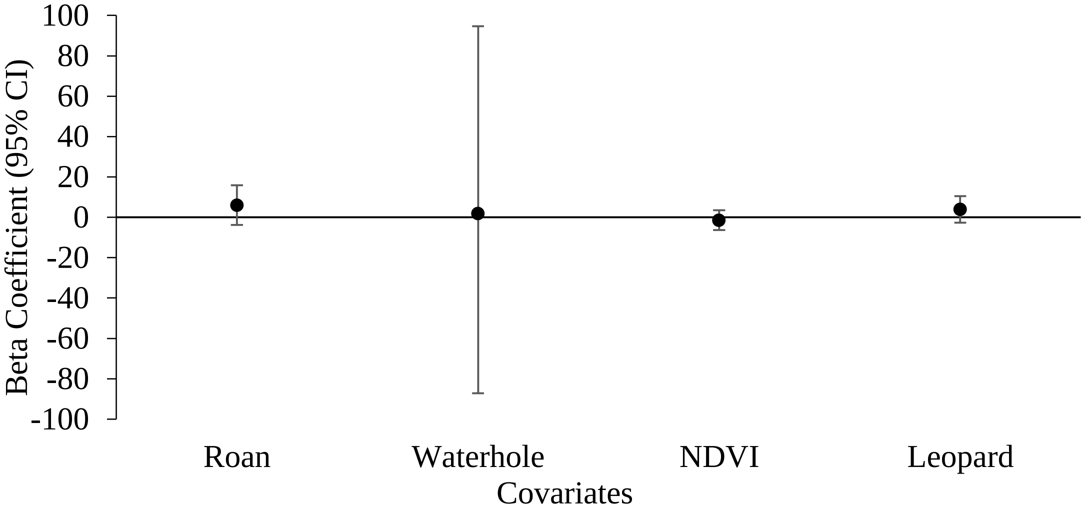

Figure 19 Mean beta coefficients of covariates influencing occupancy probability of sable during the dry season with the error bars denoting the 95% confidence interval (CI).

CHAPTER 5

5. DISCUSSION

5.1 Population dynamic estimates of roan and sable on WPP

The only reliable approach to understanding the processes occurring within a system is to monitor how the system and populations respond to natural and anthropogenic-induced changes over multiple generations. This study investigated the population dynamics and factors influencing the population abundance of roan and sable antelopes in Waterberg Plateau Park. This is the first investigation of this kind in WPP. The population dynamics of the roan and sable antelope was successfully modelled using GAM and SSM analytical frameworks based on secondary aerial count data that spanned a period of 44 years, 1975 to 2019. Both GAM and SSM fitted models followed a similar pattern with that of the observed count, which suggests that the models are describing the data accurately. The populations of both antelopes fluctuated during the 44 years periods but only the roan experienced two significant periods of change. The fluctuation in roan abundance coincided with the variability pattern in rainfall, particularly low lagged rainfall and with the increase of the buffalo population. The effect of these variables resulted in uncertainty negative growth trend. The latter was also the main driver responsible for the zero growth of the sable population. Overall, the study findings support the hypothesis with uncertainties that the most important factors affecting the roan and sable antelope population in WPP are low lagged and annual rainfall, and resource competition between the antelopes and buffalo. The effect of these variables resulted in uncertainty negative population growth trend of roan antelope and zero population growth of the sable antelope population.

5.2 Factors influencing population dynamic of roan and sable in WPP

5.2.1 Rainfall effects and resources availability

The general patterns of change in roan and sable population size in WPP were related to rainfall patterns, in particular lagged rainfall as suggested by results from the SSM analysis (Figure 11). This result is partly in agreement with that of Kasiringua, Kopij, and Procheş (2020), who observed a weak relationship between these two antelopes' abundance and annual rainfall. The population of both species responded positively to the rainfall increase and expanded during the high rainfall periods. Conversely, the temporal patterns of population change shown by the declining ungulate species suggest a direct response to the impact of changes in rainfall, particularly during periods of low rainfall coupled with severe droughts and resource availability. Exacerbating this negative effect was the cumulative effect resultant from consecutive years of low-lagged average rainfall. This is reflected by the drastic population decline of both species between 1993 and 1999. For instance, the lowest population size recorded in 1994, 1997, and 2000 were attributed to the four severe drought years that occurred in 1992, 1995 - 1996, and 1998 (Figure 1S). During these periods, rainfall was recorded to be below 250 mm (Appendix 1 Figure 1S). This reiterates existing concerns about managing these species outside their natural range with an average rainfall below 400 mm isohyet (Martin, 2003). This could have led to a decrease in food resource availability, and or reduction in the nutritional value of available forage. Grass production is positively and linearly related to rainfall once grass growth begins (Deshmukh, 1984).

Furthermore, it is well established that annual grass production is linearly related to rainfall in semi-arid savanna regions (Rutherford, 1980). As such, food production supporting the ungulate population most likely varied annually, in direct response to the amount of rainfall received during the preceding rainfall cycle. The impact of this reduction in forage resources could have intensified interspecific competition (Kasiringua, Proches & Kopij, 2019). Together these sources of distress could have had negatively impacted the survival and reproduction rate of these antelopes which are unable to escape the effects of resource depletion in drought conditions. This finding is aligned to that of previous studies that identified habitat deterioration due to an extended period of low rainfall as one of the causes of the roan antelope population decline in KNP (Harrington, et al., 1999). Correspondingly, extreme reduction in dry-season rainfall was the prime climatic variable associated with the ungulates population declines in KNP from 1977 to 1996 (Owen-Smith & Mills, 2006). Marshal, Rankin, Nel, and Parrini (2016) also established that low rainfall and poor forage from 2001 to 2005 precipitated the decrease of sable observed between 2003 and 2004 in Kgaswane Mountain Reserve. Consequently, ongoing and future interventions involving the introduction of these species in areas with low rainfall, should consider the potential impacts of climate change to improve the success of this management strategy.

5.2.2 Competition with buffalo

The study hypothesized and demonstrated that the observed increase in the buffalo population had a negative effect on both roan and sable population growth trajectories, however, the effect seems to be insignificant. Notably, roan and sable populations only increased in abundance before the introduction of buffalo in the study area, and after, it remained below 100 individuals and their subsequent apparent exponential growth (Appendix 1 Figure 1S). Roan and sable could have been impacted by this growth through interspecific competition and displacement. The buffalo growth most likely resulted in increased grazing pressure on food resources, an impact that is likely to have been severe during and after periods with low rainfall records as grass production is directly related to rainfall patterns (Deshmukh, 1984). Buffalo may not have been affected to the same extent as roan and sable because the species is predominately bulk grazer, a trait that while may have increased grazing pressure on food resources, equally explained the un-ceased growth of their population. According to Sinclair's (1973) long-term study on the African buffalo in the Serengeti, food limitation led to the evolution of specific behavioural strategies and physiological mechanisms (i.e., the eco-physiological adaptation of their digestive system) to detect and avoid food shortages.

Past studies have shown that high levels of competition, especially in national parks, were responsible for roan and sable population decline (Harrington, et al., 1999; Marshal, Rankin, Nel, & Parrini, 2016). Putman and Putman (1996) described marked overlap of habitat and nutritional niches as an indicator of potential competition among sympatric ungulate species. Buffalo, roan, and sable have similar dietary preferences. The dietary preference of buffalo includes grasses such as *Eragrostis spp*, *T. triandra*, *Heteropogon contortus*, *Digitaria eriantha*, *Sporobolus fimbriatus*, *Aristida stipitata*, and *Panicum coloratum* (Venter & Watson, 2008). Coincidently, roan and sable also prefer these grass species (Grobler, 1981; Roux, 2010; Parrini, Koen, Dalton, & Eksteen, 2016). Therefore, the abundance of these grazers could have contributed in some way to the deterioration in habitat conditions that occurred during the low rainfall periods. Harrington, et al., (1999) stated that valuable grass species as *T. triandra*, *A. stipitata*, and *D. seriata* are categorized as decreasers, those grass species that decrease in abundance and deteriorate in range condition when subjected to heavy grazing pressure. Harrington, et al., (1999) established competition from zebra and wildebeest as the causes of the roan antelope decline in the KNP.

Furthermore, competitive displacement by buffalo may explain the positive association between the decline of sable herds and the increase of buffalo. According to Macandza, Owen-Smith, & Cain (2012) sable avoided closer proximity to buffalo herds at a finer scale of movements within overlapping ranges to avoid competition, causing them to utilize habitat with poor forage production. Furthermore, the same study indicated that sable narrowed their dietary niche during the dry season, by feeding on a set of uncommon grasses that were rarely recorded in the feedings of non-ruminant zebra or buffalo zebra. Consequently, further fine-scale studies that explore aspects related to habitat and resource partitioning among these species across these species ranges are needed.

5.2.3 Introduction and auction

The hypothesized impact of management actions of auctioning and introducing individuals correlated positively to the increase of the sable population. Similarly, introductions had a positive correlation effect on roan population growth but auctioning seems not to have had an effect on roan growth. Nonetheless, the effect of the two variables seemed to be uncertain, probably because managers only sold off animals when the populations were growing. In addition, the auction was only applied 13 times for each species and ceased in 2014. While, the introduction of roan and sable occurred 5 times and 7 times in total throughout the study period, respectively.

Previous studies have attributed the ongoing decline in the population size of wildlife species in most African countries to trophy hunting and live auctioning (Ogutu, Owen-Smith, & Said, 2011; Muposhi, Gandiwa, Makuza, & Bartels, 2016). These management practices often target sexually mature individuals that coincidently are the largest in a population either in terms of body size or horns (Crosmary, Loveridge, Ndaimani, Lebel, Booth, Côté1, & Fritz, 2013). This artificial selection has been shown to negatively affect the socio-demographic dynamics of ungulates as the removed animals are often the dominant individuals and age/sex structures (Muposhi, Gandiwa, Makuza, & Bartels, 2016). For instance, Crosmary, et al., (2013) showed that the horn size of sable antelope species was declining in Matetsi Safari Area, Zimbabwe. Thus, not only do the populations of roan and sable at WPP could be at higher risk of becoming inbreed due to their small size, but auctioning could be exacerbating the loss of genetic variability and population survival. Further studies should determine the genetic variation and structure of these species' populations by comparing it with that of other populations particularly the source one. Genetic variation is an important factor influencing the long-term persistence of a population, especially in the ability of the population to respond to environmental changes (Muposhi, Gandiwa, Makuza, & Bartels, 2016).

5.3 Factor influencing the detection and distribution of roan and sable in Waterberg Plateau Farm

As far as the reviewed literature is concerned, this was the first study that explored the influence of environmental parameters on the spatial distribution of roan and sable antelopes in the Waterberg Plateau. Earlier studies at Waterberg Plateau Park focused on large ungulate including roan, sable, and buffalo waterhole use, population structure, and dynamics (Kasiringua, Procheş, & Kopij, 2017, 2019, 2020) Although these studies made use of the same dataset as the present, they differ in terms of analytical approaches, where earlier studies used linear models and this study used Generalized Additive and State Space Models, that allow for determination of the significant point of change in size, assess nonlinear patterns and account explicitly for both variance in the observation (i.e. counts) and process (i.e. trend in abundance). The present study thus extends the current knowledge by having demonstrated that the most important environmental factor influencing variability in detection probability of roan antelope during both the wet and dry seasons in WPF is the interspecific interaction with sable. For sable, the probability of detection and occupancy seemed to be significantly controlled by the forage availability, the presence, and or absence of waterholes and leopard.

5.3.1 Presence of waterholes

The presence of waterholes tended to have little to no effect on the distribution of roan in WPF, but it had a strong positive effect on the distribution of sable during the dry season. Based on the results, the detection probability rate was higher at sites with waterholes during the dry season compared to the wet season (e.g. Figure 20). This could be because these antelopes access sufficient water from rainfall-fed temporary pools during the wet season. Further, during the wet season forage are highly saturated and can act as an additional water source as opposed to during dry season when feeding on dry forage causes these obligated species to increase their water intake to be able to keep up with digestion and metabolism. Previous studies also demonstrated that access to surface water to be the main limitation on seasonal home range occupation of sable and roan in Okavango Delta, Botswana (Hensman, Owen-Smith, Parrini, & Bonyongo, 2013), KNP in South Africa (Harrington, et al., 1999; Cain, Owen-Smith, & Macandza, 2012).

These results are unsurprising, given that roan and sable are proved to be water-dependent, even in WPP (MET, 2008; Kasiringua, Kopij, & Procheş, 2017). Given this physiological trait, the availability of water is crucial for their persistence to the extent that individuals of these species were detected only on cells that were within 2.2 km and 4 km from a waterhole. This distance is within the range reported in other study areas such as in the Malilangwe Wildlife Reserve in Zimbabwe of at least 2.6 km of water sources (Capon, 2011) and 2 to 4 km on most of the nature reserves in South Africa (Wilson & Hirst, 1977). In another study conducted at Rhodes Matopos National Park, Zimbabwe they were recorded staying only 1 km away from water (Grobler, 1981).

Kimanzi and Wanyingi (2014) report that in the Ruma National Park, Kenya roan home ranges were significantly located near-surface water at distances of 1 km or less. Following this line of thought, the provision of water is an important tool that can be used to manage temporal dynamics of population distribution and species habitat use despite the contention issues but care to minimize any piosphere effect and interspecific interactions (Mukaru, 2009; Chamaillé-Jammes, Charbonnel, Dray, & Fritz, 2016).

5.3.2 Interspecific interaction

The results support the hypothesis that roan distribution was positively influenced by the co-occurrence of the other target species. Although there is a high degree of niche overlap, there was a large partitioning of detection rate amongst these species per area of occupancy during both seasons. Our findings suggest that temporal partitioning is probably not a generalized mechanism of coexistence between roan and sable; instead, the partitioning of habitat/space use and food resources may play a larger role in mediating this sympatric coexistence. Roan had a high detection probability in the area with less to no presence of sable antelope both during the wet and dry seasons, and sable detection probability varied markedly with the co-occurrence of roan, especially during the wet season. This result is likely to have been confounded in an earlier study when sable herds avoided areas with a high population abundance of buffalo and roan within the WPP (Kasiringua, Procheş, & Kopij, 2019). The observation that species had similar activity patterns in both seasons (Figure 18; Figure 21) but were not detected at the same sites further suggests that species may be employing some form of spatial-temporal avoidance strategy. The similar diurnal activity pattern exhibited by these two antelopes intensifies the potential for competition between them. This is in line with Hayward and

Hayward (2012) finding that although herbivores in southern Africa had a high degree of diurnal overlap in waterhole use, they partitioned their temporal waterhole use peak. In KNP, sable herds avoided high concentrations of wildebeest and impala (Chirima, 2009). Correspondingly, in KNP roan population distribution contracted, and population size decline when zebra and wildebeest invaded their home range (Harrington, et al., 1999). Interspecific competition has also been observed in other ungulate species. For example, Bao, et al., (2017) reports that the roe deer (*Capreolus capreolus*) influenced the occurrence probability and population density of the moose (*Alces alces*) in the Greater and Lesser Khingan mountain ranges of northeastern China. While this study provided evidence of co-occurrence influence on detection, the precise ecological and behavioural mechanism that allows roan and sable to coexist need further investigation. Knowledge about these behaviour aspects is crucial to elucidating the factors that enable their coexistence. Furthermore, an understanding of their respective activity periods is relevant to management and associated research efforts. Moreover, conduct predictions of future distributions in response to global climate change, as rates of range expansion and contraction are likely to be influenced by multispecies responses (McCullough, 2010)

5.3.3 Predation risk

The results provided evidence that the presence/absence of leopard influences the detection and distribution of sable in WPF during the dry season. That is, sable was highly detected at sites where leopards were less detected and or absent. On the other hand, for roan, results were ambiguous on both seasons because the species was detected at all sites. Accordingly, although roan had a high degree of overlap with leopard, there was an exceptionally large temporal partitioning of peak use and activity pattern amongst the two antelopes and leopard (Figure 14, Figure 16). These results are in agreement with the theory of the “landscape of fear” (Gaynor, et al., 2019). According to this theory prey behaviour is shaped based on the distribution of predation risk perception across the habitat (Gaynor, et al., 2019). Fraker and Luttbeg (2012) said that prey species commonly manage their exposure to predation risk by increasing vigilance levels and adjusting their spatio-temporal habitat use or avoiding risky habitats. These include the use of visual (i.e., predator scat’s presence), auditory and olfactory cues (Kuijper, et al., 2014).

On the other hand, the relative positive effect of leopard presence on the distribution of roan and sable may be due to the theory that the predator space use can be influenced by the increase of prey availability and or vulnerability (Kittle, Bukombe, Sinclair, Mduma, & Fryxel, 2016). For instance, Nordberg and Schwarzkopf (2019) found out that predation risk on lizards in the savannah ecosystem was not proportional to the abundance of predatory birds, but with higher predation rates at low bird abundances. Kittle, Bukombe, Sinclair, Mduma, and Fryxel (2016) confirmed that lion presence was higher in areas where prey species were abundant and vulnerable (i.e near water sources), in Serengeti National Park. Accordingly, understanding the activity patterns and predator-prey interactions thereof, is of considerable benefit in improving knowledge of these species ecologies, thus paving the way for the development of appropriate management and conservation programs.

5.3.4 Availability of forage

The study results indicated that the seasonal variation in forage availability effect was more pronounced for sable than roan (Figure 5). Forage availability significantly influenced the spatial distribution of sable predominantly during wet season in the WPF. A spatial shift in NDVI values corresponded with occupancy of sable antelope, whereby sable was highly detected in cells with higher NDVI values during the wet season and less detected in grid cells with low NDVI values during the dry season. Consistently during the dry season, sable maintained a positive association with relatively greater NDVI values however, they cease to spatially exist in an area that declines severely in NDVI values. This association suggests that sables were tracking localized resources available in the wet season in order to exploit ephemeral green flushes. The overall low detection probability of sable antelopes particularly in areas with low NDVI values suggests that they do indeed show preferences in their feeding habitat. Correspondingly, Chirima (2009) found out that the prevalence of sable in KNP was significantly correlated with areas of highest NDVI values and dropped in areas of lowest NDVI values. Wilson and Hirst, (1977) noted that wild ungulates typically display feeding habit flexibility to ensure a sufficient intake of nutrients, even in poor seasons. It appeared that sable antelope occupation could be influenced more by interactions of forage resources availability with interspecific species, presence of predators, and waterhole than just by NDVI alone.

Roan showed a consistent occurrence throughout the study area across both seasons. This suggests that forage availability seems not to have influenced their distribution patterns. Additionally, this could also be due to the WPF's small size. Nonetheless, spatial variation was noted with roan recording higher detections in areas of highest NDVI values relative to areas with lower NDVI values. This result is consistent with findings of earlier studies that roan could be sedentary and occupy the same home range during the wet and dry season if there is sufficient food and water (Wilson and Hirst, 1977, Havemann *et al*., (2016). Besides, this is probably because roan antelope would readily make use of available browse in the area when grass forage palatability dropped to a low level (Wilson & Hirst, 1977). Bao, et al. (2017) found out that the relationships between moose and roe deer appear to be mainly regulated by variations in local food conditions in the Greater and Lesser Khingan mountain ranges of northeastern China. Consequently, further studies need to be conducted on habitat and resource partitioning between roan and sable, and how they avoid interspecific competition in Waterberg Plateau.

CHAPTER 6

6. CONCLUSIONS AND RECOMMENTATIONS

6.1 Conclusions

This study aimed to improve the current knowledge about the population dynamics and factors influencing trends of roan and sable population abundance over a period of 44 years and their spatial distribution in the Waterberg Plateau with the intentions of providing scientifically-based recommendations for the conservation and population recovery of these rare antelope species. It revealed that the roan and sable populations fluctuated during the 44 years with two significant points of change in each population. The observed population growth trajectories were positively influenced by annual rainfall and the management actions, the occasional auctioning, and introduction. Inversely, these population growths were negatively influenced by the low-lagged rainfall and the increase of the buffalo population size. The study proposes that the negative impact caused by low-lagged rainfall was through reducing resource availability and potentially an associated reduction in forage nutritional values. Further, that the impact from the substantial increase of the buffalo population size place an increasing grazing pressure on food resources. Together, these drivers ultimately lead to the observed low production rate, caused by negative to zero growth rates. As such, roan and sable population decline was primarily driven by an interaction between low-lagged rainfall and buffalo.

Additionally, the seasonal detection probability and occupancy of roan and sable are strongly associated with the interaction between species, sites with high forage (high NDVI values), presence of waterholes, and low levels of predation risk. Although species activity patterns were similar there was spatial segregation between the antelopes. Further, there is an indication that the two groups of species likely occur independently of one another. This suggests that competition and facilitation are unlikely drivers of antelope occurrence, but rather that these sympatric species co-exist through the segregation in the use of food and waterhole resources. Moreover, that these two species appear to have different strategies to deal with drastic seasonal changes and environmental factors as sable occurred more on sites with higher forage values and where waterhole was present irrespective of the season while avoiding areas occupied by roan.

6.2 Recommendations

The next logical step after the identification of the potential causes suppressing a positive population growth and spatial distribution of roan and sable in the Waterberg Plateau is to implement effective adaptive managements that can halt the suppression and propel the population to recovery and ensure a suitable environment available for the species. This suppression is likely to be caused by the increasing buffalo population size and low lagged rainfall. The following recommendations are made based on these findings. First, it is recommended that there is a need to determine the carrying capacity of the park as this will help managers to guide and regulate the population sizes of species within the park. This in turn will reduce competition and habitat degradation. Carrying capacity is one of the upper limits for the size of the population within a given habitat (Kimanzi, 2011).

Second, it is recommended that the process of identifying and selecting potential sites for introductions takes into consideration these species' present-day and future environmental envelopes (IUCN/SSC, 2013). This is because population suppression is likely to be caused by the average lagged rainfall below 400 mm isohyet. Information for such assessments can be obtained by measuring key climate parameters (e.g. temperature, rainfall). Assessment of any translocation proposal should include identification of potential benefits and potential negative impacts, covering ecological and social aspects (e.g. matrilocal species). The output of this exercise should then be used to model impacts of climate change on species climate environment to identify future locations with suitable habitat.

Third, it is recommended that genetic analysis studies be conducted to determine the level of inbreeding if any, and implement a genetic management system similar to that used to monitor white rhino (*Ceratotherium simum simum*) lineages in Namibia (Guerier, Bishop, Crawford, Schmidt-Kuntzel, & Stratford, 2012). This recommendation is based on these species' demographic history particularly their persistence at low population sizes which could have lead to inbreeding despite the occasional introduction and auction of individuals. This is likely because the risk of inbreeding is often associated with small, isolated populations (Alpers, Vuuren, Arctander, & Robinson, 2004; Frankham, 2005). Furthermore, this risk is exacerbated in the target species given their polygamous mating system (Wyk, et al., 2019). The successful establishment of translocated populations often depends on the release of individuals in natural sex ratios and age classes (Ginsberg & Milner-Gulland, 1994; IUCN/SSC, 2013). This success can be enhanced by either increasing the proportion of individuals of breeding age or by favouring the proportion of juveniles.

Fourth, future studies need to assess the relationship between NDVI indices and the peak in faecal crude protein to represent temporal variability in the availability of high-quality vegetation (Hamel, Garel, Festa-Bianchet, Gaillard, & Côté, 2009). Managers should monitor the diet of these species to examine what characteristics of food items affect feeding site selection. Mostly, grass species preferences should be assessed and nutrient content from droppings should be evaluated to compare the seasonal diet quality availability. This is because the population abundance distribution of roan and sable changes according to seasonal fluctuations in NDVI values (i.e. food resource distribution).

Fifth, the study recommends that research needs to be conducted to assess predator diet, for instance through scat analysis, to determine if sable and roan are in fact being preyed upon. While in this study predation risk was included as a covariate, a more direct measure of the threat posed by predation is a determination of the proportion that roan and sable made of leopard and other predators diet across seasons (Hayward, et al., 2006) and the abundance or density of predators.

Sixth, while in this study population trends were accurately modeled from aerial count data, it is recommended that alternative surveying methods of estimating abundance and density be trialed to monitor these species populations. These may include line/strip counts, camera trapping, and spoor tracking. Applying these methods will allow for the collection of complementary data about the ecology and population structure which may not be obtained from aerial counts. The aerial counts have a significant limitation as they do not account for imperfect detection therefore false-negative errors are not accounted for or estimate effective population diversity.

Lastly, the study recommends that MEFT implements a permanent computer-based database system for data storage that can be readily accessible in a standardized format with off-site file backups. A challenge encountered in this study was difficulty in accessing existing long-term data. Currently, monitoring data (e.g. game count data and research data) are kept raw unsorted or unprocessed in archives that are not long-lasting as evidenced by torn-out pages and missing data. A centralized system will also address issues related to data being captured into single computers or hard drives.

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APPENDIX 1

Table 1S Posterior estimated effect for model parameters on the roan population growth time-series with standard deviation (SD), and 95% credible intervals (CI2.5, CI97.5).

Parameter	Mean	SD	CI2.5	CI97.5
Mean population growth	-0.02	0.06	-0.13	0.09
Observation variance	0.04	0.03	0.00	0.12
Process variance	0.06	0.06	0.00	0.2
Rainfall	0.08	0.08	-0.07	0.25
Lagged rainfall	-0.03	0.25	-0.43	0.4
Introductions	0.12	0.13	-0.15	0.36
Auctions	0.00	0.14	-0.25	0.28
Buffalo population size	-0.05	0.06	-0.18	0.07

Table 2S Posterior estimated effect for model parameters on the sable population growth time-series with standard deviation (SD), and 95% credible intervals (CI2.5, CI97.5).

Parameter	Mean	SD	CI2.5	CI97.5
Mean population growth	0.00	0.08	-0.14	0.16
Observation variance	0.07	0.08	0.00	0.3
Process variance	0.17	0.12	0.00	0.45
Rainfall	0.15	0.14	-0.13	0.43
Lagged rainfall	-0.12	0.13	-0.39	0.14
Introductions	0.05	0.25	-0.45	0.52
Auctions	0.15	0.14	-0.13	0.41
Buffalo population size	-0.05	0.09	-0.24	0.14

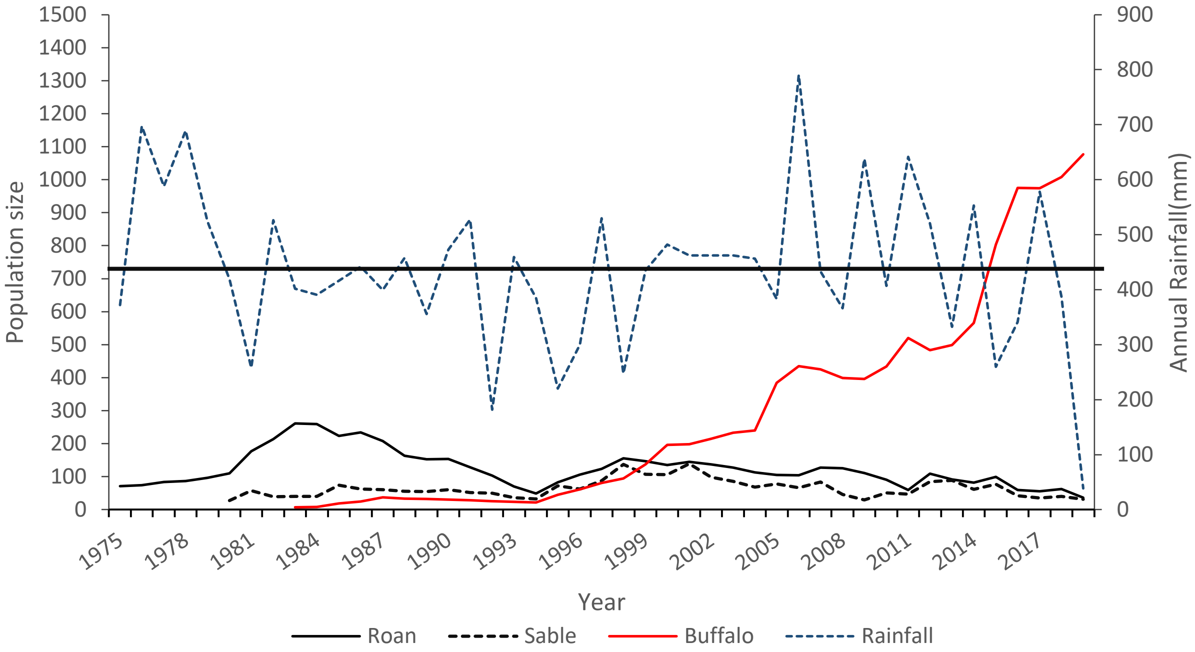
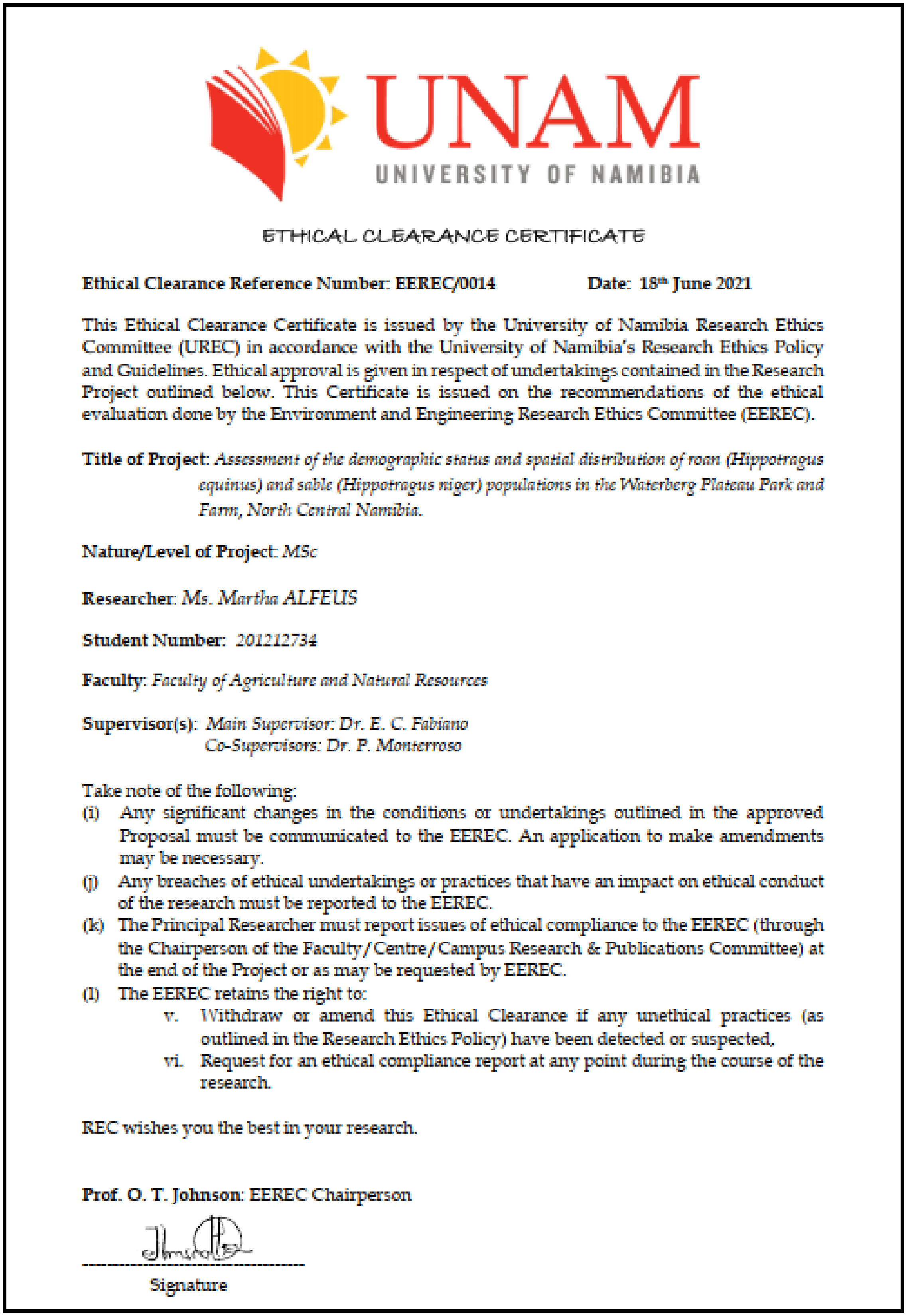


Figure 1S Yearly population size of roan, sable, and buffalo and annual average rainfall in Waterberg Plateau Park from 1975 to 2019. The solid black line indicates the average rainfall across the 44 years.

APPENDIX 2



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ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: EEREC/0014 **Date: 18th June 2021**

This Ethical Clearance Certificate is issued by the University of Namibia Research Ethics Committee (UREC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the Environment and Engineering Research Ethics Committee (EEREC).

Title of Project: *Assessment of the demographic status and spatial distribution of roan (Hippotragus equinus) and sable (Hippotragus niger) populations in the Waterberg Plateau Park and Farm, North Central Namibia.*

Nature/Level of Project: *MSc*

Researcher: *Ms. Martha ALFEUS*

Student Number: *201212734*

Faculty: *Faculty of Agriculture and Natural Resources*

Supervisor(s): *Main Supervisor: Dr. E. C. Fabiano*
Co-Supervisors: Dr. P. Monterroso

Take note of the following:

(i) Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the EEREC. An application to make amendments may be necessary.
(j) Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the EEREC.
(k) The Principal Researcher must report issues of ethical compliance to the EEREC (through the Chairperson of the Faculty/Centre/Campus Research & Publications Committee) at the end of the Project or as may be requested by EEREC.
(l) The EEREC retains the right to:
    v. Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,
    vi. Request for an ethical compliance report at any point during the course of the research.

REC wishes you the best in your research.

Prof. O. T. Johnson: EEREC Chairperson

Signature