A camera trap appraisal of mammal species richness and spatio-temporal characteristics in a private nature reserve in KwaZulu-Natal, South Africa.

by

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DECLARATION

I, Michael Samuel Henshall, declare that the contents of this thesis represents my own unaided work, and that the thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

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ABSTRACT

Globally biodiversity declined by an average of 73% between 1970 and 2022. Given the irreplaceable ecosystem services supplied by biodiversity to human populations, it is imperative that the remaining biodiversity on Earth is protected. Protected areas (PAs) have been found to be the most effective method to conserve biodiversity, with larger PAs being more impactful than smaller PAs. As the human population on Earth continues to grow, space for the proclamation of new PAs is limited, and private as well as governmental resources to adequately manage already existing PAs is insufficient. In order to best conserve remaining biodiversity it would be most effective to focus conservation efforts on Earths 35 biodiversity hotspots. Three of these hotspots occur in South Africa and vary in their threats and conservation status. Of these three hotspots, the Maputaland Pondoland-Albany hotspot (MPAh) has the greatest number of people living in it, with large portions of the area having been transformed and habitat degraded. Roughly only 25% of this hotspot still remaining in a wild, unaltered state. To ensure adequate conservation practices and management plans for PAs it is helpful to have a good understanding as to what biodiversity still remains on the PA and how the present biodiversity responds to the many anthropogenic and environmental pressures that pose a risk to the longevity and health of the PA.

One PA, within the MPAh, that is potentially to be included in a larger PA is the 11 000 ha Mawana Game Reserve (MGR). This private reserve, found in South Africa's KZN province, is made up of 85% savannah biome and around 15% grassland, one of South Africa’s most threatened biomes. Since the 1980s, after many small subsistence farms were consolidated into one larger farm, MGR has seen multiple species of medium and large herbivorous mammal (> 0.5 kg) reintroductions take place, including a herd of elephants (*Loxodonta africana*) reintroduced in 2003. To assess the current state of the medium to large mammal population on MGR a survey was conducted that used camera traps, a technology that has proven to be very useful in the assessment of mammal populations.

A four-month camera trap study was conducted on MGR over the wet season from November 2021 until March 2022. A total of 51 survey locations, spaced evenly across the landscape, using a 1.3 x 1.3 km grid, were sampled for 40 days each, with 19 and 18 camera traps moved from north to south across three separate survey blocks. A total of 29 species of medium to large mammals were observed during the survey period, while Bayesian and non-parametric estimates suggested that between 3 and 6 more species are present but went undetected. It is suggested, therefore, that a maximum of 35 medium to large mammal species occur on MGR, a number supported by the fact that 6 species detected on MGR before and since this research were not detected during the camera trap survey. The 29 species detected represents 56% of the 51 species thought to be historically present on MGR. A Bayesian analysis was performed using a hierarchical detection-based multi-species occupancy model to assess the space use of mammal species and species richness.

Ten potential predictors (covariates), - seven environmental (altitude, fire, grass biomass, heterogeneity, slope, vegetation type, visibility) - three anthropogenic (proximity to human settlement, roads and reserve boundary), were analysed to see which covariates significantly predicted mammal space use and species richness. All environmental covariates other than slope and fire were found to impact species richness. Blesbok (*Damaliscus pygargus phillipsi*) and impala (*Aepyceros melampus*) were impacted by altitude, giraffe (*Giraffa giraffa*) were impacted by fires, vervet monkeys (*Chlorocebus pygertythrus*) and bushpigs (*Potamochoerus larvatus*) were impacted by grass biomass. Giraffe, impala, plains zebra (*Equus quagga burchellii*) and black-backed jackal (*Lupulella mesomelas*) were impacted by heterogeneity, plains zebra and blesbok were both influenced by visibility. Plains zebra, blesbok, black-backed jackal, giraffe, baboons (*Papio ursinus*) and vervet monkeys all showed preferences for specific vegetation types across MGR.

Impala, nyala (*Tragelaphus angasii*) and vervet monkeys were impacted by proximity to human settlements, warthogs and baboons were affected by proximity to roads

and nyala and blesbok were affected by proximity to reserve boundaries. After spatial analyses were conducted, the medium to large mammals of MGR were assessed for temporal behavioural responses to: each other, human settlements and perceived anthropogenic and predatory risks. Both warthogs and common duiker were found to be active at significantly different times of the day to each other as well as impala and nyala for duikers and impala, nyala, wildebeest (*Connochaetes taurinus*) and zebra for warthogs.

Common duiker were found to change their behavioural patterns as they got closer to human settlements, while no species were detected changing their behavioural patterns in response to varying visibility facilitated by open or closed (dense) vegetation.

This repeatable study has assisted MGR by establishing baseline data that may be used to assess the area-specific conservation and management practices and actions that may occur on the reserve in the future. This study has allowed MGR and similar small PAs in southern Africa to gain more knowledge on the anthropogenic and environmental pressures that pose a risk to the medium and large mammals present.

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DEDICATION

For my wife, Tam, who had so much faith and patience in me to complete this thesis,

To the many thousands of rangers, researchers, conservationists and others who have dedicated their lives to protecting and understanding Africa's biodiversity.

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GLOSSARY

GIS	Geographical Information Systems
HDI	Highest Density Interval
KZN	KwaZulu-Natal
M.A.S.L	Meters above sea level
MGR	Mawana Game Reserve
MPAh	Maputaland Pondoland-Albany hotspot
PA	Protected Area
Predictors	The likely cause of a certain characteristic
Species Richness	The total number of different species in a defined area
QGIS	Quantum GIS

CHAPTER ONE:

GENERAL INTRODUCTION

1.1 Introduction

Biodiversity is the variety of life on earth and refers to the genetic variety found within a single species, the variety between different species and the variety between different ecosystems on earth (Convention on Biological Diversity, 2006). Biodiversity has increasingly been found to have significant importance in sustaining ecosystems and the services that they supply to all living creatures including humans (Lohbeck *et al.,* 2016). These findings have led to biodiversity being declared as one of the nine planetary boundaries that support human life on Earth (Rockström *et al.*, 2009). Gamfeldt *et al.* (2013) found that natural systems with a higher diversity of plant life (i.e. higher biodiversity) offered more ecosystem services than areas with a lower diversity. A few of the ecosystem services nature provides that facilitate human existence include; air filtration and oxygenation (Bolund & Hunhammer, 1999), water purification (Bolund & Hunhammer, 1999; Zedler & Kercher, 2005), carbon sequestration (Diaz *et al.*, 2009), pollination (Carvalheiro *et al.*, 2010), disease control (Ostfeld & Keesing, 2000), flood prevention (Brander *et al.*, 2012), mitigation of drought impacts (Tilman & Downing, 1994) and breeding grounds for economically important wildlife (Zedler & Kercher, 2005). Not only are biodiversity-supported ecosystem services directly linked to the success of human agricultural and medicinal requirements (Young, 1999; Minns *et al.,* 2001), but studies have found that time spent in healthy natural systems leads to improved mental and physical health (Jennings & Gaither, 2015; Ma *et al.*, 2024). An ecosystem containing a higher level of biodiversity is considered to be more robust and better able to adapt to changing species compositions and environmental characteristics than ecosystems with reduced biodiversity (Chapin *et al.*, 2000). The loss of biodiversity leads to unhealthy and altered ecosystems (Worm *et al.*, 2006; Hooper *et al.*, 2012).

It is evident therefore that the more intact the biodiversity is within a landscape, the better the landscape is at resisting catastrophic changes and support human needs.

All the critical services that are obtained from healthy, diverse environments are currently threatened by the large-scale loss of biodiversity as has been documented over the past sixty years (World Wide Fund for Nature, 2024). A decrease of 73% in globally studied populations of mammals, amphibians, birds, reptiles and plants was observed between 1970 and 2022 (World Wide Fund for Nature, 2024). This loss is largely attributed to global habitat destruction, fragmentation and the over exploitation of species and their environments (Young*,* 1999; Kideghesho *et al.*, 2006; Kraus *et al*., 2010; World Wide Fund for Nature, 2024). The main sources of habitat destruction originate from the agricultural, urbanisation and mining sectors (Kideghesho *et al.*, 2006; Bodo *et al.,* 2021). Habitat destruction, loss and fragmentation have resulted in one third of the earth's systems being intensely negatively impacted (Millenium Ecosystem Assessment, 2005; Jones *et al.*, 2018) with few healthy ecosystems still occurring on the planet.

Continued degradation of the environment at the current rate may lead to the planetary boundary of biodiversity no longer being able to renew itself and entire ecosystem crashes are projected to occur (Rockström *et al.*, 2009). Ecosystem crashes of this nature will lead to a future in which basic human needs are no longer met by the Earth (Rockström *et al.*, 2009). It is essential to continue to promote the conservation and protection of biodiversity in places where it is still largely intact (Beyer *et al.,* 2019; Bodo *et al.,* 2021). Not only will this help to maintain healthy ecosystems and therefore robust, functioning and free ecosystem services, but it will also assist in directly reaching six of the seventeen Sustainable Development Goals established by the United Nations in 2015 (United Nations, 2015).

Thirty-five separate biodiversity hotspots have been identified globally (Mittermeier *et al.,* 2011). Together these 35 hotspots still hold more than 50% of the world’s endemic plant species. Historically the 35 hotspots covered 15.9% of the earth's land surface area but that has been reduced to a mere 2.3% (Gillespie *et al.,* 2012). The loss of 13.6% is primarily due to anthropogenic habitat destruction and alteration (Mittimeier *et al.,* 2011). Around 31.8% of all humans on Earth live within the space historically occupied by the 35 hotspots and the high human density poses great risk to the remaining biodiversity due to further agricultural and urban sprawl.

Of the 35 biodiversity hotspots, seven are found in Africa (Mittermeier *et al.,* 2011). More than 20% of the world's biodiversity is found on the African continent (UNEP, 2016), however, it is estimated to undergo the largest loss in proportion of suitable habitat by 2050 (Visconti *et al.,* 2011). It is therefore important that biodiversity in Africa is protected, and especially in these seven hotspots. More than half of the 54 nations in Africa are projected to double their human population size by 2050 (United Nations, 2019), with an additional one billion people estimated to be living in sub-Saharan Africa by 2050. This population increase is set to bring unprecedented challenges and pressure to the protection of the seven hotspots and other protected and unprotected natural areas. Not only will the destruction of habitats be a pressing issue in the future, but climatic models show that southern Africa will be getting warmer and drier as human induced climate change progresses, resulting in more stress on water resources and reduced food security (IPCC, 2014). An increase in heat and droughts may also have negative impacts on biodiversity and livestock dependent on a reliable water supply, possibly leading to an increase in the reliance on bushmeat poaching, especially in smaller protected areas (PA's; Loveridge *et al.,* 2020). Sub-Saharan Africa still contains some of the most viable wildlife habitats on Earth and has the most intact wild large mammal populations in the world, making the prioritisation of local conservation efforts even more important (UNEP, 2016).

Although human population numbers do play an important role in environmental degradation, it is population affluence and the levels of inequality within a society that better indicate a country's environmental situation (Mikkelson, *et al*., 2007; Marques *et al*., 2019). South Africa has been rated as one of the most economically unequal countries in the world (May, 1998; Bhorat *et al.,* 2015; McKeever, 2024) with large disparities between the rich and poor. This economic disparity has shown little sign of improving over the last few decades (Hoogeveen & Özler, 2004; Sarkodie & Adams, 2020) and increases the urgency to preserve what nature still exists.

South Africa has three of Africa's seven hotspots within its borders making South Africa one of the most biodiverse countries in the world (Convention on Biological Diversity, 2006). These three hotspots are the Cape Floristic Region, the Succulent Karoo and the Maputaland Pondoland-Albany hotspot (MPAh, Fig. 1.1). The Cape Floristic Region is regarded to be the best documented of the South African hotspots with the region's ecosystems, ecosystemic richness, services and threats well understood (Richardson *et al.,* 1996; Rebelo *et al.,* 2006; Skowno *et al.,* 2021). The Succulent Karoo is still in need of more in-depth research, although it is at a lower risk of habitat degradation and transformation compared to the MPAh and Cape Floristic Region (Biggs *et al*., 2006). The lower risk is mainly due to the low rainfall making it less suitable for agricultural purposes although overgrazing by livestock can cause severe damage to the ecosystem (Rutherford & Powrie, 2009).

The MPAh is the most intensely used hotspot in South Africa with 19 million people living within the hotspot and large areas of the landscape having been transformed into sugar cane and timber plantations, livestock grazing and urban areas (Conservation International, 2010). Only around 24% of the hotspot remains in a near pristine state and less than 8.5% of the hotspot is protected in conservation areas meaning that the rest of the majority of the near pristine area is at risk of being transformed (Conservation International, 2010). Following the Cape Floristic Region, the MPAh has the second highest number of species of special concern (threatened or endemic species; Driver *et al.*, 2005). The species of concern (including 1900 endemic plants, 3 mammals, 36 reptiles, 11 amphibians and 20 freshwater fish), have already lost more than 75% of their historic habitat (Mittermeier *et al.*, 2011).

The intactness of the MPAh natural area is very low, resulting from high levels of fragmentation and habitat degradation (Driver *et al*., 2005; Skowno *et al*., 2021; World Wide Fund for Nature, 2022), with little space in between for wild fauna to move from one area to another safely. Although small PAs are considered to be less reliable at conserving biodiversity than large areas, these small areas can increase connectivity between larger conservation areas. This is important, as it has been shown globally, that even within large PAs, animals face population declines (Craigie *et al.*, 2010). One such small to medium sized PA that could increase connectivity between other larger protected areas of the MPAh is Mawana Game Reserve (MGR; Figure. 1.1). MGR is an 11 000 ha private reserve situated in northern KwaZulu-Natal, South Africa and falls within the MPAh (Mittermeier *et al*., 2011).

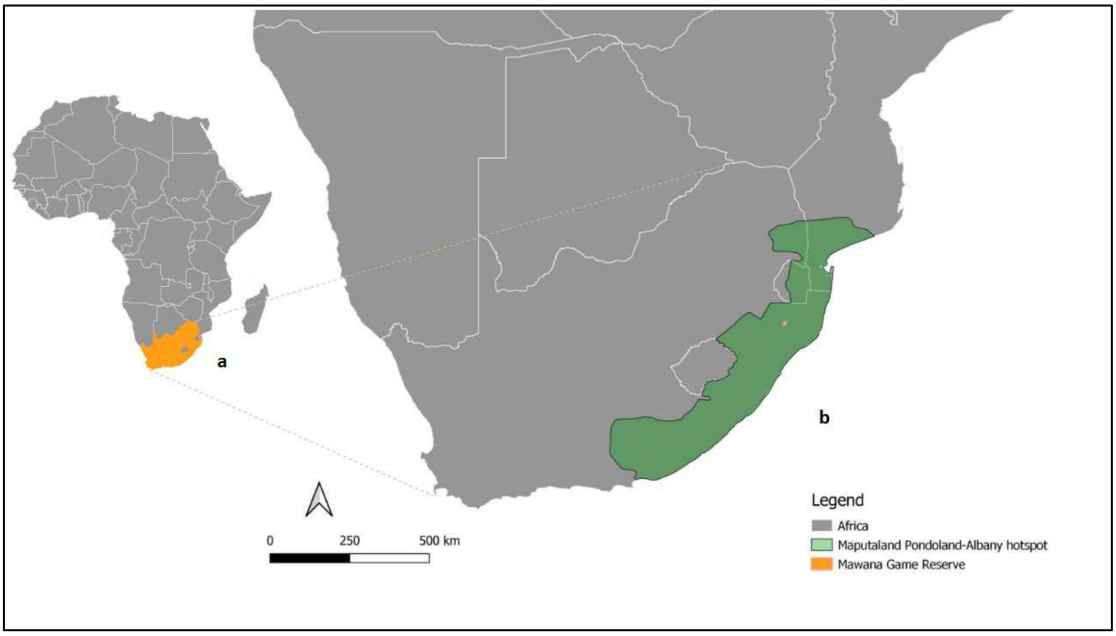

Figure 1.1: Map showing the location of (a) South Africa (orange) within Africa and (b) Mawana Game Reserve (orange) in the Maputaland Pondoland-Albany hotspot (green) within southern Africa

The reserve supports vegetation from both the savanna and grassland biomes. About 85% of the reserve encompasses the savanna biome and 15% the grassland biome, with riparian savanna vegetation found along the river edges. The grassland biome in South Africa is the biome that has been estimated to have lost the most biodiversity in the country (Biggs *et al*., 2006), and is therefore the most threatened and in need of protection wherever possible. The largest threat to this biome is habitat transformation from urban sprawl, farmlands and plantations (Driver *et al*., 2005). MGR is in the unique position of being able to play a critical role in conservation by protecting remnants of MPAh and a portion of the grassland biome, as well as by providing connectivity between other large PAs in the region (Figure 1.2).

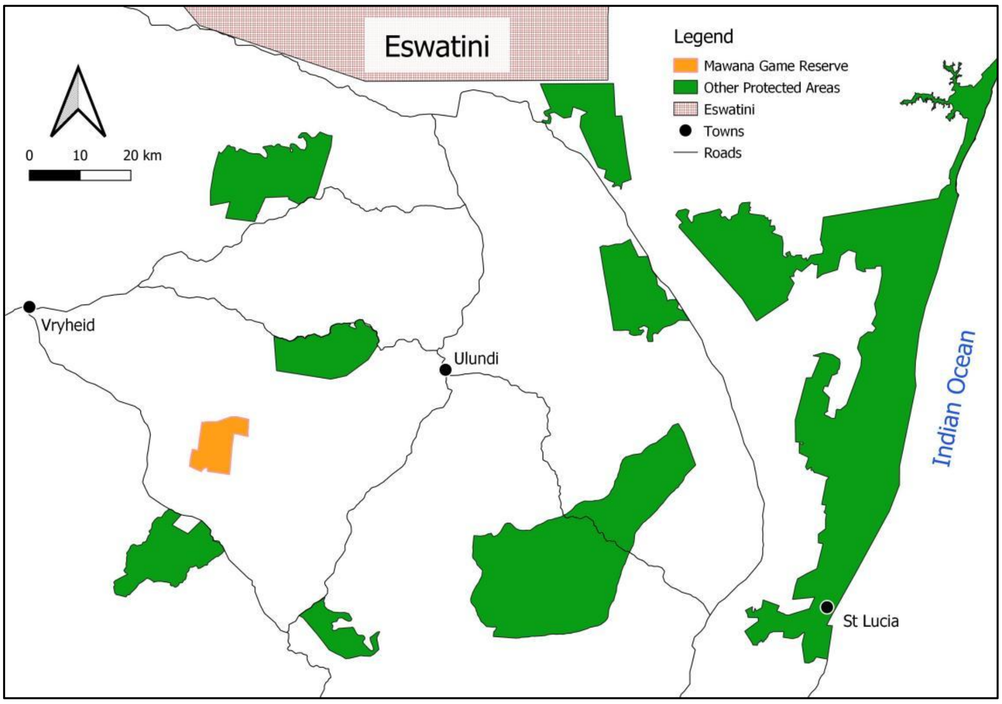

Figure 1.2: Location of Mawana Game Reserve (orange) with nearby protected areas (green) and nearby large towns within South Africa

MGR and its surrounding landscape is mostly undocumented from a biodiversity and habitat perspective and little is known about the flora and fauna of the landscape as no formal floral or faunal surveys have been completed for the reserve or surrounding area. Currently, unofficial reports account for the presence of at least 398 bird, and 35 medium and large (> 0.5 kg) mammal species (Unpublished, Reserve records). As medium and large mammals are more easily identified and observed than other taxa, they have been used as a measurement for the success and status of protected areas (Avenant, 2000; Schnetler *et al*., 2021; Nieman & Botha, 2024). Using certain charismatic mammal species as "umbrella species" also allows many areas to gain more formal and respected protection status (Rozylowicz *et al.*, 2011).

As medium and large mammals have large home-ranges and territories, they require more space for essential processes and thus require larger PAs to secure genetically viable population sizes (Ripple *et al.*, 2015). PAs large enough for viable populations of mammals are few in number and prospects to secure more such areas are slim (Patel *et al.,* 2023).

1.2 The importance of understanding mammal species richness

Mammals play a vital role in many ecosystems, providing ecological services that include; regulation of prey populations (Roemer *et al*., 2009; Ripple *et al*, 2015; Comley *et al*., 2020), seed dispersal (Matías *et al*., 2008; Rubalcava-Castillo *et al*., 2021), vegetation management (Bernes *et al*., 2018; Pringle *et al*., 2023), pollination (Goldingay *et al*., 1991; Johnson *et al*., 2011; Lacher *et al*., 2019), and the flow of energy (McNaughton *et al*., 1988; Lacher *et al*., 2019). Due to these ecological roles many mammals are considered as functionally irreplaceable (Power *et al*., 1996; Sinclair, 2003; Lacher *et al*., 2019) and good indicators of an ecosystem's health (Ritchie *et al*., 2012).

Not only do mammals hold vital ecological importance, but they also hold financial significance. Many of southern Africa’s PAs and surrounding human populations rely heavily on eco-tourism as a major source of revenue (Chiutsi *et al*., 2011). Within the eco-tourism sector, mammals and specifically “a large number and diversity of large mammals” has been cited as one of the most important attractions for tourism (Okello *et al*., 2008; Arbieu *et al*., 2018). Medium and large mammals are thus important for the financial viability of many reserves. Unfortunately, the body size and conspicuous nature of medium and large mammals often leads to these species being intensively poached and consumed in the bushmeat trade (Jerozolimsky & Peres, 2003; Becerra *et al*., 2022; Ferreira Neto, *et al*. 2023). The body parts of many medium and large mammals are also believed to have significant therapeutic abilities in traditional medicines which further leads to the persecution of these animals (Djagoun *et al*. 2018; Everatt *et al*. 2019). Compared to other regions on

Earth, mammals native to South Africa have been projected to incur the largest global loss in diversity and range by 2050 (Visconti *et al*., 2011). Intervention is needed across South Africa to reduce this projected decline. Although also facing a decline in biodiversity (Françoso *et al*., 2015; Shumba, 2019) and dependent on effective management, PAs have been found to be the best place to support and conserve biodiversity, including mammal diversity (Scholes & Biggs, 2005; Geldmann *et al*. 2013; La Saout *et al*. 2013; Rich *et al.,* 2016; Shumba, 2019). PAs will therefore be significant for future environmental, cultural and financial well-being of both people and wildlife in Africa. The success and effectiveness of a PA is intricately linked to the effective management and funding of the PA (Lindsey *et al*., 2018; Shumba, 2019; Patel *et al*., 2023). Effective management of PAs includes, among other activities, the continued monitoring of wildlife on the PA (Goodman, 2003; Françoso *et al*., 2015; Patel *et al*., 2023). For effective habitat management decisions, PAs require biodiversity monitoring to facilitate a better understanding of what exists on the PA and to monitor the success or failure of current and future management actions (Fuller, *et al*, 2016). Due to poor management, and a lack of capacity and budget, many of South Africa's PAs are ineffectively managed (Shumba, 2019; Patel *et al*., 2023), and little to no biodiversity monitoring is done. Understanding the mammal composition and diversity of an area is crucial to gauge the health of the studied system and how it functions (Kerley *et al*. 2003; Ordeñana *et al*. 2010; Lacher *et al*. 2019).

One of the more common and widely used methods describing an area's species composition is through the metric of species richness - the total number of different species found in a defined area (Chao & Chiu, 2016). Species richness has been used as the simplest method to assess and monitor biodiversity (Brown *et al.,* 2007). Both environmental and anthropogenic factors play a role in the distribution of species and thus species richness patterns (Torres-Romero & Olalla-Tárraga, 2014; Ferreira Neto *et al.,* 2023). Being able to easily and continuously repeat species richness studies will give a good indication of the effectiveness of a PA's management and conservation actions.

1.3 Understanding predictors of species richness and space use patterns of medium and large mammal species

Having a species richness list is important for monitoring purposes (Brown *et al.,* 2007), however, that alone is not enough to understand what factors may be influencing the decrease or increase of a species. For successful conservation management actions, it is essential for us to have an understanding of how animals respond to varying environmental and anthropogenic pressures.

MGR is partially fenced and surrounded by varying land use types such as peri-urban areas, crop farms, *Pinus spp.* plantations, intensive cattle farms and low-use communal livestock grazing areas. Each of these different land uses brings a unique set of circumstances and associated impacts that need to be understood and mitigated. Some sections of MGR, such as the northern boundary, are fenced and bordered by densely populated human settlements. The southern side of the reserve has sections with few standing fences and are bordered by communal grazing areas followed by sparsely populated human settlements further south. Within MGR poaching, hunting, wood harvesting and fishing still occurs (pers obs). How the surrounding land use practices as well as reserve infrastructure affect the space use of medium and large mammals within the reserve is unknown.

MGR is a heterogeneous environment with varying topography, soil types and hydrology along with multiple associated vegetation types and structures, all factors that influence mammals species richness patterns (Andrews & O'Brien, 2000; Ramesh *et al.,* 2016; Ferreira Neto *et al.,* 2021; Reece *et al.,* 2023).

This study looked at both environmental and anthropogenic predictors, to uncover area-specific ecological information and allow for appropriate conservation actions. Gaining space-use knowledge is important to inform sound management practices for MGR, and other small-medium protected areas facing similar challenges.

1.3.1 Environmental Predictors

Environmental factors predominantly known to influence mammal space use include vegetation type, hydrology and primary production (Torres-Romero & Olalla-Tárraga, 2014; Ramesh *et al.,* 2016; Nieman & Botha, 2024), but landscape features such as altitude, slope and vegetation cover are also known to play a role in mammal space use (Reece, 2020; Nieman & Botha, 2024).

Topographical landscape features

Three topographical landscape features that have been found to influence mammal species space use are altitude, slope and terrain ruggedness (Ahumada *et al.,* 2013; Reece *et al.,* 2023; Onditi *et al.,* 2023). Globally, biodiversity has been found to decrease as altitude increases (Lomolino, 2001; McCain & Grytnes, 2010), possibly owing to a reduction in ambient temperature and available oxygen (International Society for Mountain Medicine, 2001). Some species, however, have been found to be more abundant at higher altitudes than others (Ramesh *et al.,* 2016), and may be adapted to dealing with decreased temperatures and oxygen. Most past research has, however, focused on small mammal communities (Bond *et al.,* 1980; Kok *et al.,* 2012) with little information pertaining to medium and large mammals at high altitudes. High altitudes have been found to also support a dominance of grass species and other annual bulbous plants over tree and shrub species (Sieben *et al.,* 2010), resulting in a greater likelihood of grazers and less likelihood of browsers or animals preferring dense cover to be found at high altitudes.

The degree of slope also determines mammal space use, some mammals, such as eland (*Taurotragus oryx*; Marshal *et al.,* 2020) and elephants (*Loxodonta africana;* Nellemann *et al.,* 2002) prefer less steep slopes for ease of movement and access to suitable resources. Mlambo *et al.* (2024), however, found that elephants, in Hwange, make use of steeper slopes more in the wet season, when resources such as water and forage are abundant, as the need to preserve energy, by using flatter areas, is reduced. Mammals such as leopards (*Panthera pardus*), make use of slope for hunting purposes (McManus *et al.,* 2022) while animals like baboons (*Papio ursinus*) and mountain zebra (*Equus zebra zebra)* make use of steep environments as a method to avoid predation and direct competition for resources (Novellie *et al.,* 1988*;* Marais *et al.,* 2006). As the degree of slope is also known to alter the vegetation type and structure (de Knegt *et al.,* 2011), some animals may respond to change in vegetation more than the degree of slope.

Rugged environments, with reduced mobility, offer a form of protection for prey species avoiding predators less willing to move in rugged areas, such as kudu moving to more rugged areas during the night when lions are actively hunting (Davies *et al.,* 2016a). As lions are known to avoid rugged areas, other carnivores such as African wild dogs (*Lycaon pictus*) use rugged areas to avoid encountering larger predators (Davies *et al.,* 2021). Predators such as leopards are able to move through rugged areas at ease, and use the ruggedness of a landscape to improve their ambush opportunities (Hinde *et al.,* 2023). Other mammals such as bushbuck, warthogs and duiker have been found to avoid rugged areas (Reece et al., 2023) most likely due to a lack of ease in movement and their required food resources.

Vegetation types, structure, cover and heterogeneity

Given the different metabolic requirements of mammals based on their body size, dietary requirements vary widely between species (Bell, 1971; Jarman, 1974; Owen-Smith, 1988). As the quality and type of forage changes from one vegetation type to another as well as within one vegetation type over seasons, mammal space-use and species composition is expected to change too (Lunt, 2011; Smit & Prins, 2015; Nieman & Botha, 2024). Grazing species, such as buffalo, elephant and zebra have been found to increase in areas of high grass biomass (Reece *et al.,* 2023; Nieman & Botha, 2024). Woody encroachment and a general increase in browse forage availability resulted in a greater number of browsers present in an environment, such as giraffe and kudu (Smit & Prins, 2015; Nieman & Botha, 2024).

Structure of different vegetation types leads to various cover characteristics that influence the distance at which an animal can see and be seen in its environment (Davies *et al.,* 2016b). Mammals vulnerable to predation or poaching activities, require certain cover characteristics from their environment, these species therefore, associate with either open or closed vegetation types more than another, depending on their dietary and anti-predator requirements (Burkepile *et al.,* 2013; Ramesh & Downs, 2014). Open environments are generally characterised by grasslands and would, thus, be expected to host more grazers than browsers, mixed feeders with grazing preferences, such as impala, have been found to utilise open environments to increase visibility as a predator avoidance technique and access to available grasses (Burkepile *et al.,* 2013; Reece *et al.,* 2021; Reece *et al.*, 2023; Nieman & Botha, 2024). Some mammals, particularly predators, make use of decreased visibility associated with dense vegetation cover for hunting and concealment (Welch *et al.,* 2015; Owen-Smith, 2019; Nieman & Botha, 2024). Certain species, such as plains and mountain zebra, waterbuck and slender mongooses have been found to avoid open areas to utilise optimal foraging opportunities as well as relief from the heat of the sun and cover from predators (Novellie *et al.,* 1988; Ramesh & Downs, 2014; Nieman & Botha, 2024).

Vegetation type variation leads to an increase in biodiversity, especially, among herbivorous mammals both locally and globally (Kok *et al.,* 2012; Stein *et al.,* 2015 Rich *et al.,* 2016; Regolin *et al.,* 2020; Udy *et al.,* 2020). Landscapes with greater diversity in geographical features and soil types lead to varying vegetation types and a greater richness of vertebrate species too (Stein *et al.,* 2015). The more diverse the cover and forage characteristics of an environment are, the greater the number of species able to exist in these areas.

Fire and vegetation cover

Fire frequency and intensity has been known to affect vegetation structure and quality as well as cover in a landscape (Bond *et al.,* 2005; Oluwole *et al.,* 2008; Green *et al.,* 2015; Nieman *et al.,* 2021), and thus influences mammal species composition and space use (Nieman *et al.,* 2021; Reece *et al*., 2023; Nieman & Botha, 2024). Post-fire nutrient rich regrowth of plants has been found to support a large number of southern African grazers and mixed feeders (Nieman *et al.,* 2022). Many grazers and mixed-feeders, such as blesbok, blue wildebeest, impala, plains zebra, waterbuck and warthogs, have increasingly been detected in areas burnt regularly and recently (Nieman *et al.,* 2022). Browsing species, such as bushbuck, giraffe and black rhino are more commonly detected in areas with infrequent fire regimes, as this may support their browse dietary requirements (Burkepile *et al.,* 2013; Odendaal - Holmes *et al.,* 2014; Nieman *et al.*, 2022).

Vegetation cover is reduced dramatically after a fire (Levick, *et al.,* 2009; Doherty *et al.,* 2022). Alterations to cover result in varying responses not only from herbivorous species, as detailed above, but for predators too (Geary *et al.,* 2019; Gigliotti *et al.,* 2021). Interestingly, apex predators such as lions have been found to be both positively and negatively impacted by fire in different studies (Eby *et al.,* 2012*;* Gigliotti *et al.,* 2021). Positive response to fire is most probably a response to their favoured prey species using the burned patches to a greater intensity (Gigliotti *et al.,* 2021). Avoidance of burned areas in other studies is most probably a response to the reduction of concealing vegetation, and thus predators like lions avoiding detection from prey species (Eby *et al.,* 2012; Nieman & Botha, 2024). Variable responses to fire have been found by other predators too, mainly depending on the responses from larger predators as well as their prey species preferences (Gigliotti *et al.,* 2021; Nieman *et al.* 2022*,* Nieman & Botha, 2024).

Water

The presence of surface water has been found to be one of the most important predictors of mammal species space use (Reece *et al.,* 2023). As some species are more dependent on water than others, based on their feeding strategy and biology (Esmaeili *et al.,* 2021), the presence of water will have stronger impacts on some species more than others, especially during drought periods (Redfern *et al.,* 2003;Reece *et al.,* 2023; Nieman & Botha, 2024). Nieman and Botha (2024) found that large carnivores such as, lions, leopards and spotted hyena were more likely to be found nearer to perennial rivers, while meso-carnivores, such as jackals, caracals and African wild cats were more likely to be further from rivers. Large predators may prefer to be near to water, not only for hydration purposes but also as water is a positive predictor for many prey species and thus large predator hunting opportunities. Meso-carnivores are likely, therefore, to be avoiding encountering larger predators by utilising areas further from rivers (Nieman & Botha, 2024). The influence of water in a landscape can be so strong that water has been observed to override the landscape of fear created by bushmeat hunters (Kiffner *et al.,* 2013) and artificial supply of water can change habitat structure and use across entire ecosystems (de Knegt *et al.,* 2011; Sutherland *et al.,* 2018). Due to the introduction of artificial water points across Kruger National Park, elephants have altered their use of the landscape and are now found in areas that they may have avoided in the past due to a lack of water (Purdon & van Aarde, 2017). Similar impacts may have altered space use by other water dependent species in areas across the world where water has been artificially supplied, such as nature reserves or agricultural landscapes (Sutherland *et al.,* 2018; Starik *et al.,* 2020).

1.3.2 Anthropogenic Predictors

Mammal species richness in KwaZulu-Natal has been found to be lowest in habitats with anthropogenic disturbances (Ramesh *et al.,* 2016). Biggs *et al.* (2006) identified the impact that varying anthropogenic land use activities have on indigenous organisms as the most understudied component of biodiversity in South Africa. Human related aspects such as roads, reserve boundaries and human settlements play an important role in mammal species richness and space use patterns (Gascon *et al.,* 2000; Nieman & Botha, 2024; Reece et al., 2023). Human activities and infrastructure such as hiking (Procko *et al.,* 2022), poaching (Ferreira Neto *et al.,* 2023), livestock farming (Masiaine *et al.,* 2021), fences (Xu *et al.,* 2020), roads (St-Pierre *et al.,* 2022) and settlements (Creel *et al.,* 2013) influence the way in which mammals use their environments.

Roads

Although roads have a predominantly negative impact on medium to large mammals (Fahrig & Rytwinski, 2009), species such as elephants (*Loxodonta africana*) and caracals (*Caracal caracal*) have been detected more regularly closer to roads (Nieman & Botha, 2024; Reece *et al.,* 2023). Those preferring roads are likely using roads as open, easy to use areas that allow for large distances to be covered relatively quickly (St-Pierre *et al.*, 2022). Large herbivores and predators possibly make use of roads to facilitate movement in their search for food (St-Pierre *et al.,* 2022; Nieman & Botha, 2024). Busy highways, with plentiful human traffic, have been found to increase anxiety in mammals, leading to reduced use of the surrounding area, with knock-on effects of mammal genetic and population health (Naidenko *et al.,* 2021). Mammal species have been found to use roads at times of the day when less human activity is detected on the road (Benítez-López *et al.,* 2010). Within PAs medium and large mammals are more likely to make use of game trails over roads, potentially due to the danger presented by large open spaces created by roads (Fahrig & Rytwinski, 2009; Nieman & Botha, 2024).

Reserve boundaries

The boundaries of a PA, although arbitrary man-made spaces, have been found to be avoided by many mammals species (Massey *et al.,* 2014; Rich *et al.,* 2016; Reece et al., 2023). Varying land use types and potential threats occur on the outside of a PA boundary, as well as within PAs, as fences are often permeable (Massey *et al.,* 2014). Reserve boundaries pose a threat, therefore, to mammals that could come into conflict with people or are hunted for food. Overall, biodiversity has been found to be greater further inside a PA than closer to the edges (Rich *et al.,* 2016). Anthropogenic impacts outside of reserves often lead to habitat fragmentation and thus reserve boundaries are vulnerable to invasions from exotic species and diseases introduced from domestic livestock or pets (Lacerda *et al.,* 2009). Species commonly hunted for bush meat or traditional medicines are found to occur to a lesser extent near reserve edges than in the centre of a reserve, due, mainly to the fact that they are targeted and encountered more by poachers closer to human settlements near the reserve edges (Kiffner *et al.,* 2012).

Human Settlements

Many mammals, especially large predators, have been found to be detected less, closer to human settlements (Creel *et al.,* 2013; Rich *et al.,* 2016; Nieman & Botha, 2024). A meta-analysis on the impacts of human settlements and roads on mammal species showed a reduction of up to 38% in mammal abundance within 17 km of the analysed human infrastructure (Benítez-López *et al.,* 2010). Reductions in many mammal species would be linked to the settlement-associated poaching and habitat degradation (Lamprey & Reid, 2004; Kiffner *et al.,* 2013; Bar-Massada *et al.,* 2014; Penjor *et al.,* 2022). Due to a phenomenon known as the shield-effect a decrease in mammal species near human settlements would be more pronounced for predators due to human-wildlife conflict, thus settlements may offer potentially safer areas for prey species (Rodrigues *et al.,* 2023). On the contrary, biological research stations based globally in natural areas, showed a significant increase of all biodiversity within a 5 km radius around the field site (Eppley *et al.,* 2024).

Most of South Africa's PAs are small to medium fenced areas confronted with human activity, both internally and externally, involving consumptive and non-consumptive influences (Procko *et al.,* 2022), including eco-tourism, hunting and resource harvesting. Without the ability of animals to freely move off these PAs it is important to understand the impact that human factors may have on the mammals living in these PAs.

1.4 The importance of understanding temporal activity patterns of medium and large mammals

The diel cycle is the 24-hour cycle, comprising of globally, annually-equal amounts of day light and darkness (Bennie *et al.,* 2014). Different species use this 24-hour cycle in varying ways, while some are strictly diurnal (vervet monkey, *Chlorocebus* *pygerythrus*) or nocturnal (aardvark, *Orycteropus afer*) most species are active at different times in the day, often changing seasonally to suit their energy requirements. Different variables, such as temperature, visibility and predation risk affects animals in varying ways depending on whether they are active in daylight or night time hours (Kronfeld-Schor & Dayan, 2003). Animal activity patterns are also influenced by competition and predatory threats that have been shown to change depending on the type of competitors and predators present (Macandza *et al.,* 2012; Tambling *et al.,* 2015).

To enhance coexistence and reduce interspecific competition in a world with limited natural resources, partitioning of resources is essential (Kronfeld-Schor & Dayan, 2003). Fences and habitat fragmentation geographically restrict medium and large mammals exacerbating competition for limited resources, especially between species sharing similar feeding strategies and requirements (Kronfeld-Schor & Dayan, 2003). Resource partitioning can be achieved in three different ways: trophic, spatial and temporal partitioning.

Trophic partitioning occurs when animals with similar feeding strategies utilise different prey or dietary options to avoid direct conflict with one another, such as prey sizes and species partitioned between leopards (*Panthera pardus*) and caracals (Müller *et al.,* 2022) or prey preferences of black-backed jackals and fox species (Kamler *et al.,* 2012). Certain species may be found to partition resources in one instance but not another, depending on the resource availability and other forms of competition present (van der Merwe *et al.,* 2009; Yarnell *et al., 2*013). In places where species that are traditionally apex predators may be absent or in low densities, meso-carnivores such as brown hyenas and black-backed jackals may take slightly different roles (van der Merwe *et al.,* 2009). If there is a lack of larger predators black-backed jackals are more likely to kill their own prey, potentially resulting in the larger bodied brown hyena stealing their kills, ie direct competition for resources,, as observed between brown hyenas and black-backed jackals in the Waterberg Biosphere Reserve (Ramnanan *et al.,* 2016). When larger predators are present, both jackals and hyenas have been found to have wider variety of species available as prey options and exhibit decreased competition (van der Merwe *et al.,* 2009; Yarnell *et al.,* 2013). Kleynhans *et al.* (2011) found that in a fenced reserve with limited resources, (Hluhluwe-iMfolozi Park) herbivorous mammal species partitioned grass height and quality, facilitating the co-occurrence of species that would otherwise be in direct competition.

Spatial partitioning is understood as animals avoiding each other geographically and is common among sympatric meso- and large carnivores (Hearn *et al.,* 2018; Sivy, 2018), avoiding each other while hunting to decrease the likelihood of encountering the other and sustaining potentially fatal injuries. Herds of buffalo and cattle avoid grazing near each other geographically when resources are scarce, to reduce direct competition (Zengeya *et al.,* 2015). Spatial partitioning has been found to be more important than temporal partitioning in small closed areas, specifically looking at herbivore use of grazing lawns between warthogs, impala, wildebeest and zebra (Cromsigt, 2006).

Temporal partitioning occurs when different species utilise the same food sources and space but do so at different times, whether over a 24 hour period or over seasonal changes (Kronfeld-Schor & Dayan, 2003; Hearn *et al.,* 2018). Temporal partitioning, although rare, is possible when the utilised resource is able to be renewed (Kronfeld-Schor & Dayan, 2003). Most past research has focused on temporal partitioning between sympatric mammalian carnivores (Hearn *et al*., 2018; Evers *et a*l., 2022; Welch *et al*., 2023) as well as bats (Adams & Thibault, 2006; Beilke *et al*., 2020). Among herbivores, herds of sable and buffalo have also been found to partition their foraging areas, temporally, despite almost 100% home range overlap, in order to avoid grazing in the same place at the same time (Macandza *et al.,* 2012). Temporal partitioning has also been recorded in instances such as impala, kudu, roan (Hippotragus equinus) and sable (Hippotragus niger) avoiding waterholes during the times of day in which elephants are using the waterhole (Valeix *et al*., 2007). In other studies competition around waterhole use is facilitated between livestock and wild ungulates through temporal partitioning (Valeix *et al*., 2007; Connolly *et al*., 2021).

Not only have mammals been found to influence each other temporally, but the growing human population and its associated threats to wildlife can have an influence on temporal activity too. Areas in close proximity to human settlements are likely to be perceived as potentially dangerous for mammals (Oberosler *et al.,* 2017). Understanding how mammals use their environment both spatially and temporally in response to anthropogenic activities and presence will assist future management decisions and conservation of the species found on MGR. For instance, nyala (*Tragelaphus angasii*) have been found to be the most targeted species in the KZN bushmeat trade (Pillinger, 2003; Kammer, 2006) and should thus either avoid areas used by people or possibly be more active in these areas at a time when people are less likely to use the area (Kronfeld-Schor & Dayan, 2003; Salvatori *et al.,* 2023). The influence of general outdoor activities engaged in by people, whether consumptive or non-consumptive, has been shown to deter wild mammals from using areas for time periods extending beyond just when the activity is conducted (Salvatori *et al.,* 2023; Zong *et al.,* 2023). Anthropogenic activities can thus have impacts on mammal space use patterns. Threats to biodiversity from human settlements extend beyond habitat destruction, targeted killing and resource harvesting but are also linked to invasions from exotic species, as well as environmental, noise and light pollution (Keller *et al.,* 2011; Gaston *et al.,* 2013 Doherty *et al.,* 2016; Dean *et al.,* 2019; Cirella *et al.,* 2021). Previous studies have found the presence of human settlements and associated disturbances to result in a fear-based response from wild mammals similar to responses towards predation (Oberosler *et al.,* 2017; Zong *et al.,* 2023; Salvatori *et al.,* 2023). Ciuti *et al.* (2012), however, found the landscape of fear from anthropogenic presence to override the impacts of natural predators on elk and induced more profound anti-predatory responses from the elk than natural predators did.

One such anti-predatory response observed in mammals is the use of vegetation density, resulting in varying visibility, in different ways (Burger *et al.,* 2000; Owen-Smith & Traill, 2017). Some prey species prefer more open spaces for the ease of detecting predators and increased mobility away from predators or in search of food (Burger *et al.,* 2000; Reece et al., 2021; Doherty *et al.,* 2022; Nieman & Botha, 2024). Other species prefer areas with lower visibility to avoid detection from predators or people (Doherty *et al.,* 2022). Burger *et al.* (2000) found springbok to increase their time spent being vigilant in areas with taller vegetation, thus lower visibility. Ciuti *et al.* (2012) found elk (*Cervus elaphus*) to spend longer periods of time being vigilant when further from tree cover, in the open, near human settlements. Individuals spending more time being vigilant have less time available for other essential activities, such as foraging and breeding (Higginson *et al.,* 2012) potentially resulting in fitness consequences (Scheijen *et al.,* 2021). Numerous species have been found to adapt their choice of visibility classes at different times of the day in response to their main predators' temporal activity patterns (Tambling *et al.,* 2015; Owen-Smith & Traill, 2017). Gaining an understanding of how mammals on MGR respond to the surrounding and infringing anthropogenic pressures is important to thus understand the factors impacting mammal species fitness and environmental requirements within the landscape of MGR.

In order to properly protect an area and its inhabitants, a good understanding of the areas ecological importance, threats, conservation requirements and area-specific ecological knowledge is essential (Nieman & Botha, 2024). Knowing how animals respond to one another as well as how they may respond to anthropogenic pressures is important for the design and management of a PA. As MGR and other similar PAs are relatively isolated and small in size, mammals occupying these PAs will have to and are able to share resources. Gaining more information on how and when these resources are shared will assist in making better management decisions about these resources and the wildlife using them. Gaining baseline data on temporal activity patterns by using repeatable studies, will give future management of MGR the ability to compare results from future studies and shed light on the success or failure of management decisions, such as fencing, improved anti-poaching, wildlife reintroductions or the further development of tourist facilities.

1.5 Methods of assessing species richness and spatio-temporal activity patterns for medium and large mammal species

Camera trapping

Many methods exist to survey species richness of mammals in a specified area, such as pit-fall and Sherman traps for small mammals and other small vertebrates and invertebrates (Dizney *et al.,* 2008; Costa-Silva *et al*., 2019). Scat and track observations can be used for censusing elusive, shy and nocturnal medium and large mammal species (Martinoli *et al*., 2004; Suárez-Tangil & Rodríguez, 2021). Walking, driving, road or flying transects work well for large, conspicuous mammals over large distances and in big PAs (de Thoisy *et al*., 2008; Munari *et al.,* 2011; Bakala & Mekonen, 2020; Suárez-Tangil & Rodríguez, 2021). Previously mentioned methods have limitations, such as observer bias, project costs and difficulties in certain terrains when it comes to assessing mammal species richness, predictors and temporal activity patterns (Munari *et al.,* 2011; Roberts, 2011; Apps & McNutt, 2018; Suárez-Tangil & Rodríguez, 2021). Although medium and large mammals can be detected by walking, driving, road and aerial surveys (Plumptre, 2000; Martinoli *et al*., 2004; Gaidet-Drapier *et al*., 2006; Schlossberg *et al.,* 2016; Fraschini, 2024) these methods may miss elusive, shy and nocturnal species (Munari *et al.,* 2011; Suraci *et al*., 2021). Nocturnal and shy species can be accounted for through the analyses of scat and spoor, however, this is a physically demanding method that also requires a certain level of skill for accurate data collection.

Camera trap technology assists in the detection of elusive, shy and nocturnal species as well as the more common, diurnal and less shy animals through passive, constant monitoring (Kelly, 2008; Pettorelli *et al*., 2009; Apps & McNut, 2018; Cordier *et al.,* 2022). As technology and artificial intelligence advance, the use of camera traps for detecting species richness has increased as the collection and analysis of data becomes easier and more reliable (Apps & McNutt, 2018; Blount *et al*., 2021; Cordier *et al.,* 2022; Nieman & Botha, 2024; Barta, 2024). Due to the nocturnal and shy nature of many mammals, especially those in areas with detrimental human influences (Suraci *et al*., 2021), passive monitoring systems such as the use of camera traps is important to assist in the detection of species that may otherwise avoid an observer (Suraci *et al*., 2021; Fraschini, 2024). Camera trap technology offers a relatively cost-effective, easily replicable and low effort method to study medium to large mammals over a long time period (Wearn & Glover-Kapfer, 2019; Reece *et al.,* 2023; Fraschini, 2024). While camera traps have, in recent decades, been used predominantly for the monitoring of predators (Wearn & Glover Kapfer, 2019; Cordier *et al.,* 2022), more recently camera trap studies have shed light on the dynamics and health of entire PAs, ecosystems and animal communities (Schnetler *et al*., 2021; Nieman & Botha, 2024; Reece *et al.*, 2023).

When conducting a camera trap survey the methods used are crucial to make certain that the correct implications may be obtained (Kelly, 2008; Apps & McNutt, 2018; Green *et al.,* 2020; Cordier *et al.,* 2022). Camera traps should be placed in specific ways to enhance the likelihood of detecting your desired species and answering the questions that you have set out to answer (Kelly, 2008; Apps & McNutt, 2018). Camera trap studies spanning multiple habitats and vegetation types, should attempt to cover all of these habitats and vegetation types proportionately, in order to account for any habitat specialists that may occur in the surveyed area (Tobler *et al.,* 2008; Schnetler, 2020; Cordier *et al.,* 2022). Whether studies are conducting species richness inventories, occupancy assessments or targeted species specific studies, decisions such as whether cameras are placed in grid formations, non-randomly strategically or randomly across your study area are important to discern prior to placing cameras (Rovero *et al.,* 2013; Trolliet *et al.,* 2014; Apps & McNutt, 2018; Geyle *et al.,* 2020; Green *et al.,* 2020; Peral *et al.,* 2022). Surveys conducted for individually identifiable predators may need paired cameras placed in more strategic places to increase the likelihood of detection (Cordier *et al.,* 2022; Müller *et al.,* 2022). Surveys designed to assess species richness and occupancy across one or multiple PAs looking at a wide range of medium and large mammals are more inclined to place cameras using a systematic random design (grid formation), with slight alterations to camera locations based on vegetation types and practicality of placement (O'Brien, 2008; Schentler *et al,* 2021; Nieman & Botha, 2024; Reece *et al.,* 2023).

Mammal community surveys require camera trap spacing between 1 - 2 km between cameras, to ensure home ranges of multiple species are covered (Amin *et al.,* 2016). Although camera trap spacing and density is important to predetermine, camera trap efforts have been found to be more important for accurate data collection, especially the number of camera days obtained during research (Tobler *et al.,* 2008; Kays *et al.,* 2020; Schnetler, 2020). Between 30 to 60 sampling days per camera location are required for an accurate representation of species present, with the more elusive species needing longer sampling periods for detection (Si *et al.,* 2014; Kays *et al.,* 2020).

Statistical analyses - species richness and space use predictors

Camera trapping surveys result in a list of observed species (actual number of species observed during the survey) and this list is considered as the minimum number of species occupying a landscape (Ahumada *et al.,* 2011; Chao & Chiu, 2016). As animal space use is the result of multiple ecological processes and environmental pressures in a heterogeneous environment, it cannot be assumed that all species have been detected in a certain area and therefore species richness estimates are calculated too (Farnsworth *et al.,* 2002; Horne *et al.,* 2008; Chao & Chiu, 2016). Calculating species richness estimates when using camera traps can be done in multiple ways (Schnetler, 2020).

The double observer approach, as originally suggested by Cook and Jacobson (1979), can be done using a hierarchical capture - recapture model and requires two observers surveying the same space at the same time. The double observer approach works for point counts or more recently suggested for paired camera traps at each survey location in an attempt for the second observer or camera to detect any species possibly missed by the first (Cook & Jacobson, 1979; Nichols *et al.,* 2000; Nakashima *et al.,* 2022). This method works well for both species richness and population density or size for unmarked animals (Nakashima *et al.,* 2022). Having a second observing mechanism, whether person or camera, however, is costly as it requires double the number of cameras or survey effort to survey the entire area, and is less practical in long-term monitoring and large, remote areas. This survey technique may also still miss out on certain elusive, shy species that avoid human objects, such as camera traps (Rich *et al.,* 2016). Such imperfections in detection probability can be accounted for using species richness estimators that are also used when estimating richness from a single camera traps detections (Schnetler*,* 2020).

Non-parametric species richness estimates are used to estimate total species richness using the camera trap effort as well as the number of species detected over time in a survey (Schnetler *et al.,* 2021). Comprehensive species richness estimates have recently been calculated using hierarchical, detection-based, multi-species occupancy models within Bayesian frameworks, accounting for imperfect detection (Royle *et al.,* 2005; Kery & Royle, 2008; Tobler *et al.,* 2008; Nieman & Botha, 2024). Not only do these models give more insight into potentially missed, non-detected, species, but they also reveal how environmental and anthropogenic landscape characteristics may influence species richness or individual species habitat preferences (Horne *et al.,* 2008; Reece *et al.*, 2023; Nieman & Botha, 2024).

When conducting mammal occupancy surveys, using camera traps, it is important to note that multiple variables exist that can impact the probability of a species being detected, even if the species is present in the surveyed landscape (Royle et al., 2005; Rich *et al.,* 2016; Reece *et al.,* 2023). Although precautions can be taken in the planning and implementation phases of a camera trap survey to reduce the detection issues, appropriate statistical analyses may also be employed to account for imperfect detection (Royle *et al.,* 2005; Rich *et al.,* 2016; Amin *et al.,* 2022). For these models to work, in-field and desktop data need to be obtained for various anthropogenic and environmental characteristics (covariates) that will help us to understand mammal space use as well as account for the detection probability (detectability) of a species (Royle *et al.,* 2005; Reece *et al.,* 2023). While the environmental and anthropogenic space use predictors / variables are detailed in 1.3.1 and 1.3.2 above, the variables that influence detection probability of different species varies depending on technological, biological and environmental factors (Royle *et al.,* 2005; Horne *et al.,* 2008; Tourani *et al.,* 2020). Some species are more shy around human objects than others, and this may cause these species, although present in an area, to avoid human objects such as camera traps (Rich *et al.,* 2016), this biological response may be exaggerated in areas closer to a PA boundary as animals here may be exposed to a greater extent to negative interactions with people. Not all camera trap models and makes are the same and some may have greater range of vision or different infrared sensors impacting detection of species, ensuring that all the cameras used in a survey are the same, will assist in accounting for imperfect detection (Apps & McNutt, 2018). Environmentally, some landscape features are less conducive for detecting animals such as steep slopes that can alter the detection range of camera traps (Sultaire *et al.,* 2023), or landscape curvature that result in certain species being missed more than others (Anderson *et al.,* 2020). In recent years imperfect detection has been accounted for through multi-species occupancy models while using a Bayesian statistical approach (Rich *et al.,* 2016).

The Multi-Species Occupancy Model that was employed for the analyses of species richness and space use predictors accounted for the non-detected species by making use of augmented data (Rich *et al.,* 2016; Guillera-Arroita *et al.,* 2019). Using the capture rate of known species, up to 51 additional, unknown species were added into the analysis to extrapolate where unknown species may have been missing from the survey (Guillera-Arroita *et al.,* 2019).

One of the more common methods used to visualise species richness, as a function of sampling effort, is through the use of species accumulation curves that utilise presence and absence data and, plotted together, can visualise multiple richness estimate models at the same time, assisting with comparisons (Thompson & Withers, 2003; Ugland *et al.,* 2003; Schnetler*,* 2020). The species accumulation curve can assist in gaining knowledge on whether or not a survey effort has been sufficient (Thompson & Withers, 2003).

Statistical analyses - temporal activity patterns

Various methods exist to gain a better understanding of the patterns of how medium and large mammal species respond temporally to; each other, anthropogenic pressures and predation (Blake *et al.,* 2012; Green *et al.,* 2022). Temporal activity patterns can be identified using, among others, activity histograms and Kernel density estimates (Welch *et al.,* 2023). The resulting patterns can then be compared to one another using overlap indices (Frey *et al.,* 2017), allowing for a greater understanding of how the assessed factors influence changes in temporal activity patterns. Previous studies have used Generalised Additive Models (GAMs) to assess temporal activity patterns of animals compared within and between species (Aarts *et al.,* 2008; Beekmans *et al.,* 2010). While GAMs are very effective for large, complex datasets, generally expanding over multiple seasons (Wood, 2006; Podolski *et al.,* 2013), other analyses, such as Pearson's Chi-squared Tests are better for smaller, more simple datasets, such as two species over a single camera trap season (Nickel *et al.,* 2020; Green *et al.,* 2022).

The Coefficient of Overlap (Δ) is an index used to determine the temporal activity relationship between two species or single species in two contexts (Evers *et al.,* 2022; Welch *et al.,* 2023). The relationship can then be plotted in order to be effectively visualised (Welch *et al.,* 2023).

Analyses conducted for studies looking at spatial activity patterns and predictors generally use 30 minutes as the time to independence filter, temporal studies, however, have been found to gain more information on the abundant mammals, such as herbivores and ungulates by reducing or entirely eliminating the time to independence filter (Peral *et al.,* 2022). As changes to time to independence is a relatively recent idea and little data exists on what time to independence filters may be more appropriate for temporal studies, this study used the 30-minutes intervals, allowing for comparability to past studies conducted in other similar PAs.

1.6 Statement of the research problem

As biodiversity decreases globally, and Earth's human population and related resource requirements continue to grow resulting in less space to declare new PAs, focusing efforts into understanding and conserving the 35 global biodiversity hotspots, will lead to more effective biodiversity conservation. More local efforts need to be put into the Maputaland Pondoland-Albany hotspot, one of three hotspots found within South Africa, to ensure prolonged ecosystem functioning and services. MGR is in a unique position to be able to be part of a conservation area expansion while also acting as its own refugia for medium and large mammals. Gaining baseline data of the species richness patterns as well as the anthropogenic and environmental predictors that influence this, will be crucial in helping to understand the implications of the current and future MGR management actions. Apart from having a deeper understanding of the predictors of medium and large mammals space use, more species-specific biological information can be obtained from understanding the temporal activity patterns of medium and large mammals and how these activity patterns may change in response to anthropogenic pressures.

1.7 Study objectives

The aim of the study was to use camera traps to determine medium and large mammals’ spatial and temporal use of Mawana Game Reserve to provide a better understanding on how species richness patterns vary across this landscape and establish how competition and potential threats from predators and humans affect daily activity patterns.

The main objectives of the study were:

1. To determine the species richness of medium and large mammals on MGR.

2. To determine which environmental and anthropogenic predictors best explain medium and large mammal species richness patterns across MGR.

3. To determine how inter-species competition, variation in vegetation density and distance to human settlements affects medium and large mammals' daily activity patterns.

1.8 Structure of the thesis

The thesis consists of five chapters. Chapters three and four have been compiled to allow for independent publication in peer-reviewed journals.

Chapter Two explains geological, environmental, anthropogenic, historical and social backgrounds to MGR.

Chapter Three focuses on species richness estimates of medium and large mammals on MGR as well as the anthropogenic and environmental factors that may best predict mammal space use.

Chapter Four examines the daily temporal activity patterns of medium and large mammals on MGR, focusing on potential competition between large herbivore species and their reaction to human presence as depicted by distance from human settlements. We also investigate how visibility as affected by vegetation density alters medium and large species activity patterns.

Chapter Five is the concluding chapter which looks at the most critical findings of the study to make recommendations for management actions and points the direction for future studies in both MGR and similar isolated, medium sized PAs.

1.9 References

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CHAPTER TWO:

STUDY AREA

2.1 Introduction

The study was conducted on Mawana Game Reserve (MGR), a privately owned 110 km^2 protected area in northern KwaZulu-Natal, a province of South Africa. The reserve is located between longitudes 31°07'50.05"E and 31°14'53.70"E, and latitudes 27°59'21.48"S and 28°06'12.48"S and straddles the AbaQulusi and Ulundi local municipality boundaries. Numerous other large PAs fall within a 50 km radius of MGR, including the world famous Hluhluwe-iMfolozi Park, iThala Game Reserve and the newly established Babanango Game Reserve (Figure 2.1).

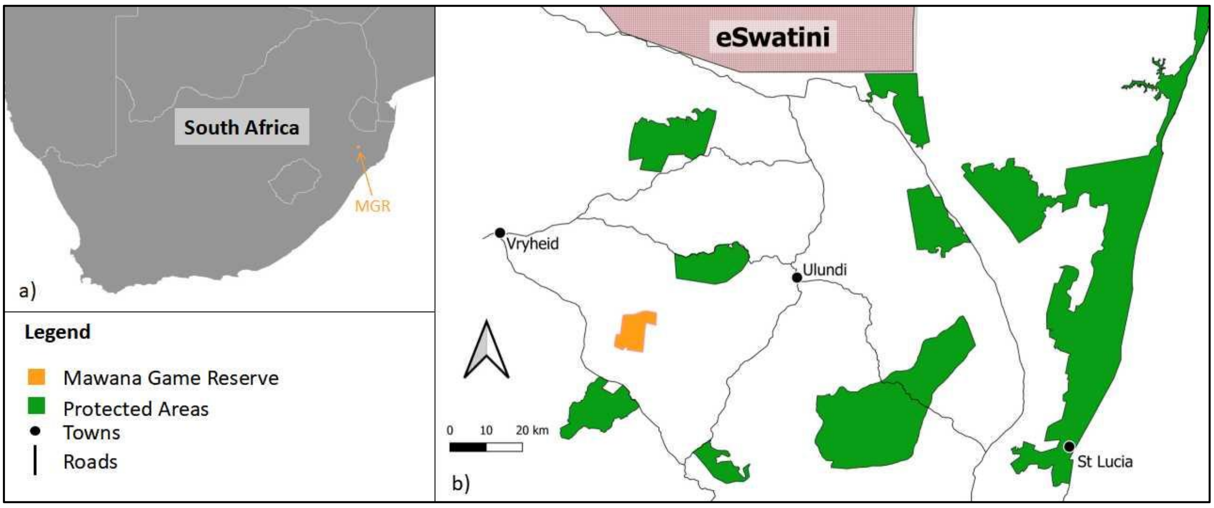

Figure 2.1: Map showing a) the location of Mawana Game Reserve (MGR) within South Africa, b) MGR in relation to other Protected Areas and towns in KwaZulu-Natal province

2.2 Historical land-use practices

Historically MGR was made up of over 30 small scale, mostly subsistence farms (per. comm. Van der Walt, 2022). The area was used for both livestock and crops such as cotton and banana fields. In 1980 the smaller farms were consolidated into a single property and managed as a unit under new ownership. At first the newly established area was used to farm cattle and some crops but in 1990 was converted into a game farm. All internal fences were removed and only a 1.2 m cattle fence remained around the property. The 1.2 m fencing was replaced by a 2.4 m high game proof fence in 2009. The breeding and live sale of game animals was the initial focus, but later biltong and trophy hunting became the primary source of income. Many native game species were reintroduced into the area including a herd of 21 elephants (*Loxodonta africana)* that were brought from Phinda Private Game Reserve in 2003. Since 2010 the north-eastern section of the farm became a research facility focusing on the study of wild Vervet monkeys (*Chlorocebus* p*ygerythrus*) by the iNkawu Vervet Project (https://inkawuvervetproject. weebly.com). Over 200 monkeys have been habituated and are monitored on a daily basis by an average of 12 local and international researchers at a time. Since 2018 commercial hunting on the reserve has been drastically reduced, and is presently no longer occurring at all. Currently the iNkawu Vervet Project is the main income stream on the property. Commercial hunting was halted in 2018 while live-game sales are maintained as a second land use. Proposals are made to include MGR into an expanded “Big 5”, 32 000 ha game reserve named Loziba Wildlife Reserve (LWR). If the proposals bear fruit LWR will be majority-owned by the surrounding communities. LWR will play a vital role in the areas’ employment and conservation opportunities and result in the long term, official protection of the area.

2.3 Climate

Based on data from the nearest South African Weather Services (SAWS) weather station in the town of Babanango (12 km to the south-west of MGR) the region can be classified as a temperate summer rainfall region, with the majority of its annual precipitation occurring between November and March (SAWS, 2022). The Babanango rainfall data correlates with rainfall data collected by the author on MGR before and during the study. The average annual precipitation of Babanango from 2011 until 2022 was 752.3 mm, 77% of the average annual total occurring between November and March (Figure 2.2). The highest average monthly rainfall from 2011 until 2022 fell in December (148 mm on average) and the lowest in July (6.8 mm on average).

The daily maximum temperature fluctuates from an average of 20.8 °C in July to 28.9 °C in January (the coolest and warmest months respectively). The daily minimum temperatures vary from 6.8 °C in July to 16.4 °C in January.

Two distinct seasonal periods can be identified. The warm, wet period occurs from December to March, and the temperature ranges between an average minimum and maximum of 15.4 °C and 27.9 °C respectively. A cool dry period occurs between April and October, with average maximum temperatures of 24.2 °C and an average minimum of 9.8 °C.

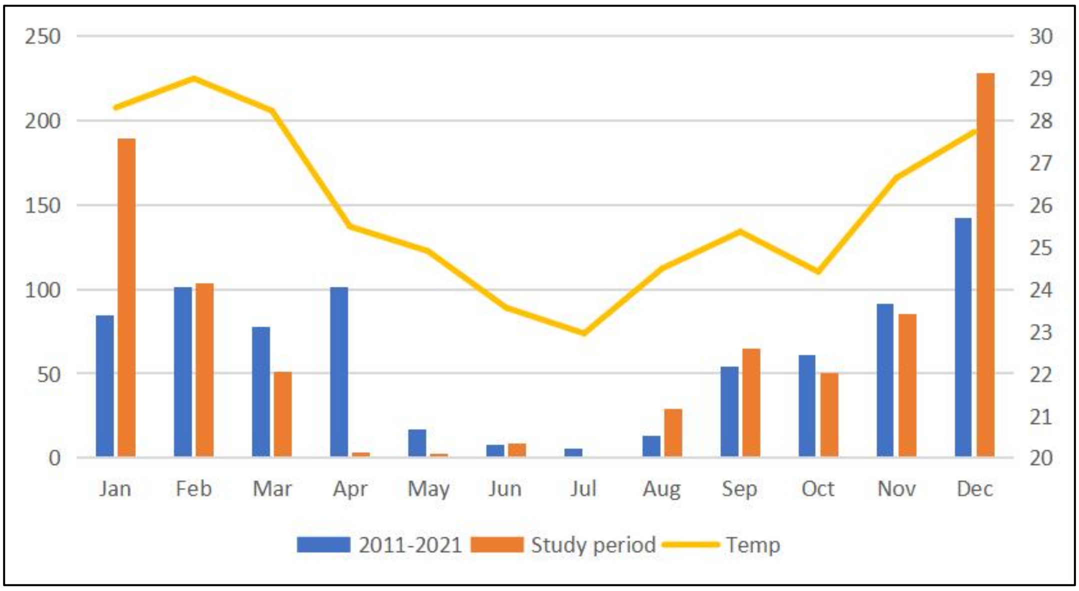

Figure 2.2: A graph showing weather data for the MGR area. The blue bars and yellow line depicts the average rainfall and average monthly maximum temperature at the Babanango weather station 12 km south west of the reserve over an 11-year period (2011-2022). The orange bars indicate the rainfall at the reserve for the months of the study (Apr 2021-Mar 2022)

During the time of the study, November 2021 until March 2022, MGR experienced higher than average monthly rainfall in December and January, nearly the same in February and less than average in March (Figure 2.2.). Frost is absent from the low lying areas of MGR, but occurs infrequently on the higher altitudes (Mucina & Rutherford, 2011).

2.4 Topography

Altitude increases from north to south in the reserve. The lowest section is in the north-east of the reserve at 599 meters above sea level (m.a.s.l.) and the highest point is Mawana Peak, at 1148 m.a.s.l. close to the southern boundary. The eastern boundary of the reserve is found along the ridge line of the Makhamasa Mountain, the highest peak of which is 1012 m.a.s.l. The landscape is highly eroded due to natural and anthropogenic influences, resulting in the central and northern sections of the reserve being deeply dissected, with undulating valley floors, erosion resistant koppies and extensive donga systems (Figure 2.3).

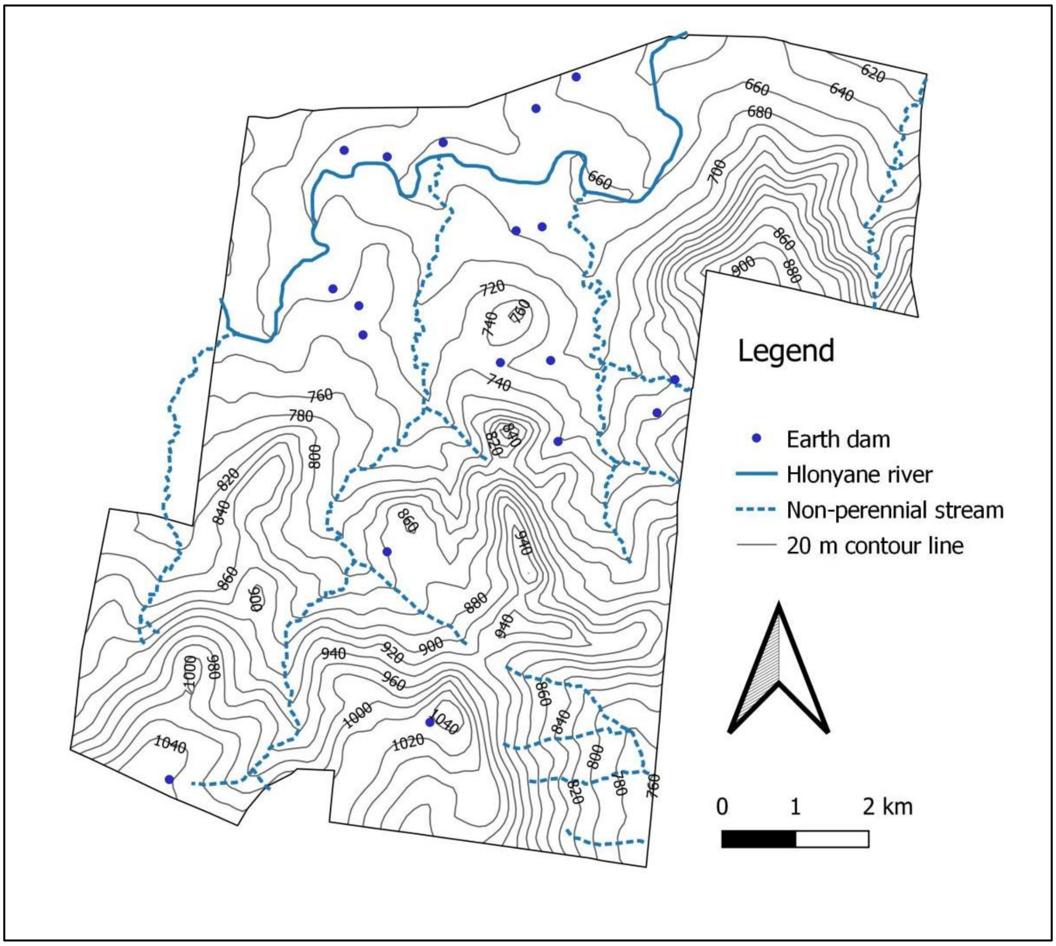

Figure 2.3: Map showing the topography and surface water drainage of MGR

2.5 Surface water drainage

The perennial Hlonyane River flows from west to east in the northern section of MGR (Figure 2.3). Two non-perennial streams, the Mkhathali and Mvuthwa run parallel from south to north through the reserve before joining the Hlonyane River. Multiple earth dams were created across the reserve while the area was used for livestock farming. Although most of these dams do not hold water all year round, they do all fill up during an average wet season. Eighteen of these dams are larger than 0.5 ha when full, and four generally hold water throughout the year. The largest of the dams is 1.4 ha in size when full.

2.6 Geology and soils

Geology

Mawana Game Reserve displays a very complex geological sequence of mostly sedimentary rock, exposed by erosion of the surrounding landscape. It includes tillite of the Dwyka Formation, with small areas of shale of the Pietermaritzburg Formation, sandstone of the Vryheid Formation and shale and quartzite of the Nsuze Group (Land Type Survey, 1986). Many sections contain dolerite dykes and sills (Land Type Survey, 1986).

Soils

This complex geological pattern gives rise to varied soil forms, including Glenrosa, Mispah, Hutton, Clovelly, Shortlands, Valsrivier, Swartland, Oakleaf and Mayo (Land Type Survey staff, 1986). More detailed descriptions of the geology and soil types associated with each vegetation type follows below.

2.7 Vegetation

MGR is found in the Maputaland Pondoland-Albany hotspot (Figure 2.4), a region of high species diversity, endemism and habitat heterogeneity (Driver *et al*., 2005; Conservation International, 2010; Mittermeier *et al*., 2011).

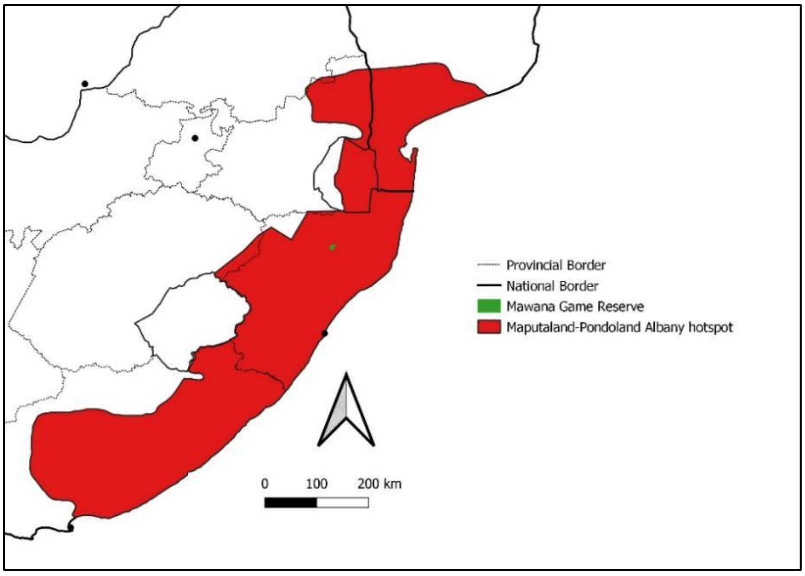

Figure 2.4: Mawana Game Reserve within the Maputaland Pondoland-Albany hotspot

Two of South Africa's nine biomes can be found in MGR, the savanna and grassland biomes (Mucina & Rutherford, 2011) and forms part of the lowveld and sub-escarpment grassland bio-regions. Five of the national vegetation types of RSA occurs within MGR (Mucina & Rutherford, 2011), namely Income Sandy Grassland, Northern KwaZulu-Natal Moist Grassland, Northern KwaZulu-Natal Shrubland, KwaZulu-Natal Highland Thornveld and Northern Zululand Sourveld. A more refined classification of the area (Figure 2.5) has recently been made by Dr. THC Mostert, a Botanist from the University of Zululand and was used in this study

The five refined vegetation units (Figure 2.5) are:

- *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands
- *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna
- *Euclea schimperi–Searsia pentheri* closed thickets
- *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands
- *Vachellia robusta–Ziziphus mucronata* riverine woodlands

The description of the five vegetation types that follows were sourced from the unpublished report of Mostert and Mostert (*in prep.*).

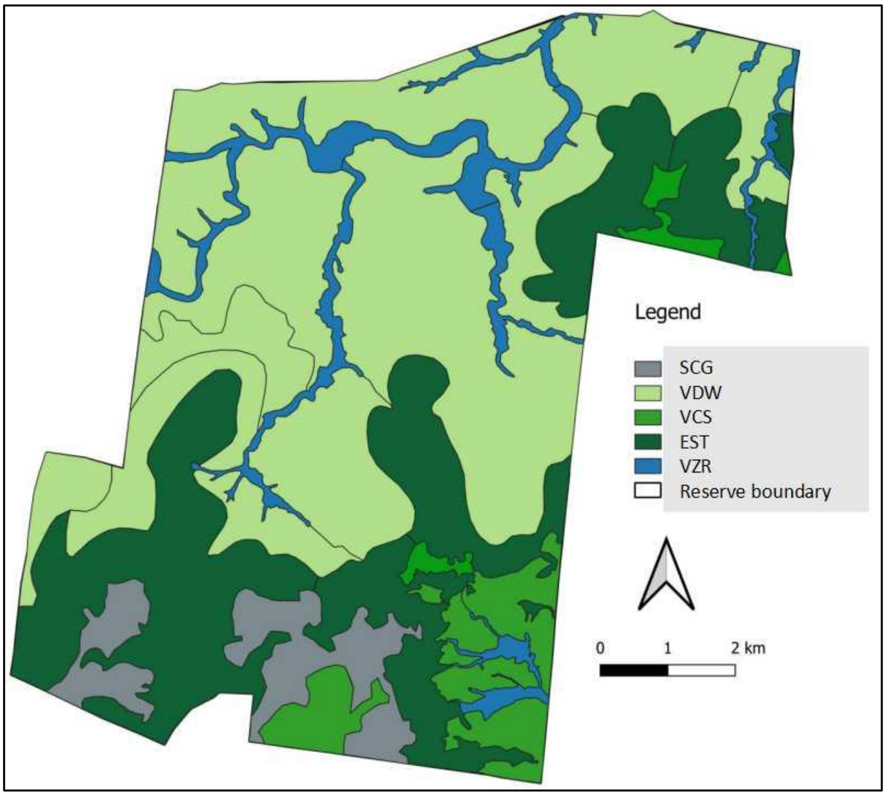

Figure 2.5: Vegetation units of Mawana Game Reserve, as mapped by Mostert & Mostert (*in prep*.) and adapted from Mucina & Rutherford (2011). SCG = Setaria sphacelata–Cymbopogon pospischilii closed grasslands; VCS = Vachellia sieberiana–Cymbopogon pospischilii sparse to dense savanna; VZR = Vachellia robusta–Ziziphus mucronata riverine woodland; EST = Euclea schimperi–Rhus pentheri closed thickets; VDW = Vachellia tortilis–Dichrostachys cinerea open to closed woodland

Setaria sphacelata–Cymbopogon pospischilii closed grasslands (SCG)

This vegetation unit is restricted to the southern sections of MGR at the highest altitudes (between 900 - 1148 m.a.s.l) on plateaus (Figure 2.5) and moderately steep slopes of <10°. Soils in this unit are shallow (< 400 mm) and derived from dolerite, underlain with sandstone.

This nutrient rich vegetation unit is a medium to tall, closed grassland. Grasses range in height from 0.4 m to 1.5 m in height, dominated by *Cymbopogon pospischilii* and *Cymbopogon excavates* (Figures 2.6 and 2.7). Due to yearly frost and frequent and intense fires, grass growth is favored over woody growth, with the exception of plants maintaining their woody growth underground (geoxylic suffrutex plants) such as *Pentanisia prunelloides,* an adaptation for a fire prone environment. Summer often brings mist to this part of MGR, creating a cooler moist environment (Mucina & Rutherford, 2011).

Figure 2.6: *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands found on plateaus above 900 m

Figure 2.7: Nutrient rich and dense grasslands, resulting in productive grazing areas

Vachellia sieberiana–Cymbopogon pospischilii sparse to dense savanna (VCS)

The VCS unit is found at lower altitudes (740 - 960 m.a.s.l.) below the SCG vegetation unit, on the lower plateaus and gentle slopes of the reserve. Soil in this unit is made from a complex rock structure, mostly sedimentary rocks. Due to the complex rock structure soil forms are also complex and include: Glenrosa, Hutton, Mispah, Clovelly, Shortlands and Swartland soil types, to name a few.

The unit has a medium to tall grass layer (0.4 m – 1.2 m) found between and underneath a sparse or open tree layer (Figure 2.8). Grasses that dominate this unit are *Cymbopogon pospischilii* and *Cymbopogon excavatus* while *Vachellia sieberianna* and *Vachellia nilotica* are the dominant tree species with *Dichrostachys cinerea* dominating the lower lying areas that border onto riparian vegetation (Figure 2.9).

Figure 2.8: *Cymbopogon pospischilii* and *C. excavatus* dominating underneath a sparse tree layer

Figure 2.9: *Vachellia nilotica* and *Dichrostachys cinerea* dominating areas bordering onto riparian zones

Euclea schimperi–Searsia pentheri closed thickets (EST)

The *Euclea schimperi–Searsia pentheri* closed thickets are associated with the steeper, stony slopes of MGR (Figure 2.10). Like VCS, these thickets grows on soil originating from a highly complex rock structure, with tillite, shale and sandstone dominating. The soil base is thus complex and includes Glenrosa, Mispah, Shortlands and Mayo types. This unit is associated with high clay contents in the soil.

The unit is short closed thickets of trees and shrubs (2 – 4m in height) dispersed in between dense medium grasses (0.3 - 1 m; Figure 2.11). Grasses dominating in this unit are *Panicum maximum* and *Panicum deustum.* The trees occurring here are *Vachellia nilotica* and *Vachellia caffra. Euclea undulata* and *Euclea schimperi* shrubs are also present in the woody layer.

Figure 2.10: *Euclea schimperi–Searsia pentheri* closed thickets found on rocky slopes

Figure 2.11: *Euclea schimperi–Searsia pentheri* closed thickets with a closed, steep thicket

Vachellia tortilis–Dichrostachys cinerea open to closed woodlands (VDW)

The *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands are found in the central and northern sections of MGR, along the undulating valley floors and koppies. The VDW vegetation unit is restricted to being between the river flood plains of VZR (below) and the steeper slopes of the EST. Due to movement of rock from higher altitudes, the soil composition is fairly complex. Soil types include Sterkspruit, Swartland, Shortlands and Oakleaf as well as Mispah in the less eroded areas. The area is easily accessible and there is therefore a history of intense ploughing and consequent degradation of the soil structure.

In areas of historical ploughing the vegetation is dominated by *Dichrostachys cinerea, Vachelia nilotica* and *Vachelia tortilis* all creating relatively low stands of thick bush with a closed canopy (Figure 2.12). Ground surfaces are either bare or dominated by herbaceous species such as *Blepharis integrifolia* and *Solanum kwebense.* The areas that escaped ploughing (Figure 2.13) have a much richer species composition and vegetation structure with *Euphorbia ingens, Berchemia zeyheri* and *Ziziphus mucronata* present at places. The ground in the unploughed areas is covered in a wider range of grasses such as *Sporobolus nitens* and *Eragrostis racemosa.*

Figure 2.12: *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands dominated by *Vachellia* spp. and *Dichrostachys cinerea* on flat sections previously ploughed

Figure 2.13: *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands seen as undulating diverse thickets in areas that escaped ploughing

Vachellia robusta–Ziziphus mucronata riverine woodlands (VZR)

Vachellia robusta–Ziziphus mucronata riverine woodlands are closely associated with the river flood plains of both the perennial and ephemeral rivers as well as, well established, deep earth dams (Figure 2.14). The underlying rock structure comprises of tillite, shale and sandstone from Dwyka, Pietermaritzburg and Vryheid Formations respectively. Soils found in the floodplains and river banks in this unit are mostly from the Oakleaf Formation.

The vegetation structure in this unit is diverse and has a tall, closed canopy up to 20 m in height (Figure 2.15). The species diversity is high and the unit can probably be subdivided into even smaller units based on the species complexity. *Ficus sycomorus, Combretum erythrophyllum* and *Schotia brachypetala* are three of a long list of tree species found in this unit. A high diversity of grasses are also found which include *Panicum maximum* and *Paspalum urvillei* along with reeds such as *Phragmites mauritianus* and the sedge *Cyperus sexangularis.*

Figure 2.14: Dense, tall growth around Earth dams and in drainage lines, as seen from above

Figure 2.15: *Vachellia robusta–Ziziphus mucronata* riverine woodlands is associated with drainage lines of all forms and diverse plant species

2.8 Fauna

Fifty-one medium to large mammal species' (> 0.5 kg) historical distribution ranges overlap with MGR, but due to agriculture and human development many of the medium to large mammal species had been extirpated from the region (Table 2.1; Skinner & Chimimba, 2005). However, during the 1990s and early 2000s many of the larger herbivorous mammals were reintroduced (per. comms. Van der Walt, 2019) and it is believed that between 35 - 40 medium to large mammal species are still present in the area

No predator reintroductions took place, and species such as the black-backed jackal (*Lupulella mesomelas*), brown (*Hyena brunnea*) and spotted hyena (*Crocuta crocuta*), serval (*Leptailurus serval*) and leopard (*Panthera pardus*) have managed to persist.

Table 2.1: List of the 52 medium to large mammals historically found on MGR. Animals in red are considered extinct in the area, while those in black are believed to have persisted in the area or were reintroduced

Name	Scientific name
Herbivore	
African Elephant	*Loxodonta Africana*
Blesbok	*Damaliscus pygargus phillipsi*
Cape Buffalo	*Syncerus caffer*
Cape Hare	*Lepus capensis*
Common Duiker	*Sylvicapra grimmia*
Natal Red Duiker	*Cephalophus natalensis*
South African Giraffe	*Giraffa giraffa giraffa*
African Savanna Hare	*Lepus microtis*
Red Hartebeest	*Alcelaphus buselaphus*
Hippopotamus	*Hippopotamus amphibius*
Impala	*Aepyceros melampus*
Klipspringer	*Oreotragus oreotragus*
Greater Kudu	*Tragelaphus strepsiceros*

Porcupine	*Hystrix africaeaustralis*
Natal Red-rock Rabbit	*Pronolagus crassicaudatus*
Mountain Reedbuck	*Redunca arundinum*
Grey Rhebok	*Pelea capreolus*
Black Rhinoceros	*Diceros bicornis*
White Rhinoceros	*Ceratotherium simum*
Steenbok	*Raphicerus campestris*
Nyala	*Tragelaphus angasii*
Warthog	*Phacohoerus aethiopicus*
Waterbuck	*Kobus ellpsiprymnus*
Blue Wildebeest	*Connochaetes taurinus*
Plains Zebra	*Equus quagga*
Carnivore	
African Civet	*Civettictis civetta*
African Leopard	*Panthera pardus*
African Wild dog	*Lyacon pictus*
Black-backed Jackal	*Lupulella mesomelas*
Brown Hyena	*Hyeanae brunea*
Cape Clawless Otter	*Aonyx capensis*
Cheetah	*Acinonyx jubatus*
Lion	*Panthera leo*
Serval	*Leptailurus serval*
Side-striped Jackal	*Lupulella adusta*
Spotted Hyena	*Crocuta crocuta*
Spotted-Necked Otter	*Hydrictis maculicollis*
Omnivore	
Aardwolf	*Proteles cristata*
African Bushpig	*Potamochoerus larvatus*
Chacma Baboon	*Papio ursinus*
Honey Badger	*Mellivora capensis*
Large spotted Genet	*Genetta tigrina*

Rock Hyrax	*Procavia capensis*
Rusty spotted Genet	*Genetta maculata*
Slender Mongoose	*Galerella sanguinea*
Thick-tailed Bushbaby	*Otolemur crassicaudatus*
Vervet Monkey	*Chlorocebus pygerythrus*
Water Mongoose	*Atilax paludinosus*
White-tailed Mongoose	*Ichneumia albicauda*
Insectivore	
Aardvark	*Orycteropus afer*
Teminck's Ground Pangolin	*Smutsia temminckii*

2.9 Fire

There is no long-term fire management plan for MGR and most areas of grassland sections (Vegetation Units 1 and 2) burn most years due to human and lightning induced fires. The majority of fires are associated with bush meat poaching incidents while runaway fires started by neighbouring livestock farmers also occurs. The reserve management tries to burn blocks where the encroachment of sickle bush (*Dichrostachys cinerea*) is perceived to be too intense for grazers and browsers to benefit from. This includes areas that are mostly within the *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands. The success of these burns are usually very low due to the low herbaceous biomass available underneath these dense canopies to drive intense fires.

Areas of steep gradients such as those found in the *Euclea schimperi– Searsia pentheri* closed thickets, burn less often, approximately every 3-4 years (per. comm. Van der Walt, 2022). Fire has not been recorded in the riparian areas (*Vachellia robusta–Ziziphus mucronata* riverine woodlands) in the last two decades, most likely due to the lack of herbaceous fuel mass at the end of the dry season within these riverine woodlands.

In the ten months of 2021 preceding the camera trap survey 1402 ha burnt in 9 independent fires (Figure 2.16). Five of these fires were uncontrolled, started outside the reserve while the remaining four were believed to be started by poaching inside of MGR. No controlled burns were started by the reserve management during this period. No fires occurred on the reserve during the study period of 1 November 2021 until 5 March 2022.

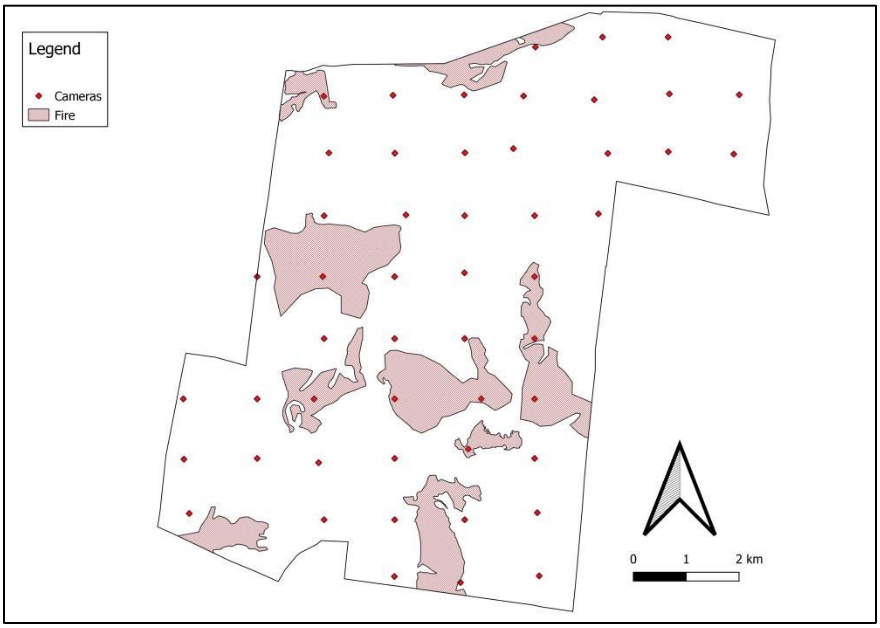

Figure 2.16: Map showing fires from 1 March 2021 until 31 March 2022 on Mawana Game Reserve with camera placements for the camera trap survey conducted after the veld fires

2.10 Infrastructure and land-use

A game proof fence of 2.4 m comprising of bonox and 2 upper 'electric' strands was erected in 2009 replacing a general 1.2 m high cattle fence, the fenced boundary of MGR is 46 km long. Due to a lack of resources for fence maintenance, unhindered movement of wildlife in and out of MGR occurs daily. Only the south-western boundary of the reserve that shares a boundary with a well-established cattle farm, has a well maintained 3 m high fence. There is no internal fencing separating the old hunting and iNkawu Vervet Project research areas (Figure 2.17). Over the past five years minimal hunting has taken place in MGR and apart from the occasional tourist there is little formal tourism or hunting infrastructure occurring on the reserve.

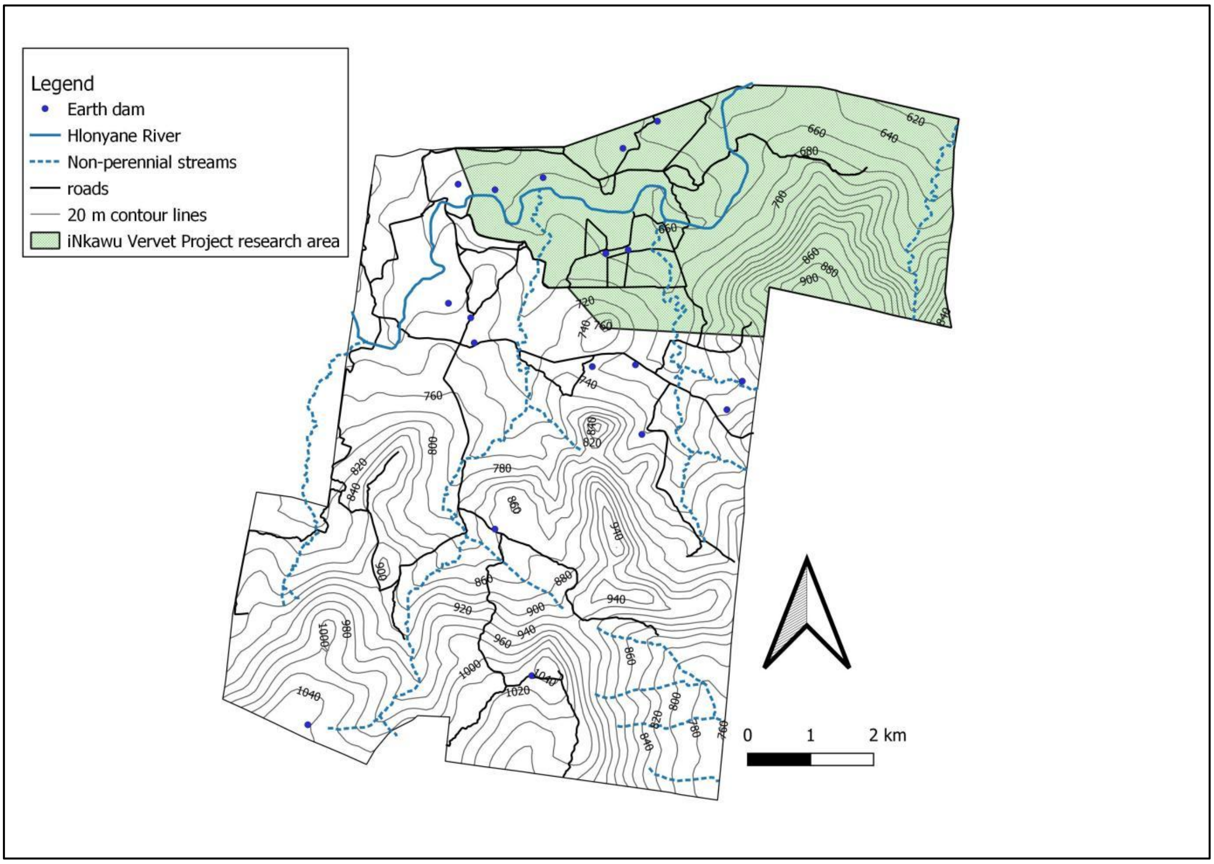

Figure 2.17: Map showing the road network on Mawana Game Reserve with the iNkawu Vervet Project research area signified in the northern and north-eastern corner of the reserve

MGR has a road network of more than 85 km. It comprises of a mixture of wide dirt roads and 4x4 tracks. No parts of the reserve are more than 3 kms from road access (Figure 2.17), although some of these roads are simple ‘twee spoor’ roads, often with little maintenance being done on them. Many of the roads in the southern section of the reserve are not used by vehicles more than once a month, and are thus often overgrown, while the northern and central roads are used daily.

The current tourist accommodation on the reserve is in the form of a single guest house that is a converted farmhouse, able to sleep up to 12 people.

2.11 Surrounding land-use

The land surrounding MGR is predominantly used for subsistence agricultural practices (Mthembu, 2021), such as livestock farming, crop production and forestry.

The intensity of farming practices vary from the predominant, small scale subsistence farming to large scale commercial operations and *Acacia* and *Pinus spp.* Plantations (Figure 2.18).

Small-scale, subsistence, free-ranging livestock and mixed-crop farming is the predominant neighbouring land use. These communal grazing areas (Figure 2.18) are largely mixed-use and generally remain in a reasonably wild state with signs of wild mammals moving in amongst the region. Cattle and goats are the most common livestock with some sheep and pigs also present. Maize (*Zea mays*) and a variety of vegetables are the subsistence crops and a few commercial lucerne (*Medicago sativa*) and cannabis farms (*Cannabis sativa*)are in the vicinity too.

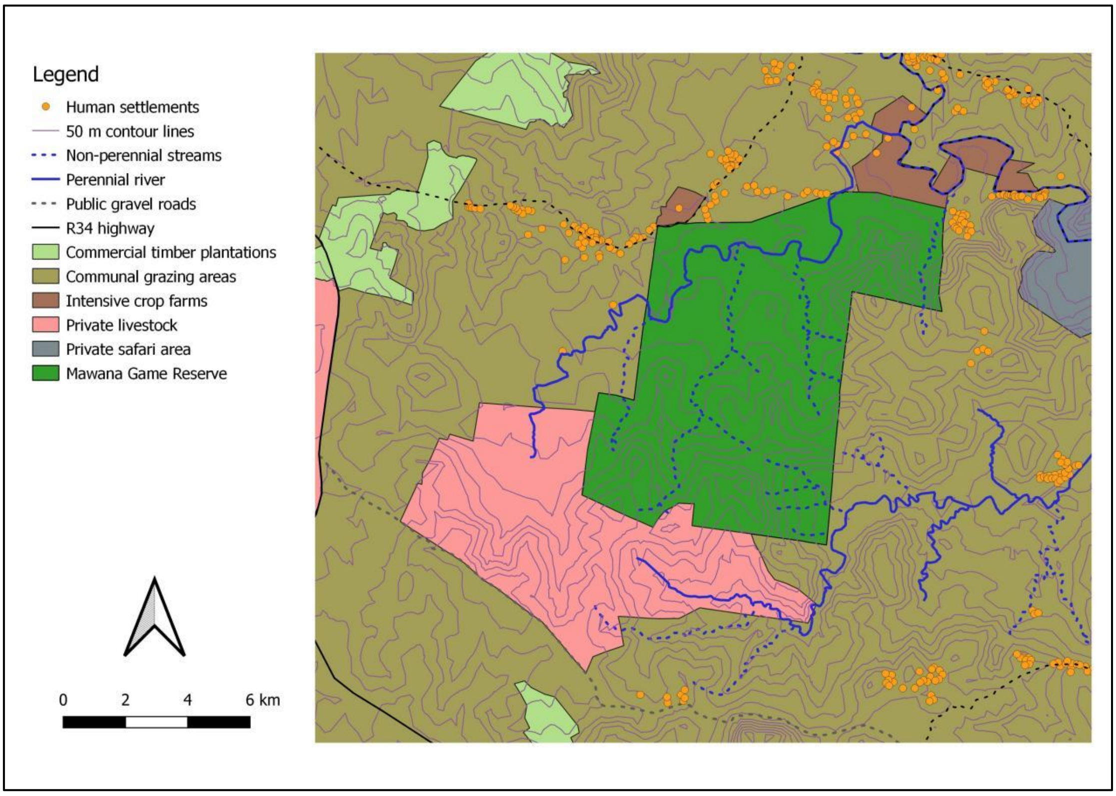

Figure 2.18: Map showing the predominant land uses surrounding Mawana Game Reserve, with communal grazing dominating the landscape

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CHAPTER THREE:

SPECIES RICHNESS AND PREDICTORS OF MEDIUM AND LARGE MAMMAL SPACE USE ON MAWANA GAME RESERVE, KWAZULU-NATAL, SOUTH AFRICA

3.1 Introduction

Mammals play a vital role in many ecosystems, providing ecological services that include; regulation of prey populations (Roemer *et al.,* 2009; Ripple *et al,* 2014; Comley *et al.*, 2020), seed dispersal (Matías *et al.,* 2008; Rubalcava-Castillo *et al.,* 2021), vegetation management (Bernes *et al.,* 2018; Pringle *et al.,* 2023), pollination (Goldingay *et al.,* 1991; Johnson *et al.,* 2011; Lacher *et al.,* 2019), and the flow of energy (McNaughton *et al.,* 1988; Lacher *et al.,* 2019). Due to these ecological roles many mammals are considered as functionally irreplaceable (Power *et al.,* 1996; Sinclair, 2003; Lacher *et al.,* 2019) and good indicators of an ecosystems health (Ritchie *et al.,* 2012).

Not only do mammals hold vital ecological importance, but they also hold financial significance as many of the southern Africa's protected areas and surrounding human populations rely heavily on eco-tourism as a major source of revenue (Chiutsi *et al.,* 2011). Within the eco-tourism sector, mammals and specifically "a large number and diversity of large mammals" has been cited as one of the most important attractions for tourism (Okello *et al.,* 2008; Arbieu *et al.,* 2018). Medium and large mammals are thus important for the financial viability of reserves. The large body size and feeding habits that make mammals popular for tourism and important in ecosystem functioning also requires mammals to have access to large areas for adequate feeding and breeding opportunities (Noonan *et al.,* 2020; Williams *et al.,* 2022).

Unfortunately, the body size and conspicuous nature of medium and large mammals often leads to these species being intensively poached and consumed in the bush meat trade (Jerozolimsky & Peres, 2003; Becerra *et al.,* 2022; de Souza Ferreira Neto, *et al.* 2023). The body parts of many medium and large mammals are also believed to have therapeutic abilities in traditional medicines which further leads to their demise (Djagoun *et al.* 2018; Everatt *et al.* 2019).

Compared to other countries mammals native to South Africa have been projected to incur the largest global loss in diversity and range by 2050 (Visconti *et al.,* 2011). Intervention is needed across South Africa to reduce the projected decline. Although also facing a decline in biodiversity (Françoso *et al.,* 2015; Shumba, 2019) and dependent on effective management, Protected Areas (PA's) have been found to be the best method to support and conserve biodiversity including mammals (Geldmann *et al.* 2013; Le Saout *et al.* 2014; Shumba, 2019). PA's will therefore be significant in the future environmental, cultural and financial well-being of all people and wildlife in Africa. The success and effectiveness of PA's is intricately linked to the effective management and funding of PA's (Lindsey *et al.,* 2018; Shumba, 2019; Patel *et al.,* 2023). Effective management of PA's includes, among other activities, the continued monitoring of wildlife on the PA (Goodman, 2003; Françoso *et al.,* 2015; Patel *et al.*, 2023). For effective habitat management decisions, PA's require biodiversity monitoring to gain better understanding of what exists on the PA and to monitor the success or failure of current and future management actions (Fuller, *et al,* 2016). Due to poor management, capacity and a lack of budget, many of South Africa's PA's are ineffectively managed (Shumba, 2019; Patel *et al.*, 2023), and little to no biodiversity monitoring is done. Understanding the mammal composition of an area is crucial in gaining a better understanding of the health of the studied system and how it functions (Kerley *et al.,* 2003; Ordeñana *et al.* 2010; Lacher *et al.* 2019).

Mawana Game Reserve (MGR) is a medium sized (11 000 ha) game reserve found in northern KwaZulu-Natal, a province of South Africa, that can make an important contribution to the conservation of South Africa's unique biodiversity. The reserve falls within the Maputaland Pondoland-Albany hotspot, one of Africa's seven biodiversity hotspots (Mittermeier *et al.,* 2011) and is earmarked to become part of the proposed larger Loziba Wildlife Reserve (Mthembu, 2021). Although MGR has had a research project studying a portion of the reserves vervet monkey (*Chlorocebus pygerythrus*) population since 2010, little is known about the mammal composition of the rest of the reserve. Little is understood about the richness of the mammals present and how they use the diverse landscape of MGR that is becoming more and more vulnerable due to increasing anthropogenic pressure from the surrounding human communities.

One of the more common and widely used methods describing an areas species composition is through the metric of species richness - the total number of different species found in a defined area (Chao & Chiu, 2016). Species richness has been used as the most simple method to assess and monitor biodiversity (Brown *et al.,* 2007). Both environmental and anthropogenic factors play a role in the distribution of species and thus species richness patterns (Torres-Romero & Olalla-Tárraga, 2014; de Souza Ferreira Neto, *et al.* 2023). Key environmental factors include vegetation type, rainfall and primary production (Torres-Romero & Olalla-Tárraga, 2014; Ramesh *et al.,* 2015; Nieman & Botha, 2024), but landscape features such as altitude, slope and hydrology also play a role (Reece, 2020; Nieman & Botha, 2024). Management related aspects such as water provision, road location and fire management have also been found to play an important role in species richness and individual species space use (Reece et al., 2023).

Vegetation preference has been cited as the strongest predictor for herbivorous mammal species space use across a landscape (Torres-Romero & Olalla-Tárraga, 2014; Ramesh *et al.,* 2015). Vegetation types vary in the quality and quantity of forage they can provide and also differ in structure and density leading to affects on visibility. Homogenous environments with a single, uniform, canopy height and structure were found to have no spatial species richness predictors (Rovero *et al.,* 2014), demonstrating the importance of a diverse landscape in hosting a wide range of mammals. Areas with a greater grass cover are more beneficial for mammal species that graze (Nieman *et al.,* 2022) while areas with a greater abundance of trees and shrubs are more beneficial to species that utilise browse forage, such as greater kudu or nyala (Dekker *et al.* 1996; O'Kane *et al.* 2013; Nieman & Botha, 2024). Although habitat diversity is important, mammal species richness has been found to be greater in areas with more grass cover than shrub cover (Soto-Shoender *et al.,* 2018). Forage diversity results in an ecosystem that can support a greater diversity of species, as has been observed that the more diverse an areas vegetation types are, the greater the species diversity that can persist, as has been found both locally and globally (Udy *et al.,* 2020; Regolin *et al.,* 2020). Changes in vegetation may also be associated with changes in altitude or slope gradient (Nadal-Romero *et al.,* 2014). Not only will slope and altitude lead to different habitat opportunities, but also result in decreases in environmental temperature (McCain & Grytnes, 2010). The degree of slope can make mobility in an environment difficult, and may result in large portions of a PA avoided by large mammals (Marshal *et al.*, 2017), resulting in a reduced species richness and abundance. Surface water availability can also be a strong predictor of especially grazing herbivore distribution across a landscape (de Boer *et al.,* 2010; Nieman & Botha, 2024), although not all mammals need regular access to open water, most will make use of it when available, resulting in increased species richness around water sources (Soykan, *et al.,* 2009; Torres-Romero & Olalla-Tárraga, 2014). Precipitation levels has been found to be, globally, one of the most important predictors of mammal species richness (Torres-Romero & Olalla-Tárraga, 2014). Certain species, such as waterbuck, have been found to have preferences for rivers over water holes (Smit *et al.,* 2007) and thus the type of water available, ie. waterhole, perennial river or non-perennial river, may result in varying species richness trends too.

Fire plays an important role in mammal space use (Burkepile *et al.,* 2016). Post-fire habitats with high quality grazing are preferred by grazing and mixed-feeding herbivores weighing less than 200 kg, such as impala and blue wildebeest (Nieman *et al.* 2022). Browsing species on the other hand have been found to prefer un-burnt areas possibly due to food availability (Burkepile *et al.,* 2013). The removal, by fire, of concealing vegetation results in greater visibility, reducing predation risk for prey species, resulting in greater abundance of prey species (Doherty *et al.,* 2022). Predators, such as leopards (*Panthera pardus*), which take advantage of concealment to stalk their prey, benefit from areas of lower visibility, and this perhaps less fire (Hinde *et al.,* 2023). Many herbivores, thus, make use of areas with greater visibility, only rarely moving into thicker areas for better forage opportunities (Burkepile *et al.,* 2013). Areas that burn less frequently generally have a greater grass biomass which has been found to both positively and negatively impact different mammal species space use (Soto-Shoender *et al.,* 2018).

Although environmental conditions and resources dictate which species can exist within a landscape the influence of anthropogenic factors are becoming increasingly important (Nieman *et al.,* 2022; Patel *et al.,* 2023). Areas exposed to greater levels of anthropogenic influence and related degradation have lower species richness than areas with greater intactness (Durán *et al.,* 2015; Ramesh *et al.,* 2015; Shumba, 2019). As Africa is experiencing the highest growth rate in human population (United Nations, 2019), it is crucial for the future of biodiversity conservation to understand what impact this will have, and manage PAs and other open areas accordingly.

Protected Areas around the world are bordered by varying land uses (Gascon *et al.,* 2000), with greater anthropogenic impacts outside than occur inside a PA. This may lead to certain animals avoiding the edges of the reserve to reduce the risks of coming into contact with human influences from outside the PA. Reserve boundaries can result in greater invasion from exotic plants and animals (Bar-Massada *et al.,* 2014), potentially resulting in an altered and unsuitable environment avoided by wildlife. Human settlements have been found to deter wildlife, due to poaching, habitat destruction and direct conflict closer to human settlements (Lamprey & Reid, 2004; Bar-Massada *et al.,* 2014; Penjor *et al.,* 2022). Species richness has been found to decline in areas modified by people (Boron *et al.,* 2019). The effects of anthropogenic presence has been found to be greater for predators, especially larger predators that may depredate livestock (Oberosler *et al*., 2017; Boron *et al*., 2019). Interestingly, biological research stations have been observed to a have a greater number and abundance of species within 5 km of the field station than surrounding areas, even within a PA (Eppley *et al.,* 2024), potentially serving as a safe haven for biodiversity, or a phenomenon known as the shield-effect.

The presence of roads allows wildlife the ability to move far at a relatively rapid speed leading to some species preferring roads over game trails (St-Pierre *et al.,* 2022). Large herbivores and predators make use of roads to facilitate movement in their search for food over a greater distance (St-Pierre *et al.,* 2022; Nieman & Botha, 2024). There is therefore a higher chance that certain animals use environments close to roads, while other species may avoid roads (Reece, 2020; Nieman & Botha, 2024), as they can present wide, open dangerous spaces.

Although difficult to accurately study, the uncontrolled, illegal, movement of people into a PA allows wildlife to be influenced by hunting through the use of domestic dogs (*Canis familiaris*) and snares, as well as other human activities such as the herding of livestock and the collection of fire wood and water from a PA (Steidl & Powell, 2006; Moore *et al.,* 2021). Human movement and the harvesting of resources on the reserve lead wildlife to being exposed to diseases such as those spread by livestock and domestic dogs (Miller *et al.*, 2013; Knobel *et al.*, 2014). Such occurrences may lead wildlife to avoiding human activities and presence as well as dogs or livestock associated with human presence. Human activity, even non-consumptive activities such as recreational hiking, have resulted in a community wide cascading effects (Suraci *et al.,* 2019; Hochreutner *et al.,* 2022). Reported cascading effects have been found to impact some species, such as large predators, negatively, through the creation of a landscape of fear, while other species, such as prey species have benefitted, potentially, from a release of predation pressure (Suraci *et al.,* 2019).

Species vary in their response to the multitude of environmental and anthropogenic factors that can affect their space use due to differences in body size, feeding requirements, vulnerability, mobility and habitat preferences (Andrade-Núñez & Aide, 2010; Nieman & Botha, 2024; Reece *et al.,* 2023). Although certain aspects such as feeding opportunities and visibility preferences may be more likely to dictate where one could find specific species (Reece *et al.,* 2023; Nieman & Botha, 2024), more diverse landscapes as well as water are found to predict greater species richness as a more productive and heterogeneous environment can support a greater number of species habitat preferences (Torres-Romero & Olalla-Tárraga, 2014). Adverse weather conditions, such as flash floods or storms, have been found to reduce an areas ability to support a diverse range of species, due to an increase in food requirement and reduction in food availability (Wang *et al.,* 2006). Adverse conditions may be more likely to impact certain vegetation types more than others, thus resulting in a greater species richness in more robust vegetation and landscape areas. Species have been found to linger for a longer duration in areas with productive vegetation types (Senft *et al.,* 1987), such behaviour may result in a higher frequency of high species richness being detected in certain areas.

Although a PA may be large, it is evident that big portions of the PA may be unsuitable habitat for certain species, and therefore possibly only a small portion of a PA is able to be occupied by a specific species (Nieman & Botha, 2024). Having a better understanding of how an area's species react to both environmental and anthropogenic factors affecting their space use, will aid in making conservation management plans more effective and reserve specific.

Camera traps can be used to gain a better understanding of not only species richness, but also the environmental and anthropogenic factors that drive individual mammal species and broader species richness patterns across landscapes (Reece *et al.*, 2023; Schnetler *et al.*, 2020; Nieman & Botha, 2024). This study aims to address the knowledge gap on MGR by establishing which mammals are present in the landscape and create a reserve-specific baseline for future studies looking at mammal species richness, while also assessing which environmental and anthropogenic factors influence mammal species richness and species space use on MGR, using a camera trap survey. A study such as this should allow future research to implement, assess and adapt related conservation concerns and strategies.

3.2 Methods

3.2.1 Study Site

The study was conducted in the 110 km^2 MGR in Northern-KZN, South Africa. Two distinct seasons, characterised by variation in temperature and rainfall, are evident: the warm wet season (November to March) and the cool dry season (April to October). Average annual rainfall is 752 mm with around 75% falling in the warm wet season. The estimated mean minimum and maximum temperatures are 6.8°C and 20.8°C in July and 16.4°C and 28.9°C in December, the coldest and warmest months respectively (SAWS, 2022).

The altitude within the reserve ranges from the highest peak at 1149 m.a.s.l. in the south to 599 m.a.s.l. in the north eastern corner. A perennial river, the Hlonyane River, runs from west to east in the northern section of the reserve, and two south-north running non-perennial tributaries connect to this in the central part of MGR (Figure 3.1). Five vegetation units are recognised on MGR (Figure 3.2). *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands (SCG) occurs on the southern high land areas while *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna (VCS) are found on the gentle slopes below the SCG. *Euclea schimperi–Searsia pentheri* closed thickets (EST) are found on the steeper, more stony, slopes of MGR. The central and northern, mostly flat, gently undulating, section of MGR is composed of the *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands (VDW) and the reserve-wide drainage lines and associated habitats are characterised by *Vachellia robusta–Ziziphus mucronata* riverine woodlands (VZR; Figure 3.2).

Thirty-two man-made earth dams are scattered across MGR, 18 of which are more than 0.5 ha in size, the largest of which is 1.4 ha in size. A network of over 85 km's of gravel roads spans the reserve (Figure 3.1). Most northern roads are kept in a workable condition and used daily, while roads in the southern section of MGR are used no more than once or twice a month and are mostly in poor condition. The reserve has a mostly permeable fence line of 46.3 km long, allowing wildlife, including elephants, to move beyond the boundaries of MGR. While the south-western corner of MGR has a well maintained fence bordering on extensive private cattle farms, the eastern and northern boundaries of MGR border on communal grazing areas with the fence flattened in some portions. The northern boundary of MGR is in close proximity to community houses, some of which are within 50 m of the fence line (Figure 3.1). The occupants mostly participate in subsistence farming of livestock and crops. For a more detailed anthropogenic and environmental description of the study site refer to Chapter two.

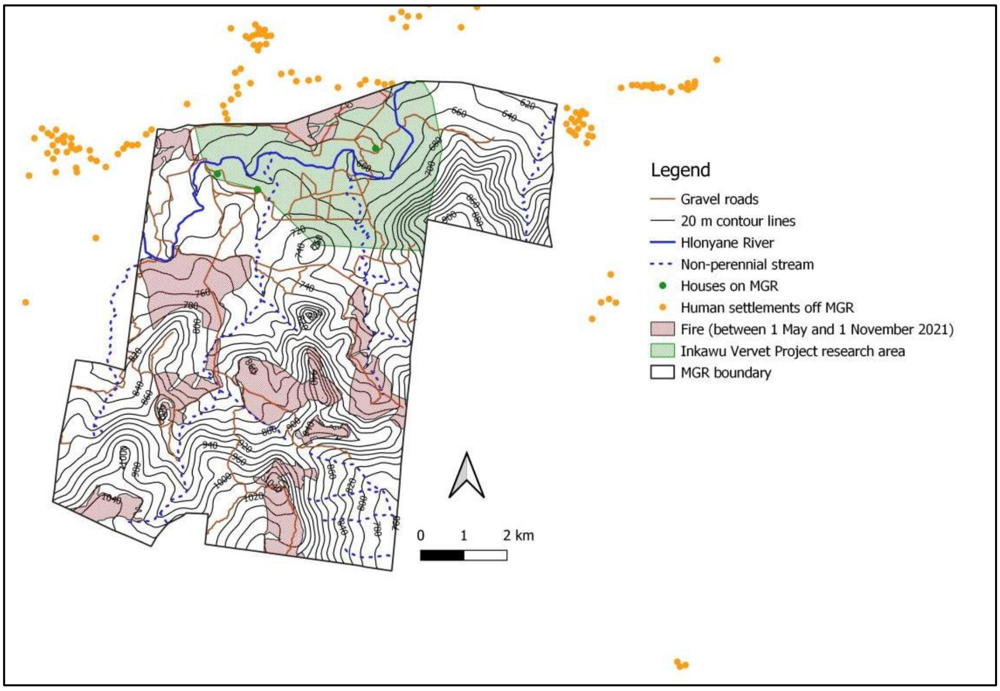

Figure 3.1: Topographical map of Mawana Game Reserve showing potential anthropogenic and environmental predictors of mammal distribution patterns

3.2.2 Survey Design

Large and medium size mammal species richness and the predictors thereof were assessed over 5 months during the wet season of November 2021 to March 2022. Fifty-one evenly spaced locations (in a 1.3 x 1.3 km grid) across MGR were systematically surveyed using 21 Bushnell model 199263C - 24MP, CORE camera traps. Only mammals of > 0.5 kg in body mass were included in the analysis with weights based on average adult male weights as stated by Skinner & Chimimba (2005).

Camera trap spacing and survey duration

A 1.3 x 1.3 km grid was overlaid onto a map of MGR using QGIS 3.1.4 (Comley *et al.,* 2020) and the center point of each grid square identified as a possible camera location, resulting in 55 camera trap locations approximately 1.3 km apart from each other. To ensure representative sampling of the five vegetation units any camera location that fell within 100 m of two different vegetation units was moved in order to cover the less represented vegetation unit (Tobler *et al.*, 2008) (Figure 3.2). Four camera locations were offset in this way. Camera availability necessitated step wise sampling, from north to south, across three survey blocks, with each block having 19, 18 and 18 cameras that were active for 40 days (Figure 3.2). Block 1 was surveyed from 01 November until 10 December 2021, block 2 was surveyed from 11 December until 20 January 2022 and block 3 was surveyed from 21 January until 02 March 2022. Cameras were serviced (memory cards and batteries) mid-way through each survey period, at 20 days.

Camera trap placement and settings

Adapting the methods of Reece (2020) and Comley *et al.* (2020) the GPS coordinates for each camera location were identified using QGIS 3.1.4 and Google Earth Engine (GEE) before going to the field. Camera location coordinates were then located in the field using a Garmin eTrex10 handheld device. Once a point was located a spiral formation was walked, away from the GPS point, until a suitable game trail was encountered, never further than 100 m away from the pre -identified coordinates (Colyn *et al.,* 2018). This trail would then be followed for up to 50 m until a suitable tree was found that allowed for a north or south facing camera (Apps & McNutt, 2018) to be placed at 40 cm above the ground (Comley *et al.,* 2020), approximately 1-2 m away from the trail. Cameras were set to a delay of 30 seconds between trigger events (Comley *et al.,* 2020) to avoid filling up memory cards and wasting battery charge from false detections, each detection was set to a burst of three images and all cameras were set to record for 24 hours with medium sensitivity. Night time images were captured using an infrared, ‘black flash’, with a mid-range setting for the flash.

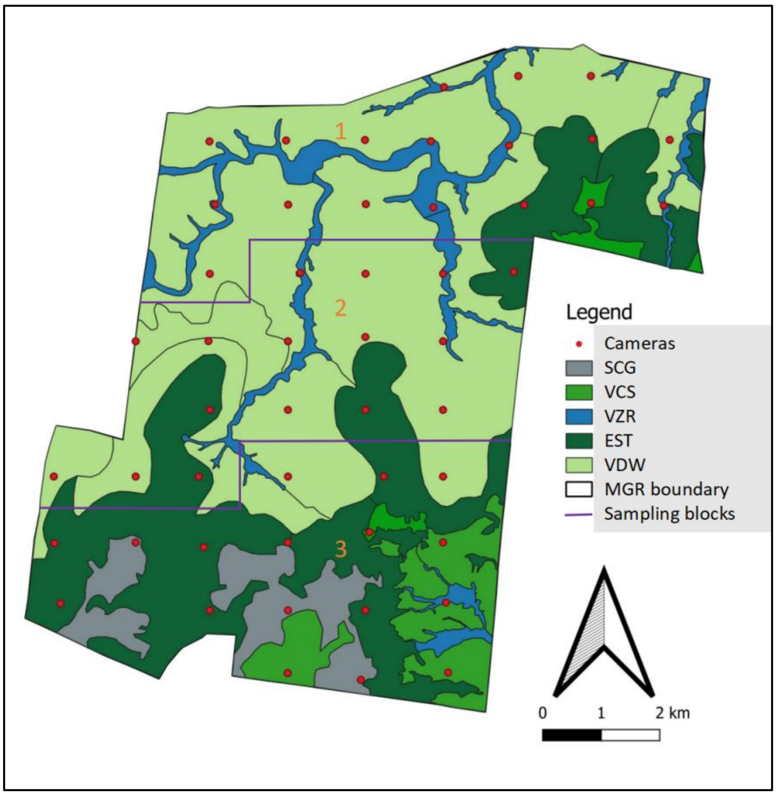

Figure 3.2: Map of Mawana Game Reserve showing the 51 camera trap locations, the reserve boundary, three separate sampling blocks indicated by the purple line and orange number and the five different vegetation types. SCG = *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands; VCS = *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna; VZR = *Vachellia robusta–Ziziphus mucronata* riverine woodland; EST = *Euclea schimperi–Searsia pentheri* closed thickets; VDW = *Vachellia tortilis–Dichrostachys cinerea* open to closed woodland

3.2.3 Predictors of mammal space use

During placement of the cameras, multiple measurements were taken at each camera location to assess which variables affects species richness and individual species detectability and space use across the landscape.

3.2.3.1 Detectability Variables

A total of four variables are hypothesised to affect the detection probability of species at any given site. The four variables measured were: distance to reserve boundary, landscape curvature, trail usage and detection distance.

- *Distance to reserve boundary*

The distance from each camera location to the nearest reserve boundary was calculated in QGIS 3.1.4, by conducting a Nearest Neighbour Analysis using the NNJoin Plugin (QGIS Development Team, 2020), measurements were stated in metres. Animals have been found to avoid human objects, such as camera traps, more when closer to reserve boundaries nearing anthropogenic disturbances, as anthropogenic presence in some places may create a landscape of fear, anthropogenic objects are avoided (Rich *et al.,* 2016; Feng *et al.,* 2021). Detection probability has been found to increase further from settlements and other anthropogenic sources (Cavada *et al.,*2019).

- *Landscape curvature*

A Digital Elevation Model (DEM) was made for MGR at a resolution of 30 x 30 m (Riley *et al.*, 1999; Reece, 2020). Each camera location was assessed by the 30 x 30 m DEM grid and reported in degrees of the slope for the grid cell in which the camera fell. Curvature was calculated for each camera point using the Terrain Analysis Tool in QGIS. The steepness, concavity and convexity of a slope can reduce the likelihood of an animal being detected by a camera (Puri *et al.,* 2015; Reece *et al.,* 2023). If an area is flat, more opportunities exist for an animal to use trails further from the camera and thus miss being detected by a camera. Cameras placed, however, on trails in steeper more rugged environments may be more likely to detect present species as an animal is forced to use the fewer trails available (Puri *et al.,* 2015). A smaller mammal, even if present, may be less likely to be detected in an area that is steep as the height difference between the cameras range and the animal is greater, if the trail is down slope of a camera (Kolowski & Forrester, 2017; Apps & McNutt, 2018; Hofmeester *et al.,* 2021).

- *Trail Usage*

Trail Usage was measured using the protocols of Reece (2020) by looking for signs of spoor and scat along the trail that the camera was placed. The trail was walked for 50 m on either side of the camera placement and if recent signs of both scat and spoor were found the trail would be considered a “3”. If no fresh signs of scat or spoor were found, but old signs existed, the trail would be considered a “2”. Trails marked as “1” had no new or old signs of usage. All trails were thus rated 1 - 3, and measured during the initial camera trap placement. As not all species use trails equally (predators more than omnivores and herbivores) it is likely that some species are detected more skewing analyses if this is not taken into account (Mann *et al.,* 2014).

- *Detection Distance*

Detection distances in front of each camera were measured by having an assistant approach the camera from three different angles - directly in front, 15 ° to the right and 15 ° to the left of the direct line. The assistant walked towards the camera from a distance of 50 m and the moment the camera detected the approaching individual identified when the person next to the camera heard the sound of the camera shutter activating. The distance at which the individual approaching the camera was at the time of activation was measured using a Bosch GLM50-27, CG Laser Rangefinder. An average detection distance, in meters, per camera trap location was calculated from the three measured distances. Vegetation cover and density as well as slope gradient can influence the distance of a cameras detection range, and thus influence the probability for some animals to be detected by certain cameras (Hay *et al.,* 2008; Palencia *et al.,* 2021).

3.2.3.2 Species Richness and Space Use predictors

Ten variables were considered to potentially influence mammal species space use and could thus influence species richness at a particular point. The 10 variables can be divided into seven environmental and three anthropogenic variables and were:

- *Altitude*

Altitude for each camera location was measured using the contour map of MGR made using Google Earth Engine (GEE) and QGIS 3.1.4. This ranged from 599 m.a.s.l to 1093 m.a.s.l.

- *Fire exposure*

For six months prior to the start of the camera trapping period (1 Nov 2021) all fires that occurred on MGR were mapped using a Garmin eTrex10 Handheld device and using GEE and QGIS these were overlaid onto a map of the camera coordinates. Camera trap locations that overlapped the mapped fires were considered burnt areas, those that did not overlap with any fires were considered unburnt areas.

- *Grass biomass*

A disk pasture meter was used to measure the grass biomass using the method of Karl and Nicholson (1987). At each camera trap location, three measurements were taken 2 m apart in each of the compass directions (N,E,S,W; 12 measurements in total). An average disk pasture meter score calculated from the twelve measurements was then assigned to each camera location.

- *Slope*

Using a 30 x 30 m resolution DEM of MGR, slope was calculated as an average in degrees around each camera location.

- *Vegetation type*

MGR is made up of two broad vegetation types, encompassing the grassland and savanna biomes. The two vegetation types were split further into five more specialized vegetation units (Mostert & Mostert, Unpublished, 2024):

Setaria sphacelata–Cymbopogon pospischilii closed grasslands
Vachellia sieberiana–Cymbopogon pospischilii sparse to dense savanna
Euclea schimperi–Searsia pentheri closed thickets
Vachellia tortilis–Dichrostachys cinerea open to closed woodlands
Vachellia robusta–Ziziphus mucronata riverine woodlands

Each camera was described as a certain vegetation unit depending on which unit it fell in.

- *Vegetation type variation*

Vegetation type variation was measured using QGIS 3.1.4 and GEE, making use of the same 1.3 x 1.3 km grid that was used for obtaining individual camera locations. The number of different vegetation units found within each cell, ranging from one to five was counted and considered as a proxy for vegetation heterogeneity in the vicinity of each camera (Torres-Romero & Olalla-Tárraga, 2014).

- *Visibility*

Visibility was measured in four directions around the camera using the methods of Hay *et al.* (2008) and Reece (2020). An assistant walked straight away from the camera and, using a range finder, the distance at which a 1 m high marker on the lower part of their body becomes obscured to the observer was measured. Visibility measurements were taken straight in front, directly behind, and at a 90° angle to the left and right of each camera. An average visibility distance per camera trap location was calculated from the four distance measurements and reported in meters.

- *Distance to reserve boundary*

The distance to nearest reserve boundary from each camera traps location was calculated using QGIS 3.1.4 NNJoin plugin and reported to the nearest meter.

- *Distance to human settlement*

Distance to nearest human settlement from each camera location was calculated in meters by plotting all human settlements on GEE and then using the QGIS 3.1.4 NNJoin plugin.

- *Distance to road*

Distance to the nearest road was measured from each camera location to the closest meter using the QGIS 3.1.4 NNJoin plugin.

3.2.4 Data analysis and modelling framework

Camera trap images were uploaded onto Camelot 1.6.14 camera trap software (Hendry & Mann, 2018). Images were then processed and only images with positive detections of medium to large mammals (> 0.5 kg; Colyn *et al*., 2018; Reece*,* 2020) were kept for further analyses. Mammals within the remaining images were identified to species level and the capture rate (number of independent captures per 100 camera days) of different species was calculated for each camera location, based on the number of days each camera was active. Multiple images of the same species from the same camera trap were considered independent detections if separated by a 30 minute interval to avoid over inflating detections due to multiple captures of the same individuals or groups passing cameras (Linkie & Ridout, 2011; Davies *et al,* 2016; Reece, 2020; Nieman & Botha, 2024). Three different species richness figures were then obtained from the data; the first being the observed species richness and the other two being estimates extrapolated by accounting for imperfect detection of species.

Observed species richness (N_{obs})

N_{obs} is calculated as the total number of different target species detected by the camera traps across MGR during the survey period. N_{obs} was calculated for each camera location as well as the reserve as a whole. N_{obs} does not take into account detectability variables and does not correct for species that may be present but not detected for various reasons. N_{obs} was recorded in a species accumulation curve displayed alongside the Jackknife and Chao estimators as described below.

Estimated species richness

Species richness estimates were calculated using the non-parametric Jacknife method and Bayesian multi-species occupancy models (Schnetler *et al.*, 2020). Jacknife estimates were calculated with non-parametric incidence based estimators using the EstimateS v 9.1.0 software, taking into account the number of camera days and time needed to detect each species. Jackknife 1, Jackknife 2 and Chao estimates were used following the methods of Schnetler *et al.* (2020) and Reece *et al.* (2021).

In order to obtain broad-scale activity patterns while accounting for imperfect detection in the camera trap survey a Bayesian analysis was performed using a hierarchical detection-based multi-species occupancy model conducted in JAGS software version 4.3.0 (Plummer, 2003; Mackenzie & Royle, 2005; Kery & Royle, 2008; Iknayan *et al.,* 2014; Rich *et al.,* 2016; Reece *et al.,* 2021; Nieman & Botha, 2024). Three Markov Chain Monte Carlo (MCMC) chains were run with 1,005,000 iterations, a burn-in of 5000 and thinning rate of 100. Trace plots were used to check chain convergence and the Gelman-Rubin statistic R-hat (Gelman *et al.,* 2004), which compares between-chain and within-chain variations. R-hat values less than 1.1 generally indicate convergence (Gelman & Hill, 2006). Data augmentation, (the artificial increase in species numbers to make a more accurate species presence estimate), was used to estimate the likely number of species that may have been missed due to imperfect detection from the camera trap survey (Royle & Dorazio, 2012; Iknayan *et al.,* 2014). The model used to estimate the predictors of species richness and individual species space use patterns was:

logit(psi[*i*, *k*]) <- b0[*k*] + bvis[*k*] * Visibility[*i*] + bgrass[*k*] * Grassbiomass[*i*] + bvegtypevar[*k*] * vegtypevar[*i*] + bfence[*k*] * Fence[*i*] + broad[*k*] * Road[*i*] + bhuman[*k*] * Human[*i*] + baltitude[*k*] * Altitude[i] + banthro[*k*] * Anthro[*i*] + bslope[*k*] * Slope[*i*] + bLUVegType[LUVegType[*i*], *k*]+ bLUFire[LUFire[*i*], *k*].

where, *k* = species; *i* = site; b0[*k*] = Intercept for species *k*; bvis[*k*] = Coefficient for Visibility at site *i* for *k*; bgrass[*k*] = Coefficient for Grass biomass at site *i* for *k*; bvegtypevar[*k*] = Coefficient for Habitat variation at site *i* for *k*; bfence[*k*] = Coefficient for the presence of Reserve Boundary at site *i* for *k*; broad[*k*] = Coefficient for the presence of Roads at site *i* for *k*; bhuman[*k*] = Coefficient for Human Settlement at site *i* for *k*; baltitude[*k*] = Coefficient for Altitude at site *i* for *k*; banthro[*k*] = Coefficient for Anthropogenic Detections at site *i* for *k*; bslope[*k*] = Coefficient for Slope at site *i* for *k*; bLUVegType[LUVegType[i],*k*] = Coefficient for Land Use Vegetation Type at site *i* for *k*; bLUFire[LUFire[i],*k*] = Coefficient for Land Use Fire history at site *i* for *k*.

The model used to assess the detection probability for each camera trap location was: logit(p[*i*, *k*]) <- a0[*k*] + adet[*k*] * Detectability[*i*] + aTU[*k*] * TU[*i*].

a0[*k*] = Intercept for *k*; adet[*k*] = Coefficient for Detectability covariate at site *i* for *k;* aTU[*k*] = Coefficient for Temporal or Use-related covariate at site *i* for *k.*

Occasions were treated as a 24 hour period from 00h00:00 - 23h59:59 per camera trap location, thus, with a total of 40 occasions for each camera location.

The above model was run separately for each species and camera in order to gain a better understanding for which environmental and anthropogenic covariates accurately predict species richness and individual species space use patterns, using the package RJAGS version 3-10 (Russell *et al.,* 2009; Plummer, 2023), on R software, version 4.2.1 (R Development Core Team, 2021). In order to assess the potential number of non-detected species for the species richness estimates, data augmentation was conducted by adding a total of 51 'unknown species' to the species list to avoid truncation of posterior distribution.

The ten environmental and anthropogenic covariates were assessed to understand which were the best predictors of mammal site-specific species richness and species-specific space use on MGR (Zipkin *et al.,* 2009; Nieman & Botha, 2024). Each covariate was considered as having a significant role as a predictor of mammal space use when beta coefficient values did not overlap with zero (95% Highest Density Intervals taken into account; Tobler *et al.,* 2015), both negatively and positively. All of the above Bayesian analyses were done using R software using the RJAGS package (Plummer, 2023).

3.3 Results

A total of 237 905 images were captured from 79 302 total trigger events over 1 855 camera days, with a total of 2960 independent detections after a 30 minutes interval was initiated. Although 2 080 camera days had been scheduled, theft, human and elephant (*Loxodonta africana*) induced damages and technical failures reduced camera days by a total of 225 days. In total 76 342 detections were either false triggers, or detections of indistinguishable or non-target animals leaving 2 960 independent detections of 29 species of medium and large mammals (Table 3.1).

The most detected mammals were impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinu*s) with 514 and 342 independent detections, captured at 37 and 40 of the camera locations, respectively (Table 3.1). The plains zebra (*Equus quagga burchellii*) and warthog (*Phacochoerus africanus*) were the most widely detected across the reserve, with zebra detected at all 51 locations, and the warthog detected at 50 of the 51 camera locations. Caracal (*Caracal caracal*), rock hyrax (*Procavia capensis*) and honey badger (*Mellivora capensis*) were all detected only once. The most detected herbivores were grazers, comprised of seven species, with 875 independent detections, mixed-feeders comprised of three species with 793 detections and, lastly, browsers comprised of five species with 758 detections.

Table 3.1: Details of camera trap detections of the 29 medium to large mammal species recorded during the survey period on Mawana Game Reserve. Species are arranged alphabetically with the number of independent detections and number of survey locations each species was detected at.

Common name	Species name	Detections	No. of locations
Aardvark	*Orycteropus afer*	35	10
African Elephant	*Loxodonta africana*	3	1
African savanna Hare	*Lepus microtis*	20	10
Baboon	*Papio ursinus*	20	5
Black-backed Jackal	*Lupulella mesomelas*	95	21
Blesbok	*Damaliscus pygargus phillipsi*	105	9
Blue Wildebeest	*Connochaetes taurinus*	342	40
Brown Hyena	*hyena brunnea*	2	2
Bushpig	*Potamochoerus larvatus*	28	8
Caracal	*Caracal caracal*	1	1
Common Duiker	*Sylvicapra grimmia*	263	42
Giraffe	*Giraffa giraffa*	73	10
Greater Kudu	*Tragelaphus strepsiceros*	340	46
Honey Badger	*Mellivora capensis*	1	1
Impala	*Aepyceros melampus*	514	37

Large-spotted Genet	*Genetta tigrina*	78	22
Natal Red Duiker	*Cephalophus natalensis*	2	2
Nyala	*Tragelaphus angasii*	279	33
Plains Zebra	*Equus quagga burchellii*	225	51
Porcupine	*Hystrix africaeaustralis*	52	21
Rock Hyrax	*Procavia capensis*	1	1
Slender Mongoose	*Galerella sanguinea*	137	25
Serval	*Leptailurus serval*	8	4
Spotted Hyena	*Crocuta crocuta*	2	1
Vervet Monkey	*Chlorocebus pygertythrus*	107	24
Warthog	*Phacochoerus africanus*	202	50
Waterbuck	*Kobus ellipsiprymnus*	12	6
Water Mongoose	*Atilax paludinosus*	6	5
White-tailed Mongoose	*Ichneumia albicauda*	7	6

The detected MGR species composition comprised of 15 herbivore species, nine omnivores, five carnivores and one insectivore. Herbivores had a total of 2433 independent detections (82% of all species detections), omnivores 479 (16.1%) detections, insectivores 35 (1.18%) detections while the five species of carnivores only had 13 independent detections in total (0.44%).

Twenty independent anthropogenic detections of humans (excluding researchers operating in the Inkawu Vervet Project research area) and collared dogs were recorded. Thirteen of these 20 events included domestic dogs (*Canis familiaris*) passing by within 2 minutes of the human detection. Two of the 20 anthropogenic detections recorded were just collared dogs, a proxy used for anthropogenic presense (Masseloux *et al.,* 2017; Dias *et al.,* 2019).

Species Richness

The observed species richness (N_{obs}) was 29 medium and large mammals species (Figure 3.3). Non-parametric Jackknife and Chao species richness estimates were calculated and Jackknife 1 estimated 32.9 (SD = 1.87) species and 34.85 (SD = 2.15) and 33.7 (95% CI = 29.24 - 44.67) from Jack 2 and Chao 2 respectively. Species richness estimated using the sample-based species accumulation curve (S[est]) was 35 (95% CI = 25.37 - 32.63; Figure 3.3). All four of these species richness estimators suggested that some species went undetected during this survey, ranging between two and six species. The observed species richness was 80.56% of the value of the mean of the highest species estimator (S[est]; Figure 3.3). The multi-species occupancy model species richness estimate was 34 (95% CI = 29-45) species.

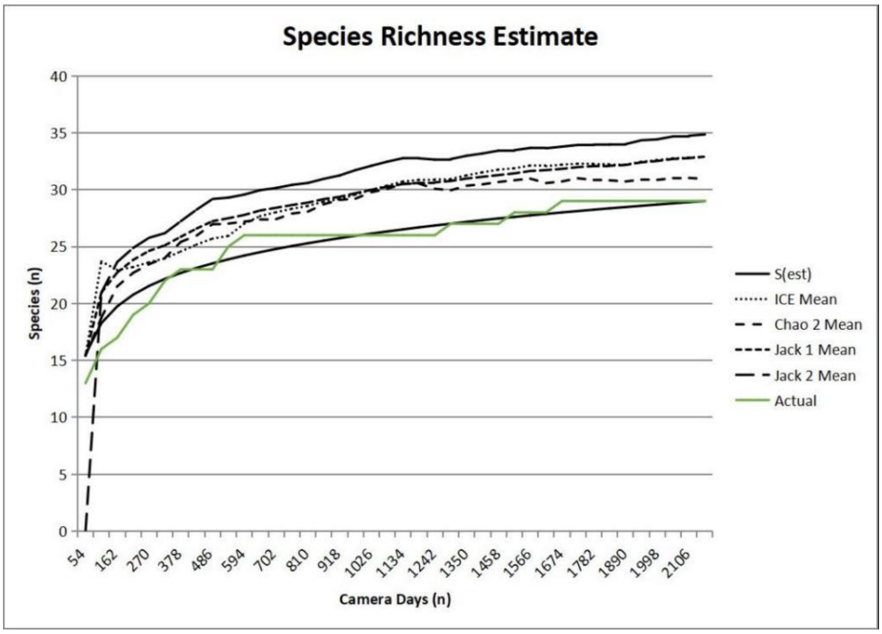

Figure 3.3: A graph showing the observed species richness detected over time with a sample-based species accumulation curve [S(est)] and three non-parametric species richness estimators Chao 2, Jack 1 and Jack 2

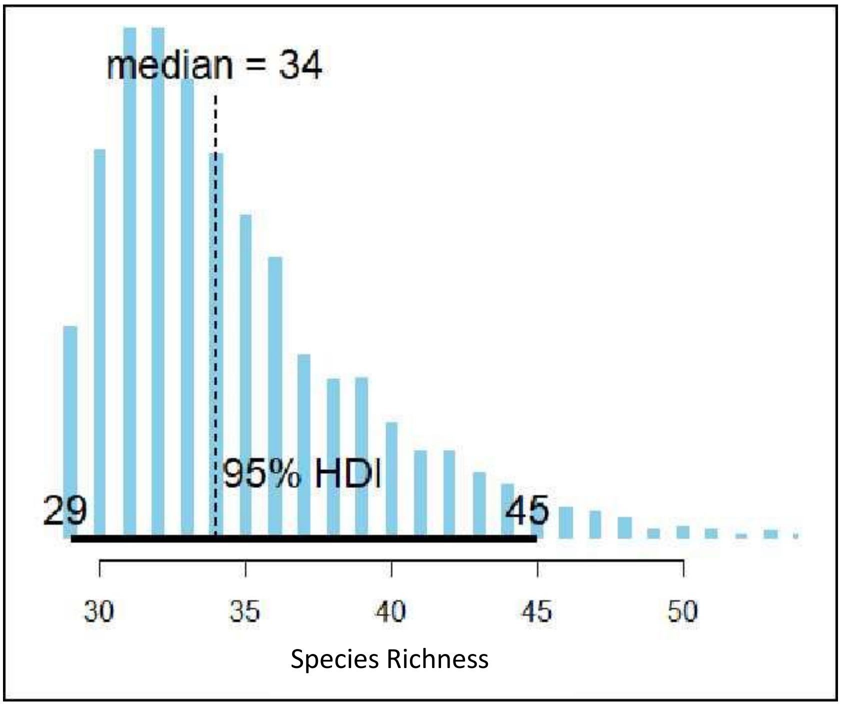

Figure 3.4: A bar graph displaying Bayesian species richness posterior distribution of medium and large mammals, with a 95% Highest Density Interval (HDI) indicating a range of 29 to 45 species on MGR with the median being 34 species

Observed species richness per camera ranged from 1 to 17, with the highest species richness numbers being recorded in the north-west of MGR, while the lowest species richness numbers were recorded in the south-eastern corner of MGR (Figure 3.5).

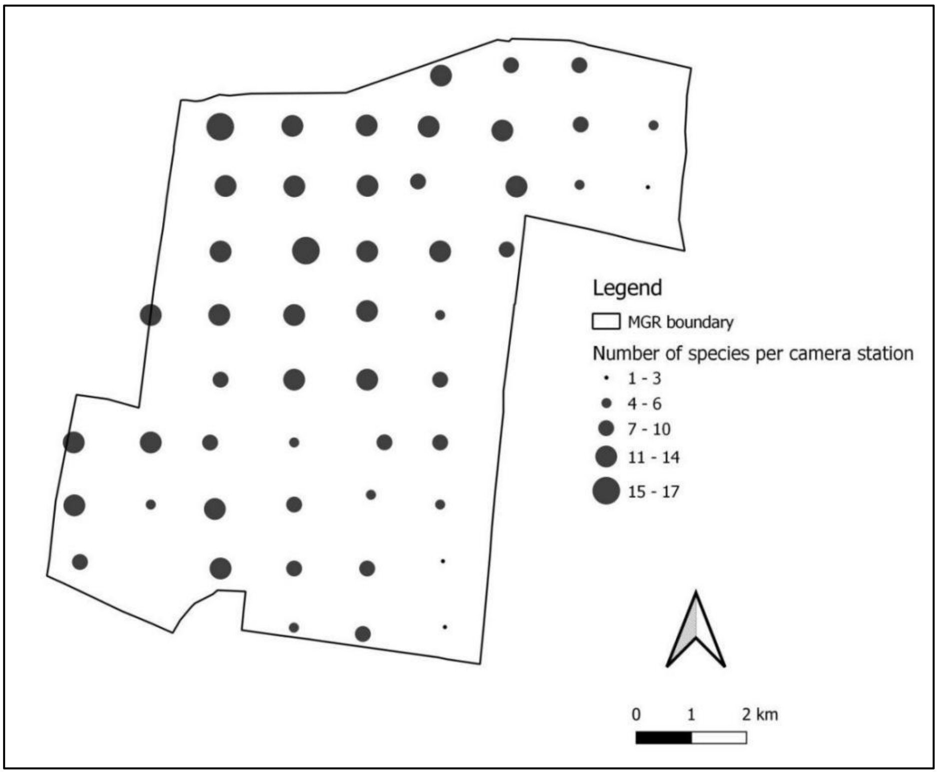

Figure 3.5: Map of Mawana Game Reserve showing the observed species richness (N_{obs}) per camera trap station with larger circles indicating a higher species richness than smaller circles. Species richness across cameras detected between one and 17 species, with the most detected in the north-central and north-western parts of the reserve

Predictors of species richness and mammal space use

Of the ten predictors of mammal space use and species richness, six significantly influenced species richness patterns across MGR, namely: altitude, grass biomass, vegetation type, vegetation type variation, visibility and distance to human settlements. However, at an individual species level nine of the predictors significantly influenced one or more of the medium and large mammal species. Slope was the only covariate not having predictive influence on mammal species.

Altitude

Species richness declined significantly (R^2 = 0.2675, p = < 0.05, F = 19.26) with an increase in altitude (Figure 3.6).

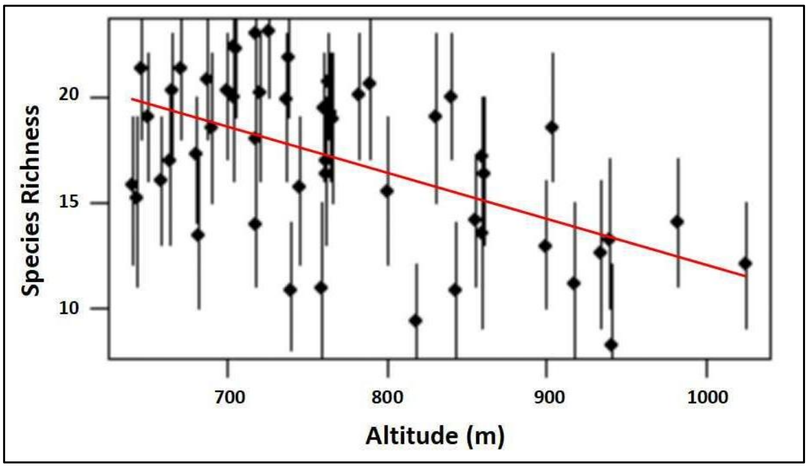

Figure 3.6: Scatter plot indicating a negative relationship between altitude and species richness on Mawana Game Reserve. Error bars represent the 95% Highest Density Interval. The red line indicates the best-fit linear regression

Blesbok and impala were detected significantly more at higher altitudes, while African savanna hare, baboon, black-backed jackal and serval tended to also be found at higher altitudes, albeit less significantly (Figure 3.7).

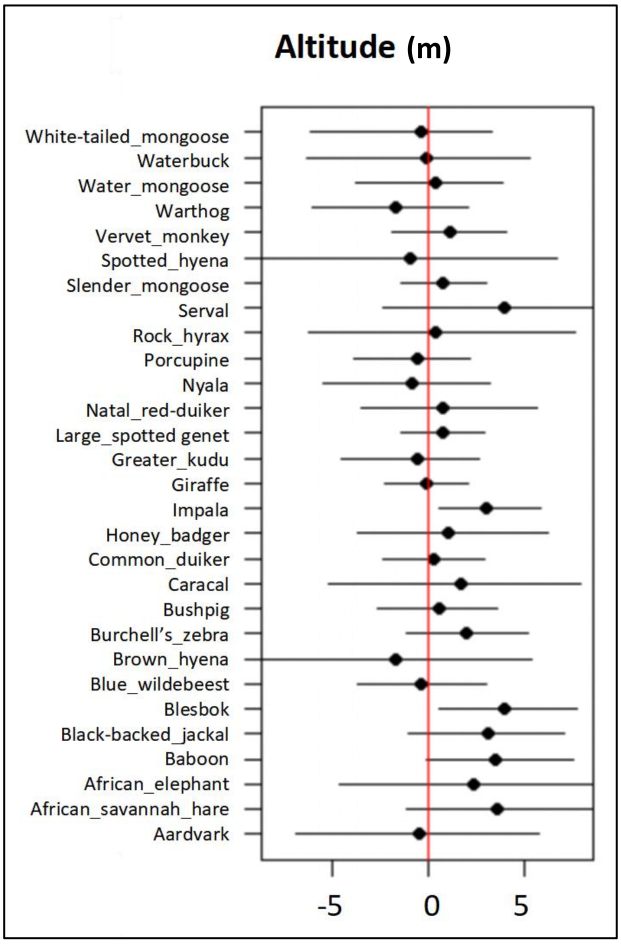

Figure 3.7: Whisker plot showing beta coefficients for the influence of altitude (m) on each individual species. The 95% Highest Density Interval is indicated by the error bars

Fire

No significant relationship occurs between species richness and fire (P = >0.05). Giraffe used recently brunt areas significantly less that unburnt areas, while black back jackal and porcupine showed a similar tendency (Figure 3.8).

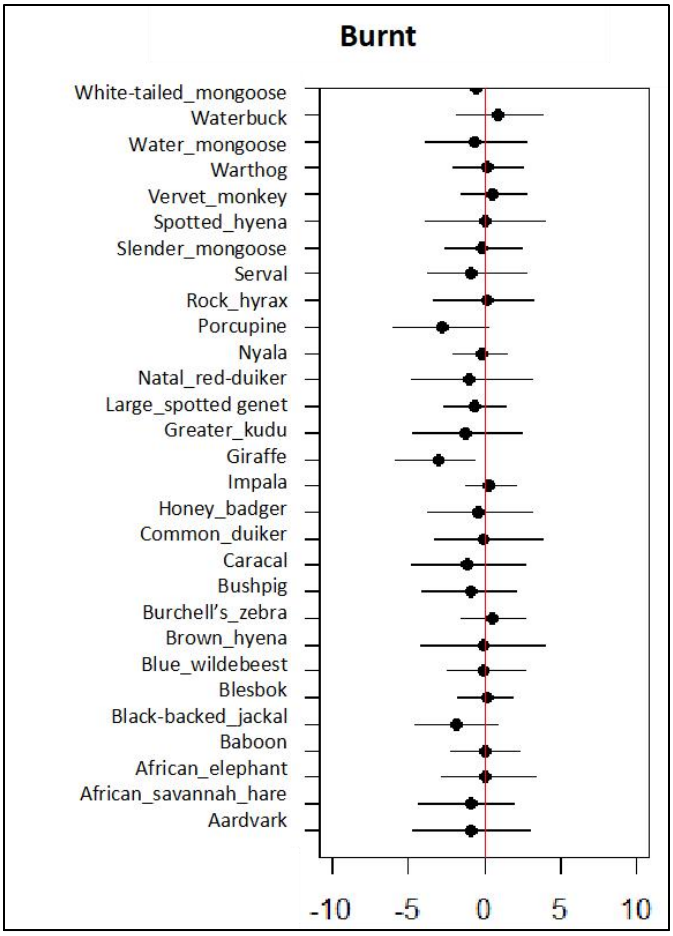

Figure 3.8: Whisker plot showing beta coefficients for the influence of fire on each individual species. The 95% Highest Density Interval is indicated by the error bars. Significant negative relationship is seen between giraffe and fire

Grass biomass

Species richness decreased significantly with an increase in grass biomass (R^2 = 0.2244, p = < 0.05, F = 15.47; Figure 3.9).

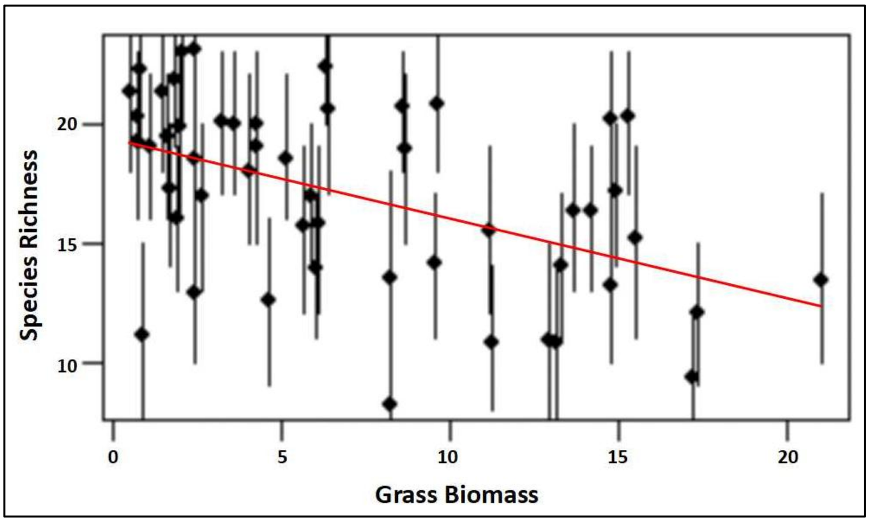

Figure 3.9: Scatter plot showing the influence of grass biomass on species richness. The 95% Highest Density Interval is indicated by the error bars. The red line indicates the best-fit linear regression

Vervet monkey and bushpig occupancy declined, significantly, with an increase in grass biomass (Figure 3.10). Plains zebra also showed a strong, but not significant, decrease in use of areas of greater grass biomass.

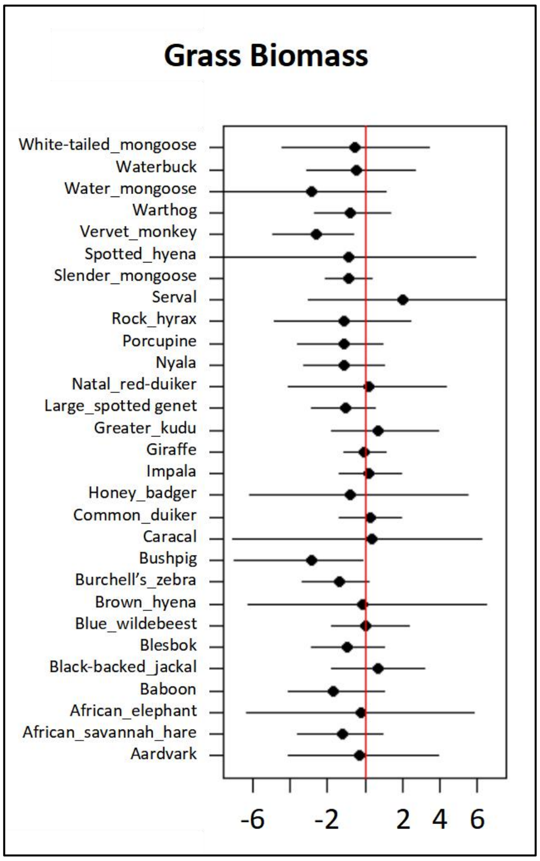

Figure 3.10: Whisker plot showing beta coefficients for the influence of grass biomass on each individual species. The 95% Highest Density Interval is indicated by the error bars. Significant negative relationship is seen between vervet monkey and bushpig with grass biomass

Vegetation type variation

Areas with greater variation in vegetation types were found to have a significantly lower species richness ($R^2 = 0.3449$, $p = < 0.05$, $F = 27.33$; Figure 3.11).

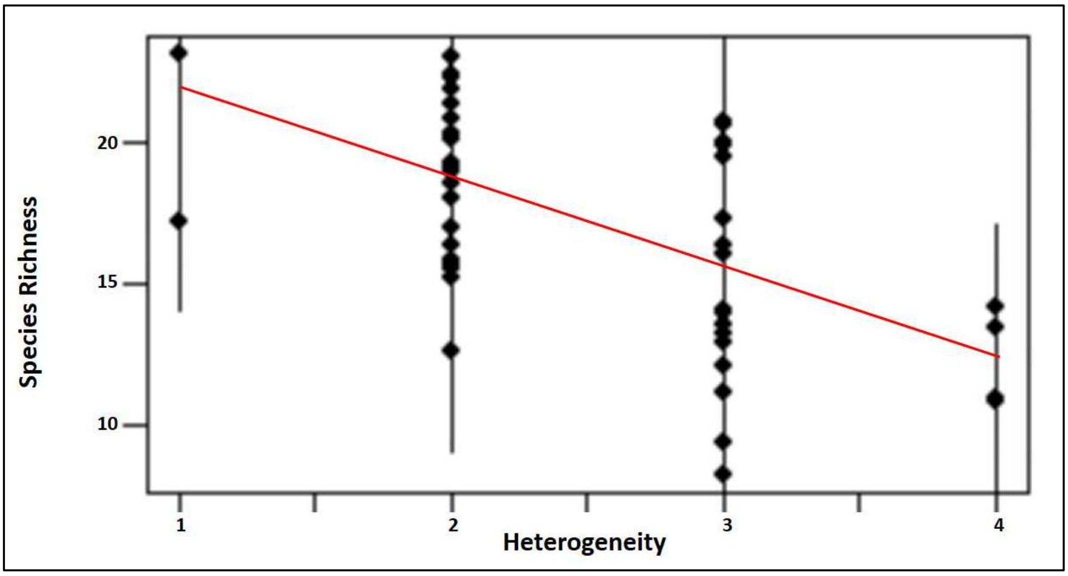

Figure 3.11: Scatter plot showing a negative relationship between vegetation type variation and species richness. The 95% Highest Density Interval is indicated by the error bars. The red line indicates the best-fit linear regression

Giraffe, impala, plains zebra and black-backed jackal occupancy decreased significantly as vegetation type variation increased. Although not significant, both primate species, the vervet monkey and chacma baboon were the only species showing a higher probability of use of areas that was more variation in vegetation types (Figure 3.12).

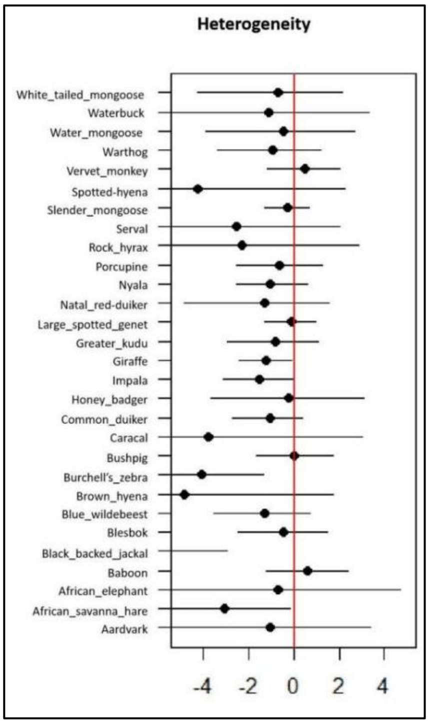

Figure 3.12: Whisker plot showing beta coefficients significant negative relationship between giraffe, impala, black-backed jackal, plains zebra and vegetation type variation. The 95% Highest Density Interval is indicated by the error bars

Vegetation type

A clear difference in species richness was noted across the five different vegetation units (Figure 3.13). The highest species richness occurred in the VDW while VCS had on average the lowest species richness of all the vegetation units (Figure 3.13).

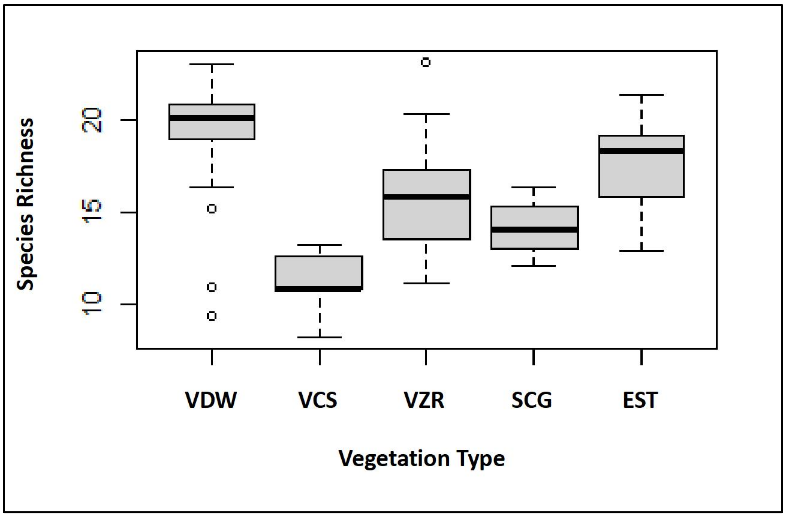

Figure 3.13: Box and Whisker plot showing median species richness found across the different vegetation units. Whisker depicts 95% confidence limits. VDW = *Vachellia tortilis–Dichrostachys cinerea* open to closed woodland; VCS = *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna; VZR = *Vachellia robusta–Ziziphus mucronata* riverine woodland; SCG = *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands; EST = *Euclea schimperi–Searsia pentheri* closed thickets

Many species showed significant positive or negative association with certain vegetation units (Figure 3.14). Vervet monkeys, blesbok and large-spotted genets were found to positively associate with EST. Baboons and giraffe had a strong positive association with VCS while black-backed jackal, blesbok and zebra showed a strong negative association with VZR. No species specific significant association was shown towards the VDW and SCG vegetation units.

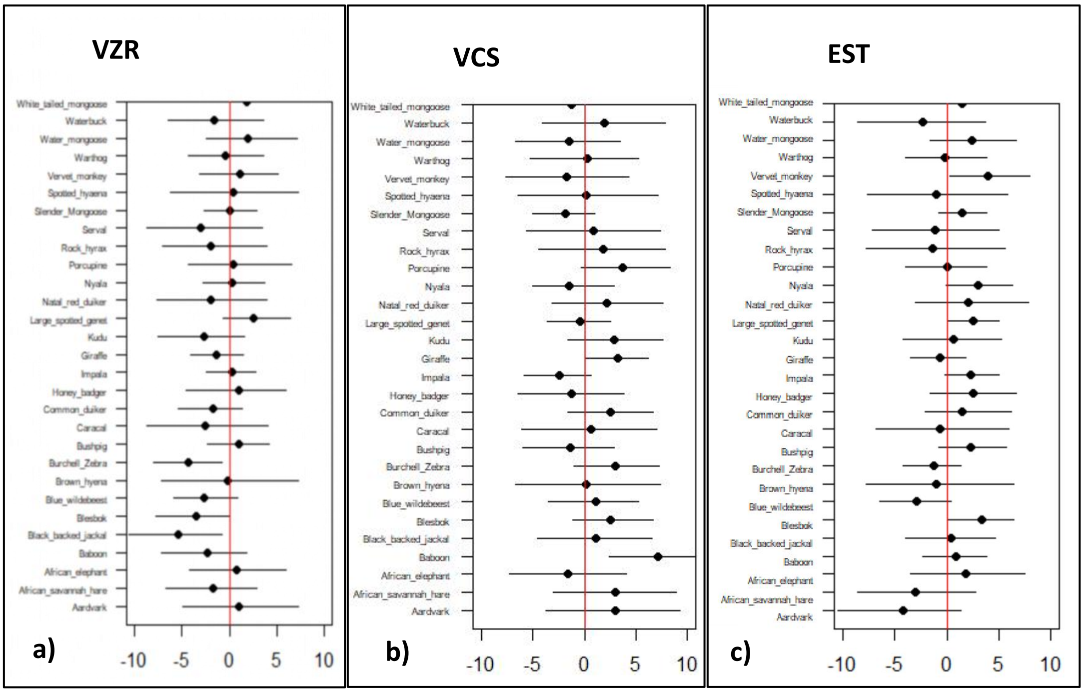

Figure 3.14 a: Whisker plot showing plains zebra, blesbok and black-backed jackal displaying a significant avoidance for *Vachellia robusta–Ziziphus mucronata* riverine woodland. **b:** Whisker plot showing giraffe and baboons displaying a significant preference for *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna. **c:** Whisker plot showing vervet monkey and blesbok preference for *Euclea schimperi–Searsia pentheri* closed thickets. Error bars represent the 95% Highest Density Interval

Visibility

An increase in visibility results in a significant increase ($R^2 = 0.157$, $p = 0.0026$, $F = 10.12$) in species richness (Figure 3.15).

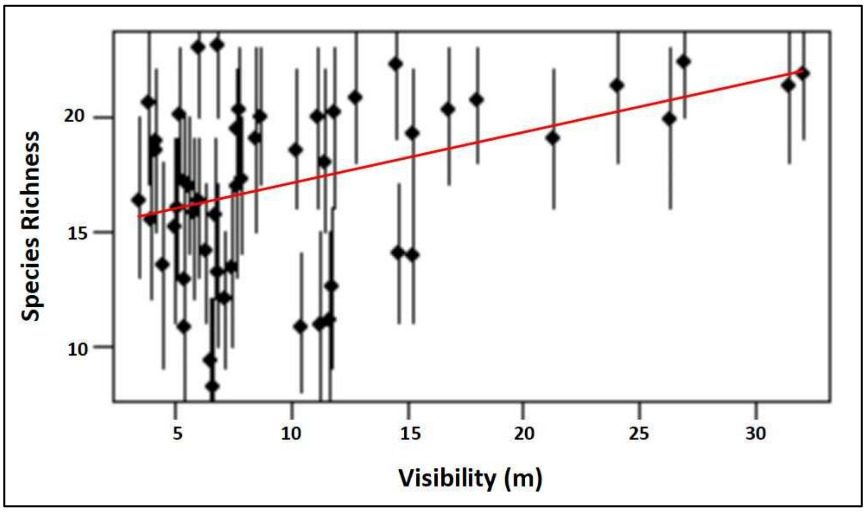

Figure 3.15: Scatter plot showing the positive relationship between species richness and visibility. The 95% Highest Density Interval is indicated by the error bars. The red line indicates the best-fit linear regression

Plains zebra and blesbok occupancy was found to significantly increase in areas of greater visibility, others such as the vervet monkey, slender mongoose (*Galerella sanguinea*), common duiker (*Sylvicapra grimmia*) and nyala (*Tragelaphus angasii*) were found to have nearly significant negative association with visibility (Figure 3.16).

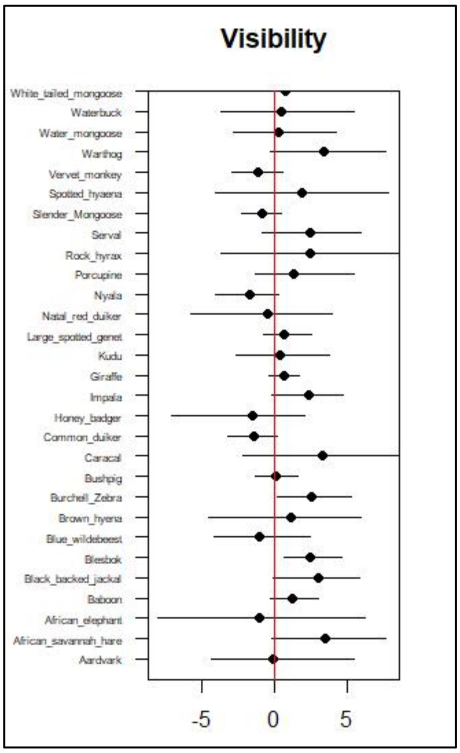

Figure 3.16: Whisker plot showing plains zebra and blesbok displaying a strong preference for areas of greater visibility. The 95% Highest Density Interval is indicated by the error bars

Distance to human settlement

A significant (R2 = 0.2613, p = 0.00008, F = 18.69) decrease in species richness occurs as distance to human settlement increased (Figure 3.17).

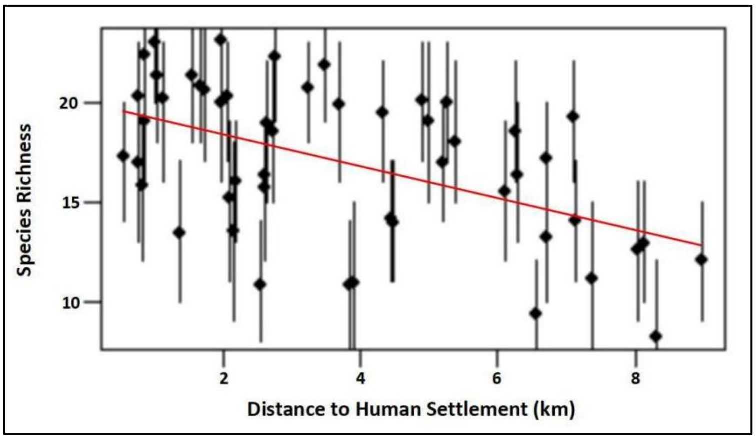

Figure 3.17: Species richness declines as distance to human settlement increases. The 95% Highest Density Interval is indicated by the error bars. The red line indicates the best-fit linear regression.

Impala, nyala and vervet monkeys were significantly more likely to be found near to a human settlement, while no species were shown to use areas away from human settlements significantly (Figure 3.18).

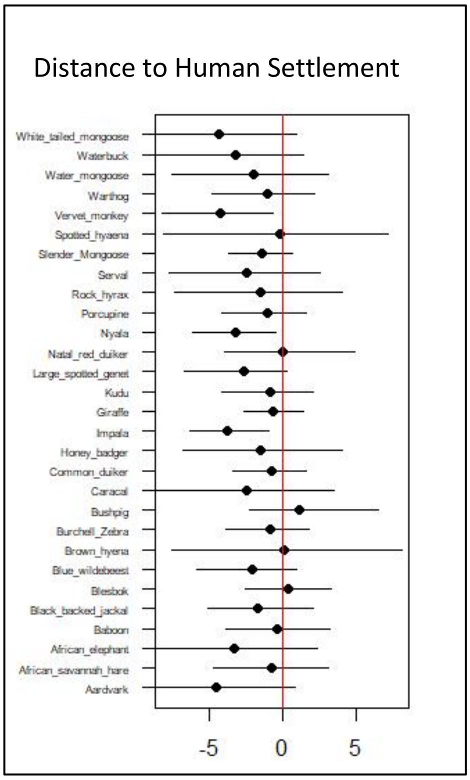

Figure 3.18: Whisker plot showing beta coefficients of all species. Whiskers represent the 95% Highest Density Index. Impala, nyala and vervet monkeys displaying a negative correlation to the distance to human settlements

Distance to roads

Although species richness as a whole did not show any significant association with distance from a road (p = 0.4928), warthogs and baboons at a species level showed a significant positive association with roads. Although not significant, giraffe, impala, blesbok and black-backed jackals also seem to use areas closer to roads more often (Figure 3.19).

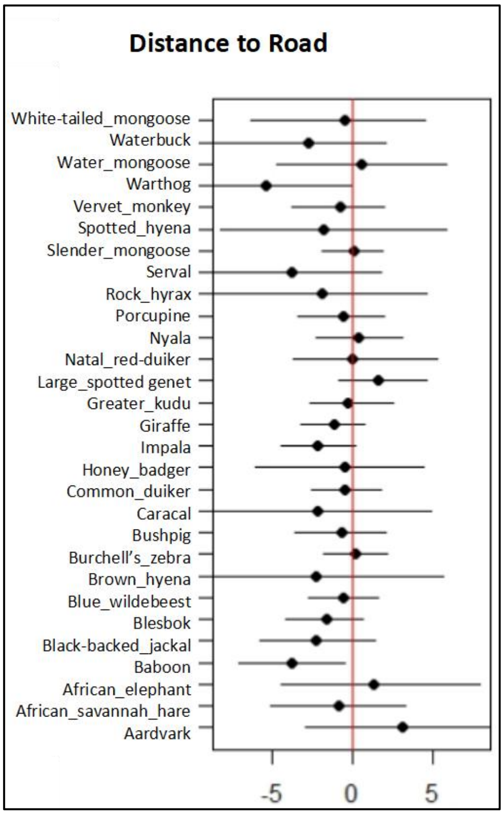

Figure 3.19: Whisker plot showing beta coefficients and significant preference for warthogs and baboons to be found close to roads. Error bars represent the 95% Highest Density Interval

Distance to reserve boundary

Species richness was not significantly impacted by the proximity to the reserve boundary (p = 0.7832), however, at species level, nyala were found more commonly further from the boundary, while the opposite, significant trend was observed with blesbok (Figure 3.20).

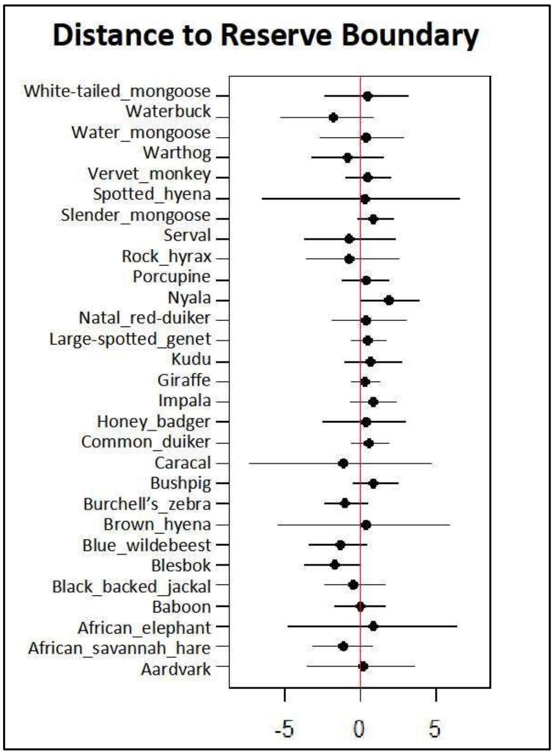

Figure 3.20: Whisker plot showing significant positive relationship for Nyala with distance to the reserve boundary and a significant negative relationship between blesbok and distance to the reserve boundary. Lines either side of points represent the 95% Highest Density Interval

3.4 Discussion

Despite multiple perceived anthropogenic threats it appears that environmental factors still have the strongest influence on the space use of mammal species and species richness across MGR, a finding supported by other studies looking at both ecological and anthropogenic predictors (Howard *et al.,* 2018; Oberosler *et al*., 2019; Reece et al., 2023). In the future, however, as the local human population and its related resource requirements increases so could the anthropogenic impacts on MGR, necessitating follow-up studies comparative to this one. The two environmental predictors with the strongest significance and impacting species richness are vegetation type variation and visibility. Distance to human settlements remained as the only anthropogenic factor influencing species richness. Although a total of 29 species were detected on MGR, all species richness estimators indicated that more camera days may have been necessary to obtain a more complete account of the MGR species richness as none of the species accumulation curves reached asymptote.

Historical species distribution maps and accounts suggest that 51 medium and large mammals used to occur in the MGR region (Skinner & Chimimba, 2005). Twenty-nine species, representing 56% of this historic figure, were recorded during this camera trap survey. Species richness estimates suggest between 32 and 35 species (between 62% and 68% of historical figures) still occur on MGR. As potentially more than two thirds of the mammal species thought to have existed here previously still occur on the reserve, MGR is in an important position to assist in the conservation of biodiversity in the Maputaland Pondoland-Albany hotspot, one of Africa's seven biodiversity hotspots. Many of the large predators (lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lyacon pictus*)) and large herbivore species (hippopotamus (*Hippopotamus amphibius*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*) and the common eland (*Tragelaphus oryx*)) are known to have been extirpated from the region close to a century ago. The potential expansion project on MGR may see the reintroduction of several of these missing medium to large mammals.

Non- and low-detection of mammals

Opportunistic sightings and other camera trapping activities conducted on MGR before and after this survey period, revealed six species that were not detected during the camera trapping period of the study. The six known species not observed during this period (Pers. Obs.) were the leopard, Cape clawless otter (*Aonyx capensis*), grey rhebok (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*), striped polecat (*Ictonyx striatus*) and aardwolf (*Proteles cristatus*). A minimum of 35 medium to large mammal species are, therefore, known to exist on MGR. As seen in Figure 3.3 the sample-based species accumulation curve [S(est)] thus provided the closest estimation of the species richness of MGR. All models used for species richness estimation indicated that a suitable change should be made to the design of the study. One potential change could be to place additional cameras outside of the centroid grid formation used for this study. The additional cameras can be placed within another cameras grid cell in locations that may target species with specialised habitat preferences, such as rivers or cliff trail, similar to the study conducted by Reece *et al.*, (2021)

The Cape clawless otter and mountain reedbuck are considered habitat specialists (Nel & Somers, 2007; Taylor & Skinner, 2006) and this is most likely the cause for non-detection. While sightings of the mountain reedbuck can be fairly common in mountainous environments on MGR they are expected to remain in a fairly low density and specialize in steep slopes and dense, tall vegetation (Taylor & Skinner, 2006), both of these are environmental characteristics that reduce detection probability when using camera traps (Riley *et al.*, 1999). The Cape clawless otter is a species with a relatively large home range restricted to riparian areas (Skinner & Chimimba, 2005) and therefore also expected to be in relatively low densities on MGR.

The leopard, although detected on MGR by camera traps late in 2020 and again in 2023 was postulated to be mostly eradicated from the region due to targeted killings resulting from human wildlife conflict and cultural beliefs. All detected individuals have been identified through spot patterns to be unique males, new to the broader area, and the area thus potentially acts as a sink for dispersing males (Fattebert *et al.,* 2015). The striped polecat is small in size (800 g) and therefore, it is possible for it to have passed in front of a camera without detection as smaller species have been recorded to do so (Apps & McNutt, 2018), despite camera trap placement attempts to avoid missing smaller animals (Tobler *et al.,* 2008). Cameras placed at a lower height (20 - 30 cm; Kelly, 2008) above the ground may have assisted in the detection of smaller mammals like the striped polecat, however, such a practice would have made identification of larger mammals difficult (Apps & McNutt, 2018). Due to their dietary requirements aardwolf are also likely to occur in low densities within MGR and it is therefore possible to remain undetected.

Two detected species, the Natal red-duiker (*Cephalophus natalensis*) and honey badger, had been presumed to be locally extinct due to a lack of sightings and no signs detected for many years. However, both species were detected during the camera trapping period (Table 1), and thus have managed to persist in the area although at low densities as suggested by the single detection of honey badger and two detections of the red-duiker.

The rock hyrax and caracal had a single detection each. The hyrax is likely to have had a low detection rate due to its habitat specialisation (Mares, 1997) while the caracal, although widespread in Africa, is understood to have a naturally low density due to their ecological requirements (Avenant & Nel, 2002). Although the absence or low densities of other larger predators should allow for caracals to be present in greater numbers (Dobamo, 2019), it is possible that livestock predation leading to human induced persecution of the species may result in less caracals on MGR than the area could sustain (Dobamo, 2019; Crookes, 2023).

The African elephant only had three detections during the camera trapping period and this is most likely due to the MGR elephant herd spending more than 84% of the camera trapping period off MGR, as observed by their global positioning systems (GPS) collar data (unpublished data). Serval, spotted hyenas and brown hyenas were also recorded in low abundance, this most probably results from low numbers due to the conflict that has been known to stem from perceived livestock predation in the region for both hyena species (Mthembu, 2021) and general low density and specialised habitat and activity preferences for servals (Webster *et al.,* 2021).

Species richness and individual species space use predictors

Overall, species richness and individual species are impacted more by ecological characteristics in MGR than by anthropogenic characteristics. Of the seven ecological covariates hypothesised to influence mammal species richness and individual species space use, five significantly predicted mammal species richness across MGR. Slope and fire history did not significantly influence species richness, while fire had a significant influence on the space use of giraffe and a near significant influence on porcupines (*Hystrix africaeaustralis*), both of which were detected less in burnt areas, most likely a result of their dietary requirements. Frequent fires are known to alter vegetation and, along with herbivory, maintain vegetation units with a relatively dominant grass component and a relatively small component of woody plants (Skarpe, 1990; Smit & Prins, 2015), thus leading to less foraging opportunities for strict browsers, such as giraffe (Scholes & Archer, 1997; Deacon, 2015). As more browse forage is available in environments known to have an absence of fire (Stevens *et al.,* 2017), it is likely that the areas of MGR that burned have less browse forage and feeding opportunities for giraffe and other strict browsers. As porcupines are also reliant on trees for consuming bark, roots and occasionally fruits (Barthelmess, 2006; Kraai, 2021), it is likely that they too may frequent the burnt areas less, opting for feeding opportunities elsewhere. From a species richness perspective, although fire may reduce vegetation cover, and thus may result in less species

Variation in vegetation types is well understood to increase mammal species richness (Torres-Romero & Olalla-Tárraga, 2014; Regolin *et al.,* 2020), however, variation of vegetation types on MGR resulted in significantly lower species richness. Although the significance on species richness was strong, only two individual species were significantly predicted by vegetation type variation, this was the black-backed jackal and plains zebra. Due to the fact that vegetation type variation is a broad scale ecological characteristic, it is more influential on species richness as a whole and could be seen to influence species diversity in a certain area more than it would influence individual species (Dorph *et al.,* 2021). Only two vegetation units are found in the central, northern and north-western parts of MGR. One of the two vegetation units in this part of MGR is VDW, a unit that proved to be a strong positive predictor of mammal species richness (Figure 3.13). Due to other environmental characteristics, such as soil types, slope gradient and aspect further south within MGR, the spatial turnover rate of vegetation units is higher than observed in the north, creating a mosaic of plant communities within a relatively small area (Figure 3.13). The high turnover of less productive vegetation types (Mostert & Mostert, *unpublished*) may result in the covariate of vegetation type variation having a negative relationship with species richness.

A decline in species richness with an increase in altitude is a well studied relationship over globally extreme altitude changes, especially in small mammal species (Lomolino, 2001; McCain & Grytnes, 2010), however, the impact on species habitat use for larger mammal species over small altitudinal shifts as seen across MGR is poorly studied. The higher altitudes of MGR are associated with the short, open SCG grasslands and VCS open, sparse savanna vegetation units. Both vegetation units have shown weaker prediction of use by medium and large mammal species (Figure 3.13). It is more likely that within the context of MGR, mammals are selecting for other vegetation units and not necessarily selecting lower altitudes, given the relatively small variance in altitude across MGR (518 m variation) having little to no impact on oxygen availability (ISMM, 2001) and temperature changes. Blesbok, however, showed a significant preference for higher altitudes, likely, again, a preference for the vegetation unit found at higher altitudes. As blesbok are strict grazers (Novellie, 1978; Venter & Kalule-Sabiti, 2016) and have been found to prefer areas of diverse short grass (Novellie, 1978), it is, therefore, not unexpected to find blesbok in the VCS and SCG units - high altitude sparse savannas and grasslands.

As grass biomass declined, species richness increased, a relationship known and expected for in mammal species such as browsers (Smit & Prins, 2015). On an individual species level only bushpigs and vervet monkey's, however, showed a clear and significant negative association with grass biomass. Of the 27 other species, although most of them trended towards a negative relationship with grass biomass, none were significant. The serval was the species displaying the most positive (although not significant) relationship with areas of greater grass biomass, something expected given their ambush hunting methods requiring thick, tall vegetation to conceal themselves (Thiel, 2011; Ramesh & Downs, 2014b). As grass quality is reduced when quantity increases (Ramoelo *et al.,* 2012) species richness is expected to decline from grazing species as well as browsers due to reduced tree abundance in the areas of greater grass biomass (Moster & Mostert, *unpublished*). Many species have been found to avoid increasing grass biomass (Reece et al., 2023) and thus species richness is likely to be reduced in MGR.

As a bulk grazer and hind-gut fermenter zebra are able to consume large quantities of poor quality grass (Bell, 1971; Mandlate & Rodrigues, 2020), and they are known to select areas of higher grass biomass as a method to avoid competition from other grazers (Mandlate & Rodrigues, 2020). Trends from the survey period on MGR, however, show that zebra are near-significantly selecting for areas with lower grass biomass, perhaps a result of their positive relationship with increasing visibility. An increase in visibility leads to higher abundance of zebra a well studied anti-predatory behaviour (Fischhoff *et al.,* 2007; Mandinyenya *et al.,* 2020).

As grass biomass increases, the general quality of forage decreases (Botero-Londoño *et al.,* 2021), and thus herbivores are likely selecting areas of better forage quality. As an increase in grass biomass is associated with fire and lower tree biomass (Scholes & Archer, 1997), it may be considered dangerous for vervet monkeys, arboreal mammals, to move through areas with few trees and tall grass, especially when predominantly hunted by aerial predators and African rock pythons (*Python sebae;* Pers. Obs.). Areas with greater density of trees provides cover for monkeys to avoid detection from raptors (McGraw & Berger, 2013), and give space to move away from terrestrial predators, including pythons, when needed (Jaffe & Isbell, 2009).

Bushpigs are omnivores (Skinner *et al.,* 1976; Breytenbach & Skinner, 1982) that have been observed to select their habitat based on food availability (Skinner *et al.,* 1976; Nummelin, 1990). As their summer diets include predominantly seed pods and fruits from trees (Breytenbach & Skinner, 1982; Nummelin, 1990) it is also more likely that bushpigs would be spending more time in areas with greater abundance of trees and therefore avoiding areas of greater grass biomass.

Not only zebra, but also blesbok have a strong positive relationship with an increase in visibility while black-backed jackal, baboons and African savanna hares, have also been found to have a near-significant positive relationship with visibility. As blesbok are strict grazers (Venter & Kalule-Sabiti, 2016) and prefer areas of short, open grassland (Novellie, 1978; Bell, 2003), a vegetation characteristic on MGR that is also characterised by fewer trees (Mostert & Mostert, *unpublished*).

Differences in vegetation composition plays an important role in the space use of mammals and species richness across MGR. As the different vegetation types are intricately linked to the landscape features in which they fall, altitude, visibility, degree of slope and other environmental factors play a role for each vegetation unit. As a dense vegetation unit, EST is a significant positive predictor of vervet monkeys, large-spotted genets and surprisingly blesbok's space use. As arboreal mammals, vervet monkeys have a strong preference for dense areas with a closed canopy and lower grass cover (Jaffe & Isbell, 2009; McGraw & Berger, 2013). Large-spotted genets have been found to have a higher detection probability in dense vegetation (Ramesh & Downs, 2014a), and although they may use other areas frequently, they are less likely to be detected in open areas. Blesbok, plains zebra and black-backed jackals were found significantly less in the riparian vegetation of the VZR. Due to the fact that all three of these species showed significant preference for areas with a greater visibility, their avoidance of the VZR is most likely due to the lack of visibility in this vegetation unit and water being abundant across MGR in this survey period, animals did not need to make use of perennial water sources during the survey period.

The northern sections of MGR are covered in predominantly two vegetation units, VDW and VZR. As species richness showed a significant increase in the VDW vegetation unit, it is likely to have also played a role in mammals being more abundant in this region than the remaining vegetation units of the reserve. The vegetation unit consistently displaying the lowest species richness was VCS, the unit furthest from human settlements.

Due to the number of small dams and rivers, no section of MGR is more than 350 m away from a water source during the wet seasons of the year, this does not take into account the small temporary puddles and streams that would give mammals access to water throughout the reserve. Due to the complexity of mapping water availability, water was therefore excluded as a potential driver for this study.

Anthropogenic predictors of mammal space use

Species richness increased closer to human settlements, a finding that appears contradictory given the perceived threat mammal species face from human presence (Nieman & Botha, 2024). Eppley *et al.*, (2024), found an increase in biodiversity within a 5 km radius of biological research stations. The presence of the Inkawu Vervet Project research station and MGR employee houses found in the northern section of MGR and active since 2010 and 1980 respectively, may thus have had an impact on the evident increase in mammal species richness found in the northern sections of MGR. A result that is likely to influence findings that mammals select for areas closer to human settlements, also north of the reserve. More protection may be gained in this region of MGR from the IVP field site than the rest of the reserve more than 5 km away from the research field site and coincidentally further from other human settlements too. A potential explanation for the increase in species richness near human settlements is the 'shield-effect' (Rodrigues *et al.,* 2023), the negative influence that human presence can have on medium and large predators that may result in less pressure being placed on the prey species and thus proximity to a human settlement is considered a safer option than being further from a settlement where more predators may be found.

Other anthropogenic factors, such as distance to fence and human detections, appear to not be considered as significant predictors of mammal species richness, however, blesbok showed a significant association with being near MGR boundaries. Nyala were significantly deterred by the MGR boundary, possibly a result of targeted poaching as nyala have been found to be the most targeted species within the KZN bushmeat trade (Pillinger, 2003; Kammer, 2006).

Management implications

Although no previous studies on large mammal species richness and space use have been conducted on MGR that allow for comparisons, future studies may be able to make use of this data to document change of the studied landscape.

Increasing human presence (Pers. Obs.) and the related resource use bordering MGR may further increase the factors affecting the manner in which mammals use their environment (Minin *et al.,* 2013). These unfolding occurrences and potential subsequent studies may result in a more comprehensive understanding of human impacts on the natural world around us. Through strategic engagement with local human communities around MGR a better understanding of the anthropogenic uses and impacts on and of mammals in and around MGR, will assist reserve management in creating a more area suitable conservation management plan. A study of this nature will play an essential part in the future conservation for mammals and protected area planning (Stephens *et al.,* 2001; Patel *et al.,* 2023) not only for MGR but other small and medium PA's in the KZN province and further afield.

Species richness varies across space and understanding this dynamic helps to gain better area-specific ecological insights, leading to more accurate and realistic conservation management plans (Nieman & Botha, 2024). Gaining the above knowledge on species-specific space-use patterns will be able to assist future conservation management for MGR and the neighbouring region.

3.5 Conclusion

With a species richness estimate of between 32 and 35 medium and large mammal species found on MGR and 29 observed during this survey period, MGR is an important refuge for mammal species of the Maputaland Pondoland-Albany hotspot. As found in other studies, vegetation types, visibility and grass biomass as well as vegetation type variation play an important role in the way mammals use their environment, indicating that dietary requirements and anti-predatory behaviour are both important factors influencing species richness and the space use of many individual species. Anthropogenic variables showed little influence over the space use of mammals on MGR, although proximity to settlements was found to have a positive relationship with species richness.

As a total of 20 events of suspected poaching incidents were detected across seven camera locations on MGR, as well as two thefts and one camera broken, further human focused studies will assist in gaining a better understanding of our species ever growing impacts on the natural world around us.

Mawana Game Reserve is an understudied nature reserve, thus research such as this camera trap survey, will act as an essential and comparative baseline for future mammal studies on the reserve and in the greater landscape to reassess the successes or failures of the regions conservation practice.

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CHAPTER FOUR:

TEMPORAL ACTIVITY PATTERNS OF MEDIUM AND LARGE MAMMAL SPECIES ON MAWANA GAME RESERVE, KWAZULU-NATAL, SOUTH AFRICA

4.1 Introduction

Biodiversity and ecological processes, essential for human life on Earth (Rockström *et al.,* 2009), are better supported within protected areas (PAs) where human impact is mitigated (Greve *et al.,* 2010) than outside of PAs. Larger PAs have been proven to be more effective in biodiversity conservation than smaller ones (Craigie *et al.*, 2010; Geldmann *et al*. 2013; Shumba, 2019), however the space needed, for establishing and declaring new PAs, is limited and governmental and private resources are often inadequate to support existing PAs, let alone new ones (Bruner *et al.,* 2004; Patel *et al.,* 2023).

Many PAs within South Africa are small, fully fenced reserves (Pirie *et al.,* 2017). Fences exist to try and prevent human wildlife conflict, and reduce negative anthropogenic influences towards biodiversity within the fenced PA (Hayward & Kerley, 2009; Massey *et al.,* 2014; Pirie *et al.,* 2017). Fences, management practices and habitat fragmentation result in wild animals within a PA having limited ability to disperse naturally (Pirie *et al.,* 2017). This inability to disperse, if not managed properly, can result in an increase in intra- and interspecific competition for environmental resources (Hayward & Kerley, 2009; Naha *et al.,* 2023). Gaining a better understanding of how animals use their environment and the stressors they face equip us to better conserve and manage the associated PA.

To avoid direct interspecific competition, animals with similar feeding strategies are known to partition resources (Kronfeld-Schor & Dayan, 2003). Resource partitioning can be achieved in three ways: spatially, trophically and temporally (Ferreiro-Arias *et al.,* 2021). Spatial partitioning is understood as animals avoiding each other geographically and has been commonly found among sympatric meso- and large carnivores, avoiding each other while hunting to decrease the likelihood of encountering the other and sustaining potentially fatal injuries (Hearn *et al.,* 2018; Sivy *et al.*, 2018; Müller *et al.,* 2022). Trophic partitioning occurs when animals with similar feeding strategies utilise different prey or dietary options to avoid direct conflict with one another. Partitioning of this sort has for instance been observed between leopards (*Panthera pardus*) and caracals (*Caracal caracal*) feeding on different prey species and prey sizes (Müller *et al.,* 2022). Temporal partitioning occurs when different species utilise the same food sources and space but do so at different times, whether over a 24 hour period or between seasons (Kronfeld-Schor & Dayan, 2003; Hearn *et al.,* 2018). Temporal partitioning has been observed in instances such as impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) avoiding waterholes during the times that elephants (*Loxodonta africana*) are using a waterhole, to avoid interspecific competition (Valeix *et al.,* 2007). Multiple predator species have also been observed to avoid each other over time as a result of competition (Welch *et al.,* 2023). Many past studies looking at temporal partitioning have focused on sympatric mammalian carnivores (Hearn *et al.,* 2018; Evers *et al.,* 2022) and bats (Adams & Thibault, 2006; Beilke *et al.,* 2020). Within herbivorous and omnivorous feeding guilds, studies have found temporal partitioning between zebra and wildebeest over seasons (Marioti, 2019), and between livestock and wild ungulates at waterholes (Valeix *et al.,* 2007; Connolly *et al.,* 2021).

As the global human population and the resources it needs increase (United Nations, 2019), so does our species impact on the natural environment and its wild inhabitants. Both consumptive and non-consumptive uses of the environment have been observed to have a negative impact on mammal species populations around the world (Oberosler *et al.,* 2017; Zong *et al.,* 2023; Salvatori *et al.,* 2023). Different mammals respond in different ways to human activity, while some avoid the activity out of fear (Bateman & Fleming, 2017), others are neutrally or positively impacted by human activity, through being ‘shielded’ from predators or exposed to an increased food source (Bateman & Fleming, 2017; Lasky, 2022). While PAs have been shown to help reduce anthropogenic impacts on biodiversity (Geldman *et al.,* 2013; Butynski & de Jong, 2024) PAs are not immune to biodiversity loss and influence from surrounding anthropogenic presence (Chape *et al.,* 2005; Jakiel *et al.,* 2024). Multiple responses from varying taxa exist in the face of anthropogenic pressure, while highly mobile animals such as birds may be able to move away when anthropogenic pressure becomes undesirable (Mikula *et al.,* 2023), other species such as large terrestrial mammals have less options, and have to adapt behaviourally to increasing pressure (Hammond *et al.,* 2019). Globally, mammal population densities have been found to be higher in human modified landscapes (Tucker *et al.,* 2021), and therefore gaining more understanding in this field is essential to know the impact our increasing species will have on the environment around us.

One such PA where anthropogenic pressure is perceived to be intense, yet proximity to human settlements was found to have a positive correlation with species richness (Chapter 3) is Mawana Game Reserve (MGR). MGR is a medium sized (approximately 11 000 ha) game reserve in KwaZulu-Natal (KZN), South Africa, that is exposed to varying anthropogenic influences from surrounding human communities as well as many environmental pressures. Due to its' relatively small size and increasing isolation from other natural areas, ecological resources for the animals of MGR are limited and wildlife is mostly restricted to living, feeding, breeding and moving within the PA. Access to sufficient feeding and breeding opportunities becomes limited further as mammals have a strong preference for certain vegetation types, areas with increased visibility and a number of other environmental characteristics (Chapter 3). Not all 11 000 ha of MGR is, therefore, suitable habitat for all species and the distribution of large mammals and their utilisation of the PA is not uniform across the landscape. Understanding how and when a species uses its environment is an essential part of a species biology and helps us to better understand a species habitat and conservation requirements (Hey *et al.,* 2003), and thus will allow MGR to make more informed conservation management decisions.

Proximity to human settlements has, unexpectedly, been proven to be a significantly strong positive predictor of mammal space use on MGR (Chapter 3) despite numerous incidences of snaring and poaching with dogs reported on the reserve

(Pers. Obs.; van der Walt pers. comm. 2021). The areas in close proximity to human settlements could be perceived as potentially dangerous for mammals (Oberosler *et al.,* 2017), and understanding how mammals use this space and respond to anthropogenic activities and presence, that potentially create a landscape of fear, will assist in further management and conservation of the species found on MGR. For instance, nyala (*Tragelaphus angasii*) have been found to be the most targeted species in the KZN bushmeat trade (Pillinger, 2003; Kammer, 2006) and should thus possibly be more active in these areas at a time when people are less likely to use the area, ie. temporal avoidance (Kronfeld-Schor & Dayan, 2003; Salvatori *et al.,* 2023). The influence of general outdoor activities engaged in by people has been shown to be a deterrence for wild mammals, whether the activities are consumptive or non-consumptive (Zong *et al.,* 2023; Salvatori *et al.,* 2023), resulting in a landscape of fear that may be created from anthropogenic activities.

Not only do human settlements pose a threat to biodiversity conservation through habitat destruction, targeted killing and resource harvesting but settlements are often linked to invasions from exotic species, as well as pollution (Keller *et al.,* 2011; Doherty *et al.,* 2016; Cirella *et al.,* 2021). Previous studies have found the presence of human settlements and associated disturbances to result in a fear-based response (landscape of fear) from wild mammals similar to responses from natural predation (Oberosler *et al.,* 2017; Zong *et al.,* 2023; Salvatori *et al.,* 2023). One such anti-predatory response observed is the use of open or closed environments in different ways that allow an animal to use the environment around it as a method to limit or increase visibility depending on its requirements. While some mammal species prefer more open spaces for the ease of detecting predators and increased mobility away from predators or in search of food (Owen-Smith & Traill, 2017; Reece *et al.,* 2021; Doherty *et al.,* 2022; Nieman & Botha, 2024), other species prefer areas with lower visibility to avoid detection from predators or people (Doherty *et al.,* 2022; Creel *et al.,* 2023). Some species have been found to adapt their choice of more open or dense habitat at different times of the day in response to their main predators' temporal patterns (Tambling *et al.,* 2015; Creel *et al.,* 2023). Gaining an understanding of MGRs surrounding and infringing anthropogenic pressures is important to help us learn how these factors impact mammal species fitness and environmental health within the landscape (Tucker *et al.,* 2021^{b}; Nieman & Botha, 2024).

Numerous other factors are known to influence where and when an animal may be found. Intra-specific competition, droughts (Gedir *et al.,* 2020) or diseases (McDonald *et al.,* 2017) may have left certain key species absent or in low-abundance from an area or forced into using or sharing limited spaces that they may have avoided doing so in the past, resulting in a potential increase in competition or facilitation. As the future, potential expansion and rewilding project, occurring on MGR, may result in changes of how inter-specific competition, predation risk and anthropogenic disturbances will impact the behaviour of the mammal populations present, it is helpful to focus this study on these three aspects in order to observe and record future shifts in behaviour.

Understanding mammal behavioral adaptations in response to each other as well as anthropogenic pressures has been greatly facilitated by the use of camera traps. These devices have not only improved our knowledge of mammal species richness and the environmental and anthropogenic predictors of space use (Reece, 2020; Schnetler *et al.*, 2020; Nieman & Botha, 2024; Chapter 3), but have also proven a useful tool to study temporal activity patterns in not only common mammals but also shy, elusive and nocturnal species (Kronfeld-Schor & Dayan, 2003; Welch *et al.,* 2023; Bollen *et al.,* 2024).

As found in Chapter 3, even if a PA may be large it is evident that certain portions of that PA may be undesirable or unsuitable habitat for specific species, and possibly only a small portion of a PA is able to be occupied by a specific species (Nieman & Botha, 2024). Similarly, many species may be unable to use all portions of the diel cycle at the optimal time that they would prefer, affecting mammal species fitness. By improving our understanding of how mammal activity patterns are affected by each other, the landscape and anthropogenic activities we can improve our area-specific understanding of threats to biodiversity and MGRs ecological importance in the larger landscape.

This study aims to address the knowledge gap pertaining to the temporal activity patterns of medium and large mammals on MGR by establishing how they alter their activity patterns in relation to the presence of humans, each other, and perceived safety risks. More specifically, this study aims to understand whether, on MGR:

a) the temporal activity patterns of large herbivores with similar dietary requirements differ in response to potential interspecific competition;

b) the temporal activity patterns of mammal species differ when closer to or further from human settlements, and

c) there is a difference in temporal activity patterns within a species when found in more open or densely vegetated areas.

4.2 Methods

4.2.1 Study Site

The study was conducted in the 11 000 ha MGR in northern-KZN, South Africa. There are two distinct seasons based upon temperature and rainfall: the warm wet season (November to March) and the cool dry season (April to October). Average annual rainfall is 752 mm with around 75% falling in the warm wet season. The estimated mean minimum and maximum temperatures are 6.8°C and 20.8°C in July and 16.4°C and 28.9°C in December, the coldest and warmest months respectively (SAWS, 2022). Daylight length at MGR varies from 12 – 16 hrs with a maximum, summer, sunlight exposure of 13 h and 54 min and a minimum, winter, sunlight exposure of 10 h and 23 min.

The altitude within the reserve ranges from 599 m.a.s.l. in the north eastern corner to 1149 m.a.s.l. on the highest peak in the south. A perennial river, the Hlonyane, runs from west to east in the northern section of the reserve, and two south-north running non-perennial tributaries connect to this in the central part of MGR (Figure

4.1). Five vegetation units are recognised on MGR (Figure 4.1). *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands (SCG) occurs on the southern high land areas while *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna (VCS) are found on the gentle slopes below the SCG. *Euclea schimperi–Searsia pentheri* closed thickets (EST) are found on the steeper, more stony, slopes of MGR. The central and northern, undulating, section of MGR is composed of the *Vachellia tortilis–Dichrostachys cinerea* open to closed woodlands (VDW) and the reserve-wide drainage lines and associated habitats are characterised by dense, tall *Vachellia robusta–Ziziphus mucronata* riverine woodlands (VZR).

The reserve has a mostly permeable fence line of 46.3 km long. While the fence in the south-western corner of MGR, bordering extensive private cattle farms is well maintained, the eastern and northern boundaries of MGR border onto communal grazing areas with the fence flattened in some areas. The northern boundary of MGR is in close proximity to human settlements, some of which are within 50 m of the fence line (Figure 4.1). Residents here are pastoralists, and mostly participate in subsistence farming of livestock, (cattle and goats) and crops (maize, citrus and cabbage).

For a more detailed description of the study site refer to Chapter 2.

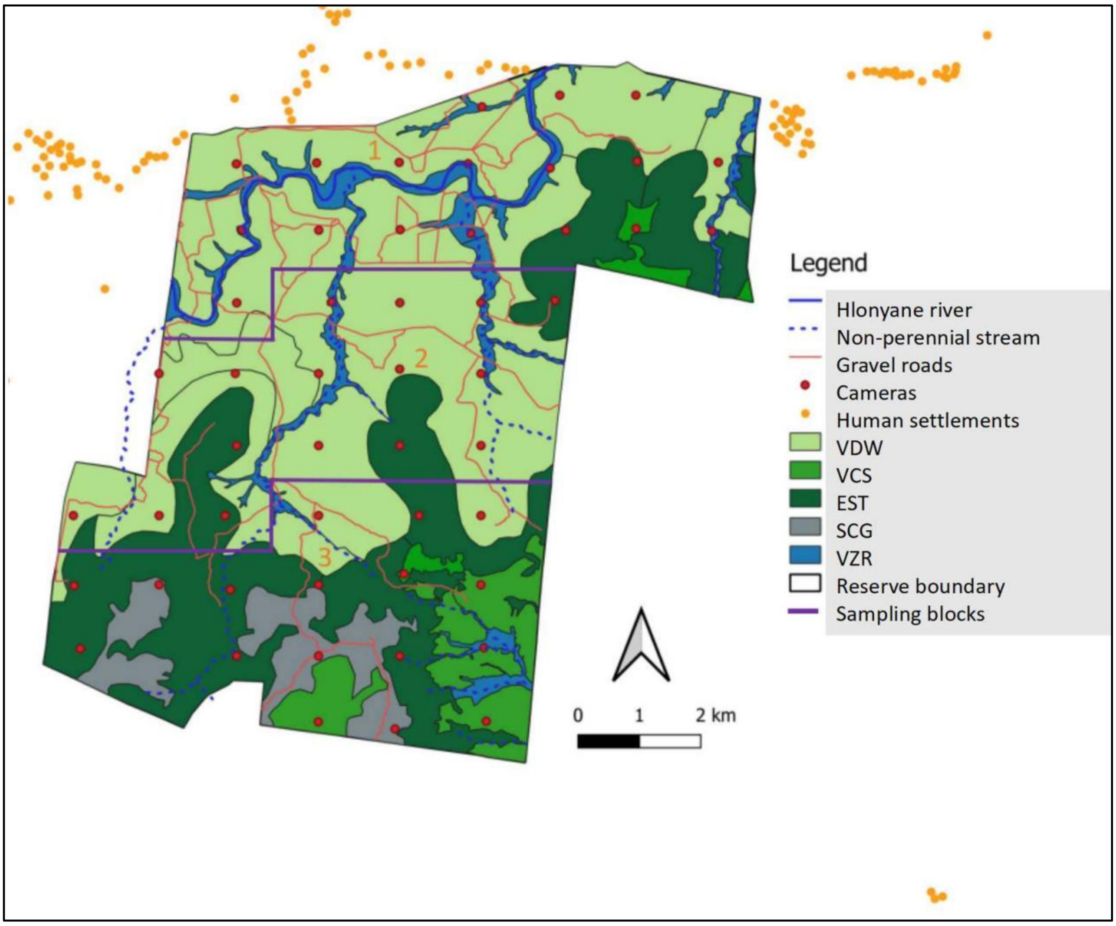


Figure 4.1: Map of Mawana Game Reserve showing the roads, the reserve boundary, rivers, human settlements, and the five different vegetation types. VDW = *Vachellia tortilis–Dichrostachys cinerea* open to closed woodland; VCS = *Vachellia sieberiana–Cymbopogon pospischilii* sparse to dense savanna; EST = *Euclea schimperi–Rhus pentheri* closed thickets; SCG = *Setaria sphacelata–Cymbopogon pospischilii* closed grasslands; VZR = *Vachellia robusta–Ziziphus mucronata* riverine woodland. Also shown are the 51 camera trap locations and the three separate camera rotation sampling blocks indicated by the purple line and numbers.

4.2.2 Survey Design

The camera trap survey of medium and large mammals was conducted across the entirety of MGR, during the wet season from 1 November 2021 to 5 March 2022. The temporal activities of medium and large mammal species were assessed over 5 months during the wet season with only mammals of > 0.5 kg in body mass included in the analyses.

Camera trap spacing and survey duration

A 1.3 x 1.3 km grid was overlaid onto a map of MGR using QGIS 3.1.4 (Comley *et al.,* 2020) and the center point of each grid square identified as a possible camera location, resulting in 55 camera trap locations approximately 1.3 km apart from each other. To ensure representative sampling of the five vegetation units any camera location that fell within 100 m of two different vegetation units was moved to cover the less represented vegetation unit (Tobler *et al.*, 2008; Figure 4.1). Four camera locations were offset in this way. Camera availability necessitated step wise sampling, from north to south, across three survey blocks, with each block having 18 or 19 cameras that were active for 40 days (Figure 4.1). Block 1 was surveyed from 01 November until 10 December 2021, block 2 was surveyed from 11 December until 20 January 2022 and block 3 was surveyed from 21 January until 02 March 2022. Cameras were serviced (memory cards and batteries replaced) mid-way through each survey period, at 20 days.

Camera trap placement and settings

Adapting the methods of Reece (2020) and Comley *et al.* (2020) the exact GPS coordinates for each camera location were identified using QGIS 3.1.4 and Google Earth Engine (GEE) before field operations began. Camera location coordinates were located in the field using a Garmin eTrex10 handheld device. Once a point was located a spiral formation was walked, away from the GPS point, until a suitable game trail was encountered, never further than 100 m away from the pre-identified coordinates (Colyn *et al.,* 2018). The game trail would then be followed for up to 50 m until a suitable tree was found that allowed for a north or south facing camera (Apps & McNutt, 2018) to be placed at 40 cm above the ground (Comley *et al.,* 2020), approximately 1-2 m away from the trail. Cameras were set to a delay of 30 seconds between triggers (Comley *et al.,* 2020) to avoid filling up memory cards and wasting battery charge from false detections, each detection was set to a burst of three images and all cameras were set to record for 24 hours with medium sensitivity. Vegetation obscuring the camera's detection zone was cut to reduce false trigger occurrences, care was taken to not alter the general vegetation characteristics. Night time images were captured using an infrared, 'black flash', with a mid-range setting for the flash. Cameras were placed in specially designed metal boxes and, to prevent theft, chained to the selected tree.

Temporal Activity analyses

To identify representative activity patterns of mammals a minimum of 30 independent detections were considered an adequate sample size (Green *et al.,* 2022). All images of the same species from the same camera were filtered by a 30 minutes to independence interval (Green *et al.*, 2022; Nieman & Botha, 2024). To simplify analyses and allow for categorical comparisons of activtiy periods the time of detection for each species was binned into one of four, six hour periods (Table 4.2). The four periods were defined as: dawn (03h00 - 08h59), day (09h00 - 14h59), dusk (15h00 - 20h59) and night (21h00 - 02h59) as conducted by Green *et al.* (2022).

Three analyses were done to establish how medium and large mammals alter their activity patterns in relation to: a) each other (competition); b) the presence of humans (anthropogenic threat); and c) varying visibility (considered as a proxy for perceived vulnerability to humans and predators). All analyses were conducted using R 4.2.1 (R Development Core Team, 2021).

a) Temporal partitioning in response to competition

Temporal partitioning between pairs of mammal species with similar feeding strategies, feeding heights and body sizes were conducted where a sufficient sample size existed for the pairwise analyses of twelve pairs of herbivorous mammals. No carnivores, omnivores or insectivores could be included due to insufficient sample sizes between species of similar feeding strategies. The twelve pairs compared were: blue wildebeest - plains zebra; nyala - greater kudu; giraffe (*Giraffa giraffa*) - greater kudu; impala - greater kudu; impala - nyala; impala - warthog (*Phacochoerus africanus*); warthog - nyala; warthog - blue wildebeest; warthog - plains zebra; common duiker (*Sylvicapra grimmia*) - nyala; common duiker - impala and lastly common duiker - warthog. Blesbok (*Damaliscus pygargus phillipsi*) were not analysed, despite 105 independent detections, due to insufficient spatial overlap observed between blesbok and their potential competitors.

b) Temporal activity shifts in response to human settlements and activity

The median distance between all 51 camera locations and the nearest human settlement was 3.29 km (Figure 4.2). A total of 20 anthropogenic detections occurred during the camera trap survey and 18 (90%) of these occurred within 3 km of human settlements (Figure 4.2). To investigate the influence that proximity to human settlement and increased human activity may have on the temporal activity patterns of medium and large mammals, all cameras were split into one of two distance classes, either "< 3 km from a settlement" or "> 3 km from a settlement". For each species with sufficient detections the activity patterns of that species within 3 km of a human settlement was compared with the activity patterns of that species further than 3 km away. As 20 anthropogenic detections are insufficient to make robust statistical conclusions, the anthropogenic activity patterns were visualised in an Activity bar chart made using the *Activity* package in R, with a trend line and 95% CI placed over bar chart (Rowcliffe, 2016), however statistical requirements were not met for further anaylsis. Anthropogenic detections included all non-study related, illegal, human detections as well as collared dogs, used as a proxy for human presence (Masseloux *et al.,* 2017; Dias *et al.,* 2019).

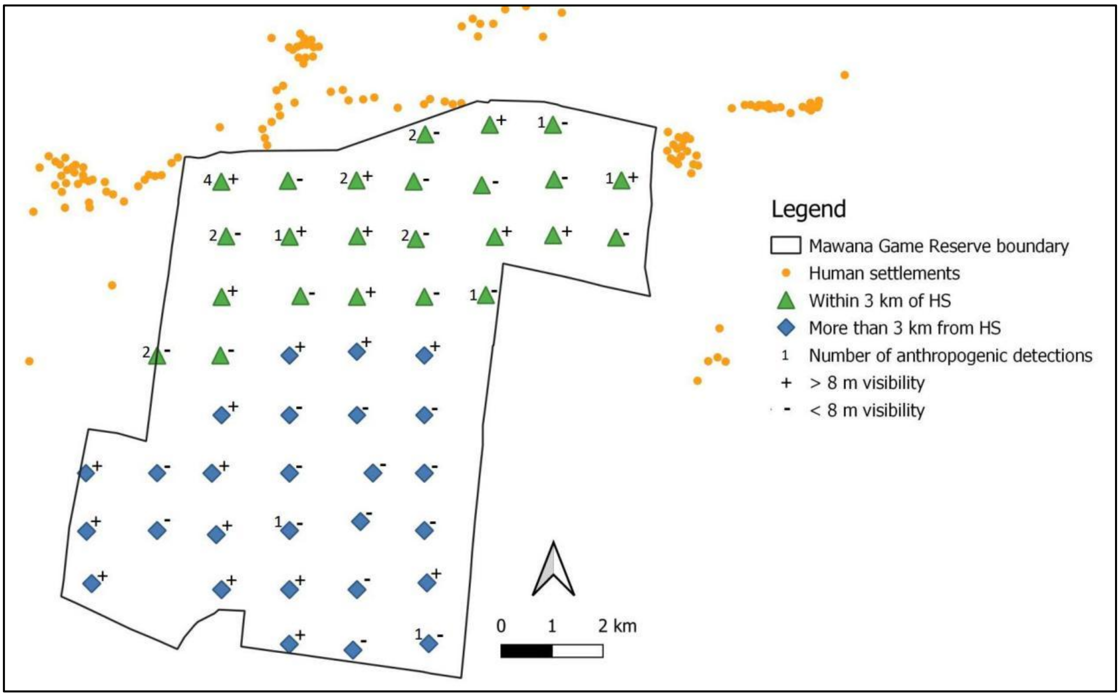


Figure 4.2: Map showing camera positions in relation to human settlements with blue diamonds indicating cameras > 3 km from settlements and green triangles cameras within 3 km. Also shown for each cameras was, whether visibility was more (+) or less (-) than 8 m. Numbers to the left of each camera indicates the number of illegal human and/or dog detections that were made by that camera

c) Temporal Activity shifts in response to variable Visibility

Visibility was measured in meters four times around each camera. An assistant walked directly away from each camera and, using a Bosch GLM50-27, CG Laser Rangefinder, the distance at which a 1 m high marker on the lower part of their body became obscured to the observer was measured as the visibility distance. Visibility measurements were taken straight in front, directly behind, and at a 90° angle to the left and right of each camera. An average visibility distance per camera trap location was calculated from the four distance measurements and reported in meters (Hay *et al.,* 2008; Reece, 2020). The median visibility for all 51 camera locations was just over 8 m. As concealment can be used by mammals as a way to limit detection from both people (Caravaggi *et al.,* 2017) and predators (Bongi *et al.,* 2008; Welch *et al.,* 2015; Nieman & Botha, 2024), temporal activity patterns within a species were compared in areas with < 8 m visibility to areas > 8 m visibility.

4.2.3 *Data analysis and modelling framework*

Individual Pearson's Chi-sqaured Tests were made to compare the number of detections per time category between species pairs (interspecific competition) and within each species for each distance class (< 3 km from a settlement and > 3 km from a settlement; < 8 m visibility and > 8 m visibility). To determine significant changes in activity patterns between the four time periods a Chi-squared Test was run with different significance values for each test, due to the application of Bonferroni corrections that reduce the chance for false positives (van der Weele & Mathur, 2018; Evers *et al.,* 2022; Green *et al.*, 2022). The Pearson's Chi-squared Tests were conducted using the 'chisq.test' function from the 'stats' package of R (R Development Core Team, 2021). To avoid violating any model assumptions, more than 80% of the expected frequencies, used in the Chi-squared tests, need to be > 5 (Cochran, 1952; McHugh, 2013), any species with insufficient data were, therefore, excluded from further analyses.

A kernel density estimate was run for all pairwise comparisons between and within species, after which the coefficient of overlap (Δ) for each pair was used as a metric to understand the degree of overlap between each pair of activity estimates. To run this estimate the 'Overlap' package in R was used (Meredith & Ridout, 2014; Mori *et al.,* 2020; R Development Core Team, 2021). To obtain confidence intervals (CIs) a total of 10 000 permutations were run for each species pair (Meredith & Ridout, 2014; Evers *et al.,* 2022). For species with more than 75 independent detections, Δ_4, was used, while species with less than 75 independent detections made use of Δ_1 (Mori *et al.,* 2020). The coefficient of overlap ranges from 0 (no overlap) - 1 (complete overlap; Ridout & Linkie, 2009). Overlap is considered to be 'low' if the coefficient of overlap is < 0.5, the overlap is considered 'moderate' when it ranges from 0.5 - 0.80 and overlap is considered 'high' if it ranges from 0.80 - 1 (Meredith & Ridout, 2014; Tian *et al.,* 2020). Whereas the Chi-squared Tests used the four binned temporal categories of 'Dawn', 'Daylight', 'Dusk' and 'Night', the non-parametric kernel density activity analyses used the actual capture times for every detection for each species, converted into radians (Krag *et al.,* 2023; Welch *et al.,* 2023). Radians resulted in the time 00h00 ranging from 0.000 radians to 23h59:59 up to 6.28316 radians, with all other times in between this depending on their fraction of the day, using the equation as laid out below (Krag *et al.,* 2023).

$$\text{Total seconds} = (\text{hour} \times 3600) + (\text{minute} \times 60) + \text{second}$$

$$\text{Fraction of the day} = \frac{\text{Total seconds}}{24 \times 3600}$$

$$\text{Radians} = \text{Fraction of the day} \times 2\pi$$

To aid understanding of the studied temporal activity patterns, activity occurrences for each analysis was visualised using the kernel density overlap plots from the ‘Overlap’ package in R (Wickham, 2016). The created plots allowed easy visualisation and comparison of activity patterns for the interspecific competition analyses, as well as the within-species comparisons for proximity to human settlement and visibility classes (Ridout & Linkie, 2008; Meredith & Ridout, 2014). Due to insufficient anthropogenic detections for Chi-squared Tests to be run, only overlap estimates were obtained and visualised for the relationships between anthropogenic activity and mammals potentially targeted in the bush meat trade.

All tests were adjusted using Holm-Bonferroni corrections to reduce the likelihood of false positives (Sinclaire *et al.*, 2013; Giacalone *et al.*, 2018). Three sets of tests were conducted: (1) interspecific competition, (2) variation in activity in response to anthropogenic factors, and (3) variation in activity based on visibility. For each of the three sets of tests, the individual p values were first ranked in ascending order and then each p-value was compared to its adjusted threshold where the adjusted threshold was determined using the following equation:

$P = \alpha / (K-1)$

Where: α represents the standard significance level ($p < 0.05$), and K is the number of tests, decreasing by one after each step. Therefore, for interspecific competition, twelve species pairs were compared, with the most significant compared against an adjusted threshold of 0.0041. The same process was then done for anthropogenic influence (most significant compared against a threshold of 0.0041, 12 tests) and visibility (most significant compared against a threshold of 0.0041, 11 tests).

4.3 Results

A total of 237 905 images were captured from 79 302 trigger events over 1 855 camera days, with a total of 2960 independent detections of targeted species remaining after the thirty-minutes time-to-independence data filter was applied (Table 4.2). Although 2 080 camera days had been scheduled, theft, human and elephant induced damages and technical failures reduced camera days by 225 days. Fifteen species met the 30 independent detections criteria and could be used for further temporal analyses (Table 4.2). Of the 15 species with > 30 independent detections the following 11 were used in the three separate analyses as they had sufficient detections in all contrasting categories; blue wildebeest, common duiker, giraffe, greater kudu, impala, large-spotted genet, nyala, plains zebra, slender mongoose, vervet monkey and warthog. Black-backed jackals lacked a similar species for comparison and thus were excluded from the interspecific species competition analyses, however had sufficient detections for the proximity to human settlements and visibility analyses.

Table 4.2: Details of camera trap detections of the 29 medium and large mammal species recorded during the survey on Mawana Game Reserve using a thirty-minute time-to-independence data filter. Species are arranged alphabetically

Common name	Species name	Total Detections
Aardvark	*Orycteropus afer*	35
African Elephant	*Loxodonta africana*	3
African savanna Hare	*Lepus microtis*	20
Baboon	*Papio ursinus*	20
Black-backed Jackal	*Lupulella mesomelas*	95
Blesbok	*Damaliscus pygargus phillipsi*	105
Blue Wildebeest	*Connochaetes taurinus*	342
Brown Hyena	*hyena brunnea*	2
Bushpig	*Potamochoerus larvatus*	28

Caracal	*Caracal caracal*	1
Common Duiker	*Sylvicapra grimmia*	263
Giraffe	*Giraffa giraffa*	73
Greater Kudu	*Tragelaphus strepsiceros*	340
Honey Badger	*Mellivora capensis*	1
Impala	*Aepyceros melampus*	514
Large-spotted Genet	*Genetta tigrina*	78
Natal Red Duiker	*Cephalophus natalensis*	2
Nyala	*Tragelaphus angasii*	279
Plains Zebra	*Equus quagga burchellii*	225
Porcupine	*Hystrix africaeaustralis*	52
Rock Hyrax	*Procavia capensis*	1
Serval	*Leptailurus serval*	8
Slender Mongoose	*Galerella sanguinea*	137
Spotted Hyena	*Crocuta crocuta*	2
Vervet Monkey	*Chlorocebus pygertythrus*	107
Warthog	*Phacochoerus africanus*	202
Water Mongoose	*Atilax paludinosus*	6
Waterbuck	*Kobus ellipsiprymnus*	12
White-tailed Mongoose	*Ichneumia albicauda*	7

4.3.1 *Forage related Temporal Partitioning*

Warthog and common duiker showed significant temporal partitioning between themselves and various other ungulate species (Table 4.3; Figure 4.3; Figure 4.4; Appendix A). No other species of similar feeding strategies or body size on MGR showed signs of temporal partitioning (Table 4.3; Appendix A). The largest Coefficient of Overlap occurred between impala and nyala, with 0.953 (95% CI = 0.885 - 0.979; Fig. 4.4 e) indicating near complete overlap in activity periods. While most herbivores tend to show crepuscular peaks of activity occurring early in the morning and again in the evening, the warthog displayed activity patterns that peak during the day and declined at sunset (Figure 4.4 f-h, l).

Table 4.2: Pearson's Chi-squared Test and overlap coefficient results for the 12 species pairs, temporal partitioning observed between pairs indicated in bold. *Spp.* 1 and *Spp.* 2 indicates number of independent detections of each species in species pair. * indicates Δ_1 used for analysis, all other pairs analysed with Δ_4

Species pairs	***Spp.* 1**	***Spp.* 2**	**X^2**	**Δ**	**p - value**
Blue wildebeest - plains zebra	342	225	0.61	0.867	0.894
Impala - nyala	514	279	1.38	0.953	0.711
Nyala - greater kudu	279	340	1.78	0.895	0.619
Giraffe - greater kudu	73	340	5.86	*0.865	0.119
Impala - greater kudu	514	340	5.37	0.921	0.061
Impala - warthog	**514**	**202**	**11.72**	**0.795**	**0.008**
Common duiker - nyala	**263**	**279**	**12.45**	**0.820**	**0.0060**
Warthog - nyala	**202**	**279**	**15.97**	**0.774**	**0.001**
Warthog - plains zebra	**202**	**225**	**28.94**	**0.721**	**<0.0001**
Warthog - blue wildebeest	**202**	**342**	**38.34**	**0.683**	**<0.0001**
Common duiker - warthog	**263**	**202**	**44.24**	**0.66**	**<0.0001**
Common duiker - impala	**263**	**514**	**23.04**	**0.823**	**<0.0001**

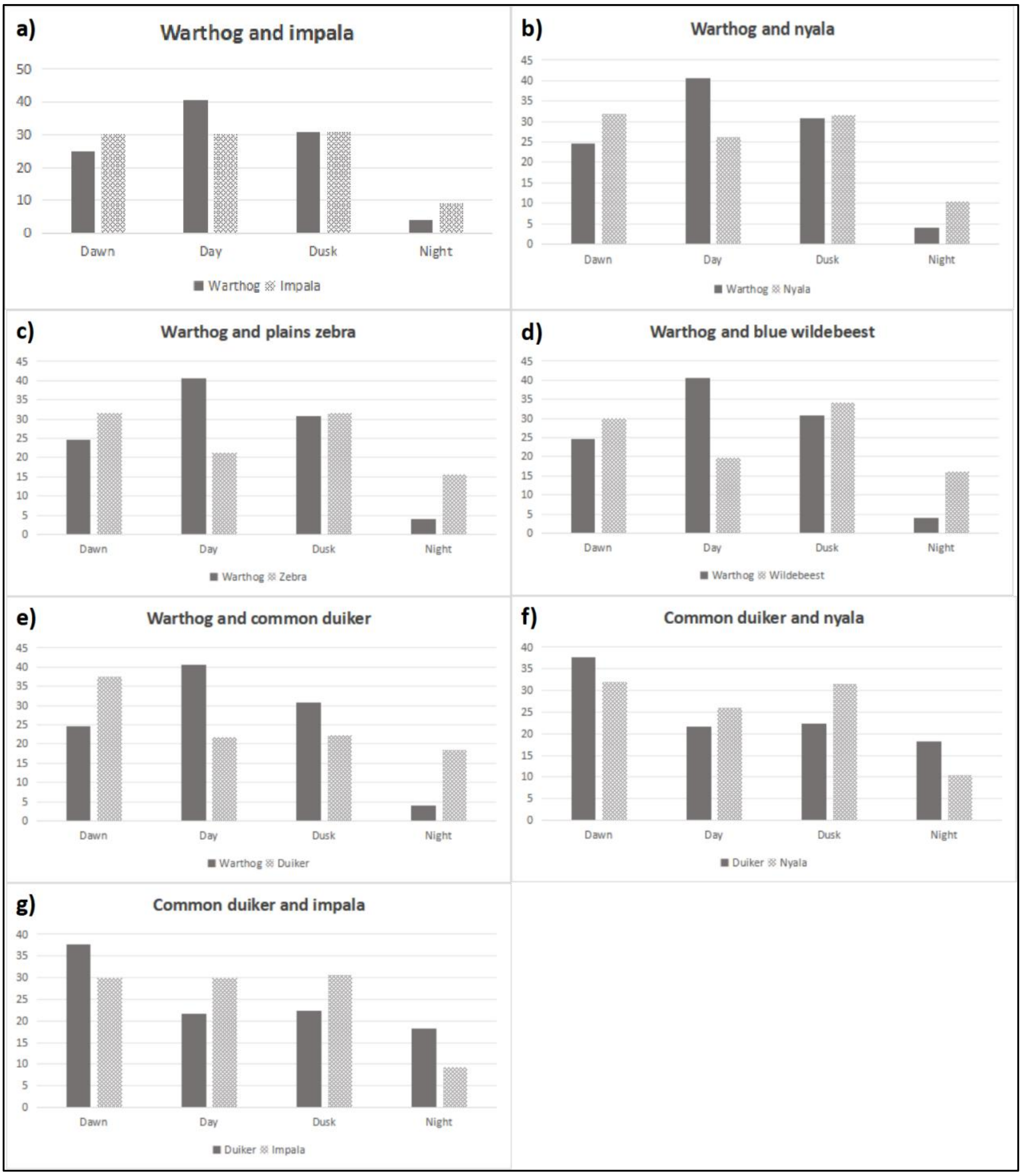
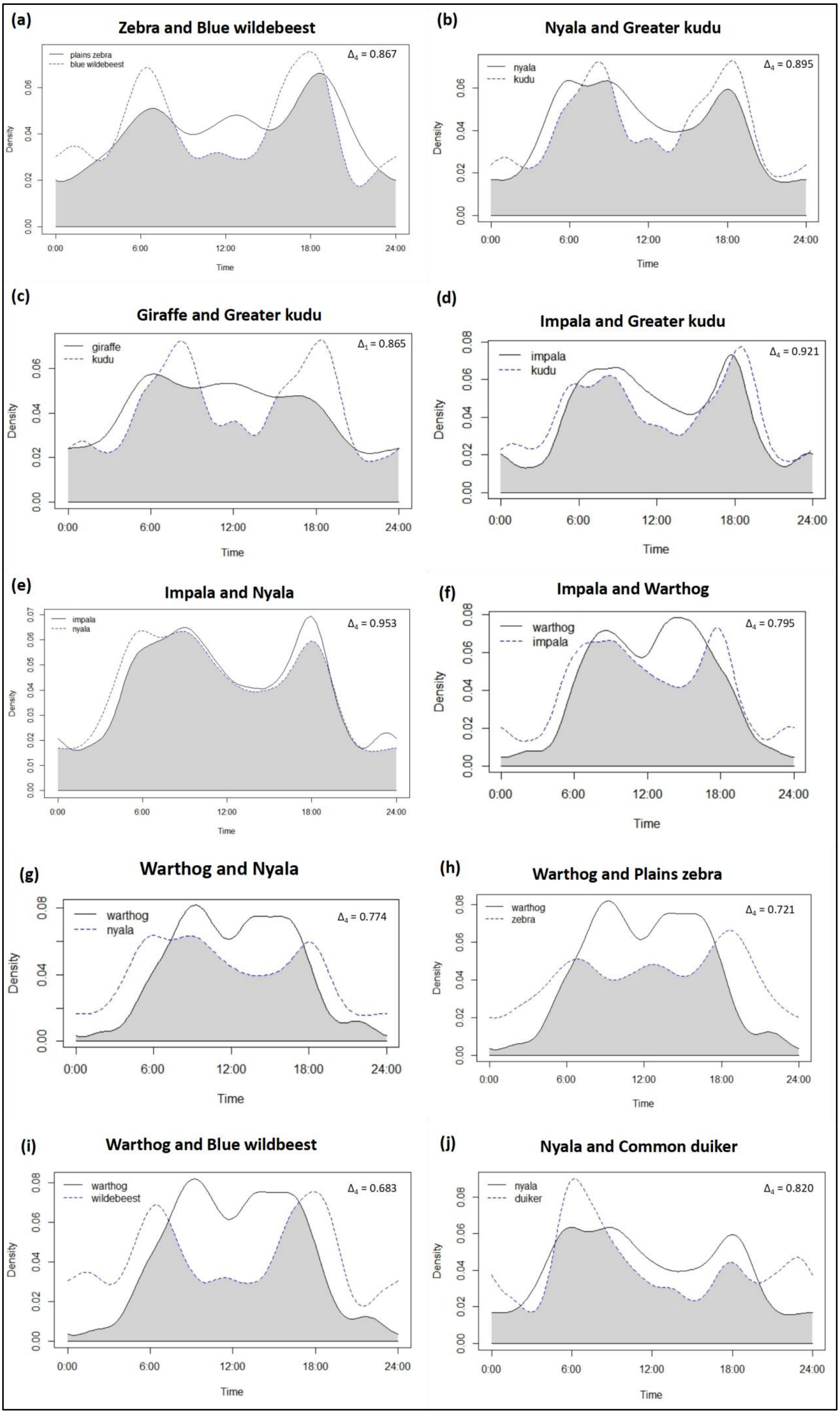


Figure 4.3: Bar charts displaying proportions of detections occurring in each time category for pairs of species (a - g) displaying significance in the differences of their temporal activity patterns


(a)
Zebra and Blue wildebeest
plains zebra
blue wildebeest
Δ_4 = 0.867
Density
0.00
0.02
0.04
0.06
0:00
6:00
12:00
18:00
24:00
Time
(b)
Nyala and Greater kudu
nyala
kudu
Δ_4 = 0.895
Density
Time
(c)
Giraffe and Greater kudu
giraffe
kudu
Δ_1 = 0.865
Density
Time
(d)
Impala and Greater kudu
impala
kudu
Δ_4 = 0.921
Density
0.08
Time
(e)
Impala and Nyala
impala
nyala
Δ_4 = 0.953
Density
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
Time
(f)
Impala and Warthog
warthog
impala
Δ_4 = 0.795
Density
Time
(g)
Warthog and Nyala
warthog
nyala
Δ_4 = 0.774
Density
0.00
0.04
0.08
Time
(h)
Warthog and Plains zebra
warthog
zebra
Δ_4 = 0.721
Density
Time
(i)
Warthog and Blue wildbeest
warthog
wildebeest
Δ_4 = 0.683
Density
Time
(j)
Nyala and Common duiker
nyala
duiker
Δ_4 = 0.820
Density
Time

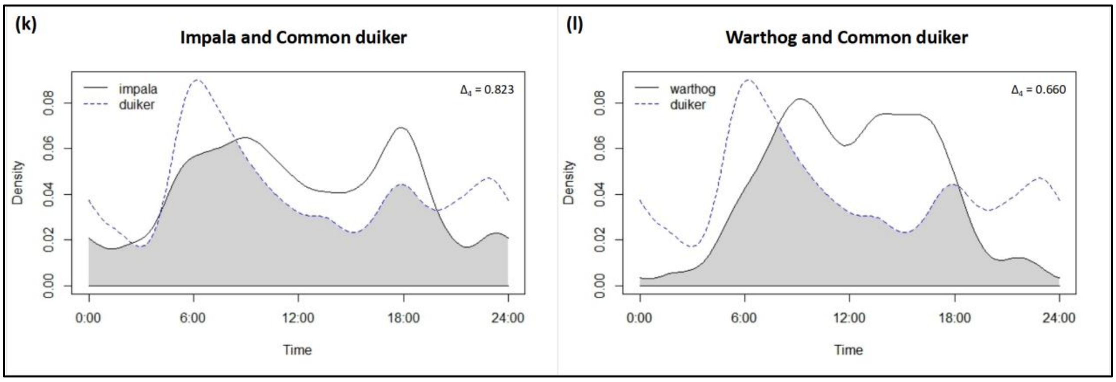


Figure 4.4: Kernel Density Estimate comparing the temporal partitioning activity patterns in 12 pairs of species **(a-l)**. Activity overlap represented by grey shading and Overlap coefficient (Δ) value indicated on each graph. Time indicating the hour of day. Density indicating the proportion of each species activity taking place at the given time of day

4.3.2 Temporal activity change in response to human settlements and activity

Anthropogenic detections indicate an increase in human activity during daylight hours, predominantly from 08h00 until 16h00, and again at midnight (Figure 4.5).

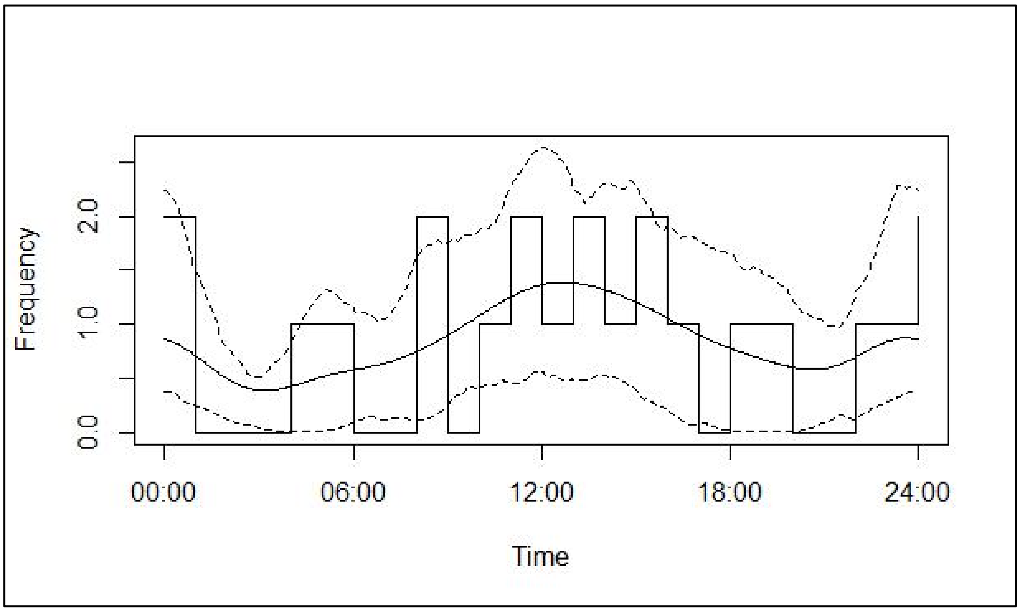


Figure 4.5: Bar chart displaying the 20 anthropogenic detections across MGR. An increase in activity is observed during the day light hours, primarily from 08h00 until 16h00. Trend line (solid) overlayed to show the general trends with the 95% Confidence Intervals (dotted lines) on either side

Twelve species had sufficient detections and thus were analysed for differences in activity patterns when detected > 3 km and < 3 km from human settlements (Table 4.3). The species analysed were black-backed jackal, blue wildebeest, common duiker, giraffe, greater kudu, impala, large-spotted genet, nyala, plains zebra, slender mongoose, vervet monkeys and warthogs.

Table 4.3: Within species differences in activity patterns when detected < 3 km and > 3 km from human settlements. Number of detections per species for > 3km and < 3km are indicated together with the chi square test results for significant differences. * indicates the use of Δ_1 for analyses, all other analyses use Δ_4. Bold indicates overall p - value significance for that model. Species ordered by total number of detections

Common name	> 3 km	< 3 km	p value	X^2 value	Δ
Black-backed Jackal	55	40	0.4189	2.8178	*0.817
Blue Wildebeest	138	204	0.737	1.2728	0.861
Common Duiker	**111**	**152**	**0.001876**	**14.49**	**0.790**
Giraffe	22	51	0.515	2.29	*0.753
Greater Kudu	187	153	0.08173	6.6172	0.839
Impala	185	329	0.04253	8.1637	0.840
Large-spotted Genet	31	47	0.1615	4.8058	*0.771
Nyala	108	171	0.1303	5.553	0.822
Plains Zebra	123	102	0.5513	2.0908	0.915
Slender Mongoose	30	107	0.7528	1.05	*0.899
Vervet Monkey	31	76	0.4427	2.4231	*0.694
Warthog	78	124	0.09012	6.2032	0.859

Common duiker exhibited significant differences in their temporal activity patterns between the two proximity to human settlement distance classes. No other species showed signs of significance in temporal activity based on proximity to human settlements (Appendix B) after the Holm-Bonferroni corrections were completed.

Common duikers detected more than 3 km away from settlements are significantly ($p = 0.0394$; Figure 4.6 a) more active during the daylight hours, than those within 3 km of human settlements. Individuals within 3 km of settlements are significantly more active during the night time than those further from settlements (p = 0.023). A moderate overlap coefficient of 0.790 occurred between both distance classes for common duikers (Figure 4.6 b).

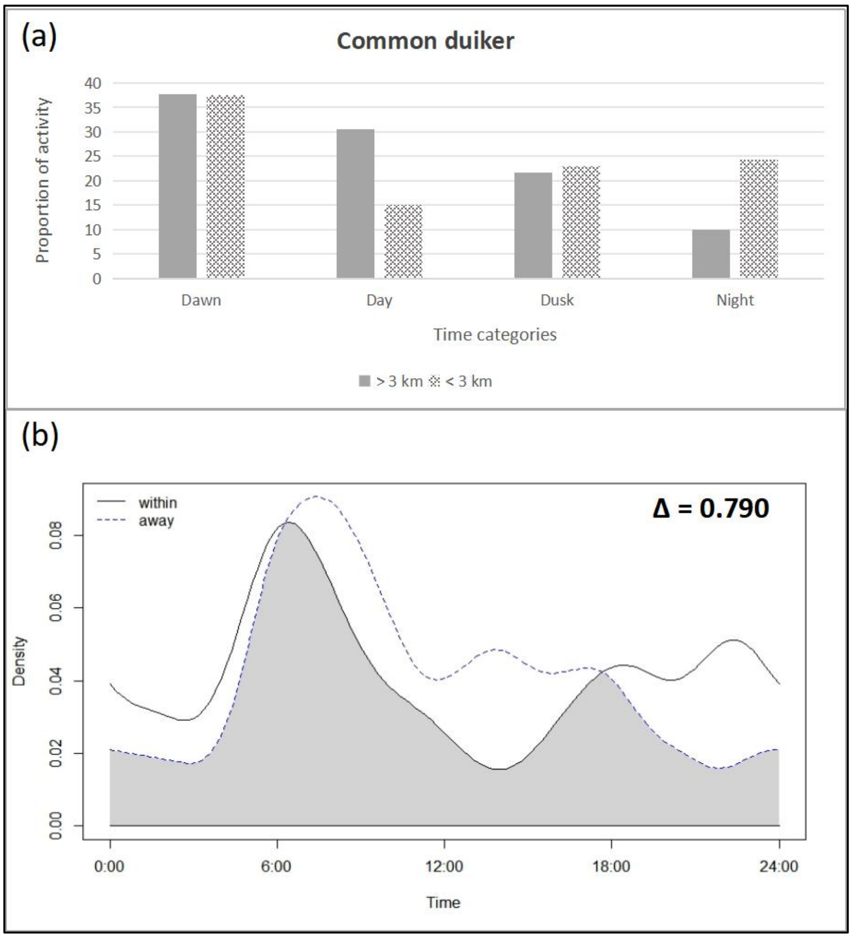


Figure 4.6: Temporal activity patterns of common duikers (a) in a bar chart displaying proportions of detections occurring in each time category and (b) a kernel density estimate graph displaying the activity patterns between the two distance class categories of > 3 km and < 3 km from human settlements

4.3.2.3 Temporal Activity shifts in response to variable visibility

Eleven species had more than 30 detections in both visibility classes (< 8 m and > 8 m), as well sufficient detections in each time category for the Chi-squared Test, these were black-backed jackal, blue wildebeest, common duiker, greater kudu, impala, large spotted genet, nyala, plains zebra, slender mongoose, vervet monkey and warthog (Table 4.5; Appendix C).

Table 4.5: Within species differences in activity patterns when detected in areas with < 8 m and > 8 m of visibility. Number of detections per species for > 8 m and < 8 m are indicated together with the Chi-squared Test results for significant differences. * indicates the use of Δ_1 for analyses, all other analyses use Δ_4. Bold indicates overall p - value significance for that model.

Species	> 8 m	< 8 m	p value	X^2 value	Δ
Black-backed jackal *	64	31	0.9917	0.1014	0.777
Blue wildebeest	192	150	0.1554	5.2353	0.851
Common duiker	108	155	0.3582	3.2254	0.885
Greater kudu	178	162	0.3115	3.5725	0.887
Impala	386	128	0.4225	2.8058	0.912
Large-spotted genet *	30	48	0.3637	3.1867	0.813
Nyala	146	133	0.0693	7.0834	0.858
Plains zebra	137	88	0.0316	8.8352	0.768
Slender mongoose *	66	71	0.0188	9.9676	0.710
Vervet monkey *	44	63	0.2385	4.2215	0.779
Warthog	96	106	0.0767	6.8546	0.844

No species showed signs of significance for temporal activity differences based on visibility (Table 4.5; Appendix C) after the Holm-Bonferroni corrections were applied.

4.4 Discussion

Findings from this study have revealed interesting aspects of mammal temporal activity patterns on MGR. Significant temporal activity differences were found to occur between warthogs and common duiker, separately, with other herbivorous species, specifically, impala, nyala, blue wildebeest and plains zebra. On the contrary impala and nyala were found to have the highest activity overlap between all pairwise comparisons on MGR. Proximity to human settlements was found to influence the temporal activity patterns of common duiker as they were less active in the daylight hours when detected closer to human settlements than individuals detected further away. No species were found to be behaviourally influenced by varying visibility classes on MGR.

Forage related Temporal Partitioning

Given the diurnal nature of warthogs (Deribe *et al.,* 2008; Tambling *et al.,* 2015; Edossa *et al.,* 2020), they are restricted to making use of daylight hours to fulfil their grazing dietary requirements (Deribe *et al.,* 2008), as they utilise burrows at night for sleeping and safety against predation (Somers, 1997; White & Cameron, 2009). Due to the sparse hair of the warthog, burrows also offer assistance for thermoregulation at night (White & Cameron 2009; Vowles, 2018). The herbivorous species to which the warthog was compared, are more crepuscular in nature, and thus benefit from foraging at the cooler, earlier and later, hours of the day (Skinner & Chimimba, 2005; Owen-Smith & Traill, 2017; Ehlers-Smith *et al.,* 2020).

Common duikers were also found to have significantly different temporal activity patterns to warthog, impala and nyala. As common duikers are a species with nocturnal and crepuscular tendencies (Mugerwa *et al.,* 2017), this antelope was detected less frequently during the daylight hours than early morning and late in the evening. Nyala and impala detections peaked during the late morning and then again late in the afternoon / dusk period. Although both species had a high overlap coefficient with duikers (Δ = 0.820 and 0.823 respectively), their activity periods were centered around sunlight hours, while the duiker was more active into the night hours. As selective feeders of high quality browse materials (Lunt & Mhlanga, 2011) not only were the diel activity patterns of common duikers different, compared with impala and nyala, but the duikers dietary requirements are more specialised. Nyala and Impala have broader dietary requirements, and both are known to change their diets based on season and forage availability (van Rooyen, 1992; Botha & Stock, 2005; Kos *et al.,* 2012). Given both the temporal and trophic separation between duikers and impala and nyala it is unlikely that these species come into competition with each other.

Impala and nyala displayed the greatest observed temporal overlap between two species on MGR (Δ_4 = 0.953; CI = 0.885 - 0.979). As these two species share similar activity periods and feeding strategies (O'Kane *et al.,* 2011) their interactions could be facilitated by slight differences in their dietary preferences (Kazembe*,* 2010).

Although both are mixed feeders (van Rooyen, 1992), nyala have been found to prefer browse resources, while impala prefer graze resources (van Rooyen, 1992; Botha & Stock, 2005; O'Kane *et al.,* 2011), especially during the wet season. Their differences in body sizes (Skinner & Chimimba, 2005) result in different dietary requirements (Kazembe*,* 2010). Nyala are known to out-compete the similar, bushbuck, in environments where they co-occur (Ehlers-Smith *et al.,* 2020), however, they do not appear to have the same impact on impala (Kazembe, 2010). Whether either of these two species, however, out-competes the other may be identified in future studies that use this study as the baseline. No spatial analyses were conducted between these two species and it is therefore possible that although they are active at, largely, the same time in a 24-hour cycle they may be active in different places to avoid competition, further analysis may help to understand this relationship better. It is also true that the particular feeding differences between nyala and impala may assist facilitation between the two rather than competition. Overlap in temporal activity may be the result of mixed-herds, which while allowing the two to outcompete other smaller single-species herds, may also aid in increased vigilance, assisting against predation (Stensland *et al.,* 2003).

As herbivorous mixed-feeders (Sponheimer *et al.,* 2003; Kos *et al.,* 2012) and given their observed difference in temporal activity patterns, it is unlikely that either nyala or impala are in direct competition with warthogs. While nyala and impala eat the small greener shoots of grass and young branches of browse (O'Kane *et al.,* 2011) warthogs more commonly eat entire grass leaves, including roots (Teklehaimanot & Balakrishnan, 2017). Although all three species utilise fallen fruits and seed pods from trees (Kos *et al.,* 2013; Teklehaimanot & Balakrishnan, 2017, Mgqatsa *et al.,* 2024), flexibility in diet may facilitate foraging in the vicinity of each other, while limiting interspecific competition.

None of the other hypothesised pairs of species with similar body sizes and feeding strategies showed signs of temporal partitioning on MGR. Zebra and wildebeest, however, have been found, in similar environments, to partition resources spatially

(Owen-Smith *et al.,* 2015), while giraffe and kudu, and kudu and impala have been found to have high overlap in resources used (O'Kane *et al.,* 2011). Given their biology, giraffe have shown a wider range of browsing heights, with a greater ability to change heights based on forage availability (O'Kane *et al.,* 2011) and therefore are unlikely to come into competition with the other ungulates in question. Although there were too few detections of elephants to conduct any statistical assessments of their competitive relationship with other species, multiple studies have found elephants to aid facilitation with other species, as bulk grazers, elephants regularly eat low quality forage avoided by other species (Odadi *et al.*, 2011*;* O'Kane *et al.,* 2011). Their feeding style also creates high nutrition feeding opportunities for other species, as they give smaller species the opportunity to access leaves and fruits usually out of reach at the tops of trees, as well as maintaining grass dominated landscapes and preventing bush encroachment (Western, 1989), a feeding strategy that has also been proven to disadvantage other smaller prey species through making dense environments more accessible to predators (Tambling *et al.,* 2013).

The lack of interspecific competition identified on MGR may indicate that the reserve has enough resources, during the wet season, to sustain the current mammal biomass. Should another similar study be conducted during the dry season these results may look quite different and more interspecific competition is likely to be identified, as is usual in dry seasons when resources are scarce (Dekker *et al.,* 1996*;* O'Kane *et al.,* 2011). As this data only examines temporal overlap, it does not rule out that competition between two species may still occur at a different level, either spatially or from a feeding mechanism that may have resulted in one animal outcompeting another from certain parts of MGR already.

Human Activity and Settlements

Despite proximity to human settlements being positively correlated to species richness and a space use predictor for individual species across MGR (Chapter 3), it appears that common duiker are influenced behaviourally by altering their activity periods due to proximity of human settlements. Common duikers detected further than 3 km from human settlements were more active in the daylight period than those detected closer to settlements. Duikers detected closer to settlements were more active during the night hours than those detected further away, a typical predator avoidance response in a landscape of fear (Swanson *et al.,* 2016*;* Beschta & Ripple, 2019; Suraci *et al.,* 2019).

The reduction in day time activity, when detected closer to human settlements, could possibly be in response to the correlated peaks in illegal anthropogenic activity patterns. Although anthropogenic detections were less than the minimum of 30 required detections for robust statistical analysis (Green *et al.,* 2022), the general trend of anthropogenic activity peaked during the daylight hours. Most past research found poaching activity to peak at night, possibly in an attempt to limit detection from anti-poaching patrols (Lindsey *et al.,* 2009; Martins & Shackleton, 2019). Anthropogenic detections on MGR, however, increased during the daylight hours, specifically between 08h00 and 16h00. As MGR had limited resources dedicated to anti-poaching before and during this study period, there was little potential for being caught and prosecuted, presumably leading to the more convenient daytime activity. As snaring is also prevalent on MGR (Pers. Obs.; van der Walt pers. comm. 2021) it is likely that people are using this period of the day to not only actively hunt, but also check or set snares as well as harvest other natural resources.

Multiple wild mammal species have shown the ability to change their behavioural patterns based on human proximity and disturbances (Grignolio *et al.,* 2011; Ohashi *et al.,* 2013; Cappa *et al.,* 2017) often with a tendency to use an area at a time of the day when people are less likely to be encountered (Gaynor *et al.,* 2018). As human disturbance factors are likely to increase closer to human settlements (Benítez-López *et al.,* 2010; Bar-Massada *et al.,* 2014) it is likely that the behaviour of duiker within 3 km of human settlements has adapted to being less conspicuous at the same time of the day when the human detections were at their highest.

Night time activity of duiker was detected significantly more closer to settlements, possibly a result of the decreased foraging opportunities during the daylight hours. Despite the common duiker being considered a nocturnal species (Skinner & Chimimba, 2005), those further from settlements were able to spend more time fulfilling their dietary requirements during the daylight hours compared to those within close proximity to settlements.

Whether people may be hunting or not, the activity patterns of duiker supports an avoidant behaviour markedly similar to anti-predatory behaviour observed in other common prey species (Tambling *et al.*, 2015; Gaynor *et al.,* 2018; Zong *et al.,* 2023). Although nyala have been found to be the most utilised species in the KZN bushmeat trade (Pillinger, 2003; Kammer, 2006), wildebeest, impala, kudu, duiker, hare species and warthogs have also been observed as targeted on MGR (Pers. Obs.). While there were insufficient detections of hare species to conduct any statistical analyses on their temporal activity patterns, no significant shift in activity periods were detected for wildebeest, impala, kudu, nyala or warthogs. Common duikers, given their smaller size than other ungulates found on MGR, may be targeted by poaching and possibly easier prey for dogs, resulting in less activity overlap with people.

Temporal shifts in activity periods, as seen in duikers, can have impacting results on species health as the advantages that comes from being active at optimal times of the day for feeding, dispersal and breeding opportunities are forfeited (Hendry *et al.,*2008; Gaynor *et al.,* 2018). Reductions in fitness would likely have compounding effects on young mammals, due to their higher energy requirements (Marshall *et al.*, 2017; Drake *et al.,* 2024), resulting in higher mortality rates in young, impacting mammal population demographics and growth within MGR.

Visibility

No species were detected to be significantly impacted by visibility classes on MGR, possibly a result of a low predator abundance (Chapter 3). In reserves where relatively high abundance of large predators do exist, as is the plan for reintroductions on MGR, many prey species tend to avoid dense areas at the time period when their predators would be most active (Thaker *et al.,* 2010; Tambling *et al.,* 2015; Owen-Smith & Traill, 2017). Observations from Kruger National Park found wildebeest herds avoiding lions by using open areas at the time of day when lions are most active (Owen-Smith & Traill, 2017). Creel *et al.* (2023) found the opposite, and observed zebra to use closed areas at the time of day when their predators would be most active, in an attempt to avoid detection. Repeating this study after predator reintroductions have taken place and fencing improved across MGR may help to inform mammal behaviour responses to predation.

Due to the low detections of carnivorous and insectivorous mammals on MGR, no assessments could be made of their response to the proximity of human settlements and varying environmental visibility. Given past research findings, it is likely that carnivorous mammals are highly impacted by human presence (Creel *et al.,* 2013; Sévêque *et al.,* 2021; Burton *et al.,* 2024). Carnivore-targeted studies on MGR may, therefore, be able to shed more light on how this group of mammals adapts their behaviour temporally in response to anthropogenic pressures. Repeating this study in the years to follow as MGR may undergo varying degrees of protection and associated change in anthropogenic pressures will assist in the reserve management planning and conservation of the species currently found on MGR.

Although temporal overlap or partioning has been observed for many species on MGR, this does not necessarily signify a competitive nature, unless the interaction leads to a negative side effect for one species (Cronk & Pillay, 2020). Some species may, on the other hand, have no true influence on each other, despite being found to associate with one another spatially and temporally.

This research focused on three aspects that influence mammal spatial activity, however, many other factors contribute to the spatial patterns of mammals. Occurrences such as disease outbreaks, droughts (Gedir *et al.,* 2020) and rainfall patterns (Ahlers *et al.,* 2015) lead to mammals selecting certain places at certain times of the day or year, in response to the altered environmental conditions. Anthropogenic activities, beyond settlements themselves, have been found to influence mammal behaviour, such as livestock presence and movements (Masiaine *et al.,* 2021). Intra-specific competition is also an important biological trait as species compete within themselves for the best resources and access to feeding and mating opportunities, such interactions may result in skewed temporal activity patterns at different times throughout a day or year, such as a large number of males gathering together for rutting observed in impala (Murray, 1982). As MGR remains a poorly studied nature reserve many of the above mentioned aspects governing mammal biology and conservation strategies on the reserve should be looked at in further detail.

4.5 Conclusion

Although no unexpected resource partitioning was observed between species pairs in response to feeding resources, it was shown that both warthogs and common duikers maintain significantly different diel activity patterns to the species with which they were compared. Given the rigid diurnal and mostly nocturnal habits for the warthog and common duiker respectively, it is not a surprise that both of these species displayed unique temporal activity patterns to other herbivorous mammals.

While the number of anthropogenic detections was insufficient to test for significance in the relationship between anthropogenic activity and the temporal activity patterns of mammals, proximity to human settlements maintained a significant influence on common duikers. Duikers were found to decrease their day time activity when detected in close proximity to settlements, potentially a fear-based response to the disturbances associated with settlements.

No species showed any significance based on the visibility characteristics of the area.

Analyses of mammal responses to proximity of human settlements and varying habitat density should once again be studied when fencing and anti-poaching operations on MGR have improved and large predator reintroductions have taken place. Future studies of this nature will help gain a better understanding of the impacts that management practices have on wildlife in PAs across South Africa, and make more informed management plans for MGR.

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CHAPTER FIVE:

RESEARCH FINDINGS AND MANAGEMENT IMPLICATIONS

Globally wildlife populations have declined by 73% in the past 54 years (WWF, 2024). The importance of biodiversity and the related ecosystem services required for sustained human life on Earth cannot be separated (Rockström *et al.*, 2009). Our species reliance on a healthy functioning planet is not fully understood, but there is strong evidence that biodiversity plays an integral role in the longevity of a living planet (Millenium Ecosystem Assessment, 2005; Rockström *et al.*, 2009; WWF, 2024). Focusing conservation efforts onto biodiversity hotspots will be the best method to ensure preservation of the most valuable areas for biodiversity conservation (Mittermeier *et al.,* 2011). As seven of the Earth's 35 biodiversity hotspots occur in Africa, with approximately 20% of all of Earth's species on the same continent, more conservation efforts across Africa are crucial to protect a large portion of Earth's biodiversity. The sub-Saharan region of Africa is expected to undergo, globally, the largest increase in human population by 2050 (United Nations, 2019). With three biodiversity hotspots in South Africa alone, the country ranks as one of the most biodiverse countries in the world (Convention on Biological Diversity, 2006). South Africa's three hotspots have varying levels of protection and threats, the most threatened by land transformation is the Maputaland Pondoland-Albany hotspot (MPAh; Mittermeier *et al.*, 2011) found along the South Africa's east coast, as well as in Eswatini and southern Mozambique. Gaining a better understanding of the success and failure of conservation efforts in this hotspot rely on biodiversity assessments and monitoring. One understudied reserve in the MPAh that allowed an opportunity to study both anthropogenic and environmental factors effect on medium and large mammals is Mawana Game Resrve (MGR) that can contribute significantly to the conservation of the MPAh as well as South Africa's most threatened biome, the grasslands.

As a medium sized (11 000 ha) fenced reserve, MGR, experiences many anthropogenic and environmental pressures from both outside and within the reserve. The growing human presence around the reserve, as well as an environmentally diverse landscape, results in many factors that may influence the fitness of wild medium and large mammal species. Many wild mammals were already on MGR, having never been extirpated, but since 1980 other large mammal reintroductions have taken place and plans are currently underway to include MGR into an expanded (30 000 ha) protected area. As an understudied reserve, no official data existed on what still occurs on the land after decades of poaching and hunting have occurred. The baseline data gathered here, together with future monitoring, will help with understanding how the system of MGR and surrounds works and can be best managed. Should the proposed PA expansion occur, referred to in Chapter two, and large predators and more mega-herbivores be reintroduced, it is recommended that this study be repeated to reveal the impact that the reintroduction of these species may have in an environment. Repetition of this study may also shed light on whether improved fencing and anti-poaching actions can change the medium and large mammals space and time use.

Species richness and its predictors

This camera trap study confirmed the presence of 29 mammal species (56% of historical estimates; Chapter 3), with another six known to occur on MGR. Bayesian and incidence-based species richness estimators suggest between three and six species may be missing in addition to the 29 detected species which therefore lead to a fairly accurate estimate of 35 species of medium and large mammals still occurring on MGR. Although these estimators indicate that the study efforts resulted in missed species, the study has created a baseline on which future surveys will be able to build. Species missed in this survey, yet known to occur on MGR, included, the African leopard (*Panthera pardus*), Cape clawless otter (Aonyx capensis), striped polecat (*Ictonyx striatus*), aardwolf (*Proteles cristata*), mountain reedbuck (*Redunca fulvorufula*) and grey rhebok (*Pelea capreolus*). Visual confirmation, additional camera trapping and spoor assessments have confirmed these species to still occur on the reserve prior to and since this study. Given the local *Vulnerable* IUCN status of the leopard (IUCN, 2024), it is recommended that further targeted camera trap surveys are carried out across MGR and the greater landscape, strengthened by partnerships with organisations such as Panthera or Wildlife ACT. For this study, paired cameras could be set up along well used trails, near popular water points and around fresh carcasses opportunistically found around MGR. Targeted capture - recapture studies of this nature, may help to gain better information on the presence and population dynamics of leopards and other predators, such as spotted hyenas (*Crocuta crocuta*) and the *Near Threatened* brown hyenas (*Parahyena brunnea;* IUCN, 2024), as individuals for all of these species can be identified from camera trap images. Both the honey badger (*Mellivora capensis*) and the Natal red duiker (*Cephalophus natalensis*), previously assumed to be locally extinct on MGR prior to the study, were confirmed to be present on the reserve during the study, and both have been detected again since this camera trap survey took place.

Other than black-backed jackal (*Lupulella mesomelas*) all other medium and large predatory species had very low detections, most likely a result of years of persecution from neighbouring human settlements and farms. After black-backed jackals, serval were the most detected predators but with just 7 detections overall. Of the herbivores impala, blue wildebeest and greater kudu were the three most numerously detected species, with 502, 342 and 340 detections respectively, while the Natal red duiker had two and the rock hyrax had a single detection.

Of the ten predictors considered to be influential on species richness patterns that were assessed (Chapter 3), seven were environmental and three anthropogenically derived. Environmental covariates were found to have a larger impact on mammal species-specific as well as species richness space use patterns than anthropogenic factors. The only environmental predictor that was assessed and found to have no influence on mammal species richness patterns nor individual species space-use was ‘slope’. The other six environmental predictors were found to not only predict species richness patterns overall, but also certain individual species space use patterns in particular. These six predictors were: altitude, fire, grass biomass, vegetation types, vegetation type variation and visibility. Given that this study occurred over the wet season, proximity to water was not considered when assessing species richness predictors, as water was readily available (within 350 m from any given location) and the near impossibility to map all temporarily available pools and pans. Species richness as a whole declined as altitude increased, although it is believed that this is more likely a result of other changing environmental characteristics such as vegetation type, rather than altitude, given the relatively small change in altitude over MGR (ISMM, 2001). Blesbok and impala were both detected significantly more at higher altitudes, very likely a selection for the dietary opportunities found in these areas, such as diverse, short grass species, something blesbok select for (Novellie, 1978). Whether areas were recently burnt or not had no overall impact on species richness but proved to be a significant predictor for giraffe which preferred unburned areas, likely a result of their dietary requirements of browse forage being found predominantly in habitats that do not burn as frequently, due to a reduced grass biomass (Kraaij & Ward, 2006; Smit & Prins, 2015). Species richness decreased significantly as grass biomass increased, with vervet monkeys and bushpigs being the two species to significantly show this trend. Vegetation type variation was a strong predictor of species richness declines, species richness was, unusually, greater in areas with less variation in vegetation types than areas with more variation. Species wise, giraffe, impala, plains zebra and black-backed jackal, particularly were found to occupy areas with less variation in vegetation types than areas with more variation. Most research into the effects of vegetation variation have found habitat and vegetation heterogeneity to be a strong positive predictor of mammal species richness on a global and local scale (Kerr & Packer, 1996; Tews *et al.,* 2004; Regolin, *et al.,* 2020). It is unlikely that the landscape characteristic of increased vegetation diversity, on MGR, was the predictor of species richness decline itself. The method used to describe vegetation type variation looked only at the number of different vegetation units within each block of the 1.3 x 1.3 km grid cells, this method did not take into account the diversity of habitat structures and plant species diversity within each vegetation unit. The northern section of MGR, also the area with the lowest number of vegetation units, is dominated by the unit that appears to be most selected for by many mammal species and was itself a positive predictor of mammal species richness. The vegetation unit (*Vachellia tortilis - Dichrostachys cinerea* open to closed woodlands; VDW) found in the northern sections of MGR, is a flat, slightly undulating, environment that has a diverse range of habitat structures and is made up of *Dichrostachys cinerea* as well as *Euphorbia ingens* open and closed, diverse, savanna with generally a high visibility (Mostert & Mostert, *in prep.*). These habitat characteristics may explain the mammal species compositions.

Of the five different vegetation types, clear species richness preferences were found for the VDW while the vegetation type used the least was the *Vachellia sieberiana–Cymbopogon plurinodis* sparse to dense savanna, this vegetation unit was found in the southern section of MGR, on the lower altitude slopes, mostly dominated by short grasslands. A significant species richness increase was observed with an increase in vegetation openness (visibility), but the only species showing a significant preference for areas of greater visibility were the plains zebra and blesbok, both grazers, preferring areas of higher visibility most likely due the characteristics of grazing areas as well as anti-predatory behaviour (Palmer, 2018; Lasky, 2022).

Of the three anthropogenic covariates, only proximity to human settlement was found to be a significant predictor of species richness space use. Ex-situ human settlements were found to be a positive predictor of species richness, and specifically positive for impala, nyala and vervet monkeys. Proximity to roads and reserve boundaries were not found to have any significant influence over mammal species richness, however, at species levels, warthogs and baboons showed a strong positive correlation to roads. Blesbok were more commonly found near the reserve boundary while nyala were more common further from the boundary, most probably a response to increased in anthropogenic activities in the areas near the reserve edges, a factor limiting the effective protected area size for nyala.

As no previous studies have been conducted on MGR looking at the mammal assemblage, this study can be used as a baseline for future studies. Further, proposed increases in the reserve size as well as improvements to fences and reintroductions of more megaherbivores and large predators to the reserve should lead to fascinating changes in mammal species compositions and the predictors of the mammal space use on MGR. It is recommended that similar studies are repeated throughout this process. To gain a better insight into the current meso- and large predator populations on the reserve it is suggested to look into conducting further baited or targeted camera trapping surveys across MGR to increase the likelihood of detecting the species missed in this study.

Mammal Temporal Activity Patterns

The study of the medium and large mammals space use patterns was followed by an investigation into the temporal activity patterns of medium and large mammals that co-occur and hence potentially compete for the same resources. In addition the effect that perceived anthropogenic and predation threats might have on species temporal activity was also studied by using vegetation density (i.e. visibility) and distance from neighboring human settlements as a proxy for predation and anthropogenic threats respectively (Chapter 4).

Temporal partitioning was observed between warthogs and a number of other herbivorous species such as impala, nyala, plains zebra, blue wildebeest and common duiker. There was also temporal partitioning observed between common duikers and nyala, and common duikers and impala on MGR. The partitioning observed between warthogs and other herbviores may be explained by the dirunal nature of the warthog (Botha & Stock, 2005; Kos et al., 2012; Edossa *et al.,* 2020), as a species which spends nights in burrows for safety and thermoregulation, no activity is detected during the night time hours (Somers, 1997), while other species may be more crepuscular and make use of the cooler, safer hours of the day for foraging. Similarly the common duiker is a species with slightly more nocturnal /

crepuscular tendencies (Mugerwa *et al.,* 2017), and therefore is less active at times of daylight when other species may be more active.

Eighteen of the 20 (90%) illegal anthropogenic detections (people and collared dogs) occurred within 3 km of neighboring human settlements, this distance was thus considered a potential danger zone for animals within which they might alter their time use patterns to limit encounters with humans. Of the 12 mammal (herbivores and omnivores) species with enough detections, within, and further than 3 km from human settlements, to allow statistical analyses, only the common duiker was found have significantly different temporal activity patterns close and far from human settlements. Duiker exhibited a decline in daily temporal activity patterns when detected within 3 km of human settlements which coincide with the time of peak human detection 12 (60%) of the 20 detection were between 08h00 and 15h00. Although only common duikers demonstrated significant reductions in midday temporal activity patterns, the general trend among other herbivorous and omnivorous mammals was similar. Individuals detected more than 3 km away from settlements exhibited activity patterns displaying increases to their midday activity compared to their counterparts near settlements. Further studies looking at the relationship between settlement proximity and mammal activity patterns are recommended to assess the full extent of the influence anthopogenic disturbances may have on mammals on MGR. If indeed, it is the case that mammals are impacted by settlements this may have wider impact on species across MGR than was detected, more than just mammals too, with possibly exaggerated impacts in the dry season when resources are scarce. Impacts such as altered temporal activity patterns are likely to be long lasting and lead to reduced species fitness on MGR, resulting from the inability to be active at the optimum time of day.

Of the 11 species that could be analyzed in areas with varying visibility two species, none were found to use areas with varying visibility characteristics differently throughout the diel cycle. Although both zebra and slender mongoose showed to have significant responses to visibility when compared to traditional p value of < 0.05, Holm-Bonferroni corrections resulted in this changing. perhaps as a predator avoidance technique, or selection of favoured feeding areas. Individual zebras detected in areas with > 8 m of visibility were detected significantly more in the hours of dawn, most likely taking advantage of grazing opportunities before anthropogenic activity and ambient temperatures increased. The non-significance displayed from species may be a result of predators on MGR occuring in a relatively low abundance (Chapter 3), other studies have found the impacts of predators present may be enough to result in similar temporal change in both wildebeest and zebra (Martin & Owen-Smith, 2016; Owen-Smith & Traill, 2017).

For mammals, altering activity periods due to the perceived and real threats from anthropogenic factors on MGR, can negatively influence the fitness levels of the mammals present on the reserve, having lifetime knock-on effects (Marshall *et al.,* 2016) as feeding and moving at the optimum time of day may not be an option. As there were too few detections of predators and insectivores on MGR, the influence of anthropogenic threats on these groups of mammals remains unknown, however, based on previous findings it likely that the anthropogenic impacts on predator species is strongly negative (Oriol-Cotterill *et al.,* 2015; Nieman & Botha, 2024) and further monitoring to investigate this is encouraged. Monitoring how the temporal activity patterns of mammals in response to anthropogenic pressures changes over time, will give the MGR management team a good indication as to the success or failure of management actions put in place to attempt to reduce poaching incidents and other illegal activities.

Concluding remarks

To help us understand the impacts that anthropogenic activities may have on the future of biodiversity conservation across Africa past research has emphasised the need for repeatable studies to be conducted in small reserves isolated within mosaics of other land-uses (Ahumada *et al.*, 2013; Reece, 2020). The findings produced in this study will assist management to refine and improve decisions guiding conservation actions across MGR, and hopefully other reserves facing similar challenges. With more than 2/3 of the species thought to exist on MGR historically, still present, the reserve is in a position to act as a refuge for these species and other species scheduled for reintroduction, some of which are threatened with extinction such as cheetahs (*Acinonyx jubatus*), white (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*) and pangolin (*Smutsia temminckii*). Although anthropogenic pressures on wildlife are evident across MGR, it appears that these impacts are, at this stage, still manageable and not as detrimental as generally perceived. However, there are indications that some species are already altering their behavior in reaction to human presence with potential long term consequences. It is thus advocated that more financial resources be put towards improved fencing and increased anti-poaching patrols conducted on MGR.

The hope is that this study has been able to contribute to not only baseline data on mammal species present and the environmental and anthropogenic factors influencing their spatio-temporal activity patterns, but that it may also guide many more reserve wide studies to come. This study has also shed light on to the importance of MGR in the conservation of biodiversity within the MPAh and highlights the importance for MGR to be included in the larger protected area proposed for the landscape. With the proposed expansion project and involvement from neighbouring human communities, the future of MGR can be bright but it needs decisive action before the anthropogenic threats and associated disturbances increase further. With the appropriate law enforcement, environmental education and reinforcing of the reserve boundaries and other infrastructure, MGR can play a vital role in the conservation of the Maputaland Pondoland-Albany hotspot as well as assist South Africa in reaching the 30 x 30 biodiversity goals set out by the UN (United Nations, 2015).

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APPENDICES

Appendix A: X^2 values and Pearson's Chi-squared Test results for all 12 of the species pairs tested for interspecific competition. Period of significant differences in diel activity indicated in bold. p -value (overall) indicates the overall significance from the Pearson's Chi-squared Test

Species	p-value (overall)	Dawn p-value	Day p-value	Dusk p-value	Night p-value
Zebra & wildebeest	0.894	0.810	0.652	0.632	0.878
Nyala & kudu	0.619	0.976	0.299	0.622	0.474
Giraffe & kudu	0.119	0.879	0.133	0.067	0.557
Impala & kudu	0.061	0.641	0.029	0.435	0.184
Impala & nyala	0.711	0.637	0.340	0.847	0.649
Impala & warthog	**0.008**	0.240	**0.026**	0.992	**0.020**
Warthog & nyala	**0.001**	0.150	0.006	0.869	0.012
Warthog & zebra	**0.000002**	0.187	**0.0003**	0.873	**0.0002**
Warthog & wildebeest	**<0.0001**	0.231	**<0.0001**	0.525	**<0.0001**
Duiker & nyala	**0.006**	0.257	0.286	**0.042**	**0.015**
Duiker & impala	**<0.0001**	0.076	**0.040**	**0.038**	**0.0008**
Duiker & warthog	**<0.0001**	**0.015**	**0.0002**	0.0835	**0.0001**

Appendix B: Pearson's Chi-squared Test results for all 12 of the species with > 30 detections in both < 3 km and > 3 km visibility. Overall model significance observed in common duiker and impala, with significant time periods indicated in bold. p - value (overall) indicates the overall significance from the Pearson's Chi-squared Test

Species	**p-value (overall)**	**Dawn p-value**	**Day p-value**	**Dusk p-value**	**Night p-value**	**X^2 value**
Black-backed Jackal	0.4189	0.2919	0.6918	0.1048	0.5223	2.82
Blue Wildebeest	0.7370	0.0109	0.4812	0.9275	0.3552	1.27
Common Duiker	**0.0019**	0.0814	**0.0394**	0.8296	**0.0230**	14.49
Genet	0.1615	0.8348	0.8702	0.8903	0.1292	4.81
Giraffe	0.5152	0.3206	0.9752	0.7873	0.2682	2.29
Greater Kudu	0.0817	0.1112	0.0138	0.2628	0.8385	6.62
Impala	0.0427	0.0490	0.0047	0.1941	0.9338	8.16
Nyala	0.1303	0.0186	0.0237	0.1042	0.2259	5.55
Plains Zebra	0.5513	0.4152	0.4056	0.4001	0.6146	2.09
Slender Mongoose	0.7528	0.7503	0.8913	0.4676	0.8790	1.05
Vervet Monkey	0.4427	0.8974	0.3819	0.1621	0.9253	2.42
Warthog	0.0901	0.3299	0.0317	0.0219	0.4235	6.20

Appendix C: Pearson's Chi-squared Test results for all 11 of the species with > 30 detections in both < 8 m and > 8 m visibility. Overall model significance observed in plains zebra and slender mongoose, with significant time periods indicated in bold. p -value (overall) indicates the overall significance from the Pearson's Chi-squared Test

Species	**p-value (overall)**	**Dawn p-value**	**Day p-value**	**Dusk p-value**	**Night p-value**	**X^2 value**
Black-backed jackal	0.9917	0.8712	0.9089	0.8502	0.8712	0.1014
Blue wildebeest	0.1554	0.3048	0.0729	0.4728	0.5018	5.2353
Common duiker	0.3582	0.3989	0.9543	0.6860	0.1255	3.2254
Greater kudu	0.3115	0.3560	0.5081	0.2995	0.2722	3.5725
Impala	0.4225	0.9587	0.4235	0.8961	0.1430	2.8058
Large-spotted genet	0.3637	0.1709	0.8137	0.9374	0.2636	3.1867
Nyala	0.0693	0.0965	0.6087	0.0582	0.4932	7.0834
Plains zebra	**0.0316**	**0.0167**	0.1136	0.4382	0.9258	8.8352
Slender mongoose	**0.0188**	0.3305	**0.0136**	0.2330	0.2193	9.9676
Vervet monkey	0.2385	0.2790	0.1723	0.4846	0.4033	4.2215
Warthog	0.0767	0.5183	0.1682	0.0881	0.2017	6.8546