SPECIES RICHNESS AND SPATIAL USE PATTERNS OF MEDIUM AND LARGE MAMMALS IN MAJETE WILDLIFE RESERVE, MALAWI

by

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DECLARATION

I, Sally Jean Reece, 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.

Reece.

Signed

12 November 2020

Date

ABSTRACT

Human population numbers are increasing exponentially across Africa, with the associated effects of urban and agricultural expansion fragmenting landscapes and largely confining medium and large mammals to protected areas (PAs). The PAs themselves do not escape the anthropogenic pressure on their boundaries. Smaller reserves are particularly vulnerable, needing intensive management and interventions to maintain core habitat characteristics. To ensure that management actions have the desired outcomes it is important to understand how interventions influence the mammal community and associated biodiversity, within the context of each PA's unique environmental characteristics. Monitoring variables such as species richness and mammal space use can provide valuable insight on how anthropogenic and environmental variables influence mammal species and communities.

Majete Wildlife Reserve (MWR) is a small (691 km^2) and isolated PA in southern Malawi within the Miombo woodland ecoregion. The reserve lies within a transformed matrix of agricultural and rural land use. MWR has had a turbulent past with most large mammal species lost to poaching by the end of the 20th century. However, since 2003 numerous large mammal reintroductions have taken place and the reserve is recovering. Historical species lists suggest that at least 41 medium and large mammal species (> 0.5 kg) used to occur in MWR, but no rigorous inventory has been made and the space use of these mammals is largely unknown. The aim of this study was to first determine the species richness of the terrestrial medium and large mammals at MWR, and secondly, assess the space use patterns and anthropogenic and environmental drivers thereof for the ungulate species.

A six month systematic camera trap study was undertaken at MWR during the 2018 dry season (July – December) whereby 140 locations, spaced evenly across the landscape, were sampled for 40 days each, using 47 camera traps moved across three blocks. Species richness estimators (Frequentists and Bayesian) were used to estimate species richness. Ungulate space use was assessed against a suite of nine potential environmental and anthropogenic drivers (i.e. landscape curvature, fire, vegetation type, visibility, grass biomass, relative predator abundance, distance to water, distance to road and distance to fence) using an occupancy modelling framework.

Over a period of 5 456 camera days, a total of 120 239 photographs were recorded, of which 12 202 were independent detections of 35 medium and large mammal species (20 herbivores, seven carnivores, six omnivores and two insectivores). This figure represents 85% of the medium and large mammal species historically present. The species richness estimators estimated that between 1-5 species were missed by the current survey, and both direct and indirect observations confirm the presence of another four species in MWR. Most species missed have specific habitat requirements such as aquatic habitat and rocky outcrops which were not specifically accounted for in the camera trap survey design. The mammal community structure was found to be atypical for Miombo woodland with megaherbivores (specifically, elephants *Loxodonta africana*) underrepresented.

Ungulate space use patterns were mainly driven by environmental drivers with distance to water, vegetation type and visibility strongly influencing species. Distance to water affects hippo (*Hippopotamus amphibius)*, elephant (*Loxodonta africana*), plains zebra (*Equus quagga)*, eland (*Tragelaphus oryx livingstonii*), kudu (*Tragelaphus strepsiceros)* and impala (*Aepyceros melampus)*, while bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), nyala (*Tragelaphus angasii*)*,* impala (*Aepyceros melampus*), black rhino (*Diceros bicornis*), elephant, waterbuck (*Kobus ellpsiprymnus*) and hartebeest (*Alcelaphus lichtensteinii*) are affected strongly by the distribution of the different vegetation types. Waterbuck use dense vegetation more, and buffalo (*Syncerus caffer*) eland, impala, zebra and sable (*Hippotragus niger*) prefer more open areas. The anthropogenic activity around the reserve impacts black rhino and plains zebra space use negatively with their probability of space use increasing away from the reserve boundary. The space use of elephant and impala decreases with distance from roads.

This study demonstrates the efficacy of a systematic camera trap survey and occupancy modelling framework in producing medium and large mammal species distribution data in Africa. Furthermore, a scientifically verifiable baseline measure of species richness and ungulate space use has been produced providing the basis from where the impact of future changes (natural and anthropogenic) can be assessed, and the success of conservation objectives evaluated.

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DEDICATION

For my Father, Peter Reece,
who had a deep love of the natural world and conservation,
and who nurtured my interest from an early age

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GLOSSARY

Acronyms/Abbreviations

AIC	Akaike's Information Criterion
CI	Confidence Interval
GIS	Geographic Information Systems
GPS	Global Positioning System
ha	Hectares
ICE	Incidence-based Coverage Estimator
Km	Kilometres
MWR	Majete Wildlife Reserve
QGIS	Quantum GIS
RAI	Relative abundance index
SD	Standard deviation
SE	Standard error
VIF	Variance Inflation Factor

CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

In 2014 the world population reached 7.2 billion people, and projections suggest it will reach between 9.6 and 12.3 billion by 2100 (Gerland *et al*., 2014). The majority of this increase is expected to occur in Africa (Gerland *et al.,* 2014), with 26 of the 54 African countries expected to expand to at least double their current population size by 2050 (United Nations, 2017). This projected population growth and consequent increasing human needs will likely undermine the protection of biodiversity and result in an increase in urban and peri-urban land occupation, reducing and degrading natural habitat due to expanding development and agriculture (Newmark, 2008). Habitat loss and fragmentation are regarded as the most important threat to biodiversity (Millenium Ecosystem Assessment, 2005) and Africa is expected to be amongst the continents with the largest projected habitat loss between 2000 and 2050 (Visconti *et al.*, 2011).

One third of global protected areas (PAs) are under intense human pressure (Jones *et al.,* 2018). This pressure on protected natural habitat is driven by habitat loss and degradation, as well as anthropogenic driven climate change and pollution (Alkemade *et al.,* 2009; Tittensor *et al*., 2014). African PAs benefit people living adjacent to such areas, with average human population growth rates on PA borders double that of rural areas suggesting that these regions hold considerable value for local people (Wittemyer *et al.*, 2008; Naidoo *et al.,* 2019). However, the resultant overcrowding and pressure of edge effects on PA boundaries also threatens biodiversity conservation efforts and PA effectiveness (Wittemyer *et al*., 2008; Jones *et al.*, 2018). The direct threats to PAs from large human populations on their borders include direct habitat loss due to encroachment, disease transmission, alien species infestation, poaching and uncontrolled burning (Newmark, 2008; Lindsey *et al.*, 2014). PAs also become increasingly more isolated as settlements, road networks and fences around PAs increase (Newmark 2008; Lindsey *et al.* 2014; Newbold *et al.*, 2015; Ibisch *et al.,* 2016; Liu *et al.*, 2020).

The loss of connectivity and consequent isolation of PAs due to habitat fragmentation threatens species persistence within these areas (Hayward & Kerley, 2009; Kool *et al.*, 2013; Wegmann *et al*., 2014). Threats include the halt of natural processes such as dispersal and migration (Kool *et al.*, 2013; Xu *et al.*, 2019), a reduction in genetic variability (Wegmann *et al*., 2014; Miller *et al.*, 2015), limitation of metapopulation dynamics (Hodgson *et al*., 2009; Miller *et al.*, 2015), and averting natural potential responses to climate change (Wasserman *et al.*, 2012).The strength of these threats depends on the context and size of the PA (Cerdeira *et al*., 2010; Wegmann *et al.*, 2014). PAs that lie in a more converted landscape matrix of human settlement and agriculture are naturally more susceptible to the threats of isolation, with smaller PAs tending to be in more converted landscapes compared to larger PAs (Parks & Harcourt, 2002). The theory of island biogeography (Macarthur & Wilson, 1967) predicts that small PAs (habitat islands) are likely to lose species at a faster rate than larger PAs due to the smaller PAs holding lower population numbers. Small PAs (< 1000 km^2; Miller *et al.*, 2015) are also more susceptible to human-induced disturbances due to them having a large perimeter-to-area ratio. This results in less core habitat to buffer external threats and leads to higher exposure to human disturbance (Newmark, 1996; Parks & Harcourt, 2002; Joppa *et al*., 2008; Cerdeira *et al.,* 2010; Wegmann *et al*., 2014). Species richness thus tends to increase with PA size (Ramesh *et al.*, 2016a). Additionally, large carnivores are particularly vulnerable in small PAs due to their wide-ranging behaviour and inherently low population densities (Woodroffe & Ginsberg, 1998).

With the current predictions of habitat loss in Africa, the importance of PAs and their ability to function independently, regardless of their size, is critical for the conservation of the remaining biodiversity (Wegmann *et al.*, 2014). However, in recent years large mammal population numbers within African PAs decreased by 50% and this is attributed to human-induced threats and poor management (Caro & Scholte, 2007; Craigie *et al*., 2010; Lindsey *et al.*, 2014). There are large regional differences though, with southern African PAs faring better than those in east and west Africa (Craigie *et al.,* 2010). The effective management of these PAs, all of which are unique in their anthropogenic threats and ecological characteristics, is therefore vital to ensure African mammal population persistence.

In comparison to large and unfenced PAs, small, fenced and isolated PAs generally require more intensive management to maintain sound ecosystem functioning (Cumming, 2004; Hayward *et al*., 2007; Cant-Salazar & Gaston, 2010; Di Minin *et al.*, 2013; Miller *et al.*, 2013; Massey *et al*., 2014). Necessary management interventions in small PAs typically include medium and large mammal (> 0.5 kg) translocations to maintain genetic diversity (Miller *et al.,* 2015), perimeter fencing to mitigate external threats and prevent human-wildlife conflict (Hayward & Kerley, 2009; Massey *et al*., 2014), surface water provision (Smit *et al*., 2007), and fire management (Bond & Archibald, 2003). Furthermore, the placement of roads is necessary to perform management functions (van der Merwe & Saayman, 2014) Being able to predict how these management interventions will impact medium and large mammal populations is vital for PA decision-making. However, the impact of interventions must be considered alongside the unique ecological characteristics of a PA which promote or limit medium and large mammal species' use of a landscape (Mkonyi *et al.,* 2018). Through biological monitoring, an understanding of how management interventions and the ecological characteristics of a PA influence energy transformation and matter cycling from the combined activity of living organisms i.e. ecosystem functioning, can be gained (Yoccoz *et al.*, 2001)

(Ghilarov, 2000). Species richness and distribution (or occupancy) are variables often used to evaluate how anthropogenic and environmental drivers influence mammals (Ramesh *et al.*, 2016a; Ramesh *et al.*, 2016b; Mkonyi *et al.*, 2018; Oberosler *et al*., 2020).

Majete Wildlife Reserve (MWR) in south-west Malawi is a small (691 km^2), fenced and isolated PA (Figure 1), lying within a transformed matrix of agricultural and rural land use. The reserve has had a tumultuous past, with the majority of medium and large mammal species lost to poaching in the 1970's (Staub *et al.*, 2013). In 2003 African Parks took over management of the reserve, improving infrastructure, law enforcement and building good community relationships. In addition, numerous large mammal (> 20 kg) species reintroductions have taken place, and the reserve is recovering well with growing population numbers of most large mammal species (African Parks, 2020). To ensure that this PA continues on its road to recovery and fulfils its conservation mandate, it is vital for key baseline measures to be in place against which the success of management efforts can be evaluated. Such measures include an assessment of medium and large mammal species richness and space use within the reserve.

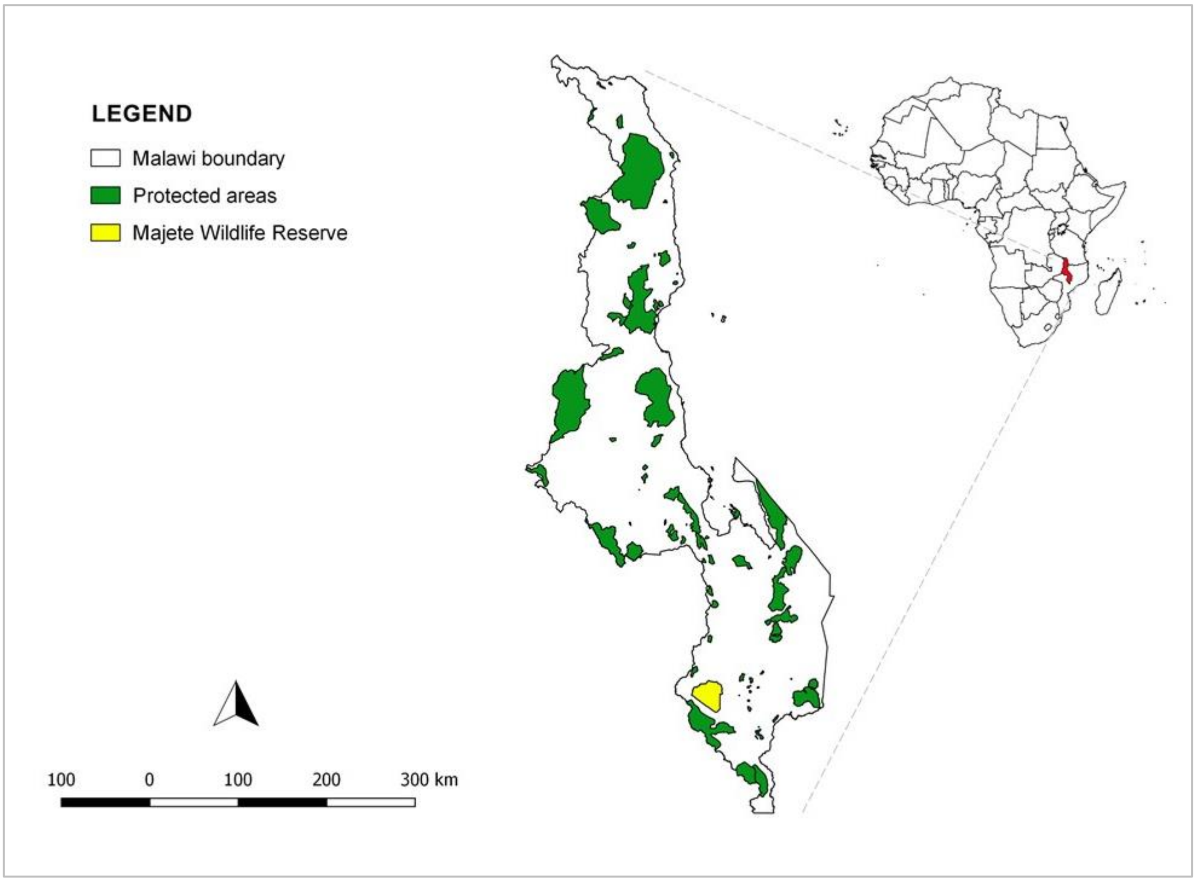

Figure 1.1: Map of Malawi indicating the protected areas, highlighting their fragmentation. Majete Wildlife Reserve is indicated in yellow, and a map of Africa (inset) indicates the location of Malawi

1.2 The importance of understanding medium and large mammal species richness and community structure

Medium and large mammals are crucial to ecosystems as they have substantial effects on the structure and function of landscapes (Ripple *et al.,* 2014; Ripple *et al.*, 2015). These mammals modify abiotic processes involving nutrient cycles, soil properties, hydrology and primary production which can have cascading effects on other species including small mammals, birds, invertebrates and herpetofauna (Ripple *et al.,* 2014; Ripple *et al.*, 2015). The loss of medium and large mammals can thus alter ecosystem functioning, stability and resilience (Ripple *et al.,* 2014; Ripple *et al.*, 2015; Lacher *et al.*, 2019). It is therefore essential that medium and large mammals are monitored in PAs to enable active adaptive management.

Assessing the medium and large mammals species richness is the simplest and most common measure used to evaluate their status in an area (Yoccoz *et al.,* 2001) and is used to assess anthropogenic and environmental impacts, with the number of species present used as an indicator of PA integrity (Ahumada *et al.*, 2011; Gibson *et al.*, 2011; Newbold *et al.*, 2015; Boron *et al.*, 2019). Richness may naturally vary across PAs based on gradients of plant-available nutrients and moisture which regulate species based on nutritional requirements (Olff, *et al.*, 2002), and the dynamics between trophic groups and feeding guilds (Fritz *et al.*, 2002; Hopcraft *et al.*, 2010). Generally, species richness serves as an indicator of site diversity and aids with the refinement of distribution maps (Tobler *et al.*, 2008; Burton *et al.*, 2015). However, with mammal populations decreasing in African PAs, and small PAs likely to lose species at a faster rate than larger PAs, it is especially important to assess current species richness patterns within PAs so that it can act as a baseline against which conservation efforts can be evaluated and improved.

It is not only important to gain insight on the overall species richness but also the community structure (composition and abundance) which can be broadly categorised by the functional traits of body size and trophic category (Wallgren *et al.*, 2009; Ahumada *et al.*, 2011). The landscape surrounding a PA has been shown to leave a strong signature in the structure of a PAs mammal community with fragmented landscapes having lower functional diversity (Perault & Lomolino, 2000; Wallgren *et al.*, 2009; Ahumada *et al.*, 2011). The structure of mammal communities plays a significant role in the functioning of ecosystems, with herbivores specifically shaping the structure and function of landscapes in which they occur (Ahumada *et al.*, 2011; Ripple *et al.*, 2015). As landscapes surrounding PAs are becoming increasingly transformed, it is important that the community structure of a PA is understood, altered where necessary and protected from adverse alterations.

1.3 Understanding medium and large mammal space use and the drivers

With medium and large mammals in general decline worldwide (Caro & Scholte, 2007; Craigie *et al*., 2010; Ripple *et al.,* 2014; Ripple *et al.*, 2015) and most now confined to PA's (Caro & Scholte, 2007), it is imperative to ensure their persistance in the last remaining refugia (Lindsey *et al.*, 2014; Wegmann *et al*., 2014; Oberosler *et al.*, 2020). A sound understanding of how medium and large mammal's are using PAs and what environmental and anthropogenic factors are driving their space use is essential if management are to clearly define and implement effective conservation actions (Caro, 1999; Mkonyi *et al*., 2018). Numerous factors influence the space use of mammals, which may be of natural or anthropogenic origin. Some natural drivers are also often manipulated by humans as PA management interventions, with intentional and unintentional effects on mammal space use.

Topography and terrain

The variability of the terrain of a PA impacts how medium and large mammals will use space, with landscape ruggedness (the degree of concavity or convexity of a landscape; Sappington *et al.,* 2007) and slope being influential (Puri, 2015; Anderson *et al.,* 2020). For example, more rugged terrain may allow herbivores to conceal themselves from prey and provide ambush cover for predators (Davies *et al.,* 2016). Some species, such as black rhino (*Diceros bicornis*) prefer to use less undulating slopes that allow ease of movement due to their large size and the energy needed to move through steep terrain (Odendaal-Holmes *et al.,* 2014).

Vegetation characteristics

Plant species and vegetation structure vary across the landscape in relation to climatic and geomorphic conditions (Jennings *et al.*, 2009; De Cáceres & Wiser, 2012), and will also differ seasonally, spatially and between plant growth stages (du Toit, 1995; Fynn *et al.*, 2014). This gives rise to areas of varying vegetation quality and quantity as well as cover, which in turn influences mammal distribution due to their differences in nutritional demands and vulnerability to predation. Herbivores utilise forage resources differently based on their metabolic requirements governed by body size (Bell, 1971; Jarman, 1974; du Toit, 1995). Smaller herbivores have higher energy requirements compared to larger herbivores, so require high quality forage to meet metabolic needs, whereas larger herbivores can tolerate low quality but require it in greater quantities (Bell, 1971; Jarman, 1974).

Predator-prey interactions

Trade-offs exist between forage quality and availability, and the risk of predation (Anderson *et al.*, 2010; Tambling *et al.*, 2015; Owen-Smith, 2019). For example, herbivores form groups to lower their risk of predation, however the maximum group size which affects their predation risk is determined by the availability of food and its distribution (Jarman, 1974; Hopcraft *et al.*, 2010; Fritz *et al.,* 2011; Hopcraft *et al.*, 2012). Herbivores may alter their behaviour and space use so that they are more difficult to encounter, detect and capture (Thaker *et al.*, 2011; Makin *et al.*, 2017; Owen-Smith, 2019) with responses to predators differing depending on predation risk (Laundré *et al.*, 2010). Herbivore behavioural changes vary in space and time, resulting in them avoiding areas that pose a greater risk than others (Valeix *et al.*, 2009; Laundré *et al.*, 2010; Tambling *et al.*, 2015). Greater grass height and vegetation cover improve ambush predator hunting success (Funston *et al.*, 2001; Owen-Smith, 2019), and in response, herbivores may use more open areas (Valeix *et al.*, 2009). For example, herbivores in Hwange National Park preferentially use open habitats when ambush predators such as lion (*Panthera leo*) are in the vicinity (Valeix *et al.* 2009). Therefore, understanding how prey species respond to predator presence is a key factor in interpreting why and where prey species occur within a PA (Tambling *et al.,* 2015; Owen-Smith, 2019).

Water

The location of water influences medium and large mammal spatial ecology, with impacts varying between species based on species-specific water dependence (Smit *et al.*, 2007; Kihwele *et al*., 2020). The regular need to access water constrains certain mammal species from moving too far from water, with the distribution of water influencing species in the dry season (Western, 1975; Redfern *et al*., 2003; Smit *et al*., 2007; Valeix, 2011). A herbivore species' water dependence can be quantified based on feeding type, with grazers tending to be more water dependent than browsers or mixed feeders which obtain some water through their diet (Western, 1975; Owen-Smith, 1996; Redfern *et al*., 2003; Smit *et al.*, 2007). More recently, ungulate water dependence has been quantified using species' functional traits (Kihwele *et al*., 2020), with species such as African elephants (*Loxodonta africana*) particularly sensitive to water availability (Smit & Grant, 2009; Purdon & van Aarde, 2017).

Artificial waterholes can change the distribution of large African herbivores even in a landscape where natural water is available (Smit *et al.*, 2007). Species utilise artificial waterholes and rivers differently, with some species, such as waterbuck (*Kobus ellipsiprymnus*) dependent on the habitat and forage associated with natural water sources (Smit *et al*., 2007). The positive association that water-dependent species have with water becomes most notable in the dry season in areas with high soil nutrients when the availability of moist, green and nutritious forage decreases with increasing distance from water (Smit *et al.,* 2007). However, wetter habitats, such as floodplains, are characterised by relatively tall, less nutritious grass species that may result in grazers dispersing away from permanent water (Hopcraft *et al*., 2012). Furthermore, trade-offs are often made in the dry season whereby grazers mitigate limitations in nutritional requirements by foraging further from water (Redfern *et al.*, 2003). Additionally, prey will make temporal adjustments in their use of waterholes to avoid dangerous periods coinciding with high predator activity (Valeix *et al.,* 2009). Thus, herbivore distribution in relation to water is often confounded by other factors such as habitat needs, food availability and predation risk (Redfern *et al.*, 2003; Valeix *et al.* 2009; Kihwele *et al.*, 2020).

Augmenting surface water supplies by providing artifical waterpoints is often used in PAs to manipulate mammal distribution patterns (Owen-Smith, 1996). Understanding how the placement of these waterpoints effects mammals is essential to ensure waterpoint placement is ecologically successful.

Fire

Fire influences medium and large mammal space use through changes in forage quantity and quality by reducing biomass and changing plant species composition (Anderson *et al.*, 2007; Burkepile *et al.*, 2013). Post-fire grass regrowth is of higher nutrient value than unburnt grass, and in savanna systems grazers are attracted to this higher quality forage, particularly at the start of the wet season (Tomor & Owen-Smith, 2002; Archibald & Bond, 2004; Sensening *et al*., 2010). Furthermore, fire reduces vegetation cover and tree density increasing visibility which effects predation risk since cover for ambush predators is reduced (Hopcraft *et al*., 2005; Burkepile *et al.,* 2013). The trade-off between predation risk and food quality is however species-specific, dependent on nutritional requirements, body size and prey escape tactics (Burkepile *et al.,* 2013).

Fire is used as a PA management tool to restrict the extent of wildfires, to reduce alien vegetation, and where necessary to promote heterogeneity of grass veld age by applying patch mosaic burning (Bond & Archibald, 2003; Freckleton, 2004; van Wilgen, 2015). It is also used to ensure good quality grazing at key times of the year (Bond & Archibald, 2003).

Roads

The presence of roads in PAs can influence medium and large mammal space use through either their preferential use or avoidance of them (Fahrig & Rytwinski, 2009; Taylor & Goldingay, 2010; Leblond *et al.,* 2013; Muposhi *et al*., 2016). Mammals may avoid roads due to the perceived, and often real, risk from vehicle traffic (Forman & Alexander, 1998; Fahrig & Rytwinski, 2009). Elephants have been shown to use roads as low-resistance corridors, notably in the dry season in order to easily reach water sources (Gaynor *et al.*, 2018), with large predators and carrion feeders often using lightly traveled roads as movement corridors (Forman & Alexander, 1998; Rich *et al.*, 2017). In addition roads can change patterns of water run-off which in turnalters the adjacent vegetation which may attract mammals (Trombulak & Frissell, 2000).

Roads are essential infrastructure in PAs which allow management activities such as patrols, fire management, fence and artificial waterhole maintenance as well as research to take place. It also provides access for tourism activities (Gaynor *et al.*, 2018).

PA borders and fences

Isolated PAs that lie in a matrix of anthropogenic land use often need the erection of fences to separate and protect species from negative human influences such as poaching, resource harvesting and habitat loss (Hayward & Kerley, 2009). Fences also serve to keep wildlife within PAs, reducing human persecution by mitigating human-wildlife conflict from megaherbivores and large carnivores in particular (Marnewick *et al.*, 2007; Osipova *et al.*, 2018). While physically protecting both wildlife and people, fences can also become threats by creating hard boundaries hindering most medium and large mammal movement, which makes immigration and emigration virtually impossible (Hayward & Kerley, 2009; Massey *et al.*, 2014) In transformed landscapes, anthropogenic activity often abuts PA boundaries at their fence line (Wittemyer *et al.*, 2008), and with some medium and large mammals particularly sensitive to human activity, the extent of species space use will often increase towards the interior of a reserve (Everatt *et al.*, 2014; Wang *et al.*, 2015; Rich *et al.*, 2016; Rich *et al.,* 2017). This avoidance of the hard boundary effectively reduces the amount of space in the PA for medium and large mammal species to utilise with potential repercussions for their population persistence (Rich *et al.*, 2016).

1.4 Assessing medium and large mammal species richness and space use using camera traps

Methods to collect occupancy and species richness data include direct observations and live-traps (Wearn & Glover-kapfer, 2017; Crunchant *et a*l., 2020), with the chosen method largely dependent on financial and time constraints but also the target species (Silveira *et al.*, 2003; Munari *et al.,* 2011). Cameras that are triggered by movement have been in existence for more than a century, evolving from a primitive trip wire focused on bird ecology to sophisticated cameras that can send data remotely for research and management purposes (Wearn & Glover-kapfer, 2017). In recent years in particular, the use of camera trapping to survey and monitor wildlife has increased with technological advances leading camera traps to become a non-invasive, long term cost-effective means to monitor wildlife (Rovero *et al.*, 2013; Burton *et al.,* 2015). They are particularly useful for monitoring rare and elusive, wide ranging species (Tobler *et al.*, 2008; Linkie & Ridout, 2011; Bischof *et al.,* 2014; Li *et al.,* 2018), with the single most common use of camera traps in recent years being to estimate the abundance of felids (Tobler & Powell, 2013). However, cameras are now widely used at ecosystem and landscape level scales to inform conservation management decisions (Ahumada *et al.*, 2011; Swanson *et al*., 2015; Bruce *et al.*, 2018; Pyšková *et al.*, 2018; Welch *et al.*, 2019) and have been used extensively to collect data on species richness and animal occupancy in surveys across Africa (Pettorelli *et al*., 2010; Andresen *et a*l., 2014; Ramesh *et al.*, 2016a; Rich *et al*., 2016; Mkonyi *et al*., 2018; Oberosler *et al*., 2020) and the rest of the world (Puri, 2015; Wang *et al.*, 2015; Li *et al.*, 2018; Boron *et al*., 2019).

Camera trap survey design

Wearn & Glover-Kapfer (2017) state that for any sampling design, including the use of camera traps, standard ecological sampling design methods are applied, which include: 1) the random selection of sampling units, 2) replication with independent sampling units, and 3) stratification according to distinct features (e.g. habitat types). Camera trap sampling units, or sites, could be either grid squares or sampling points (Burton *et al*., 2015). Sampling units are selected at random using either a simple random design, a clustered random design or a systematic random design (such as within a grid) which is considered to yield more precise estimates of state variables due to having lower variance (Burton *et al*., 2015; Wearn & Glover-kapfer, 2017). When the objective is to determine the species richness of an area, a systematic random design is considered desirable (O'Brien, 2008).

Camera trap spacing, their placement and trapping period are important considerations when designing a survey (Foster & Harmsen, 2012), and will vary depending on the survey location and state variable to be measured (Colyn *et al*., 2018). Trap spacing can directly influence the capture probability of target species or species assemblages (Foster & Harmsen, 2012), and notably so when using an occupancy modelling framework (O'Brien, 2008). Camera trap placement varies depending on target species and survey goals with cameras being placed on wildlife trails (Ramesh & Downs, 2015), along roads (Rich *et al.,* 2016), in trees (Bowler *et al*., 2017) or at rivers and animal dens (Tobler *et al.*, 2008). Placing cameras on trails is often used in order to maximise capturing multiple species for mammal community studies (Ahumada *et al.,* 2011). Rotating camera traps to new sites is more efficient at estimating species richness than leaving cameras at fewer sites for a longer period (Si *et al*., 2014). The minimum number of camera days (number of cameras multiplied by survey period) recommended to record the most common species varies between studies and different habitats, while it is the more elusive species that determine how much time is needed to complete a survey (Tobler *et al.,* 2008). For example, species richness estimates in a savanna-forest mosaic require at least 3000 camera days (Hedwig *et al.*, 2018), while in open scrubland at least 1000 camera days is sufficient (Colyn *et al*., 2018).

Species richness estimates using camera traps

The broad spectrum sampling capabilities of camera traps lend themselves well to the counting of species (Wearn & Glover-kapfer, 2017). Tobler *et al*. (2008) found that survey effort was the most important factor determining the number of species recorded on camera traps. Species accumulation curves are commonly used to determine a survey's completeness, by estimating how many more species may have been detected if the camera was set out longer (Tobler *et al.*, 2008). Species richness assessments include observed species richness (sum of the number of species captured by the camera traps; Ahumada *et al.*, 2011; Samejima *et al.*, 2012) and estimated species richness which are based on observed species richness, and attempt to correct for imperfect detection (the fact that a species is present at a site but was undetected; Tobler *et al.*, 2008; Boron *et al.*, 2019). Camera trap surveys designed to determine other state variables, such as species occupancy, often produce reliable species richness estimates as a useful by-product (Tobler *et al.*, 2008).

Occupancy modelling

Occupancy modelling requires presence/absence site data and examines the probability of a species being present at a site or not (i.e. the proportion of area occupied; Mackenzie *et al.*, 2006). Occupancy modelling is highly suitable for studying broad-scale species distribution patterns, and the drivers of these patterns, while accounting for imperfect detection (Mackenzie & Royle, 2005; Mackenzie *et al.*, 2006; Tobler *et al.*, 2015). Calculating detection probability allows the examination of variables that influence the probability of a camera detecting a species, given that the species is present (Mackenzie & Royle, 2005). Occupancy modelling assumes that sampling units are closed to changes in species occupancy during the sampling period and that the detection of a species at one site is independent of detecting the species at other sites. Camera trap placement (distance between sampling sites) is important here as often a sampling site will cover a small proportion of a mammal's home range, such as for wide-ranging, low density carnivores (Mackenzie & Royle, 2005). Thus, if a species is present at a site at random points in time during the sampling period, this alters the interpretation of occupancy and the probability of area occupied becomes probability of area used (MacKenzie & Nichols, 2004).

1.5 Statement of the research problem

The ability of PAs to function independently and sustain viable populations of wildlife is becoming increasingly important for biodiversity conservation as landscapes become more fragmented and PAs smaller and more isolated. Medium and large mammals play a particularly important role in ecosystem functioning. Species richness of medium and large mammals is unique to each PA, with their space use patterns a function of the PAs environmental and anthropogenic characteristics. There is an urgent need to assess and understand each PAs medium and large mammal species richness and space use patterns so that it can act as a baseline from which the effects of threats and management interventions can be measured. MWR in Malawi is an isolated PA within the important Miombo woodland ecoregion surrounded by rural settlements and agricultural land. The species richness of the terrestrial medium and large mammal species within MWR has not been rigorously assessed and the space use of these species is largely unknown.

1.6 Study objectives

The aim of this study was to generate rigorous baseline information on the presence of the terrestrial medium and large mammals at MWR and to assess the space use patterns and drivers thereof, for the ungulate population.

The main objectives of the study were:

1. To determine the species richness of the terrestrial medium and large mammals at MWR.
2. To determine the space use patterns of the ungulates across the landscape of MWR.
3. To identify variables that are influencing the observed space use patterns of the ungulates at MWR.

1.7 Structure of the thesis

The thesis consists of five chapters of which Chapters 3 and 4 have been compiled as independent manuscripts to facilitate publication in peer-reviewed journals.

Chapter 2 provides contextual background to MWR, in terms of its location, climate, physical features, vegetation, historical context and anthropogenic influences.

In Chapter 3 the species richness and community composition of the terrestrial medium and large mammals in MWR is determined from data obtained through a comprehensive camera trap survey. A comparison of the community composition of the reserve was made to that considered typical of the Miombo Woodland Ecoregion.

Chapter 4 examines the space use patterns of the ungulate population across MWR. Using a modelling framework, covariates that were hypothesised to influence mammal detection probabilities and space use were modelled to determine the drivers of space use.

Chapter 5 is a synthesis chapter which aims to relate the most important findings of the study to recommendations for reserve management action.

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CHAPTER 2

STUDY AREA

2.1 Introduction

The study was conducted in the Majete Wildlife Reserve (MWR) which is a 691 km^2 protected area in the south-west of Malawi (Figure 2.1). The reserve is located between longitudes 34°26'36.56"E and 34°45'29.84"E, and latitudes 15°46'20.14"S and 16° 6'11.44"S and lies within both the Mwanza and Chikwawa administrative districts.

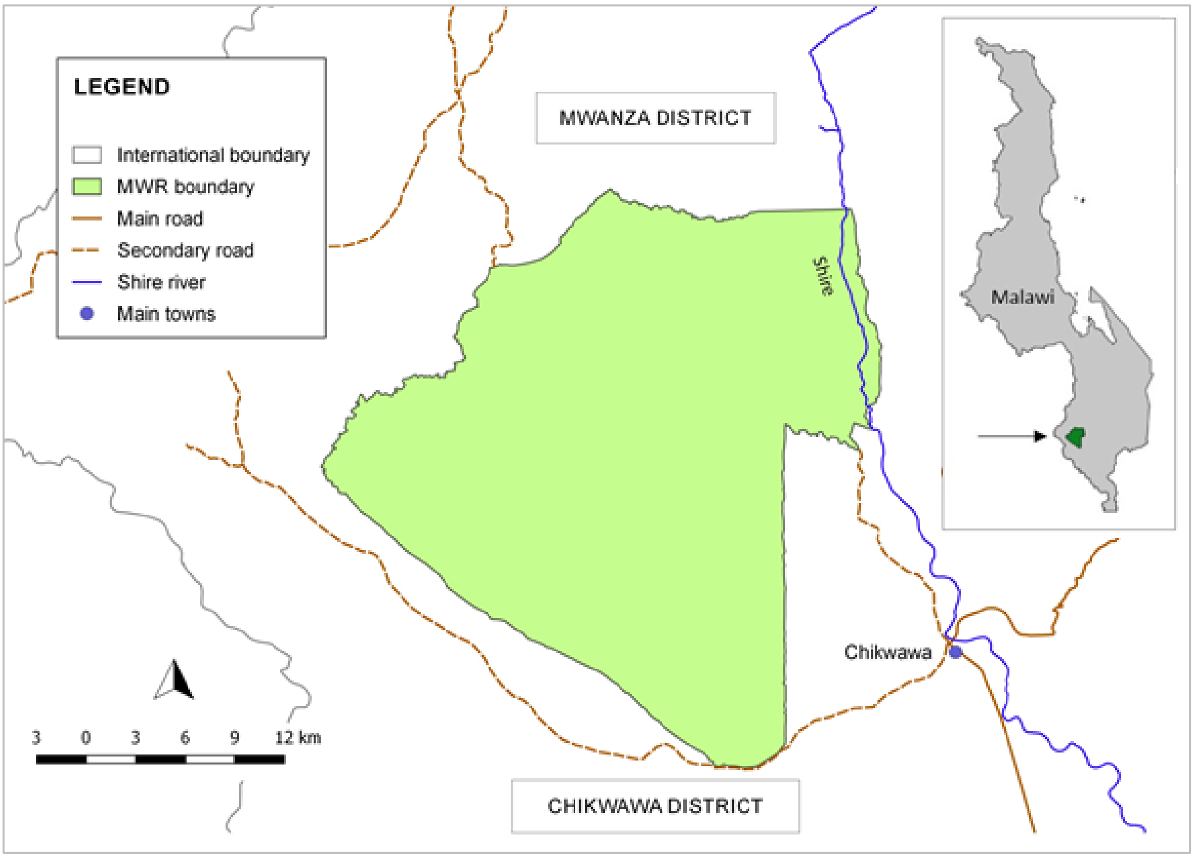

Figure 2.1: Map indicating the international boundary with Mozambique, the boundary of Majete Wildlife Reserve (MWR), the districts surrounding MWR, the surrounding roads and the major towns. The location of MWR is shown within Malawi (inset)

Since its inception as a game reserve in 1955, MWR has had a troubled history, with large-scale poaching in the 1980's leading to the extirpation of many mammal species (Staub *et al.,* 2013). In 2003, African Parks Ltd. took over the management of the reserve with a focus on combating poaching and reintroducing large mammal species.

2.2 Climate

MWR is situated in a tropical climate zone with semi-arid conditions (Staub *et al.,* 2013). The reserve's topography influences the rainfall gradient with the lower lying eastern areas receiving between 680 – 800 mm of precipitation per annum, and the higher lying western slopes receiving 700 – 1000 mm (Wienand, 2013).

The average annual rainfall for the area in the ten years preceding this study was 661 mm as measured at the meteorological station at Chikwawa, fifteen kilometres south-east of MWR's main gate (the monthly averages can be seen in Figure 2.2). This is the closest weather station to the park with reliable rainfall data for the area. The year of this study, 2018, received 754 mm (Figure 2.2) of rainfall that is higher than the average. However, it is important to note that the dry season of 2018 was preceded by an exceptionally dry wet season with the 2017/18 rainfall season (Nov – April) only receiving 346 mm in comparison to the previous 10 years wet season average of 635 mm. Another anomaly to occur during the study year was an unprecedented 60 mm of rain in July that on average receives less than 4 mm.

The estimated mean minimum and maximum temperatures are 12.5°C and 26.3°C in June and 20.9°C and 34.8°C in November (Martin, 2005), with these months the coldest and warmest months respectively. Higher elevations in the north-west of the reserve are slightly cooler than the low lying south-east. Sherry (1989) notes that the lowest temperature recorded in the south at Chikwawa was 11°C whilst the highest was 45°C.

According to Hall-Martin (1975) three distinct seasons can be identified based upon temperature and rainfall:

a) The hot wet season that lasts from November to April is characterised by high relative humidity and rainfall. Most of the reserve's rainfall (96%) is received during this period.

b) The cool dry season that lasts from May to August generally experiences cooler temperatures, high relative humidity and no significant rainfall.

c) The hot dry season that occurs from September to October experiences high temperatures but low relative humidity and hardly any rainfall.

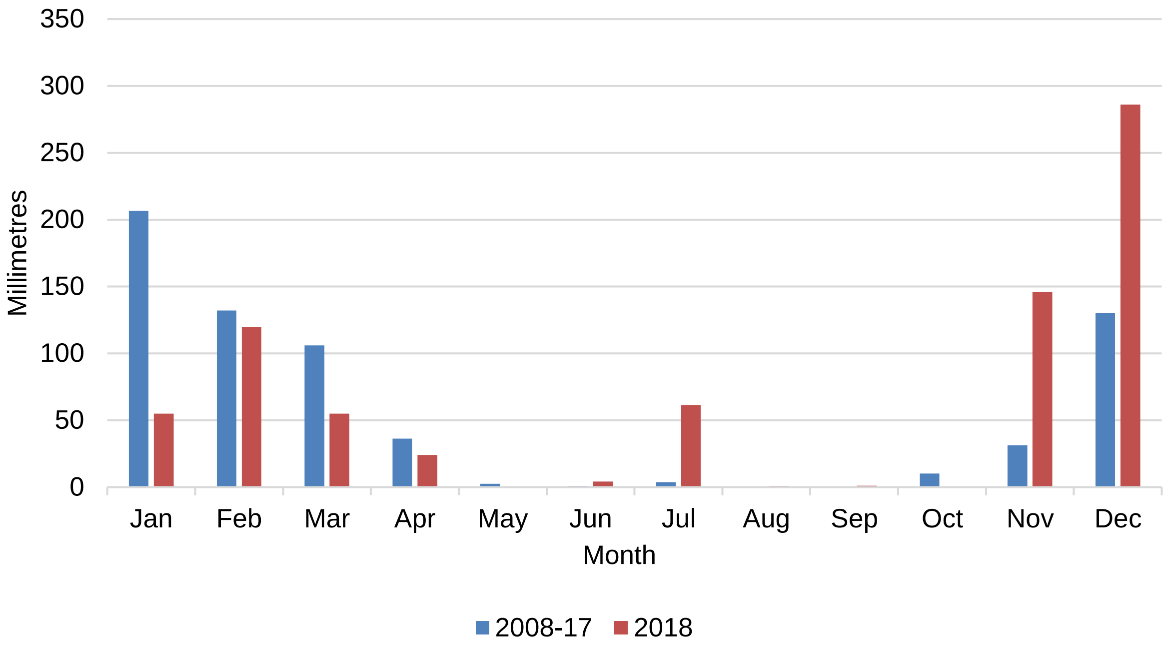

Figure 2.2: The average monthly rainfall at Majete Wildlife Reserve for the 10 years preceding the study (2008-2017) are indicated in blue, while the rainfall experienced during the study year (2018) is indicate in red

2.3 Topography

MWR is situated in the Shire valley that forms the southern end of the African great rift valley (Sherry, 1989). A fault line running north-south down the centre of the reserve demarcates it into two distinct sectors. The western sector with steep hills and large outcrops, is more rugged and at a higher elevation compared to the eastern sector which is lower and slopes progressively down from the western hills to the Shire river (Bell, 1984).

The altitudinal gradient decreases from approximately 455 metres above sea level (m.a.s.l) in the north-west to approximately 150 m.a.s.l in the south-east. Granite outcrops occur in the west of the reserve with the highest point being Majete Hill in the centre of the reserve (766 m.a.s.l; Figure 2.3). Seasonal sand rivers and gullies run in a south-east direction towards the Shire river, many of which are deeply incised creating ravines below the level of the surrounding terrain (Bell, 1984).

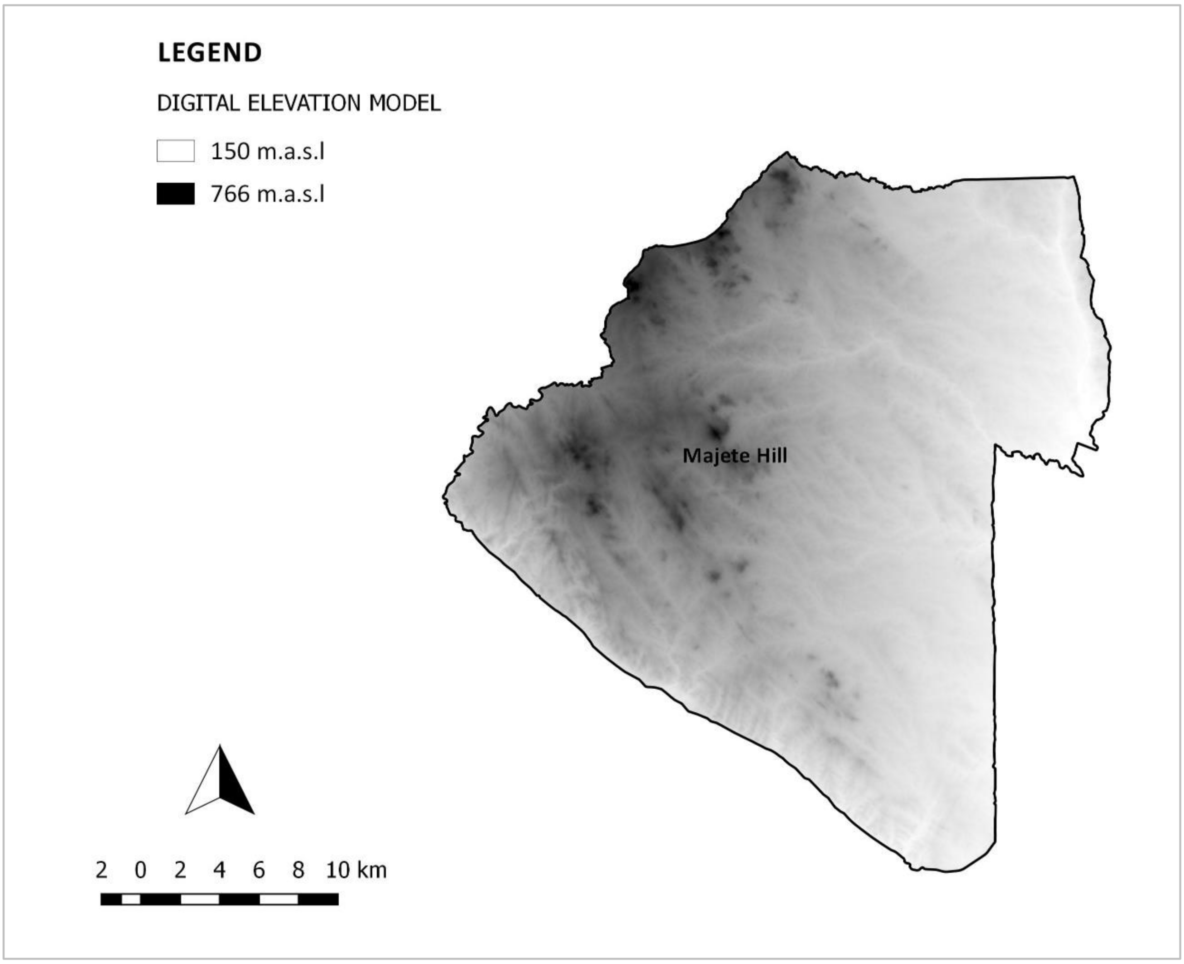

Figure 2.3: A digital elevation model (DEM) showing the altitudinal gradient in the reserve with the dark areas indicating high lying areas in the west and the lighter coloured lower areas in the east of Majete Wildlife Reserve. Majete Hill is the highest point in the reserve. DEM obtained from African Parks (Majete) Pty Ltd

2.4 Geology and soils

The majority of MWR is Horneblende-Biotite Gneiss from the Precambrian Metamorphic Basement Complex (Bell, 1984). In addition to this, long bands of quartz-schists and granulites occur in the Majete escarpment area in the south with shorter bands of psammite gneisses, biotite gneisses and quartz microsyenites outcrops occuring in the north of the reserve (Bell, 1984). Dolerite dykes occur throughout MWR but are most common in the south, standing several metres above the surrounding landscape (Bell, 1984).

The ancient soils of the Basement Complex in south-central Africa covered by the Miombo woodlands have nutrient poor soils, which are typically acidic and low in nitrogen (Frost, 1996; Walker & Desanker, 2004). Published reports describing the soils of MWR and the region are scant, however Bell (1984) and Sherry (1989) refer to a Shire Valley Agricultural Development Programme Atlas from 1975, that describes the majority of the soils of MWR as lithosols and shallow, stony, gravelly, ferruginous soils or lithosols with sandy and loamy soils of low fertility.

The atlas further describes limited areas of more fertile, alluvial soils occurring along some of the rivers; the alluvial Shire river valley floor extends into the south-east of the reserve for a few square kilometres with the presence of this fertile alluvium.

Bell (1984) noted the soils of the western uplands of MWR to be generally red-brown clay loams and dark grey sandy clay loams in the eastern slopes, with a depth of several metres in places. The numerous dolerite dykes within MWR would have undergone some weathering over time, and with dolerite having high biological potential, would contribute to localised nutrient-rich soils (Bell, 1984; Frost, 1996). Overall, the soils in MWR would be considered of low nutrient potential with areas of concentrated high nutrients along the rivers.

2.5 Hydrology and artificial water points

Two perennial rivers, the Shire and the Mkulumadzi, transect the north-east corner of MWR (Figure 2.4). The level of the rivers fluctuate seasonally with the highest flow during December/January and the lowest during August/September, following rainfall events. The Shire river is a major tributary of the Zambezi river, and flows out of lake Malawi. The Mkulumadzi river flows for seven kilometres through the north-eastern corner of the reserve before joining the Shire river.

Numerous seasonal and ephemeral rivers and streams run in a south-easterly direction across the reserve and serve as drainage channels during the wet season. Some pools may persist in the stream beds until late into the dry season (Martin, 2005), with water also made available by animals (especially elephants *Loxodonta africana*) digging in the sandy stream beds (Bell, 1984). During the field work undertaken for this study, only one such digging was observed (Figure 2.5).

There are nine known natural springs in MWR (Figures 2.6 and 2.7) which I visited during the dry season of 2018. All nine held water and had clear signs of use by mammals. One is a hot spring in the south western corner of the reserve and being the only water source in this area is actively used by mammals, despite being hot water (Figure 2.6). Surface water is supplemented in MWR by ten artificial borehole-fed waterholes, which serve as additional dry season water sources (Figure 2.4 and 2.8).

By the end of the dry season surface water is restricted to the two perennial rivers, nine natural springs and 10 artificial water points. During the wet season, surface water increases across the reserve as the seasonal streams and rivers start to flow. Additionally, during the wet season concave and shallow waterlogged areas, generally with clay soils (von der Heyden, 2004), also fill up with water to form pans or “dambos”.

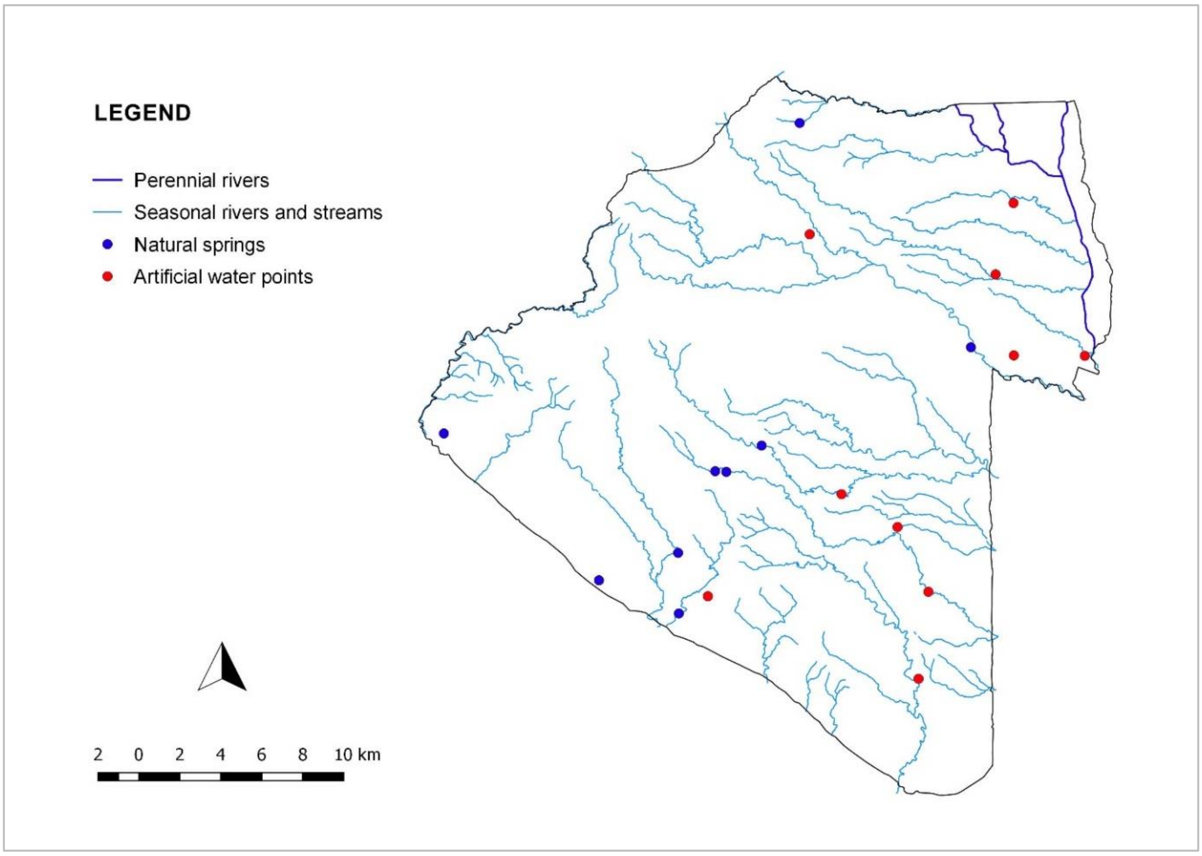

Figure 2.4: The distribution of the two perennial rivers, multiple seasonal streams, nine natural springs and 10 artificial water points within Majete Wildlife Reserve

Figure 2.5: Water in a dried river bed in Majete Wildlife Reserve exposed by elephant digging

Figure 2.6: The hot spring in the south-west corner of Majete Wildlife Reserve along the fenceline with clear signs of mammal use

Figure 2.7: Phwadzi spring in the south of Majete Wildlife Reserve during the 2018 dry season

Figure 2.8: Nakamba artificial water point in the Sanctuary area of Majete Wildlife Reserve

2.6 Vegetation

MWR falls within the Miombo Woodland Ecoregion, that is the most extensive ecoregion in Africa south of the equator, covering about 2.7 million km^2 from central Mozambique through Tanzania and west through Angola, Zambia and Malawi (Balme *et al*., 2007; Frost, 1996; Walker & Desanker, 2004). Miombo woodland holds approximately 8 500 species of higher plants of which 54% are endemic (Sedano *et al.,* 2005), making the region a biodiversity hotspot (Mittermeier *et al.,* 2010). This ecoregion is threatened by settlement, agriculture, illegal charcoal production and uncontrolled fires (Frost, 1996; Syampungani *et al*., 2009; WWF, 2012).

At a finer scale MWR falls within the Zambezian regional centre of endemism (White, 1983), specifically the Southern Miombo woodland ecoregion (WWF, 2012), which is associated with dry deciduous woodland and thicket, as well as deciduous riparian vegetation (White, 1983). Differences in species composition and structure are more apparent on a local scale which are determined by soil nutrients, moisture and altitude (Frost, 1996; Ribeiro *et al.,* 2012).

Structurally, miombo woodland is distinguished from other African savanna, woodland and forest formations by stands of trees composed of a 10-20 m high, partly closed canopy of mostly pinnate-leafed, deciduous trees dominated by species in the genera *Brachystegia, Julbernardia* and *Isoberlinia* (Frost, 1996). An understorey of broadleafed shrubs and a patchy herbaceous layer of forbs, small sedges and C4 grasses is present (Frost, 1996). Dry miombo woodland, receives less than 1000 mm of rainfall annually and under which southern Malawi where MWR is located, is classified (Frost, 1996; Ribeiro *et al.,* 2012).

The vegetation community composition of MWR changes with altitude and the associated rainfall gradient, with the high altitude tall miombo woodland in the west gradually changing into more open mixed tall woodland in the centre and east. Riverine associations are confined to river valleys throughout MWR with thicket associated with rivers and river junctions in the east of the reserve (Sherry, 1989).

Sherry (1989) identified six broad vegetation types within MWR (Figure 2.9) and these are described below. Vegetation descriptions are those described by Sherry (1989) unless otherwise indicated.

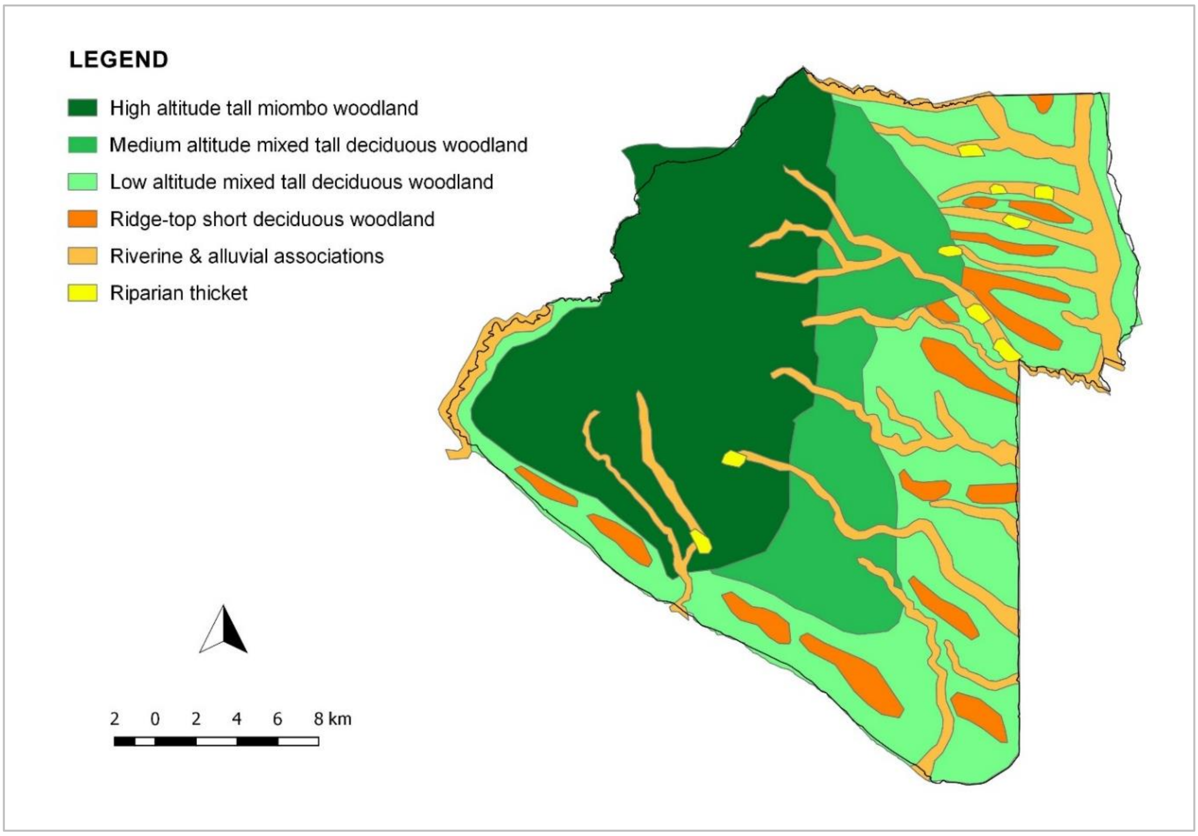

Figure 2.9: Vegetation types of Majete Wildlife Reserve adapted from Sherry (1989)

High altitude tall Miombo woodland

This vegetation type makes up the woodlands of the western uplands of MWR where altitude is between 410-770 m.a.s.l. It is well developed miombo woodland with tall trees (average height is 15 m) making up a medium to closed canopy and an open understorey (Figures 2.10 and 2.11). High rainfall and sandy clay loam soils with low nutrient levels produce vegetation with poor nutritional value but with an overall medium to high biomass. The tree canopy is dominated by *Brachystegia boehmii*, *B. spiciformis* and *Julbernardia globiflora* and the shrub layer by *Bauhinia petersiana, Bridelai cathartica* and *Ormocarpum kirkii.* The grass layer is tall and made up predominantly of nutritionally poor *Andropogon, Diheteropogon, Heteropogon* and *Hyparrhenia* species; *Oxytenanthera abyssinica* bamboos are locally common. Some of these grass species are nutritionally valuable during the early growing season but soon produce thick, unpalatable stems with high biomass.

Sherry (1989) argues, based on soil nutrient status and water infiltration capacity, that this vegetation type's plant biomass should be considered as high but the nutritional level of digestible material in the plants as poor (Figure 2.12).

Figure 2.10: High altitude tall miombo woodland in the dry season in Majete Wildlife Reserve

Figure 2.11: High altitude tall miombo woodland in the wet season in Majete Wildlife Reserve

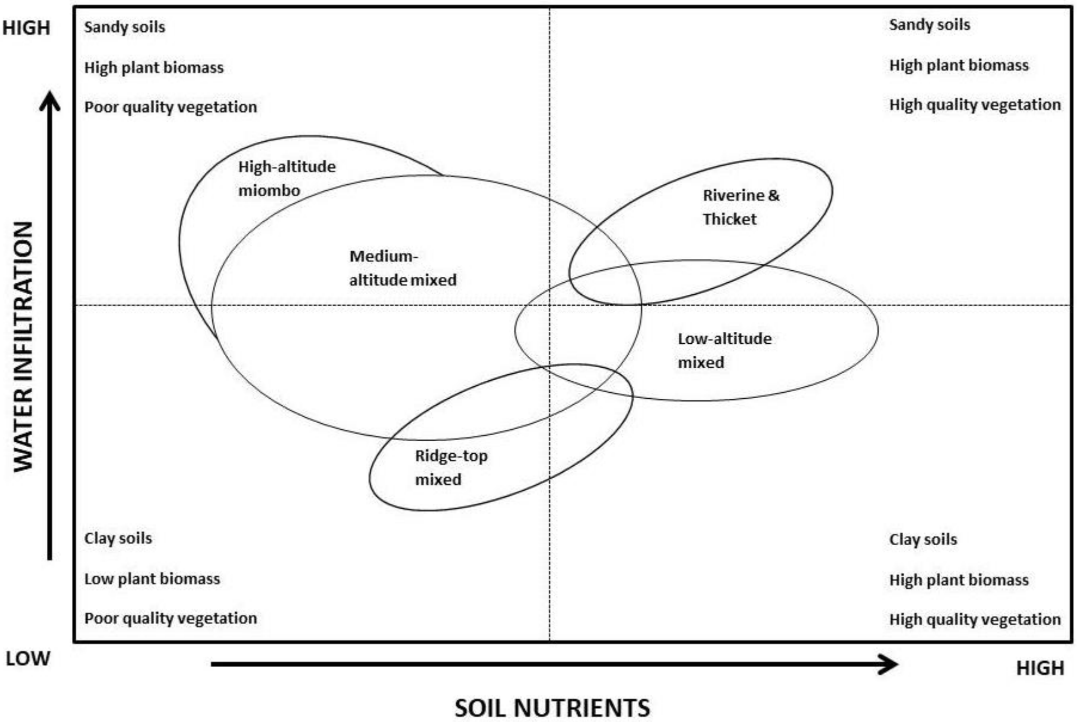

Figure 2.12: The relationship between the vegetation associations in terms of water infiltration and nutrients, adapted from Sherry (1989)

Medium altitude mixed tall deciduous woodland

This vegetation type forms a band of intergradation (between 230 and 410 m.a.s.l) separating the high altitude tall miombo woodland from the low altitude mixed tall deciduous woodland, and thus represents an ecotone of their characteristic vegetation. Tree biomass is highest of all vegetation types in MWR though average height is relatively short at five metres (Figures 2.13 and 2.14). *Brachystegia boehmii* is dominant by virtue of a few large mature trees, with other dominant species being smaller and in dense clumps, such as *Combretum fragrans*. The shrub stratum is short (average height is one metre) and dense with low biomass, dominated by *Pterocarpus rotundifolius*. Overall the species composition is less diverse than in the other vegetation communities.

Sherry (1989) considers the plant biomass production of this vegetation type as lower than that of the high altitude tall miombo woodland, but of a similar low quality (Figure 2.12).

Figure 2.13: Medium altitude mixed tall deciduous woodland in the dry season in Majete Wildlife Reserve

Figure 2.14: Medium altitude mixed tall deciduous woodland in the wet season in Majete Wildlife Reserve

Low altitude mixed tall deciduous woodland

These woodlands are shorter and more open than the high altitude tall miombo woodland and occur between 205 and 280 m.a.s.l. (Figures 2.15 and 2.16). The tree stratum is denser than adjacent riverine areas and with a much greater biomass. The dominant tree species is *Sclerocarya caffra* with *Combretum imberbe* and *Terminalia sericea* prominent. The shrub layer is relatively sparse with the lowest overall biomass. The grass layer is medium to tall comprised mostly of perennial species such as *Heteropogon*. The sandy clay loams here produce vegetation of medium quality (Bell, 1984). Sherry (1989) classifies the plant biomass production of this vegetation type as similar to that of the medium altitude mixed tall deciduous woodland but considers the vegetation quality to be better (Figure 2.12).

Figure 2.15: Low altitude mixed tall deciduous woodland in the dry season in Majete Wildlife Reserve

Figure 2.16: Low altitude mixed tall deciduous woodland in the wet season in Majete Wildlife Reserve

Ridge-top mixed short deciduous woodland

This woodland is confined to flat ridge tops and upper slopes of higher ground (220 – 300 m.a.s.l) between the tributaries of the Shire river and is most common in the east of the reserve. A short tree stratum is present (average height is five metres), with a medium density and low biomass (Figures 2.17 and 2.18). *Terminalia sericea* and *Diospyros kirkii* are dominant. The shrub layer is short (average height is one metre) of a high density but with relatively low biomass. *Diplorhynchus condylocarpon* and *Bauhinia petersiana* are the dominant shrubs. The grass layer is relatively sparse. This vegetation type supports the lowest overall plant biomass and quality of all the plant communities owing to poor soils which are shallow and gravelly and support stunted tree growth (Sherry, 1989; Figure 2.12).

Figure 2.17: Ridge-top mixed short deciduous woodland in the dry season in Majete Wildlife Reserve

Figure 2.18: Ridge-top mixed short deciduous woodland in the wet season in Majete Wildlife Reserve

Riverine and alluvial associations

This vegetation type is made up of riverbed, river bank and alluvial communities confined to river valleys throughout MWR (Figures 2.19 and 2.20). Deep, sandy alluvial soils and relatively high soil nutrient levels account for overall high biomass and productivity within this vegetation type. However, the tree stratum has a relatively low biomass compared to the other vegetation communities (average height is seven metres) and is made up of tall and sparse species dominated by *Vachellia tortilis, Kigelia africana* and *Croton megalobotrys.* Shrub species composition is highly diverse with *Combretum mossambicensis* and *C. paniculatum* dominant. The large shrub size make up the majority of the high biomass found here. The riverine terraces along the Shire support a dense mat of high quality grasses including *Panicum*, *Echinochloa* and *Paspalum* species (Bell, 1984). The plant biomass and plant quality of this vegetation type is considered high by Sherry (1989; Figure 2.12).

Figure 2.19: Riverine and alluvial associations in the dry season in Majete Wildlife Reserve

Figure 2.20: Riverine and alluvial associations in the wet season in Majete Wildlife Reserve

Riparian thicket

Riparian thicket is associated with the rivers and river junctions in the east of MWR, particularly in level areas where tributaries meet, and is associated with deeper, sandy alluvial soils with high nutrients. Tributaries act as effective firebreaks which suggest that thicket is the climax vegetation of alluvial soils in this area.

Tree biomass is high although the average height is short (five metres), with the regular occurrence of *Adansonia digitata* contributing largely to the high biomass (Figures 2.21 and 2.22). Characteristic tree species here are *Diospyros quiloensis*, *Euphorbua ingens* and *Markhamia acuminata.* The shrub layer gives the highest biomass of all the vegetation types and is relatively tall with *Grewia* species clearly dominant. Overall species diversity is high with deep, sandy alluvial soils producing high quality vegetation as nutrient-rich forage. Like the riverine and alluvial associations, Sherry (1989) thus considers this vegetation type to have both high plant biomass and good quality forage (Figure 2.12).

Figure 2.21: Riparian thicket in the dry season in Majete Wildlife Reserve

Figure 2.22: Riparian thicket in the wet season in Majete Wildlife Reserve

2.7 Fauna

There are currently 41 medium and large terrestrial mammals believed to occur in MWR (Table 2.1; Martin, 2005). Medium and large mammals are defined as those with a body mass above 0.5 kg (Amin *et al.*, 2018).

All the listed species are considered native, however, there are no historic reports of nyala (*Tragelaphus angasii*) in MWR (Bell, 1984). Lengwe National Park, approximately 20 km from MWR, was established to protect declining numbers of nyala (Morris, 2001), and is considered to hold more favourable habitat for nyala than MWR (Martin, 2005).

In 2003 when African Parks assumed management of MWR, few medium and large mammal species were present, with the only significant numbers being those of kudu, waterbuck and hippo (Hall-Martin, 2011; Martin, 2005). From 1986 to 1992, the reserve's entire elephant population was poached. Between 2003 and 2012 African Parks undertook a large wildlife reintroduction programme, whereby more than 3 000 individual animals of 13 species (11 herbivore and two carnivore species) were reintroduced to MWR, with the aim to restore ecosystem functioning of the reserve. The mammal reintroductions were undertaken in stages (see Appendix A; African Parks, 2018a) with initial releases happening in the 140 km² Sanctuary area (see below in Infrastructure and the location in Figure 2.23) which at the time was the only area that was fenced, with releases into the wider reserve happening after the entire reserve was fenced in 2008. The Sanctuary fence was removed between May and September 2011, allowing the wildlife to disperse into the wider reserve. Appendix B shows 2018 estimates of the population sizes of the medium and large mammals (African Parks, 2018b).

Table 2.1: The 41 medium and large terrestrial mammals historically recorded in Majete Wildlife Reserve (Martin, 2005)

Common name	Species
Herbivore	
African elephant	*Loxodonta africana*
African savanna hare	*Lepus microtis*
Black rhinoceros	*Diceros bicornis*
Bushbuck	*Tragelaphus scriptus*
Cape buffalo	*Syncerus caffer*
Common duiker	*Sylvicapra grimmia*
Common eland	*Tragelaphus oryx*
Common reedbuck	*Redunca arundinum*
Greater kudu	*Tragelaphus strepsiceros*
Hippopotamous	*Hippopotamus amphibius*
Impala	*Aepyceros melampus*
Klipspringer	*Oreotragus oreotragus*
Lichtenstein's hartebeest	*Alcelaphus lichtensteinii*
Livingstone’s suni	*Neotragus moschatus*
Nyala	*Tragelaphus angasii*
Plains zebra	*Equus quagga*
Porcupine	*Hystrix africaeaustralis*
Sable antelope	*Hippotragus niger*
Sharpe's grysbok	*Raphicerus sharpei*
Warthog	*Phacohoerus aethiopicus*
Waterbuck	*Kobus ellpsiprymnus*
Carnivore	
African civet	*Civettictis civetta*
African clawless otter	*Aonyx capensis*
Caracal	*Caracal caracal*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Serval	*Leptailurus serval*
Side-striped jackal	*Canis adustus*
Spotted hyaena	*Crocuta crocuta*
Spotted-necked otter	*Hydrictis maculicollis*
Omnivore	
Banded mongoose	*Mungos mungo*
Bushpig	*Potamochoerus larvatus*
Honey badger	*Mellivora capensis*
Large grey mongoose	*Herpestes ichneumon*
Large-spotted genet	*Genetta tigrina*

Slender mongoose	*Galerella sanguinea*
Vervet monkey	*Cercopithecus pygerythrus*
Yellow baboon	*Papio cynocephalus*
Yellow-spotted rock dassie	*Heterohyrax brucei*
Insectivore	
Aardvark	*Orycteropus afer*
Ground pangolin	*Smutsia temminckii*

2.8 Fire

Prior to 2004 no fire management took place in MWR, and due to high anthropogenic pressure on the reserve boundary, large and continuous areas of the reserve burnt every year. This pressure still exists with uncontrolled, recurring wildfires an ongoing management challenge. The current fire management goal is to prevent these extensive annual burns by practicing early dry season controlled burning, creating firebreaks in order to contain the spread of these wildfires across the landscape (Hay, pers. comm. 2018; MWR Park Manager).

The fire return interval for MWR's high altitude miombo and medium altitude mixed woodlands is 1.96 years, while the low altitude mixed woodland experience fire less often at a return interval of approximately every four years (Nieman, Unpublished data). Fire is actively excluded from the Sanctuary area in the north-east of the reserve, where reserve infrastructure is concentrated. Large areas of the reserve continue to burn every year, notably in the south and west of the reserve, where suppression and maintaining firebreaks is more challenging.

2.9 Infrastructure

MWR's perimeter fence is 142 km in length, made up of 1.5 m high mesh with an additional four wire strands above this making the fence two metres tall. Four live and four earth strands run on offsets from the bonnox. At the fence base, 20 cm off the ground, an anti-burrow hot wire runs independently from the main fence. In 2003 a 140 km^2 "Sanctuary" area (see Figure 2.23) was fenced off in the north-east of the reserve to facilitate the reintroduction of mammals between 2003 and 2008, while the larger reserve's fenceline was being completed. In 2011 the Sanctuary fenceline was removed.

The road network is concentrated in the Sanctuary area where the majority of reserve buildings are situated, and with all the accessible 2x4 roads is the main area for tourism activities. The roads in the remainder of the reserve are used for management activities such as patrols, fire management, research and road, fence and artificial waterhole maintenance. All roads are graded gravel roads.

Within the Sanctuary there are two tourist lodges accommodating approximately 20 guests each, as well as a campsite and restaurant. Management buildings refer to the office, staff housing, research camp and a workshop. The scout camps are fenced areas with housing for each of the scouts and their families. The scout camp on the boundary of the Sanctuary houses 20 scouts and the three outside the Sanctuary house eight scouts each. Scouts patrol from their camp on foot or by motorbike and will be transported by vehicle into the reserve for long patrols.

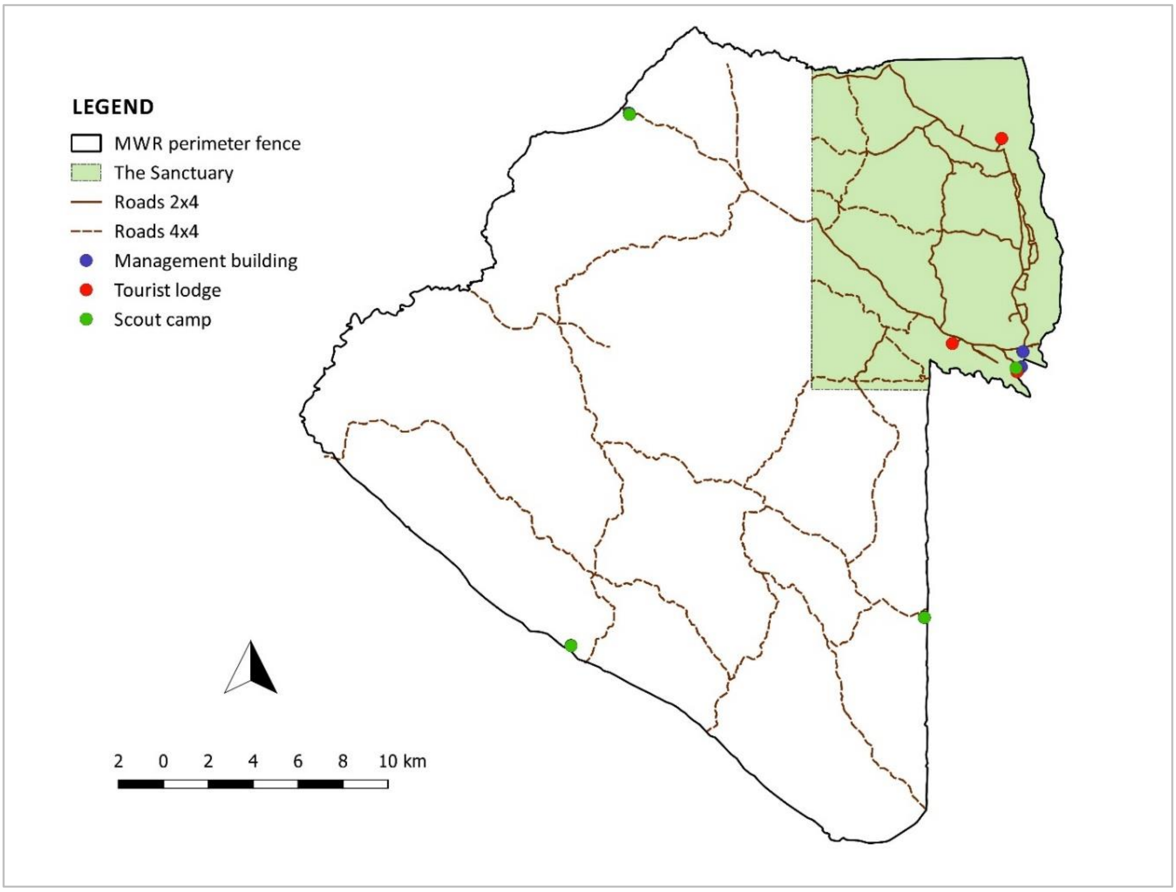

Figure 2.23: Map indicating the reserve fenceline, the Sanctuary, road network and buildings within Majete Wildlife Reserve

2.10 Surrounding land use and human impact

Malawi is a small country with a high population density of 186 people/km^2 (Government of Malawi, 2018). This high population density means that the national parks and forest and wildlife reserves, are increasingly threatened by settlement and human encroachment (Frost, 1996; Walker & Desanker, 2004) with MWR no exception. The primary land use outside the reserve is subsistence agriculture. Cattle (*Bos indicus*) numbers are low but there is an abundance of goats (*Capra spp*.) and pigs (*Sus spp*., Martin, 2005). Agriculture is especially prevalent on the southern, eastern and north-western boundaries of the reserve (Figure 2.24). Illegal timber extraction is high around the outside perimeter of the reserve.

The Mwanza district bordering the northern part of MWR is densely populated with approximately 173 people/km^2, but only the western section of the northern boundary is exposed to agricultural practices. The Chikwawa district that surrounds the rest of the reserve is less densely populated than Mwanza, holding approximately 116 people/km^2. The entire south-western fence line is directly exposed to agricultural practices with the southern part of the eastern boundary similarly exposed (i.e. no buffer zone).

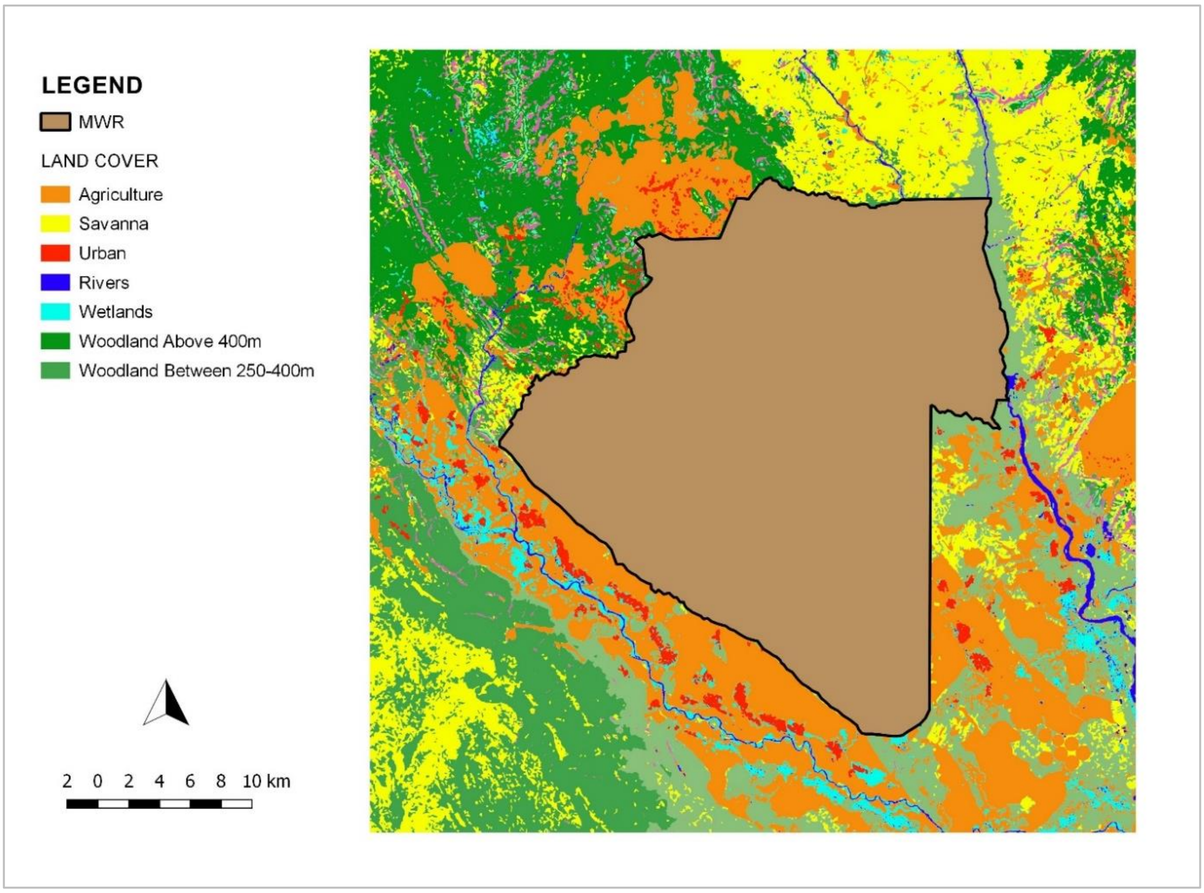

Figure 2.24: Map of land cover around Majete Wildlife Reserve, indicating agricultural areas abutting the reserve boundary, notably along the southern and south-eastern boundaries

2.11 References

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CHAPTER 3

A CAMERA TRAP APPRAISAL OF SPECIES RICHNESS AND COMMUNITY COMPOSITION OF MEDIUM AND LARGE MAMMALS IN MAJETE WILDLIFE RESERVE, MALAWI

3.1 Introduction

Sound protected area management requires area specific biological information for effective decision making (Margules & Pressey, 2000; Yoccoz *et al.*, 2001). Biological monitoring can be defined as the process of gathering information about the state of a system and observing any changes which may occur over time (Yoccoz *et al.*, 2001; Cowell *et al.*, 2020). Monitoring data are collected through the measuring of variables, with the decision of what to monitor determined by management objectives (Cowell *et al.*, 2020). Variables such as species diversity, species richness, community structure, population size and distribution are measured and are critical for planning and evaluating nature conservation strategies (Tobler *et al.*, 2008; O’Brien, 2008; Yoccoz *et al.*, 2001).

Mammal species richness, defined as the number of mammal species in an area, is the most common measure used to assess and predict anthropogenic impacts on biodiversity (Gibson *et al.*, 2011; Newbold *et al.*, 2015; Boron *et al.*, 2019). For example, highly fragmented sites and those subject to habitat degradation have a lower mammal species richness than contiguous and intact sites (Gibson *et al.*, 2011; Ahumada *et al.*, 2013; Ramesh *et al.*, 2016). Species richness is also used to evaluate the state of biological diversity in an area (Yoccoz *et al.,* 2001). The measure is thus useful to identify biodiversity hotspots on a global scale (Myers *et al.*, 2000), but can also provide baseline species data on a local scale, as a simple characterisation of diversity that is easy to interpret. Mammal species richness estimates provide a simple baseline measure from which future comparisons can be made and the effectiveness of mammal related management actions evaluated over time (Tobler *et al.*, 2008; Yoccoz *et al.*, 2001; Amin *et al.*, 2018; Cowell *et al.,* 2020).

The use of camera traps has become a popular method to monitor medium and large terrestrial mammal species richness information (Silveira *et al.*, 2003; Tobler *et al.*, 2008; Roberts, 2011). They offer a rapid, long term, low cost (over the long term) and easily replicable method (Ahumada *et al.*, 2011; Rovero *et al.*, 2014; Rich *et al.*, 2017; Li *et al.*, 2018; Rocha *et al.*, 2019), and are especially effective in targeted monitoring of rare mammal species (Kelly, 2008; Tobler *et al.*, 2008). The use of camera traps provides the opportunity for long term, standardised monitoring of terrestrial mammals that can be of value locally as well as globally across numerous sites and international projects (Ahumada *et al*., 2011; Ripple *et al.*, 2014; Rich *et al.*, 2017; Li *et al.*, 2018).

When assessing medium to large mammal species richness, both observed species richness (Ahumada *et al*., 2011; Samejima *et al.*, 2012) and estimates based on observed species richness (Tobler *et al.,* 2008; Wearn *et al.*, 2016; Orban *et al.,* 2018; Boron *et al*., 2019) are used. Observed species richness produces a minimum estimate (McNew & Handel, 2015) and does not account for imperfect detection (the fact that a species may be undetected because it is rare, inconspicuous or temporarily absent from a sampling area) which may lead to biased estimates (Kéry & Royle, 2008; Marc & Royle, 2009; McNew & Handel, 2015). A more accurate measure of estimated species richness is to use models that account for imperfect detection, which leads to estimates that can reliably be used to provide baseline species richness estimates for incorporation into monitoring programmes (Dorazio & Royle, 2005; Kéry & Royle, 2008).

Camera trap data can also provide information about animal community structure (composition and abundance), which are also used to assess negative anthropogenic impacts in an area, such as habitat fragmentation (Ahumada *et al.,* 2011; Wearn & Glover-kapfer, 2017). Community structure is characterised by populations of several species that are associated with a particular habitat, and can be broadly categorised by the functional traits of body size and trophic category (Ahumada *et al.,* 2011; Paker *et al*., 2014). The abundance and diversity of body sizes and trophic groups play a significant role in the functioning of ecosystems (Ahumada *et al.,* 2011; Fritz *et al*., 2011), which is influenced by rainfall and soil nutrient gradients (Olff, *et al*., 2002) and the dynamics between trophic groups and feeding guilds (Fritz *et al*., 2002; Hopcraft *et al*., 2010). Community structure will therefore vary between systems such as African savanna and tropical rainforests where environmental gradients differ (Bell, 1985; Ahumada *et al.*, 2011; Amin *et al.*, 2018).

Camera trap capture frequencies (captures/100 camera days) are often used as a relative abundance index (RAI) when absolute abundance is difficult and costly to measure (Amin *et al*., 2015; Palmer *et al*., 2018). However, camera trap capture frequencies, from which RAIs are derived, should be used with caution as they do not account for imperfect and variable detection and are often criticised (Tobler *et al.,* 2008; Foster & Harmsen, 2012; Sollmann *et al*., 2013). The reliability of RAIs from camera traps has been tested against robust density estimates, with correlations found to be positive and linear (Rovero & Marshall, 2009; Carbone *et al.*, 2001). They were also tested by Palmer *et al.* (2018) who compared RAIs from a camera trap study in the Serengeti to aerial count data from the same area and found camera trap RAIs to be reasonably accurate and precise. Despite the controversy that RAIs invoke, their use can thus still offer some meaningful insights into wildlife populations (Wearn & Glover-kapfer, 2017).

The Miombo Woodland Ecoregion holds the most extensive seasonal and floristically rich woodland and dry forest formation in Africa, receiving > 700 mm mean annual rainfall on nutrient poor soils, and typically has a low diversity of mammal species (Frost, 1996; Syampungani *et al.*, 2009; Timberlake, 2018). Mammal diversity increases with the inclusion of non-Miombo habitat patches such as riverine vegetation and savanna (Frost, 1996). Megaherbivores comprise the majority of the biomass of herbivore communities in ecosystems with high rainfall and low nutrient soils, such as Miombo woodlands, as they can tolerate the low quality vegetation which is available in high quantities (Fritz *et al*., 2002). As such, the biomass of the herbivore community of untransformed Miombo woodland comprises of almost two thirds mixed feeders (predominantly elephants *Loxodonta africana*), one third bulk grazers (buffalo *Syncerus caffer* and zebra *Equus quagga*) and a small proportion (~5%) of browsers (generally less than 100 kg; Bell, 1985). Specifically, elephants, zebra and buffalo are expected to make up between 75 and 90% of the herbivore biomass in Miombo woodland (Frost, 1996). Spotted hyaena (*Crocuta crocuta*) make up the majority of the predator biomass in Miombo woodland (Fritz *et al*., 2011).

Majete Wildlife Reserve (MWR) in Malawi lies within the Miombo Woodland Ecoregion, and experienced large-scale poaching during the second half of the 20th century. Since 2003 conditions improved with African Parks taking over management to control poaching. African Parks reintroduced locally extinct large mammal species to improve ecosystem functioning and boost tourism to provide critical revenue for management of the reserve. It is now an important refuge not only for these reintroduced species, but also the less charismatic and often overlooked mammal species that managed to persist despite the persecution of the past. MWR is found in a landscape increasingly threatened by agriculture and settlement (Coulibaly *et al.,* 2015) which might ultimately lead to complete isolation from other natural areas. It is thus important to ascertain which mammal species still remain within the boundaries of MWR and to monitor their persistence which will contribute to sound ecosystem functioning.

Little is known about the mammal species richness patterns and community structure across MWR as a systematic survey has never been undertaken. Based on observations from the 1980’s, at least 41 terrestrial medium and large (> 0.5 kg) mammal species are reported to occur in MWR (Martin, 2005). This chapter aimed to provide updated scientifically verifiable information for terrestrial medium and large mammal species richness and community structure within MWR through a comprehensive and systematic camera trap survey.

3.2 Methodology

3.2.1 Study site

The study was conducted in the 691 km^2 MWR in south-western Malawi (34°26'36.56"E - 34°45'29.84"E, 15°46'20.14"S - 16° 6'11.44"S). The reserve lies within a tropical climate zone with semi-arid conditions, characterised by a hot wet season (November – April), a cool dry season (May – August) and a hot dry season (September – November; Hall-Martin, 1975) . The reserve's topography influences the rainfall gradient - the lower lying eastern areas receive between 680 - 800 mm of precipitation, and the higher lying western slopes receive 700 – 1000 mm (Wienand, 2013). The estimated mean minimum and maximum temperatures are 12.5°C and 26.3°C in June and 20.9°C and 34.8°C in November (Martin, 2005b). The reserve lies within the Miombo Woodland Ecoregion with the vegetation broadly made up of high, medium and low-altitude woodland, ridgetop woodland, riparian thicket and riverine associations (Sherry, 1989). Two perennial rivers transect the north-east corner and numerous seasonal and ephemeral streams run throughout the reserve. See Chapter 2 for a detailed description of the study site.

3.2.2 Survey design

The camera trap survey took place during the dry season of 2018, between 7th June and 5th December. The study used 47 Cuddeback X-Change™ camera traps (Model 1279) with a colour strobe flash. Each camera was deployed inside a protective metal case.

Camera trap spacing

Quantum GIS (QGIS) 2.18.15 Vector Grid Research Tool (QGIS Development Team, 2018) was used to divide MWR into 140 five km^2 grid squares (2.25 km x 2.25 km). Cameras were placed in each of these grid squares in a systematic manner by sub-dividing the reserve into three sampling blocks of approximately 230 km^2 each (Figure 3.1). These blocks had 47, 47 and 46 camera survey sites respectively and the blocks were surveyed one after the other.

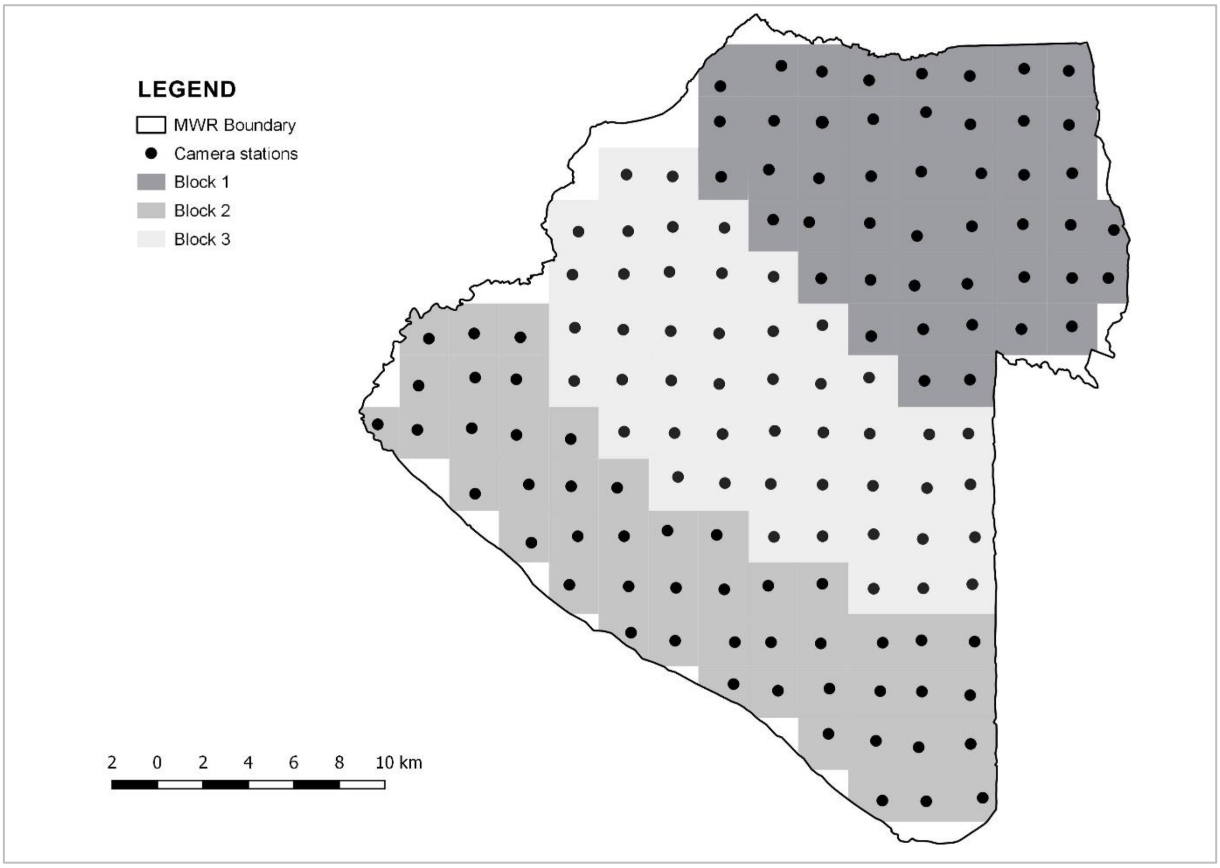

Figure 3.1: The locations of the 140 camera trap sites across Majete Wildlife Reserve. The sites were surveyed using 47 camera traps moved between three sampling blocks (different grey areas)

Camera placement protocol

The centre point of each grid cell was determined using the QGIS Polygon Centroid Geometry Tool (QGIS Development Team, 2018) from which the geographic coordinates were extracted and uploaded onto a handheld GPS device (Garmin eTrex10) for use in the field. Within a 100 m radius of the area surrounding each grid cell centre point, a systematic search for the most frequently used wildlife trail was done and a camera placed next to the most used trail. Signs of scat and spoor were used as indicators of use (Colyn *et al.,* 2018). A tree was chosen on which to secure the camera, facing either north or south to mitigate the over exposure of photographs by direct sunlight (Apps & McNutt, 2018). Cameras were secured vertically, 50 cm above the ground and positioned to photograph the flanks of passing animals (Tobler *et al*., 2008; Swanson *et al.*, 2015; Rich *et al.*, 2016).

The cameras were programmed to take three photographs at each trigger event with a delay of one minute between each trigger (Swanson *et al.*, 2015). At night cameras took only one photo every minute due to the flash having to recharge. Cameras were set to their highest sensitivity and the strobe flash activated after dark. The camera's zone control shutter was set in a wide angle view to allow an image to be captured as an animal entered the camera's movement detection range (and not limited to when it is centrally located to the camera), minimising the chances of missing a species if it rapidly moved past the camera. Vegetation within the camera's detection zone was trimmed to prevent false trigger events, but not to the extent of altering the immediate habitat. If practically possible, the cameras were serviced fortnightly to change batteries, download photographs and ensure cameras were fully operational. The cameras were not baited.

Trapping period

Effort was made to achieve a sampling period of 40 days per camera placement location in each of the three survey blocks (Ahumada *et al.*, 2013; Si *et al*., 2014; Colyn *et al.*, 2018; Kays *et al.*, 2020). The first block was surveyed between June and August, the second between July and September and the third between September and December 2018.

3.2.3 Data analysis

Photographs were collated using the camera trapping software Camelot 1.4.5 (Hendry & Mann, 2018). The photographs were filtered according to species using 30 minute intervals to ensure independence, which is considered a fair compromise between the likelihood of capturing the same group multiple times and the likelihood of missing groups (Linkie & Ridout, 2011; Davies *et al.*, 2016). Species were then filtered to include only medium and large mammal species (> 0.5 kg; Amin *et al.*, 2016) using body mass values from Skinner & Chimimba (2005), and to exclude arboreal species.

Observed and estimated species richness

Observed and estimated species richness was determined across the entire reserve (γ-richness). Observed species richness was calculated by counting the number of species detected. Estimated species richness was calculated by firstly using non-parametric incidence based estimators in the programme package EstimateS 9.1.0 (Tobler *et al.,* 2008; Colwell & Elsensohn, 2014), and secondly using a hierarchical Bayesian community model that accounts for imperfect detection based on species-specific models of occurrence (Dorazio & Royle, 2005).

Using EstimateS, a sample-based rarefaction graph was generated for the reserve. Non-parametric incidence based estimators were employed to produce species richness estimates and accumulation curves, where the shape of the curves and the asymptote were compared to one another. The estimators used were the Incidence-based Coverage Estimator (ICE), Chao 2, Jackknife 1 and Jackknife 2 (Tobler *et al.,* 2008). All these estimators serve to extrapolate species data to the presumed asymptote (Gotelli & Chao, 2013). The estimators use information on the frequency of rare species in a sample to estimate the number of undetected species, based on the concept that rare species carry the most information about the number of undetected species (Gotelli & Chao, 2013). A comparison was made between the estimated species richness and the anecdotal species list developed in the 1980's (Martin, 2005; See Chapter 2, Table 2.1 for species list).

In addition to the non-parametric incidence based estimators, a hierarchical Bayesian community model that accounts for imperfect detection based on species-specific models of occurrence (Dorazio & Royle, 2005) was run. The species community model based on species-specific models of occurrence was implemented in the program JAGS version 4.3.0 (Plummer, 2003) accessed through the program R, version 3.6.0 (R Development Core Team, 2019) using the package RJAGS version 3-10 (Plummer, 2014). It ran three Markov Chain Monte Carlo (MCMC) chains with 1005,000 iterations, a burn-in of 5000 and a thinning rate of 100. Chain convergence was checked with trace plots and the Gelman-Rubin statistic R-hat (Gelman *et al*., 2004), which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman & Hill, 2006).

Rarefaction curves ignore the spatial component of the data, losing information on how richness may vary across an area (Sollmann, 2018). Consequently, a map was created to display the recorded species richness of each camera station which provides an indication of the spatial variation of species richness across MWR.

Community structure

A basic assessment of community structure (i.e. abundance and composition) was estimated by comparing the camera trap RAIs of species (independent detections per 100 camera trap days; O'Brien *et al*., 2003; Sollmann *et al.*, 2013; Amin *et al*., 2015) within and between feeding guilds. As not every camera was operational for the full 40 day survey period, the RAI for each species at each camera location was calculated and then averaged across the 140 sites to estimate species relative abundance across the reserve.

The community structure was visually displayed by plotting the RAI of a species within a particular feeding group against the species body weight (Amin *et al.*, 2018). Average female body mass estimates were used for each species and obtained from Skinner & Chimimba (2005).

To make the herbivore community composition comparable to the results of other Miombo woodland studies, the biomass contribution of the herbivore species of each feeding guild (browser, grazer and mixed feeder) were divided into three size classes (mega: > 1000 kg, medium: 100 – 1000 kg and small < 100 kg; Bell, 1985). Buffalo and zebra were separated into their own category as bulk grazers (Bell, 1985; Frost, 1996). The relative biomass contribution of each size class for the respective feeding guilds were calculated by multiplying the camera trap capture frequency of the respective species within each class, with the average female body mass of that species and then summing these. These relative biomass estimates were then compared to those of Bell (1985) for Miombo woodland (moist oligotrophic savanna communities with woodlands).

To assess how well the RAI measure compares to other abundance estimates, and hence reflects community structure, the camera trap RAIs of large herbivores were compared to the results of MWR's 2018 dry season aerial census (African Parks, 2018; Palmer *et al.,* 2018) Large herbivore species (> 20 kg) were counted using a Bell 206 helicopter which flew 500 m wide transects over three days following the protocol of Macpherson (2012). Three comparisons were made between the aerial count data and calculated RAI. Aerial count data was expressed as: 1) total aerial count numbers of individual animals per species, 2) total aerial count numbers of individual animals per species corrected for undercounting, and 3) total number of independent encounters (individuals if alone, or groups when together) per species during the aerial census. The corrected aerial count numbers were obtained by using correction factors for each species from Owen-Smith & Mills (2008) calculated for the savannas of Kruger National Park, South Africa, which originate from the work of Redfern *et al*. (2002) and Mills & Biggs (1993). All the MWR large herbivore species also occur in Kruger National Park except for Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) where the value for common tsessebe (*Damaliscus lunatus*) was used as proxy (Owen-Smith & Mills, 2008).

3.3 Results

The camera trap survey lasted 5 456 camera days (mean 39 days/camera) out of an anticipated 5 600 days. Of the 140 cameras, 15 (11%) were in the field and functional for less than the 40 day trapping period (Figure 3.2), resulting in a loss of 146 camera days or 2.6% of the expected number of camera days. The loss of data was due to disturbance of camera orientation by elephant (three cameras) and warthog (one camera), batteries running out (four cameras), SD cards reaching capacity (one camera) and a logistical error leading to the removal of six cameras one day before the targeted 40 days were reached.

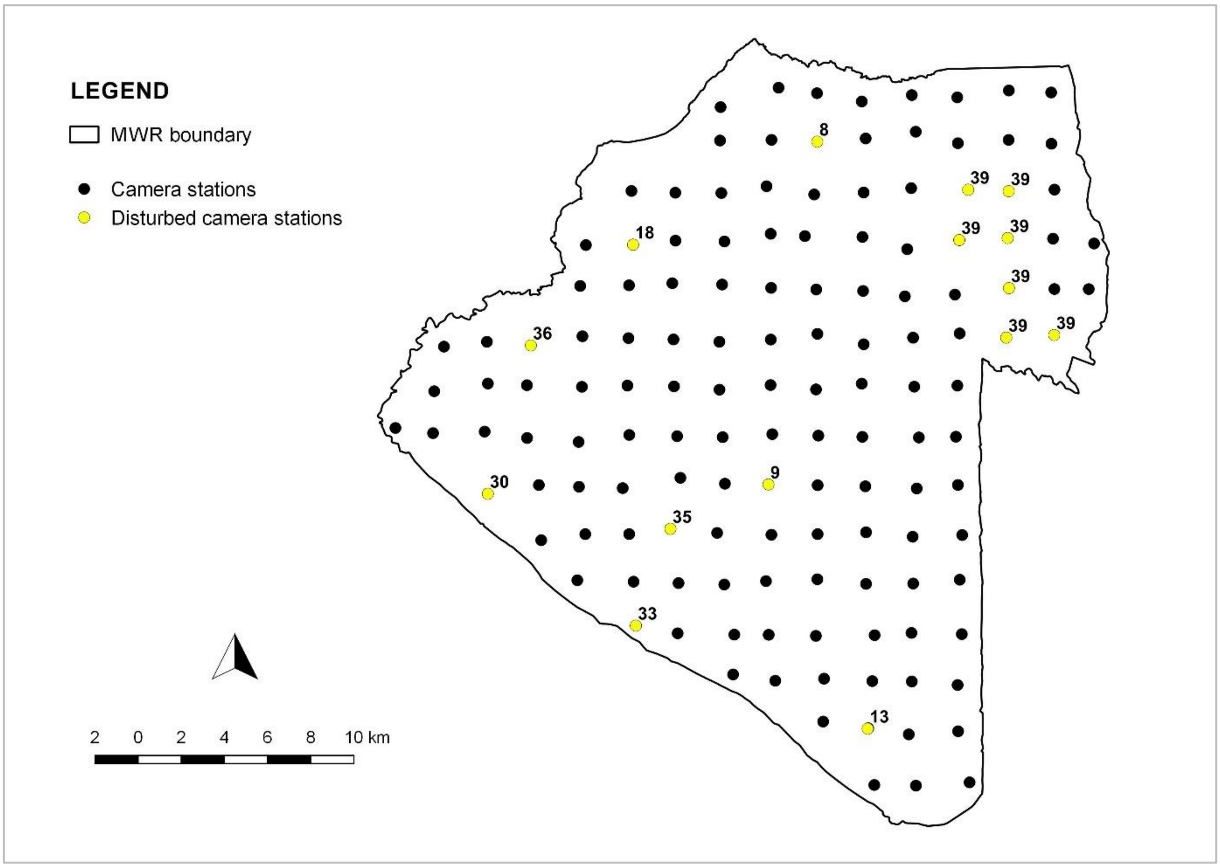

Figure 3.2: Map of Majete Wildlife Reserve showing the location of the camera stations that were operational for the full 40 day survey period (black dots) and the 15 camera stations that were operational for only a portion of the time (yellow dots). The number of survey days accrued by the cameras not running for the full 40 days are indicated above the yellow dots

A total of 120 239 photographs were recorded, of which 12 202 were independent detections of 35 medium and large mammal species (Table 3.1). The mean number of species detected per camera trap location was 11, ranging from 0 – 20 (Figure 3.3). The species detected most widely were kudu, warthog, sable antelope and baboon which were captured at more than 100 camera locations, while side-striped jackal, slender mongoose, pangolin, honey badger and vervet monkey were each recorded at less than five locations. The most frequently recorded species was warthog, followed by waterbuck, impala and kudu which all had more than 1000 detections each. Slender mongoose, side-striped jackal and honey badger had three or less detections each.

Table 3.1: Camera trap statistics for the 35 medium and large mammal species that were detected during the camera trap survey at Majete Wildlife Reserve. Species are arranged according to feeding strategy with the number of independent detections, number of camera locations a species was detected at, and species capture frequency (captures/100 camera days) indicated next to each species name

Common name	Species	No. of detections	No. of locations detected at	Capture frequency
Herbivore		**11 093**		
African elephant	*Loxodonta africana*	267	73	4.82
African savanna hare	*Lepus microtis*	14	8	0.26
Black rhinoceros	*Diceros bicornis*	47	21	0.84
Bushbuck	*Tragelaphus scriptus*	562	84	10.24
Cape buffalo	*Syncerus caffer*	626	75	11.25
Common duiker	*Sylvicapra grimmia*	460	96	8.28
Common eland	*Tragelaphus oryx*	192	56	3.47
Common reedbuck	*Redunca arundinum*	55	25	1.01
Greater Kudu	*Tragelaphus strepsiceros*	1 043	131	19.06
Hippopotamous	*Hippopotamus amphibius*	31	8	0.55
Impala	*Aepyceros melampus*	1 100	67	19.76
Klipspringer	*Oreotragus oreotragus*	17	8	0.3
Lichtenstein's hartebeest	*Alcelaphus lichtensteinii*	160	39	2.86
Nyala	*Tragelaphus angasii*	165	29	2.97
Plains zebra	*Equus quagga*	598	73	23.03
Porcupine	*Hystrix africaeaustralis*	140	51	2.59
Sable antelope	*Hippotragus niger*	773	112	14.2
Sharpe's grysbok	*Raphicerus sharpei*	64	36	1.24
Warthog	*Phacohoerus aethiopicus*	3 510	131	63.6
Waterbuck	*Kobus ellpsiprymnus*	1 268	78	22.77
Carnivore		**240**		
African civet	*Civettictis civetta*	70	23	1.26
Caracal	*Caracal caracal*	10	9	0.18
Leopard	*Panthera pardus*	43	26	0.84
Lion	*Panthera leo*	14	7	0.25
Serval	*Leptailurus serval*	19	14	0.34
Side-striped jackal	*Canis adustus*	1	1	0.02
Spotted hyaena	*Crocuta crocuta*	83	32	1.5
Omnivore		**779**		
Bushpig	*Potamochoerus larvatus*	122	59	2.29
Honey badger	*Mellivora capensis*	3	3	0.05
Large-spotted genet	*Genetta tigrina*	37	14	0.68
Slender mongoose	*Galerella sanguinea*	1	1	0.02
Vervet monkey	*Cercopithecus pygerythrus*	9	4	0.16
Yellow baboon	*Papio cynocephalus*	607	108	10.89
Insectivore		**91**		
Aardvark	*Orycteropus afer*	86	45	1.6
Ground pangolin	*Smutsia temminckii*	5	3	0.09

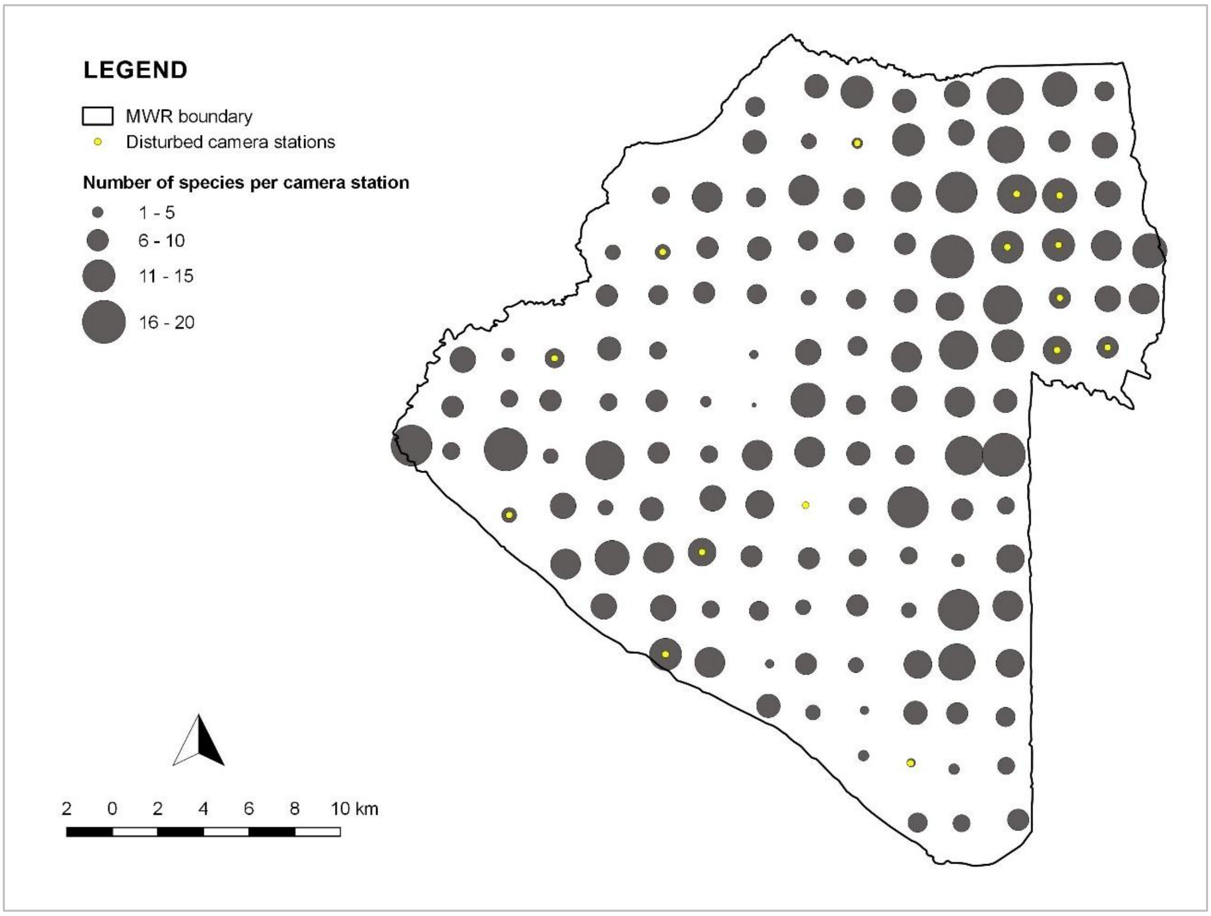

Figure 3.3: Map of Majete Wildlife Reserve showing the location of the 140 camera trap stations with the size of the circle indicating the number of species detected per station. The stations that did not reach the full effort of 40 days are indicated with a yellow dot

Species richness estimators

Based on the rarefied species accumulation curves, all the observed species were recorded after approximately 5 000 camera days (Figure 3.4). Chao 2 and Jack 1 levelled off at approximately 4 500 days, while Jack 2 levelled at approximately 5 000 days. ICE and Chao 2 produced similar estimates of 36.35 and 35.49 species respectively, while the Jackknife estimators, Jack 1 and Jack 2 produced higher estimates than these, with 36.95 and 37.92 species. Jack 2 thus produced the closest estimate (37.92) to the 41 species contained in the species list of the reserve. The Bayesian analysis estimated nearly two species more (36.5 species, 95% CI = 35 - 40) than the 35 observed species (Figure 3.5).

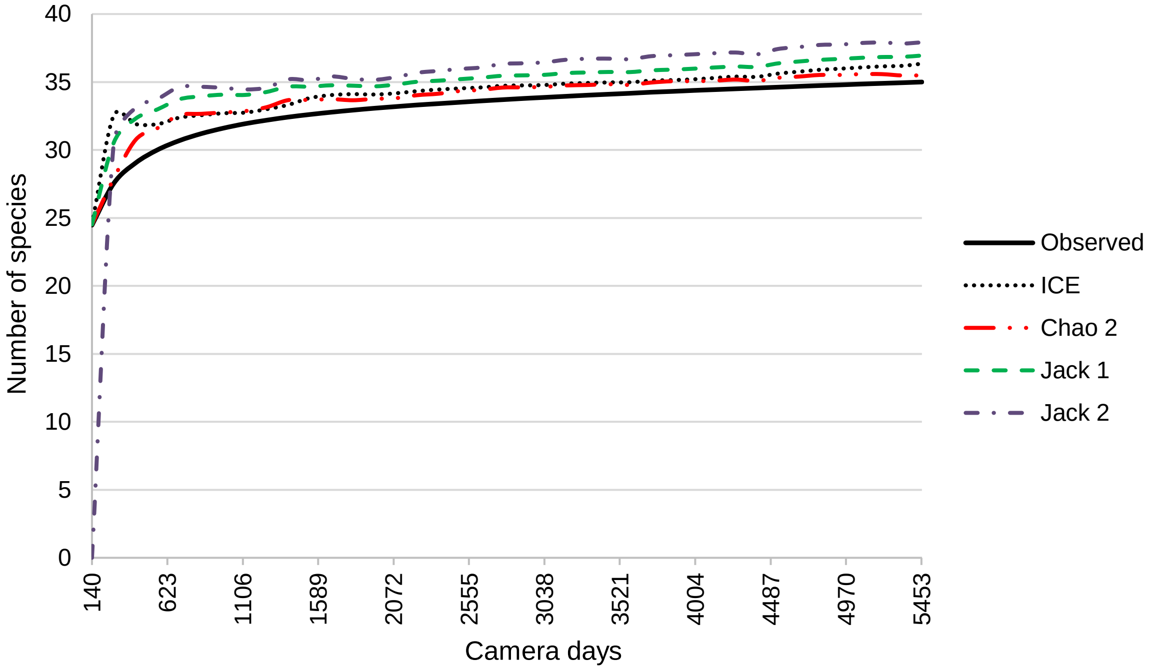

Figure 3.4: The observed (actual) and predicted (non-parametric estimators) medium and large mammal species richness estimates at Majete Wildlife Reserve in relation to the sampling effort as calculated using EstimateS

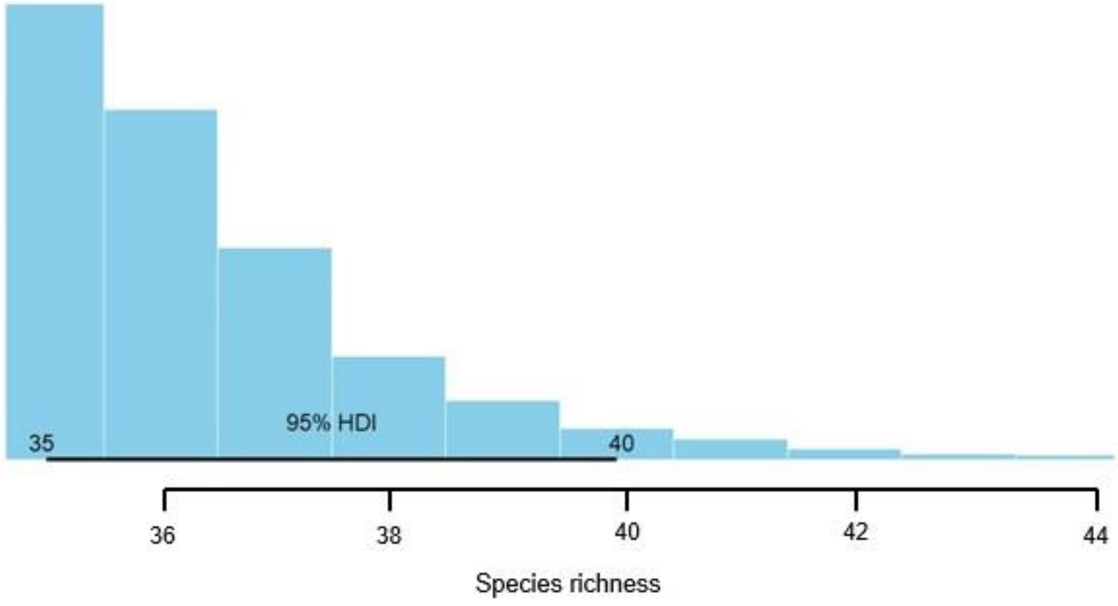

Figure 3.5: Bayesian species richness posterior distribution for medium and large mammals at Majete Wildlife Reserve. The 95% Credible Interval (35 – 40 species) is also shown

Community structure

Herbivores made up the largest component of the medium to large mammal community with 20 species, followed by carnivores with seven species, omnivores with six species and insectivores with two species (Figure 3.6, Table 3.1). The most frequently encountered trophic guild was herbivores, followed by omnivores, carnivores and insectivores (Figure 3.6, Table 3.1). Of the herbivores the most encountered species were grazers (eight species with 7 021 detections), followed by browsers (six species and 2 193 detections) and mixed feeders (four species with 1 724 detections).

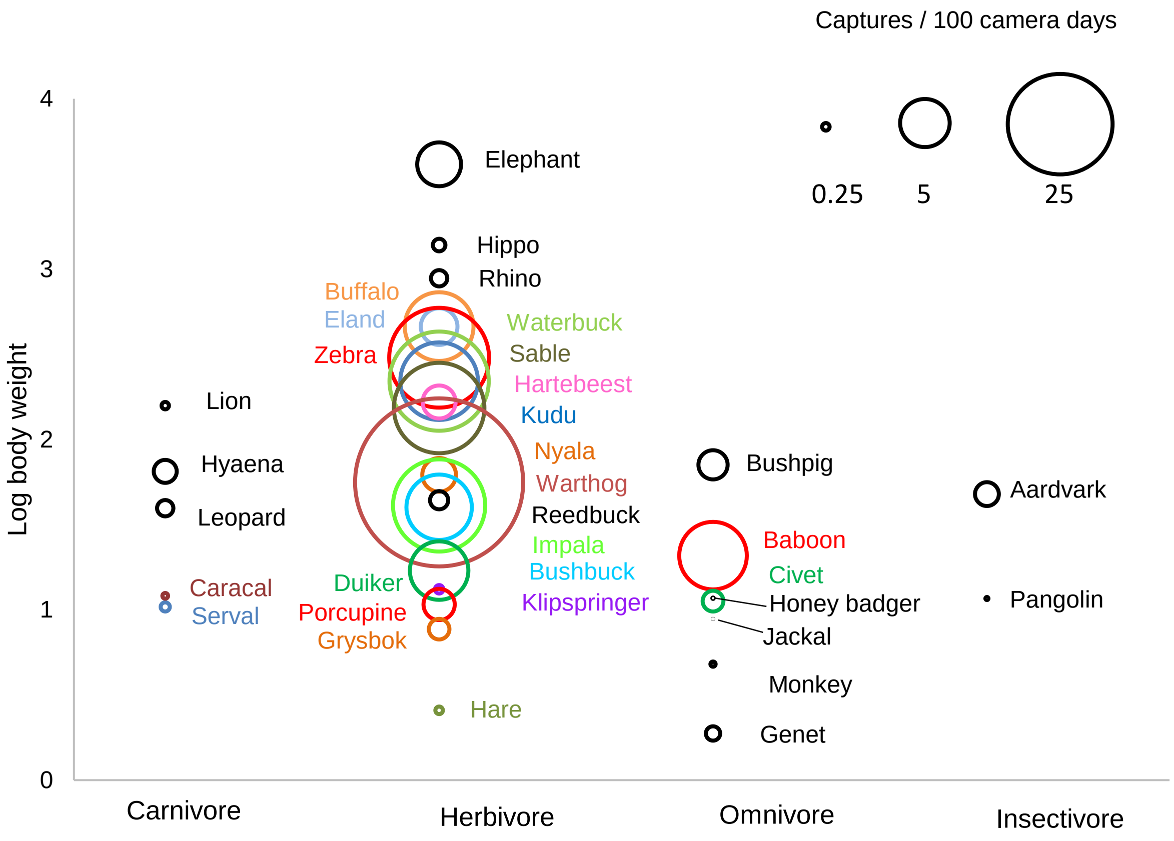

Figure 3.6: A representation of the abundance of each species in each feeding group at Majete Wildlife Reserve based on body size (expressed in a log scale) and feeding group, with each circle proportional to the RAI (captures/100 days) for that species

When the herbivore community is explored from a biomass contribution perspective, grazers contribute 48%, browsers 7.3% and mixed feeders 43% (Figure 3.7, Table 3.2) to the overall medium and large herbivore biomass. Large herbivores make up 41% of the herbivore community, medium herbivores 49% and small herbivores only 9.3% (Table 3.2).

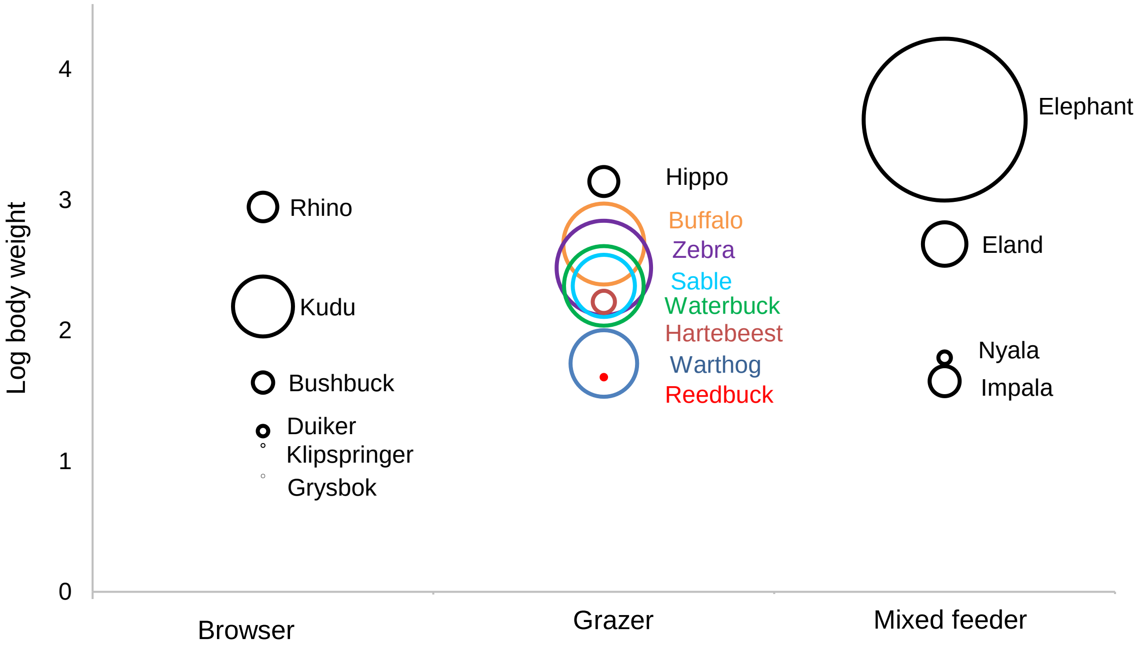

Figure 3.7: A representation of the herbivore community structure based on relative biomass contribution per feeding guild at Majete Wildlife Reserve. Species are presented in relation to their body size (expressed in a log scale) and feeding guild category, with the size of each circle representing a species biomass contribution as calculated by multiplying the camera trap capture frequency of a species by the adult female body mass of that species

Table 3.2: A comparison of the total herbivore biomass apportionment (expressed as a percentage) between that expected for moist oligotrophic savanna communities with woodlands based on Bell (1985; in brackets) and the results from Majete Wildlife Reserve where camera trap capture frequencies per species were used as the basis for biomass contribution calculations (see text for more detail)

Size class	Grazer	Browser	Mixed	Total
Large > 1000 kg	2 (1)	1 (0.5)	38 (55)	**41 (56.5)**
Medium > 100 kg	17 (11)	6 (1.5)	3 (3.5)	**26 (16)**
Buffalo & zebra	23 (22)			**23 (22)**
Small < 100 kg	7 (1.5)	0.3 (3.5)	2 (0.5)	**9.3 (5.5)**
Total	**49 (35.5)**	**7.3 (5.5)**	**43 (59)**	

Relative abundance measurement comparison

The comparison between the camera trap capture frequencies and total aerial count data (Appendix D) resulted in a weak positive relationship (R^2 = 0.08; Figure 3.8), with warthog a clear outlier. The relationship strengthened when the comparison is made to the corrected aerial count data (R^2 = 0.21; Figure 3.8), but warthog persist as an outlier. When warthog was removed from the analysis the strongest relationship is observed (R^2 = 0.55; Figure 3.8).

When comparing independent encounter rates on both axes (camera trap capture frequencies and aerial census encounter rate), a weak positive relationship resulted (R^2 = 0.36; Figure 3.9). However, the strongest positive relationship overall was seen when comparing encounter rates, with the outlier warthog removed (R^2 = 0.65; Figure 3.9).

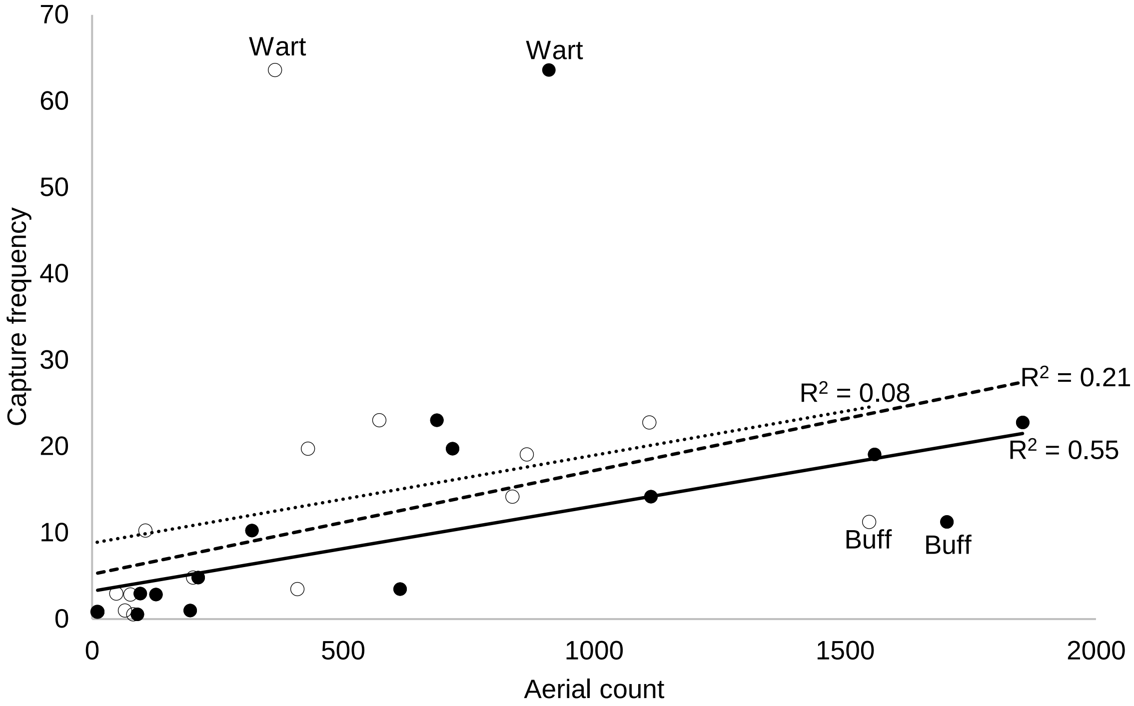

Figure 3.8: A comparison between the camera trap capture frequency and the uncorrected aerial count data (dotted line and open circles), the corrected aerial count data including warthog (dashed regression line with solid circles), and the corrected aerial count data excluding warthog (solid line), at Majete Wildlife Reserve. Species mentioned in discussion are labelled: Wart = warthog and Buff = buffalo

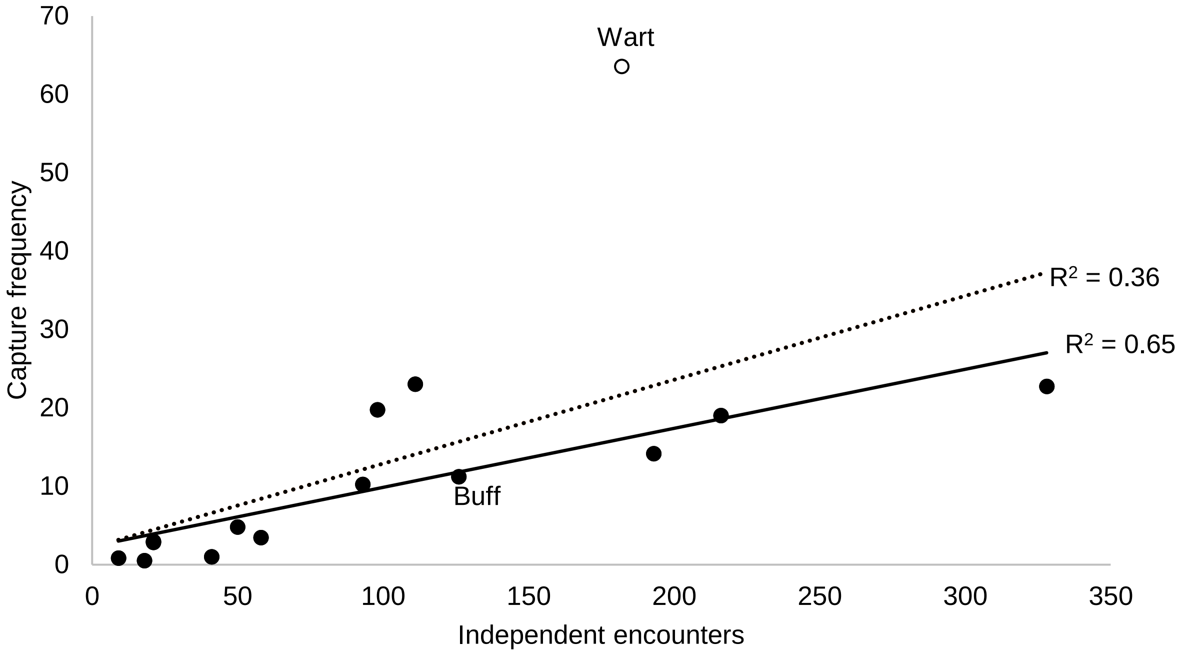

Figure 3.9: A comparison between the camera trap capture frequency and the total encounters per species during Majete Wildlife Reserve's 2018 aerial census, calculated as the total number of independent encounters (individuals if alone, or groups when together) per species during the aerial census. The dashed regression line comparison includes warthog (closed circles with warthog an open circle) and the solid line is the same comparison excluding warthog (closed circles). Species mentioned in discussion are labelled: Wart = warthog and Buff = buffalo

3.4 Discussion

Thirty-five species were detected which represents 85% of the 41 medium and large mammal species believed to be historically present, with the species richness estimators confirming species were missing from the survey. This compares well with another study in the Miombo Woodland Ecoregion (35 species in a study by Caro, 1999), as well as more species rich savanna ecosystems, where 40 mammals species were found in Tanzania (Swanson *et al.,* 2015) and 27 in south-west Zimbabwe (Welch *et al*., 2019). From a herbivore biomass contribution perspective, the community structure is not typical of a Miombo woodland system (Bell, 1985) - notably the megaherbivore component and in particular elephants are underrepresented. Camera trap frequencies as a measure of RAIs are comparable to aerial census encounter rate data but less so to overall count data, suggesting that caution should be applied when using camera trap frequencies to interpret community structure.

The medium and large mammals on the reserve species list (Martin, 2005) that were not recorded by the camera traps are Livingstone's suni (*Neotragus moschatus)*, African clawless otter (*Aonyx capensis)*, spotted-necked otter (*Hydrictis maculicollis)*, yellow-spotted rock hyrax (*Heterohyrax brucei),* banded mongoose (*Mungos mungo)* and large grey mongoose (*Herpestes ichneumann)*. Suni, both otter species, and rock hyrax are habitat specialists

(Skinner & Chimimba, 2005). Suni is a shy, territorial forest-dwelling species (Skinner & Chimimba, 2005) believed to be present in extremely low numbers in MWR. Both otters species are elusive, semi-aquatic species favouring riverine habitat (Purves & Somers, 1996; Perrin & Carugati, 2000), which have proven a challenging species to detect in camera trap surveys if riparian zones are not specifically targeted (Stevens *et al*., 2004; Majelantle *et al.*, 2020).Yellow-spotted rock hyrax inhabit rocky outcrops or piles of loose boulders (Skinner & Chimimba, 2005) and may have been missed because of this specialised habitat. Similarly, Welch *et al*. (2019) conducted a study in Zimbabwe and also did not record yellow-spotted rock hyrax despite its presence being known. O'Brien (2008) cautions against making deductions when comparing richness estimates with species lists, as lists do not necessarily represent the current species assemblage. However, suni, hyrax and signs of otter have been detected in the year after the survey was completed at MWR (Pers. obs. 2019; Nieman, pers. comm. 2019); these species' absence in the survey is most likely a product of the random systematic sampling design, which did not target their specialised habitat requirements.

There are three medium-sized mongoose species at MWR according to the list of Martin (2005): the slender mongoose, of which there was one detection, and the large grey and banded mongooses which were not detected. The banded mongoose has been sighted in MWR in the last year (Nieman, pers. comm. 2019), but there are no recent confirmed reports of the large grey mongoose. The large grey mongoose has been detected in camera trap studies in South Africa (Ramesh & Downs, 2015) and Uganda (Fuda *et al*., 2018), and the banded mongoose in Tanzania (Rovero *et al.,* 2017) and Zimbabwe (Welch *et al.*, 2019). Some mammal species exhibit either avoidance or preference towards using trails, often in relation to predator presence (Trolle & Kéry, 2005; Mann *et al*., 2015). The large grey and banded mongooses were however detected along trails in the aforementioned studies, and in areas with predators, therefore trail avoidance is unlikely. Smaller mammals are more likely to pass in front of a camera without triggering it compared to larger mammals (Tobler *et al.,* 2008). Lowering a camera to 20-30 cm above the ground will likely increase detections of smaller mammals (Kelly, 2008). With the cameras in MWR deployed at 50 cm height it is thus possible that cameras failed to detect these mongoose species, however similar sized species like large spotted genet had 37 detections across 14 cameras. An explanation for this may be that increased differences between ambient temperature and animal surface temperature are associated with increased detection probabilities (McIntyre *et al.*, 2020). The undetected fast-moving, diurnal mongoose species were therefore likely to be less detectable by the cameras compared to analogous nocturnal mammals because of the comparatively high background surface temperatures during the day. The undetected species may thus have low detection probabilities, as well as low abundances or patchy distribution in MWR, as has been found in similar studies for other mongoose species (Fuda *et al.,* 2018; Moore *et al.,* 2020).

The non-parametric incidence based estimators all indicate that 1–2 species remained undetected in the survey (range 35.5 – 37.9). The Bayesian model estimated 36-37 species present with an upper 95% limit of 40 species, which is considered a more robust estimate due to it accounting for imperfect detection (Kéry & Royle, 2008). When considering the observed species, the signs of the missing species and the fact that the large grey mongoose may be absent from the reserve, the Bayesian upper estimate of 40 species appears likely.

The megaherbivore component of the herbivore community in MWR is underrepresented in comparison to other Miombo woodland areas, where elephants alone make up as much as 55% of the total biomass (Bell, 1985; Frost, 1996). In MWR elephant contribute just 38%. The bulk grazers, buffalo and zebra, make up 23% of the biomass which is in line with the 22% of what Bell (1985) considers appropriate for Miombo woodland. Frost (1996) suggests elephants, buffalo and zebra should make up 75 – 90% of biomass in Miombo, while Fritz *et al.* (2002) and Fritz *et al.* (2011) also suggest megaherbivores should dominate in areas with high rainfall and low soil nutrients. The large body size of megaherbivores allows them to utilise the abundant low quality vegetation in Miombo woodlands, and elephants can reach substantial amounts of browse unavailable to other species (Frost, 1996). In addition, medium-sized grazers and browsers make up a greater biomass proportion than Bell (1985) suggests is natural in Miombo woodland, albeit at a smaller proportional difference than the megaherbivores (40% grazers and 6% browsers in MWR vs. 33% and 1.5% suggested by Bell, 1985). The riverine and open woodland habitats (non-miombo patches comprising 45% of MWR), underlain by higher soil nutrients, may be able to support a different species composition. This may account for the increased browser biomass who are dependent on higher quality forage than what is available in the Miombo Woodland (Hopcraft *et al.*, 2010). Spotted hyaena is the dominant predator in MWR which is considered natural in this habitat type (Fritz *et al*., 2011).

The species capture frequencies, as a measure of RAIs, were used to inform community structure. The correlation between the RAI and the corrected aerial census data had a better fit than the uncorrected census data with both comparisons providing weak positive relationships when the clear outlier warthog is included. Rodwell *et al.* (1995) recommended excluding warthog from aerial censuses as their counts are too inaccurate due to their poor detection potential, however warthog is included in other studies using aerial census data (e.g. Redfern *et al*., 2002 and Palmer *et al.,* 2018). The study of Palmer *et al.* (2018) in particular found RAIs based on camera trap data to compare very well to aerial count data, and their data set include warthog. However, in this case even when correction factors are used, warthog remains a strong outlier. We hypothesise that this effect may be due to their over detection on the camera traps. The camera traps in this study were placed on trails, and warthog have been shown to be detected more on trail-based cameras than on those placed randomly (Cusack *et al*., 2015). Correlation between corrected aerial count data and camera trap RAI improve markedly without warthog. Comparing the camera trap data with the aerial census encounter rate resulted in a stronger positive relationship than when compared to the corrected absolute count data which makes sense since individuals were not counted in the camera trap photographs. For this reason, buffalo are not an outlier when based on encounter rates. Buffalo form herds (Skinner & Chimimba, 2005), and notably large herds in Miombo woodland (Caro, 1999), which was observed in MWR (Pers. obs.). RAIs based on camera trap frequencies can be used to investigate community structure but should be undertaken with caution. A better understanding of the inconsistencies between aerial counts and RAIs derived from camera traps for some species is needed before species abundance estimates can be used with great confidence.

It is important to note that MWR is a manipulated system. The majority of the medium and large mammals at MWR have been reintroduced since 2003, with some medium and large mammals, including 150 elephants, translocated out of the reserve in 2016 and 2017. Despite the potential shortcomings in analysing community structure using camera traps, it seems the current community structure is not typical of a natural Miombo system. Due to the small size of the reserve, its enclosed nature, and anthropogenic pressure on the boundary, it is unlikely that community structure typical of Miombo will return naturally. Improving ecosystem functioning by reintroducing historically occurring mammal species to MWR is a priority of park management, as is increasing diversity to encourage critical tourism-based revenue for management purposes. Based on current community composition, it is recommended that reserve management consider allowing the elephant population to increase so that the megaherbivore component representative of Miombo woodlands can re-establish.

3.5 Conclusion

Majete Wildlife Reserve is one of the last remnants of natural habitat in Malawi. In addition, it represents an intact remnant of Miombo woodland, which has a species richness representative of the Miombo Woodland Ecoregion. This study is the first comprehensive and systematic survey for MWR which has provided valuable updated species richness and community structure data for both the reserve and the Miombo Woodland Ecoregion. The methodology used is repeatable which is particularly important to allow meaningful understanding over time of how the threats of increasing settlement and agriculture surrounding the reserve might affect the reserve and its isolation in the larger landscape. When managing closed and isolated conservation areas, the manipulation of mammal populations is necessary, however, care should be taken to ensure that the community composition of an area allows for the area’s optimal ecosystem functioning. This is especially the case when important remnants are becoming increasingly threatened by the effects of habitat fragmentation, threatening the loss of representative mammal species assemblages. In the next chapter the drivers of ungulate and megaherbivore species space use differences across the landscape will be explored.

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CHAPTER 4

PATTERNS AND DRIVERS OF UNGULATE SPACE USE ACROSS MAJETE WILDLIFE RESERVE, MALAWI

4.1 Introduction

Historically, the African landscape was home to large populations of resident and migrating mammals (Harris *et al.*, 2009; Hempson *et al.*, 2017). However, due to increasing human population numbers in Africa and the associated effects of urban and agricultural expansion, medium and large mammal populations are now largely confined to protected areas (PAs; Caro & Scholte, 2007). PAs have consequently become critical for the conservation of the remaining mammal populations (Wegmann *et al.,* 2014). However, since the 1970's there has been a 50% decrease in medium and large mammal population abundance within African PAs, attributable to human-induced threats (Caro & Scholte, 2007; Craigie *et al.*, 2010) and poor management (Lindsey *et al.*, 2014). Furthermore, the fragmentation and consequent loss of connectivity between PAs due to increasing human settlement, roads and fences, results in PAs becoming isolated and static natural remnants (Newmark, 2008). These remnants are susceptible to considerable anthropogenic edge effects, which strongly influence patterns of biodiversity persistence (Lindsey *et al.*, 2014; Tobler *et al.*, 2015; Ramesh *et al.*, 2016). For example, mammal species presence often increases with increasing distance from anthropogenic activity close to PA perimeters (Everatt *et al*., 2014; Wang *et al.*, 2015; Rich *et al*., 2016; Rich *et al.*, 2017). This avoidance of PA boundaries reduces the effective reserve size available to species with potential knock on effects for population viability and their conservation (Rich *et al*., 2016).

Due to PA isolation and the matrix of anthropogenic land uses PAs are embedded in, the fencing of PAs is often considered to be the only solution to protect the PAs biodiversity from negative human influences and to mitigate potential human-wildlife conflict (Hayward & Kerley, 2009). While serving the purpose of physically protecting both wildlife and people, fences create an artificially closed and confined space, which is not equally occupied by all species. Furthermore, closed reserves limit the amount of space, food and water resources available for mammals (Newmark, 2008). This scenario creates the need for more intensive management of both mammal species and their environment (Hayward & Kerley, 2009; Miller *et al*., 2015; Selier *et al.*, 2018), with small fenced reserves (< 1000 km^2; Miller *et al.*, 2015) in particular having high management requirements to maintain interior characteristics (Hayward *et al.*, 2007; Massey *et al.,* 2014).

Savanna ecosystems are difficult to manage as isolated, fenced systems due to their intrinsic heterogenous and dynamic characteristics (Gaylard *et al.*, 2003; Rogers, 2003). Management interventions such as water provision and fire management thus become necessary, but influence animal space use (Owen-Smith, 1996; Bond & Archibald, 2003). The manipulation of the spatial-temporal variability of surface water availability influences animal space use but species specific water-dependence influences the magnitude of piosphere related affects (Andrew, 1988; Smit *et al.,* 2007). Additionally, the manipulation of fire to mimic a natural fire regime and to prevent the spread of wildfires entering PAs influences mammal distribution due to changes in plant quality and quantity through changes in plant species composition and above ground biomass, which in turn influences predation risk (Anderson *et al.,* 2007; Burkepile *et al.,* 2013). Combined with water and fire manipulation, reserve infrastructure such as roads may influence how mammals use a landscape, with some carnivore species tending to use roads, while some herbivores avoid them due to the perceived risk from humans and vehicles (Fahrig & Rytwinski, 2009; Taylor & Goldingay, 2010; Leblond *et al.,* 2013; Muposhi *et al.*, 2016).

Along with anthropogenic influences, the potential of a PA to conserve viable populations of medium and large mammals, largely depends on the ecological characteristics of the PA such as topography, vegetation type, the quantity and quality of forage available and species interactions, which all influence how mammals use space (Wegmann *et al.*, 2014; Ramesh & Downs, 2015; Ramesh *et al.,* 2016; Rich *et al.,* 2016). Terrain heterogeneity can influence mammal space use, with landscape curvature - the degree of concavity or convexity of a landscape - and slope being particularly strong drivers of mammal space use (Sappington *et al.*, 2007; Puri, 2015; Anderson *et al.,* 2020). Rainfall and soil nutrients regulate the quantity and quality of food available to herbivores, which is utilized differently by herbivores of varying body size due to their metabolic requirements (Jarman, 1974; du Toit, 1995). Vegetation types also differ in plant structure, climatic conditions and soil nutrients (Jennings *et al.,* 2009; de Cáceres & Wiser, 2012) and influence where herbivores are found across a landscape.

The presence of predators in an ecosystem may alter prey behaviour so that they are more difficult to encounter, detect and capture, resulting in the creation of a landscape of fear (Lima, 1998). Herbivores avoid areas that pose a greater risk than others, and can change the structure of habitats in relation to their use (Valeix *et al.*, 2009; Laundré *et al.*, 2010; Tambling *et al.*, 2015). Therefore, interpreting how prey species respond to predators is a key factor in understanding how, why and where prey species occur in the landscape (Tambling *et al.,* 2015; Owen-Smith, 2019).

Majete Wildlife Reserve (MWR) is an isolated, small (691 km^2), fenced reserve situated in the south-west of Malawi, within the Miombo Woodland Ecoregion, with the majority of the reserve surrounded by subsistence agriculture and settlement. The reserve experienced large-scale poaching during the second half of the 20th century, but since 2003 conditions have improved with African Parks assuming management to control poaching and reintroduce locally extinct large mammal species (Staub *et al.,* 2013; Briers-Louw *et al*., 2019). Understanding how these mammal species are using the landscape of MWR and what is driving mammal space use is not clear. This information is important for improved understanding of how environmental features, management actions and infrastructure, impact species and ecosystem functioning in this small and isolated reserve. Furthermore, published research on the ecology and distribution patterns of medium and large mammals in Miombo woodland habitat appears to be limited with only the study of Caro (1999) found after intensive search.

Species' space use patterns and the impact of management interventions, anthropogenic disturbance and the ecological characteristics of a landscape on mammal communities can be evaluated using an occupancy modelling framework (Yoccoz *et al.*, 2001; O'Brien, 2008; Ramesh & Downs, 2015; Boron *et al.,* 2019). This framework also accounts for imperfect detection (Mackenzie & Royle 2005; Mackenzie *et al.,* 2006; Tobler *et al.,* 2015). The use of camera traps is a popular method used worldwide to determine occupancy and the drivers thereof (Rich *et al.*, 2016; Li *et al.,* 2018; Mkonyi *et al.,* 2018; Boron *et al.,* 2019). This chapter aimed to assess the space use patterns of ungulates in MWR and the drivers thereof, by using a systematic camera trap survey and an occupancy modelling framework. The specific objectives were to: a) determine the space use patterns of the ungulates across the landscape of MWR, and b) identify variables (management and natural) that are influencing the observed space use patterns of the ungulates.

4.2 Methodology

4.2.1 Study site

The study was conducted across the entirety of the 691 km^2 of MWR in south-western Malawi. There are three distinct seasons based upon temperature and rainfall: the hot wet season (November to April), the cool dry season (May to August) and the hot dry season (September to October). Average annual rainfall is 680 – 800 mm in the lower lying eastern areas (approximately 150 metres above sea level; m.a.s.l) with the higher lying western slopes receiving 700 – 1000 mm (approximately 455 m.a.s.l; Wienand, 2013). The estimated mean minimum and maximum temperatures are 12.5°C and 26.3°C in June and 20.9°C and 34.8°C in November (Martin, 2005). Overall, the soils are considered to have low nutrient potential which together with the rainfall gradient, influence the species composition and structure of the vegetation (Frost, 1996). Six vegetation types are recognised in the area - high altitude tall miombo woodland in the west of the reserve gradually changes into a more open mixed tall woodland in the centre and east, with riverine and thicket vegetation associated with streams and rivers in the extreme east of the reserve (Sherry, 1989; Frost, 1996; Figure 4.1). There are nine known natural springs and ten artificial waterholes in the reserve and two perennial rivers transect the north-east corner of MWR (Figure 4.1). The road network (Figure 4.1) and tourism vehicle traffic is concentrated in the north eastern section of MWR with the roads in the remainder of the reserve used minimally for management and research purposes. The study site is discussed in more detail in Chapter 2.

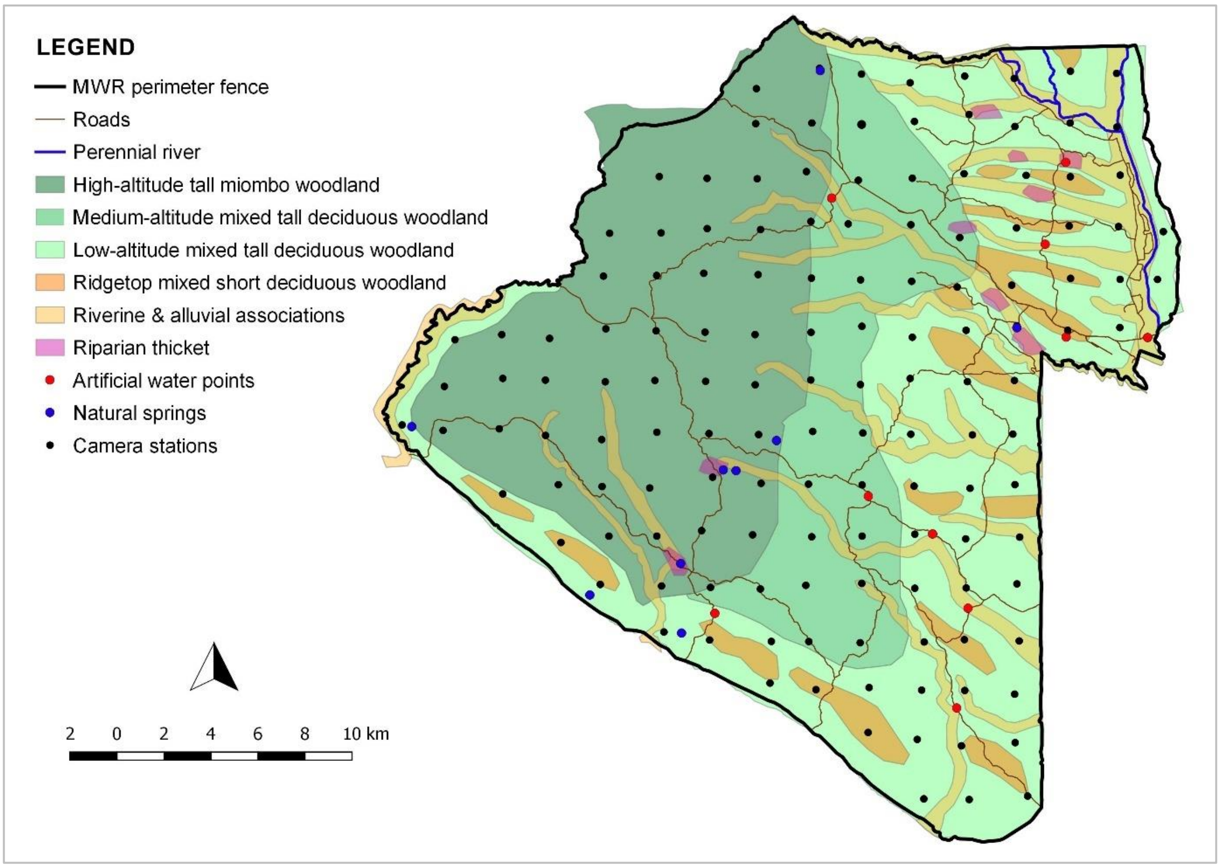

Figure 4.1: Map of Majete Wildlife Reserve indicating the perimeter fence line, roads, distribution of surface water, vegetation types and the 140 locations where cameras were placed to determine the space use of ungulate species

4.2.2 Survey design

The camera trap survey of medium and large mammals took place during the dry season of 2018, between 7th June and 5th December. One hundred and forty camera trap locations (Figure 4.1), identified as the centre points of 5 km^2 grid blocks projected over MWR, were systematically surveyed in three consecutive phases using three sampling blocks containing 47, 47 and 46 camera trap locations each. Effort was made to deploy the 47 Cuddeback X-Change™ camera traps (Model 1279) for a sampling period of 40 days at each camera placement location before moving them to the next block. The first block was surveyed between June and August, the second between July and September and the third between September and December 2018. Cameras were placed next to the most used wildlife trail in close proximity of the predetermined camera trap location points, with signs of scat and spoor as indicators of use (Colyn *et al.,* 2018). Vegetation within the camera's detection zone was trimmed to prevent false trigger events, but not to the extent of altering the immediate vegetation characteristics (See Chapter 3 for a detailed account of the camera trap placement protocol).

4.2.3 Predictors of space use

Both the space use patterns of the ungulates and the effect of anthropogenic and environmental covariates on that space use was investigated. This was done by jointly modelling the detection probability and presence/absence of species to evaluate the effect of site covariates on occupancy by using single-species occupancy models (MacKenzie *et al.*, 2006). The "probability of use" (Ψ) was used as opposed to "probability of occupancy" as the assumptions of closure and independence were not met due to some species' home ranges considered to be larger than a single 5 km^2 survey site (Mackenzie & Royle, 2005). As occupancy models correct for imperfect detection, detection probability (p) was modelled as a function of site-specific covariates thought to impact how likely a species is to be detected when it is present (Sollmann, 2018). The variables hypothesised to influence probability of use comprised of both categorical and continuous data types and were measured at each camera trap location.

4.2.3.1 Detection probability variables

Four variables were hypothesised to influence a species probability of being detected by a camera trap, given that the species is present at a site, and these were measured for each camera trap location. The four variables were:

Visibility

The density of vegetation could influence whether a species is obscured by vegetation or not, with greater vegetation density reducing the probability of detection. Following the methodology of Hay *et al*. (2008) to calculate visibility of the area around the camera station, a field assistant walked away from the observer who stood at the camera station. The distance, in meters, at which the lower part (one metre from ground level) of the assistant became obscured by vegetation was measured using a range finder (Nikon Prostaff 5) and recorded in metres. Distance measurements were made in each of the four cardinal compass directions and then averaged to estimate the site-specific vegetation density.

Distance to fence

Animal vigilance and associated avoidance of anthropogenic impacts and objects may increase in relation to poaching pressure, which is argued to be of higher probability closer to PA boundaries (Rich *et al.*, 2016). Close to the fence, an animal may thus avoid human-related objects, such as cameras, more readily than when they are far from the fence, with a consequent unequal detection probability on the cameras. The distance, in metres, from each camera location point to the closest point of the perimeter fenceline was calculated in Quantum GIS (QGIS) 2.18.15, by using the NNJoin Plugin and conducting a Nearest Neighbour Analysis (QGIS Development Team, 2018).

Landscape curvature

The degree of concavity or convexity of a landscape can effect whether or not an animal will be detected by a camera, given that it is present (Anderson *et al.*, 2010; Puri, 2015). Landscape curvature was calculated at each camera trap location by using terrain ruggedness (Terrain Ruggedness Index, TRI; Riley *et al*., 1999) in the Terrain Analysis Tools in QGIS and the Digital Elevation Model (DEM) for MWR. The DEM was provided by African Parks (Majete). TRI uses the pixels of the DEM layer and calculates the mean difference in elevation between a pixel and the eight cells surrounding it for each camera location (Riley *et al*., 1999). The values at MWR ranged from 0.25 – 16.62, (least rugged – most rugged).

Trail usage

The level of use of a trail may influence the likelihood of a species being detected (Mann *et al.*, 2015). A trail usage criteria was used to assign one of three categories to the trail where the camera had been placed, where Level 1 indicated trail present with no animal signs, Level 2 indicated trail present with minimal animal signs (old or minimal scat and/or spoor present) and Level 3 where trail was present with abundant animal signs (fresh scat and/or spoor of two or more species present). It was expected that the detection probability of a species in any given area would be higher if a camera was placed on a frequently used trail instead of a lesser used one.

4.2.3.2 Space use variables

Ten ecological and anthropogenic covariates, hypothesised to influence medium and large mammal space use in MWR, were estimated for each camera location. The 10 variables are:

Visibility

The success of attacks by ambush predators such as lion (*Panthera leo*) and leopard (*Panthera pardus*) tend to improve with increasing grass height and vegetation cover (Funston *et al.*, 2001). Habitats with poor visibility may thus have a higher predation risk influencing herbivore space use of these areas (Hay *et al*., 2008; Burkepile *et al*., 2013). The same visibility values as calculated for the detection probability estimates were used here.

Grass biomass

Grass biomass represents a measure of grass forage availability which may influence the space use of grazers (Shipley, 1999). The comparative yield/dry weight rank method was used to estimate grass biomass availability as it takes both the horizontal and vertical grass components into account (Haydock & Shaw, 1975; Friedel *et al.*, 1988). At each camera station, four 1 x 1 metre quadrats located 10 metres from the camera trap location in each of the four cardinal compass directions were selected. A grass biomass score was then assigned to the quadrat based on a predetermined ranking of one to nine, whereby one was low grass biomass (0 – 3 tons/ha) and nine the highest grass biomass (25 – 27 tons/ha). Calibration of the biomass scores was conducted by preselecting 1 x 1 metre quadrats of grass of varying yields representing the visual ranking from one to nine. These rankings from one to nine were then verified by harvesting the grass, air drying it to constant weight and weighing it using a hanging scale. Quadrats were harvested throughout the study to compare against the reference scale (Appendix E) to ensure that there was consistency in the allocation of rank scores to the quadrats at each camera location.

Vegetation type

Vegetation types vary in terms of vegetation structure, and the quantity and quality of forage they provide and therefore influence where mammals are found across a landscape (du Toit, 1995; de Cáceres & Wiser, 2012). The vegetation types at MWR were therefore predicted to influence mammal space use. The vegetation map of Sherry (1989; Figure 4.1) was used to assign one of the six vegetation types to a camera station location. See Chapter 2 for a detailed description of each vegetation type.

Fire

The fire history of a site influences its use by mammals through changes in forage availability and quality, as well as vegetation density which may affect a herbivores ability to detect predators, and a carnivores ability to stalk prey (Hopcraft *et al.*, 2005; Anderson *et al.*, 2007; Burkepile *et al.*, 2013). At the time of camera deployment, the area around each camera trap station was categorised as either burnt or unburnt depending on whether it had burnt during the dry season survey period of 2018.

Distance to water

A species' physiological dependence on water influences their space use in relation to surface water distribution (Redfern *et al.*, 2003; Smit & Grant, 2009). The distance from the camera station to the nearest permanent water source (river, spring or artificial water point) was calculated in Quantum GIS (QGIS) 2.18.15 by using the NNJoin Plugin and conducting a Nearest Neighbour Analysis (QGIS Development Team, 2018) which provided the distance in metres.

Distance to fence

Mammals may be deterred from using areas close to a fence due to anthropogenic activity on or near a fence line (Everatt *et al*., 2014). Therefore, fences were considered to potentially influence mammal space use in MWR. The same distance to fence values calculated for the detection probability estimates were used here.

Distance to road

Roads in MWR may influence mammal space use through mammals either favouring or avoiding them for movement (Fahrig & Rytwinski, 2009; Muposhi *et al.*, 2016). All roads in MWR are graded gravel roads. The distance, in metres, from the camera station to the closest road was measured in QGIS by using the NNJoin Plugin and conducting a Nearest Neighbour Analysis (QGIS Development Team, 2018).

Landscape curvature

Terrain accessibility as governed by topographical and geomorphological features affects mammal use of an area (Sappington *et al*., 2007). The same landscape curvature values calculated for use in the detection probability estimates were used here.

Slope

Mammals may avoid or prefer steep slopes (Oberosler *et al.,* 2017). Slope was calculated for each camera station by using the Slope feature in the Terrain Analysis Tools in QGIS and the DEM (Ahumada *et al.,* 2013). The slope feature is measured as the angle of inclination of the terrain at each camera station and is expressed in degrees (QGIS Development Team, 2018). Slope values at the camera stations ranged from 0 – 34°. Slope varies from landscape curvature as it takes in the gradient of a land surface only, whereas landscape curvature takes in the topographic aspect and gradient components of a surface (Sappington *et al.*, 2007).

Relative large predator abundance

It was hypothesised that the presence of the large predators, viz: lion, leopard and spotted hyaena (*Crocuta crocuta*) may influence the space use patterns of some herbivore species (Rich *et al.*, 2017). Relative predator abundance indices were calculated as the number of independent large carnivore detections divided by sampling effort (camera days) and multiplied by 100. Independent detections were calculated by filtering the photographs of large predator species using 30 minute intervals, with one photograph within a 30 minute period considered to be one independent detection (Davies *et al.*, 2016; Rich *et al.*, 2017). Predators were not considered to have a significant influence on the space use of elephant, black rhino (*Diceros bicornis*) and hippo (*Hippopotamus amphibius*) as they do not usually form part of even the largest predators diet (Sinclair *et al.*, 2003; Radloff & Toit, 2004; le Roux *et al.,* 2018). The presence of leopard was also considered not to have an effect on the space use of buffalo (*Syncerus caffer*), zebra (*Equus quagga*) and eland (*Tragelaphus oryx livingstonii*) as they do not form part of the usual diet of leopard in this area (Briers-Louw & Leslie, 2020).

4.2.4 Modelling framework

Photographs taken at each of the 140 camera trap locations during the 40 day sampling period were collated using the camera trapping software Camelot 1.4.5 (Hendry & Mann, 2018). Species were then filtered to include only large predators (lion, leopard and spotted hyaena) and ungulate species.

Binary matrix detection histories were created for each of the ungulate species using the independent captures for that species at each camera station. In order to estimate species detection probability, the detection history was condensed from the 40 sampling days into eight sampling occasions, where any presence in a five-day period was counted as one in the detection history (Bischof *et al.*, 2014). Considering the length of the survey, this occasion length is considered a fair compromise between having too many zeros and thus obtaining low estimates of detection probability, and having too few zeros and losing valuable information that goes into estimating detection probability (Bischof *et al.*, 2014; Sollmann, 2018).

All statistical analysis were performed in R software, version 3.6.1. (R Core Team, 2013). Collinearity between the continuous covariates was assessed using Variance Inflation Factors (VIF) in the R package car, version 3.0-9 (Fox & Weisberg, 2019). VIF is used as an indicator of multicollinearity which occurs when two or more covariates are correlated and provide redundant information (Thompson *et al*., 2017). If a VIF value of > 5 resulted for a covariate it was considered to covary with another (Dormann *et al*., 2013) and only the covariate which was considered the most pertinent retained. A correlation was found between landscape curvature and slope covariates, as a VIF score of 18 confirmed collinearity between these two variables. Slope was dropped and landscape curvature was retained for further analysis

(Appendix F). Due to the difference in measuring units and large range of recorded data values, the retained continuous covariates were scaled into standardised z-scores for all analysis (Comley *et al.,* 2020).

The species-specific probability of detection and probability of use were then estimated using single-species occupancy models (Mackenzie *et al.,* 2006) in the R package unmarked, version 0.13-1 (Fiske & Chandler, 2011). The linear combinations of the detection and probability of use estimates were back-transformed. First, a null model was developed to calculate detection estimates for each species. Species with detection probabilities of < 0.15 were not considered for further analysis as they produce probability of use estimates that are considered inaccurate and limit resulting inference (O'Connell *et al.*, 2006; Rogan *et al.*, 2019). The covariates influencing detection for each species were determined by holding Ψ constant and allowing the detection variable to vary, i.e. Ψ(.),*p*(covariate). The best performing model was selected based on the Akaike information criterion (AIC) corrected for small sample sizes (AICc) using the R package AICcmodavg, version 2.2-2 (Mazerolle, 2019), whereby all possible combinations were run and the model with a ΔAICc score of < 2 was considered the best fit to the data (Burnham & Anderson, 2002; Mackenzie *et al.,* 2006). If multiple models were within two ΔAICc, then the most parsimonious model was selected. The detection covariate, or combination thereof, which resulted in the top detection model was retained for estimating probability of use and the drivers thereof.

In the probability of use modelling process, the space use covariates were allowed to vary, with all possible combinations of covariates run and assessed, while holding the detection covariates determined above constant, i.e. Ψ(covariate),*p*(covariate). Where mathematical convergence issues were encountered due to too few detections for a categorical variable, the variable was removed from further analysis. This occurred once and resulted in the removal of the fire variable from the modelling of hippo. The model with a ΔAICc score of < 2 was selected as the top model and most likely to predict space use. If there was more than one top model (within < 2 ΔAICc), model-averaging was performed with the function available in the R package MuMIn (Barton, 2015; Burnham & Anderson, 2002). The beta coefficient values produced for each covariate in the top model were assessed and those beta coefficient values that did not overlap zero (when taking into account the SE) were considered as having a strong influence on the probability of use (Tobler *et al*., 2015).

To visually display the importance of a single predictor variable on a species space use, the remaining variables in the top model were held constant at their median so that probability of use was allowed to vary as a consequence of just that single variable being assessed. The beta coefficient of the single variable was then plotted as a function of probability of use, with the 95% confidence intervals and the direction and strength of the relationship allowing inferences to be made.

4.3 Results

A total of 5 456 camera days were achieved out of an anticipated 5 600 days. Cameras at 15 of the 140 locations were functional for less than the 40 day trapping period, resulting in a loss of 146 camera days or 2.6% of the expected number of camera days. The data from these 15 cameras was however retained and used in the analysis by including the presence/absence data within the achieved sampling occasions (see Figure 3.3 in Chapter 3 for days of operation and location of these cameras). The 140 sites yielded 120 239 photographs, of which 11 078 were independent detections of 18 ungulate species (10 938 detections; Figure 4.2) and 140 detections of the three large predator species (14 lion, 43 leopard and 83 spotted hyaena).

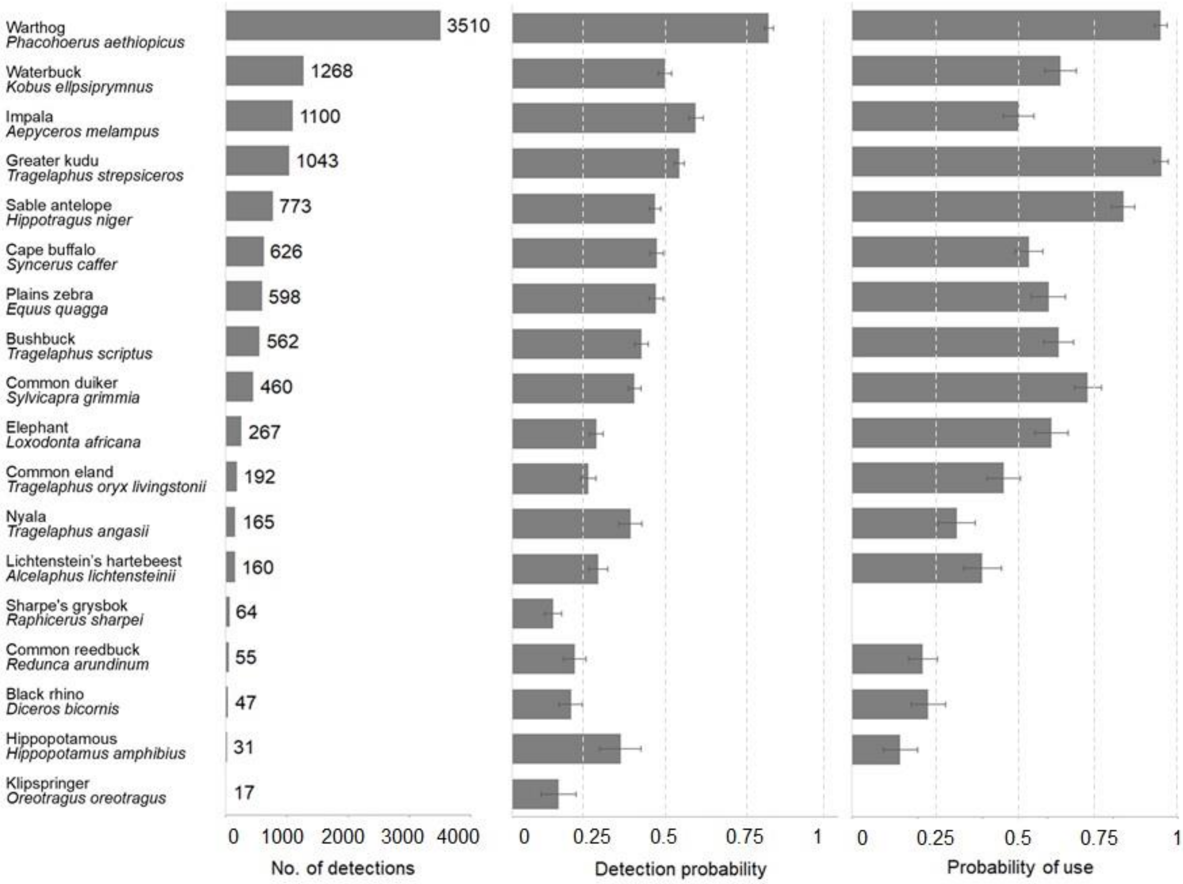

Figure 4.2: A graphic representation of the number of detections, the detection probabilities, and probability of use without covariates across all camera stations for the ungulates that were detected during the camera trap survey of Majete Wildlife Reserve. Species are ranked from highest to lowest number of detections

Detection probability

Species detection probability ranged from 0.12 for Sharpe's grysbok to 0.79 for warthog (Figure 4.2 and Table 4.1). After warthog, impala (p = 0.56, SE = 0.02) had the highest detection probability followed by kudu (p = 0.51, SE = 0.02) and waterbuck (p = 0.47, SE = 0.02; Figure 4.2 and Table 4.1). Sharpe's grysbok and klipspringer had detection probabilities of < 0.15 and so were excluded from further analyses.

Detection variables were included in the modelling of space use for 13 species. Distance to fence was retained in the largest number of models, influencing 11 species (Table 4.1). Trail usage influenced the detection of eight species. Landscape curvature and visibility influenced seven species each. None of the detection covariates were identified to influence the detection probability of reedbuck, buffalo or eland. The detection probability of the three megaherbivores were influenced by only a single covariate, with elephant and hippo influenced by distance to fence and rhino detection affected by landscape curvature. The detection probability of the remaining species were influenced by a combination of either two, three or four of the detection variables.

Probability of use

Probability of use for all species retained ranged from 0.15 – 0.95. Kudu was most widely distributed, using approximately 95% of MWR (Ψ = 0.95, SE = 0.02), followed closely by warthog (Ψ = 0.94, SE = 0.02) which had 2467 more detections than kudu. Sable followed warthog as the third most widely distributed species (Ψ = 0.83, SE = 0.03; Figure 4.2 and Table 4.1). Hippo (Ψ = 0.15, SE = 0.05) and reedbuck (Ψ = 0.22, SE = 0.04) had the most restricted use out of the retained species.

Predictors of space use

No single model emerged as the top ranking model for any of the species except for nyala, so the model-averaged estimates of probability of use were used (Table 4.1).

The nine variables hypothesised to influence space use were all found to have some influence on the species (see Appendix G and H). However, only seven of the nine drivers strongly influenced ungulate probability of use (Appendix I), with landscape curvature and fire not found to be strong drivers. The number of variables in well-supported models ranged from one to seven, with vegetation type, visibility and distance to water influencing the most species (eight, six and six species respectively), followed by distance to road and grass biomass (four and three species respectively). Distance to fence and relative predator abundance influenced three and two species, respectively.

Table 4.1: The probability of use (ψ) and probability of detection (*p*) estimates for the ungulates that were detected during the camera trap survey at Majete Wildlife Reserve, and the best model combination considered most likely to predict probability of use and detection. The detection estimates of klipspringer and Sharpe's grysbok are included but no further analysis were performed for these species. The covariate abbreviations in the model are: road = distance to road, veg = vegetation type, biomass = grass biomass, water = distance to water, fence = distance to fence, vis = visibility, curve = landscape curvature, preds = relative predator abundance and trail = trail usage

Common name	***p* ± SE**	**ψ ± SE**	**Best model combination**
African elephant	0.26 ± 0.02	0.61 ± 0.05	Ψ(biomass+road+veg+water+fence),*p*(fence)
Black rhinoceros	0.18 ± 0.03	0.23 ± 0.05	Ψ(fence+veg+vis+burnt+water+road),*p*(curve)
Bushbuck	0.40 ± 0.02	0.63 ± 0.04	Ψ(fence+preds+veg+curve+road+water),*p*(vis+fence+trail)
Cape buffalo	0.44 ± 0.02	0.54 ± 0.04	Ψ(biomass+preds+road+vis+water+fence),*p*(.)
Common duiker	0.37 ± 0.02	0.72 ± 0.04	Ψ(veg+water+curve+road),*p*(vis+curve+fence)
Common eland	0.23 ± 0.02	0.47 ± 0.05	Ψ(biomass+preds+vis+water+veg),*p*(.)
Common reedbuck	0.19 ± 0.03	0.22 ± 0.04	Ψ(curve+water+biomass),*p*(.)
Greater kudu	0.51 ± 0.02	0.95 ± 0.02	Ψ(burnt+water+road+curve+vis+fence+preds),*p*(trail+fence)
Hippopotamous	0.33 ± 0.06	0.15 ± 0.05	Ψ(burnt+water+fence+curve+vis+road),*p*(fence)
Impala	0.56 ± 0.02	0.5 ± 0.05	Ψ(burnt+preds+road+veg+vis+water),*p*(curve+fence+trail+vis)
Klipspringer	0.14 ± 0.05		
Lichtenstein's hartebeest	0.26 ± 0.03	0.4 ± 0.06	Ψ(preds+road+veg+biomass+curve+fence),*p*(fence+vis+curve+trail)
Nyala	0.36 ± 0.03	0.32 ± 0.05	Ψ(veg),*p*(trail+fence)
Plains zebra	0.44 ± 0.02	0.60 ± 0.052	Ψ(biomass+burnt+fence+vis+water+preds+curve),*p*(curve+fence+trail+vis)
Sable antelope	0.44 ± 0.02	0.83 ± 0.03	Ψ(preds+road+vis+curve+fence+water),*p*(fence+trail)
Sharpe's grysbok	0.12 ± 0.02		
Warthog	0.79 ± 0.01	0.95 ± 0.02	Ψ(preds+road+biomass+curve+burnt+fence+vis),*p*(curve+vis)
Waterbuck	0.47 ± 0.02	0.64 ± 0.05	Ψ(road+veg+vis+water+fence+burnt+curve),*p*(fence+trail+curve+vis)

Distance to fence

Distance to fence had a strong influence on black rhino, zebra and bushbuck. The probability of use increased for zebra and black rhino with increased distance from the fence (Figure 4.3a, b), but the opposite was true for bushbuck (Figure 4.3c).

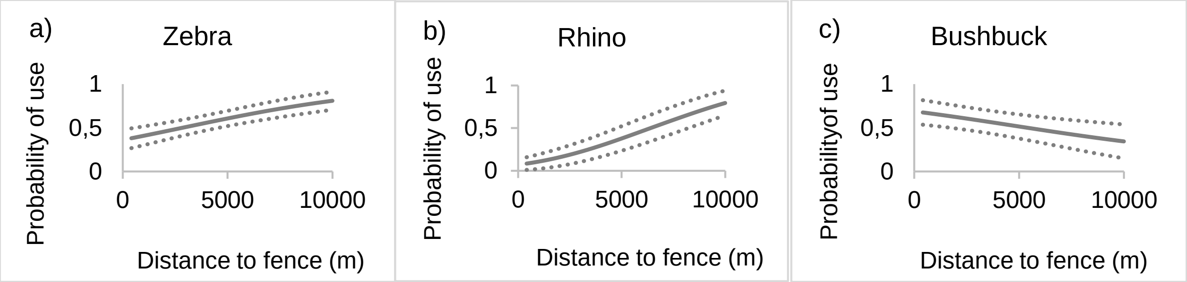

Figure 4.3: The probability of use of a) zebra, b) rhino and c) bushbuck in response to distance to fence at Majete Wildlife Reserve. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals

Distance to road

The probability of use by elephant, impala, waterbuck and warthog was strongly affected by the presence of roads. The probability of use of elephant and impala decreased steadily from a road to a distance of 3700 m from it (Figure 4.4a, b). The change is from 0.82 to 0.36 (difference = 0.46) for elephant and 0.55 to 0.17 (difference = 0.38) for impala. Waterbuck and warthog probability of use also decreased over a distance of 3 700 m (Figure 4.4c, d). However, the effect was less strong for waterbuck where probability of use varied by only 0.19 (0.74 – 0.55), and even less for warthog with a difference of 0.15 (0.95 – 0.67).

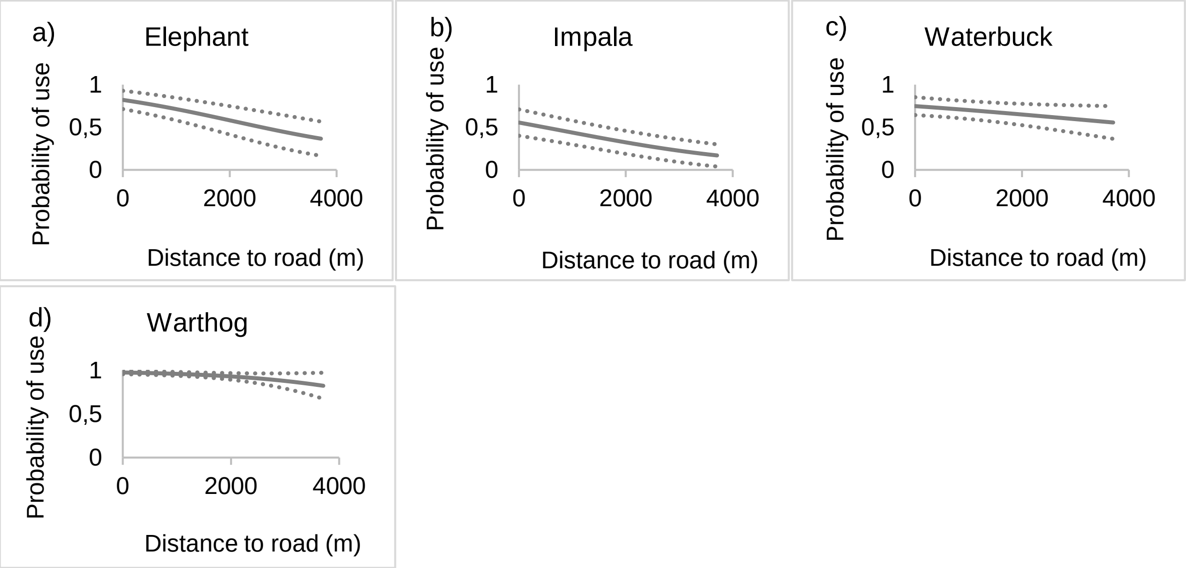

Figure 4.4: The probability of use of a) elephant, b) impala, c) waterbuck and d) warthog in response to distance to road at Majete Wildlife Reserve. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals

Distance to water

The probability of use by elephant, hippo, zebra, eland, kudu and impala was strongly influenced by the presence of water. Hippo's probability of use was most affected, with them predicted not to use areas further than 3 800 m away from water (Figure 4.5a). The probability of finding elephant close to water was close to 1 with a drop to below 0.5 more than 5 000 m from water (Figure 4.5b). Zebra and eland probability of use was similarly affected at similar distances from water (Figure 4.5c, d). Kudu and impala probability of use was also affected by water. Kudu space use was only affected further than 4 000 m from water (Figure 4.5e). The effect on impala was marginal with a variation of only 0.28 (0.55 – 0.27) over a distance of 10 000 m (Figure 4.5f).

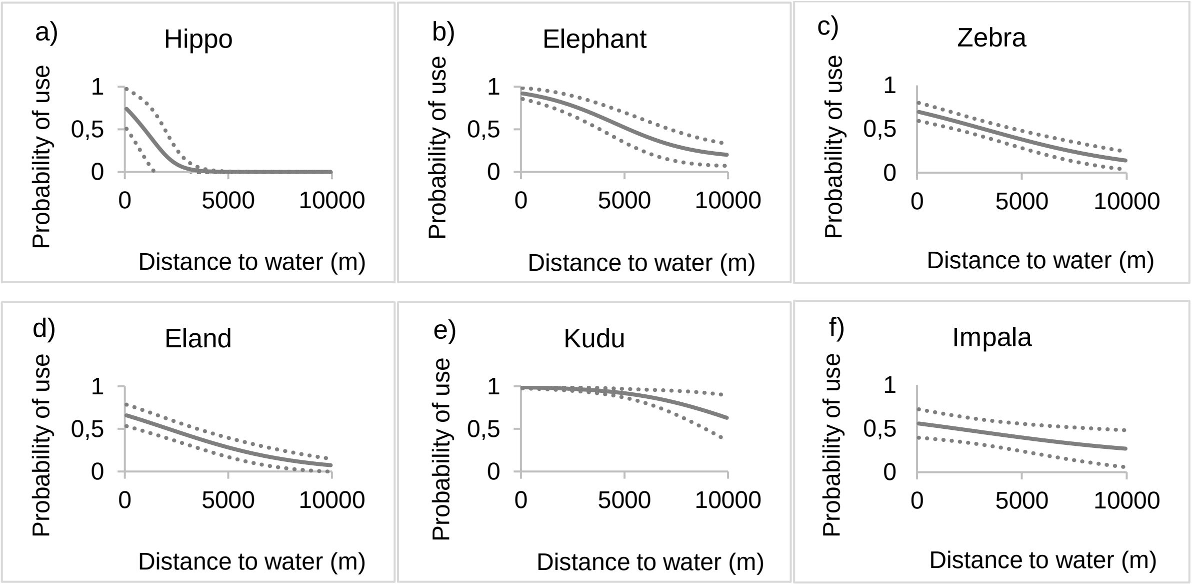

Figure 4.5:.The probability of use of a) hippo, b) elephant, c) zebra, d) eland, e) kudu and f) impala in response to distance to water. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals

Grass biomass

Elephant, eland and buffalo's probability of use were positively influenced by increasing grass biomass. The influence was lowest for elephant with a difference of only 0.32 (from 0.59 to 0.91) when confronted with a range of grass biomass from 0 to 12 tons per hectare (Figure 4.6a), followed by buffalo with a variation of 0.38 (0.33 – 0.71; Figure 4.6b) and eland with 0.43 (0.28 – 0.71; Figure 4.6c).

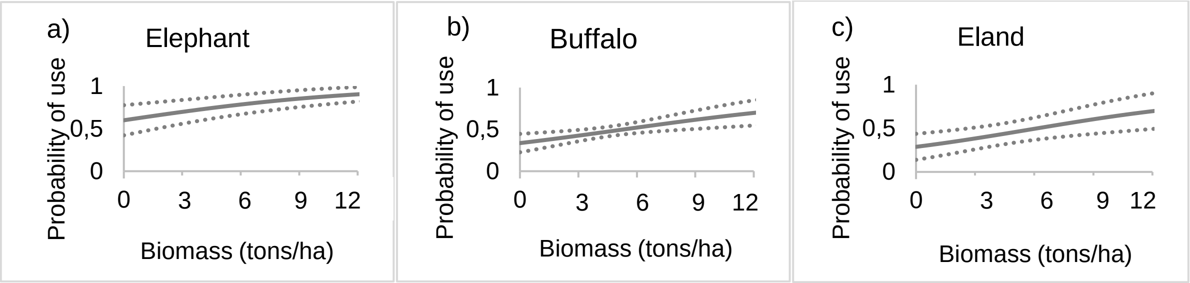

Figure 4.6: The probability of use of a) elephant, b) buffalo and c) eland in response to grass biomass at Majete Wildlife Reserve. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals

Visibility

Visibility influences the probability of use of buffalo, eland, impala, zebra, sable and waterbuck. All species were more likely to be found in more open habitat except waterbuck which shows a strong opposite trend. The relationship between visibility and probability of use was similar for buffalo, eland, impala and zebra (range 0.20 - 0.98; Figure 4.7a, b, c, d) as visibility improves from 10 to more than 70 metres. Sable showed the lowest effect with only a 0.34 difference in probability of use as visibility improves from 10 to 70 metres (Figure 4.7e).

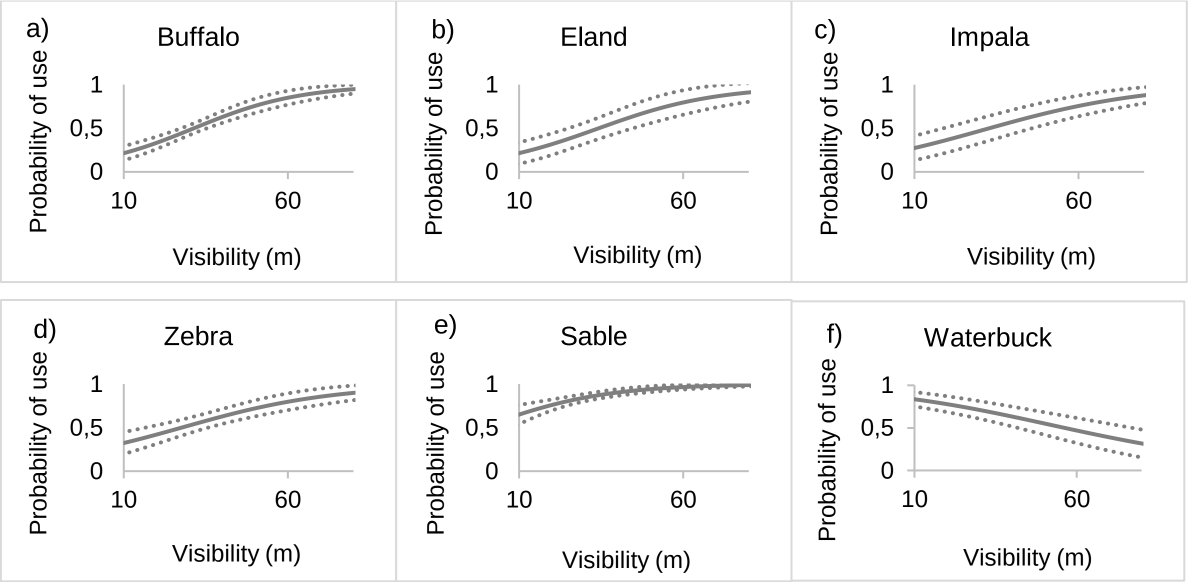

Figure 4.7: The probability of use of a) buffalo, b) eland, c) impala, d) zebra, e) sable and f) waterbuck in response to visibility at Majete Wildlife Reserve. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals

Relative predator abundance

Bushbuck and buffalo probability of use was positively associated with the presence of large predators (Figure 4.8a, b).

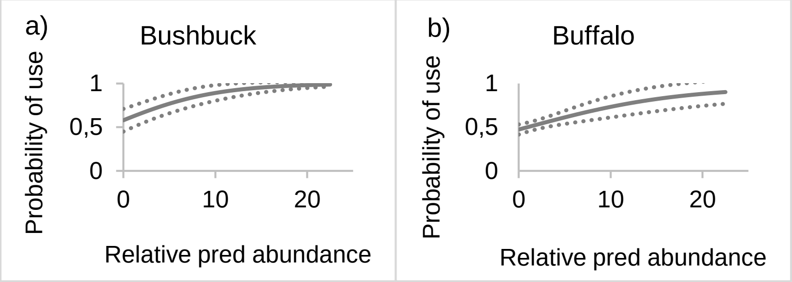

Figure 4.8: The probability of use of a) bushbuck and b) buffalo in response to relative predator abundance at Majete Wildlife Reserve. The solid line represents the probability of use and the dotted lines represent the 95% confidence intervals. The abbreviation pred = predator

Vegetation type

The probability of use by duiker, bushbuck, rhino, elephant, nyala, impala, hartebeest and waterbuck was strongly influenced by vegetation type. Bushbuck use high-altitude vegetation in higher proportions than other vegetation (Figure 4.9a). Duiker use ridge-top vegetation less than any other vegetation type (Figure 4.9b). In contrast, nyala uses ridge-top more and high-altitude miombo vegetation less than any other vegetation type (Figure 4.9c). Another mixed feeding ungulate, the impala, also uses high-altitude miombo vegetation in low proportions (Figure 4.9d). Black rhino use low and high-altitude miombo vegetation less than the other vegetation types, with ridge-top being used the most (Figure 4.9e). Elephant use ridge-top vegetation most and high-altitude miombo vegetation least, but there is much overlap in the confidence intervals that makes definitive inference difficult (Figure 4.9f). Waterbuck use riverine vegetation more than the other vegetation type apart from ridge-top areas (Figure 4.9g). Hartebeest use ridge-top and high-altitude miombo vegetation in low proportions with high-altitude miombo being used less than riverine, medium- and low-altitude vegetation (Figure 4.9h).

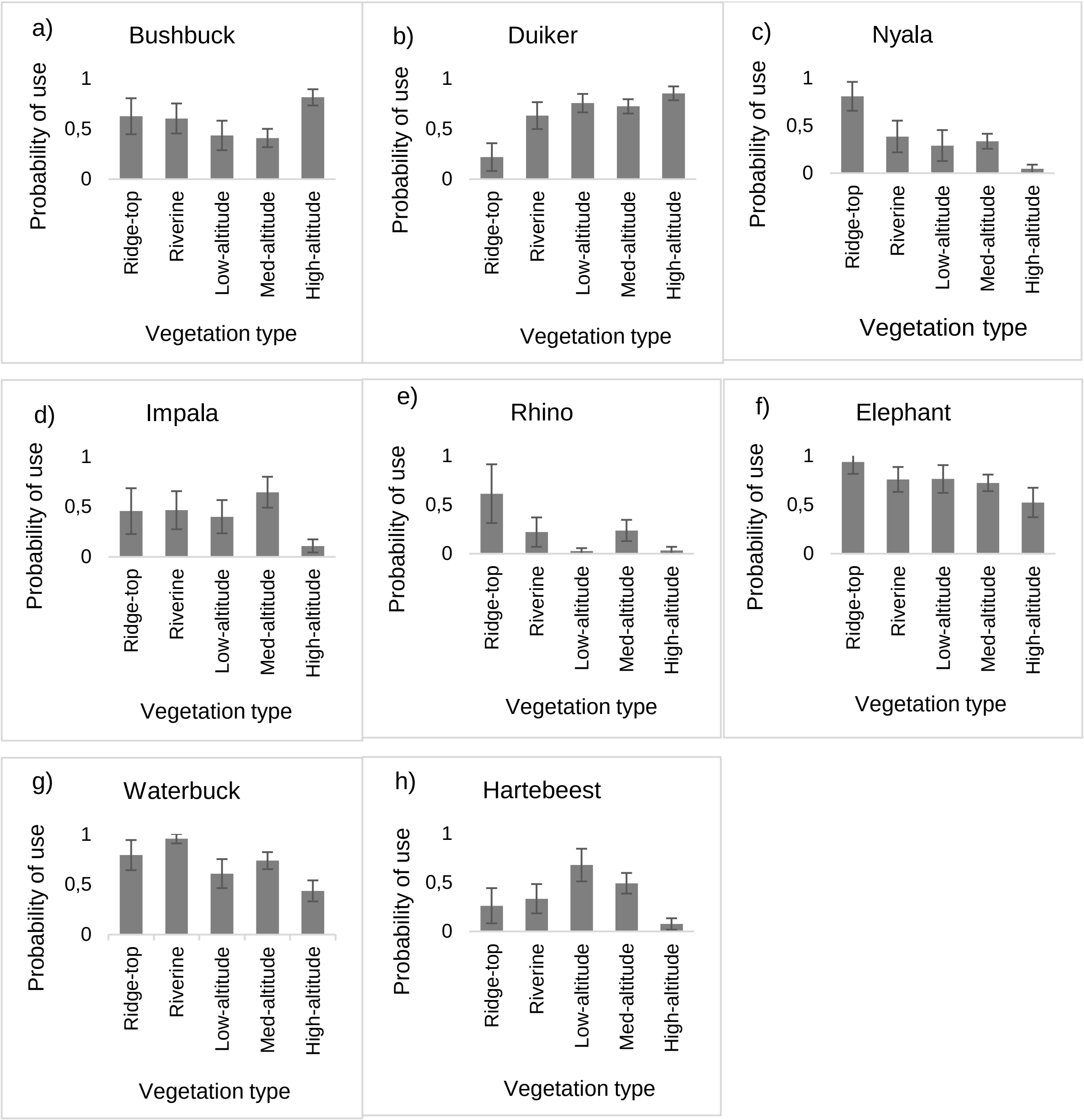

Figure 4.9: The relationship between vegetation type and the probability of use of a) bushbuck, b) duiker, c) nyala d) impala, e) rhino, f) elephant, g) waterbuck and h) hartebeest in Majete Wildlife Reserve. The 95% confidence intervals are indicated. The vegetation type abbreviations are, Ridgetop = Ridgetop mixed short deciduous woodland, Riverine = Riverine and alluvial associations, Low-altitude = Low-altitude mixed tall deciduous woodland, Med-altitude = Medium-altitude mixed tall deciduous woodland and High-altitude = High-altitude tall miombo woodland

4.4 Discussion

The results from this study uphold the predictions that anthropogenic and environmental variables influence the probability of use of ungulates in MWR. However, the results suggest that the measured environmental drivers affect more species (12 species) in MWR than anthropogenic drivers (10 species), with vegetation type, distance to water and visibility influencing the most species. Other occupancy studies had similar findings with environmental variables having a greater impact on mammal space use than human-induced disturbance (Fuda *et al*., 2018; Oberosler *et al.*, 2019). The use of the different vegetation types varied considerably between species, and it was surprising that some water-dependent species' (buffalo, warthog, waterbuck and black rhino) space use was not strongly influenced by the presence of permanent water. As predicted, the anthropogenic activity around the reserve was influential, with two species' probability of use negatively affected by the fence line.

Kudu, warthog and sable were the most widely distributed species in MWR. It is interesting to note that Bell (1984) recorded that kudu and warthog were the most common and widely distributed species in MWR in 1984. Kudu and warthog are two species that were not reintroduced into MWR from 2003 and their current and past common occurrence and wide distribution suggest that these two species are well adapted to the conditions in MWR. Sable are a characteristic species of Miombo woodland (Frost, 1996; Hinde *et al.*, 2001). Bell (1984) reported the widespread presence of sable in the reserve in the early 1980's and after the successful re-introduction of sable into MWR in 2003, they are widespread once again. In contrast, hippo and reedbuck had the most restricted distribution in the reserve. Hippo is a habitat specialist, requiring open water where they spend most of the day (Skinner & Chimimba, 2005). Similarly, reedbuck have essential habitat requirements; they are associated with reed beds or herbaceous cover adjacent to permanent water so their distribution tends to be discontinuous and patchy (Skinner & Chimimba, 2005).

Black rhino and zebra's probability of use increased with distance from the fence, indicating avoidance of the reserve perimeter, which is likely due to anthropogenic-associated disturbance along the reserve boundary (Hayward & Kerley, 2009; Massey *et al*., 2014). This effectively reduces the available space for these species to utilise within the reserve (Woodroffe & Ginsberg, 1998; Rich *et al.,* 2016). This is important information for rhino especially, as they use high- and low-altitude woodland significantly less than other vegetation, which further limits their available space. Large-bodied herbivores in particular are sensitive to anthropogenic activities (Selier *et al.*, 2015), and black rhino space use is negatively affected by human disturbance in other small, fenced reserves (Odendaal-Holmes *et al*., 2014), as well as in larger, open landscapes in Africa (Walpole *et al.,* 2003; Gadiye & Koskei, 2016). Similarly, Hartmann's zebra in Namibia were found to strongly avoid areas of human activity (Muntifering *et al.*, 2019), while Young *et al.* (2005) found plains zebra to avoid human activity areas associated with livestock. Conversely, the probability of use of bushbuck decreased with distance from the fence, which may be an effect of their low use of the medium-altitude vegetation that occurs in the centre of the reserve, rather than bushbuck preferring to be closer to the fence.

The probability of use of elephant and impala was higher closer to roads, contrasting with other studies where some herbivore species, including elephants and impala, avoided roads due to human presence (Leblond *et al.*, 2013; Mulero-Pázmány *et al.,* 2016; Muposhi *et al.*, 2016; Gaynor *et al.,* 2018). Vehicle traffic on the majority of the roads in MWR is extremely low with lodge accommodation for only 36 tourists and minimal day visitation when compared to other tourism hotspot PAs. Tourism vehicles are restricted to the north eastern section (20% of the reserve). The degree to which the roads are avoided by animals due to traffic is therefore considered minimal. Elephants use roads as low resistance movement corridors as roads may provide the fastest and most direct route to water (Gaynor *et al.*, 2018; Tsalyuk *et al.*, 2019). Water is channelled off roads into the roadside ditches encouraging the growth of greener vegetation, which may also be attracting both elephant and impala (Trombulak & Frissell, 2000; Tsalyuk *et al*., 2019). However, this is likely not a significant factor as other species that require high quality forage may otherwise have been similarly influenced by roads.

Zebra, elephant and hippo strongly associate with water and are known to be water dependent (Skinner & Chimimba, 2005; Smit *et al*., 2007; Kihwele *et al.*, 2020). However, distance to water is not a reliable indicator of water dependency since herbivore distributions are confounded by other factors such as predation risk and food availability (Kihwele *et al.*, 2020). Buffalo which are considered water dependent (Skinner & Chimimba, 2005; Smit *et al*., 2007; Kihwele *et al.*, 2020), were not found to be associated with water but rather were associated with high grass biomass. This may indicate a trade-off between surface water needs and food quantity during the dry season (Redfern *et al.,* 2003). Smit *et al.* (2007) indicated that waterbuck have a greater association with rivers than waterholes, which was suggested to be due to the habitat associated with rivers that waterbuck are known to be dependent on rather than the fact that waterholes are artificial. Waterbuck used riverine vegetation more than any other vegetation type in MWR and were associated with areas with low visibility. Thus the finding that distance to water is not a driving factor of waterbuck space use is more likely a result of there being no water-associated vegetation around artificial waterholes rather than them not associating with water (Smit *et al.,* 2007). Impala are reported to be water dependent (Skinner & Chimimba, 2005) but in the recent study by Kihwele *et al*. (2020) their physiological water requirements were found to be medium to low, and indeed their association with water in MWR is weak. Eland as another mixed feeder is generally considered water-independent as they tend to browse in the dry season from which they can obtain some moisture (Taylor, 1969; Skinner & Chimimba, 2005). However, the results of this study suggest that they are affected by water availability which corraborate the findings of Kihwele *et al.* (2020) that suggest they have medium water requirments. Distance to water influenced probability of use for the highly water-dependent black rhino, however the result was not strong; equally surprising was that warthog presence, also considered highly water-dependent, appears not to be influenced by water (Skinner & Chimimba, 2005; Kihwele *et al*., 2020).

Buffalo, eland and elephant space use are positively influenced by grass biomass. As large ruminants with relatively low energy requirements, buffalo and eland both feed unselectively on a wide range of grasses that may be low in nutritive value but which they require in high quantities to meet their nutritional needs (Jarman, 1974; Owen-Smith, 1988; Hopcraft *et al.*, 2010; Fritz *et al.,* 2011; Hopcraft *et al.*, 2012). Similarly, elephant as a megaherbivore and hindgut fermenter have low metabolic needs and can tolerate low quality forage but require it in large quantities (Owen-Smith, 1988; Clauss & Hummel, 2005; Hopcraft *et al.*, 2010).

An increase in visibility positively influenced the probability of use of buffalo, eland, impala, sable and zebra with only waterbuck showing a negative response to increased visibility. This corresponds with waterbuck preference for dense, riverine vegetation also seen in other studies (Owen-Smith, 1996; Smit *et al.*, 2007). Greater grass height and vegetation cover are important for predator hunting success (Funston *et al.*, 2001; Owen-Smith, 2019). Buffalo, eland and zebra used more open areas possibly as a mechanism for avoiding ambushing lions (Funston *et al.*, 2001; Hopcraft *et al.*, 2005; Owen-Smith, 2019). These species are not preferred prey items of lions in MWR and make up a small proportion of lion diet, and notably buffalo are strongly avoided here (Briers-Louw & Leslie, 2020), which may be due to these species' success in avoiding lion predation by using open areas. In addition, predation risk was shown to shape the vigilance behaviour of zebra bachelor herds in MWR (de Vos *et al.*, 2020). Impala form a large proportion of leopard diet in MWR (Briers-Louw & Leslie, 2020) and elsewhere (Hayward *et al.*, 2006). By using more open areas they may be avoiding leopard habitat (i.e. habitat with intermediate cover; Balme *et al.*, 2007) which enables successful ambushing, which was found in a small fenced reserve in South Africa (Thaker *et al.*, 2011). A positive association between bushbuck and predator presence exists which may be driven by leopard's preference of bushbuck as a prey item (Briers-Louw & Leslie, 2020). Conversely, buffalo are also positively associated with predator presence, though as previously mentioned, they probably avoid being killed in high numbers by using open areas (Briers-Louw & Leslie, 2020).

Species' probability of use of the different vegetation types in MWR varied between species. The high-altitude miombo woodland was used considerably less by nyala, impala and black rhino than any other vegetation type in MWR, whereas bushbuck utilised this vegetation type the most. High-altitude miombo woodland has been shown to have the lowest browse availability and habitat suitability for black rhino in MWR (Gyöngyi & Elmeros, 2017) which supports the findings here. Nyala and impala are mixed feeders, consuming both graze and browse selectively (Gagnon & Chew, 2000; Skinner & Chimimba, 2005). Strong interspecific competitive interactions have been recorded between browsing bushbuck and nyala, where nyala outcompeted bushbuck resulting in their spatial and temporal segregation (Ehlers Smith *et al.*, 2020). Similarly, it was shown that as resource depletion increases in the dry season, interspecific habitat-usage overlap between impala and nyala decreases indicating competition between these species (Botha & Stock, 2005; O'Kane *et al.,* 2013). It may be that due to competitive interactions between nyala, impala and bushbuck, bushbuck have reverted to using high-altitude vegetation. Ridge-top vegetation is nutrient poor, with the lowest biomass in MWR, which is perhaps why it is least used by duiker, a small browser that requires sufficient habitat cover and high quality forage to meet nutritional needs (Skinner & Chimimba, 2005). Nyala may be using ridge-top vegetation to avoid impala, despite vegetation quality being low.

Large portions of the reserve burnt during the study period (2018 dry season) and particularly towards the end of the dry season. Although fire came up as a driver for several species (Table 4.1), the results were not strong for any of them. Grazing ungulates are attracted to high quality grass regrowth following dry season fires (Tomor & Owen-Smith, 2002) which predominantly occurs at the start of the wet season (Archibald & Bond, 2004) which is in November in MWR. With many fires occurring towards the end of the 2018 dry season, and the survey period (7th June – 5th December 2018), perhaps the effect of species moving onto the green flush did not occur. Furthermore, the first seasonal rain fell in the last week of November 2018, so a green flush may not have occurred before the end of the survey period. However, Archibald & Bond (2004) found that grazer movements varied between years as a result of varying patterns of the spatial and temporal distribution of burns, and thus there may have been other factors at play which were not accounted for in this study.

4.5 Conclusion

The assessment of the patterns and drivers of ungulate space use at MWR provided insight on the functioning of this ecosystem, and may be useful for managers of other small, isolated, and fenced reserves in the Miombo Woodland Ecoregion, for which data are sparse. Insight into vegetation type use by the different species can be used to inform carrying capacity estimates, while the effect that distance to water has on some species space use may be useful for artificial water point placement planning. This study further demonstrates the efficacy of a systematic camera trap survey and occupancy modelling framework in producing mammal species distribution data in Africa. Considering the fragmented nature of the reserve, and the high levels of anthropogenic land use bordering it, it is somewhat surprising that more species were not influenced by the anthropogenic drivers. However, zebra and black rhino were shown to be particularly sensitive to the fence, while the space use of elephant and impala in relation to roads may alter in the future as tourism increases. In saying this, the fact that the environmental characteristics are predominantly driving ungulate landscape use indicates the critical importance of maintaining the natural interior characteristics of the reserve. Furthermore, the overall high value of MWR as a protected area and an intact natural remnant within the region has been shown. This research highlights the need for similar studies to be undertaken in other isolated protected areas, which are equally unique in their ability to conserve the biodiversity characteristics of the larger landscape.

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CHAPTER 5

RESEARCH FINDINGS AND MANAGEMENT IMPLICATIONS

Protected areas (PAs) in Africa face numerous threats as a result of a rapidly expanding human population (Gerland *et al*., 2014; Jones *et al.*, 2018). Direct threats such as habitat loss, poaching and regular, uncontrolled burning are common (Newmark, 2008; Lindsey *et al.*, 2014). Indirect and more subtle threats such as increasing road networks, fences and settlements fragment intact natural landscapes around parks and add further pressure (Newmark, 2008; Ibisch *et al.*, 2016). Small, fenced and isolated PAs result from these cumulative threats that then require intensive management to maintain ecosystem functioning (Cumming, 2004; Hayward *et al*., 2007; Miller *et al.*, 2013). Furthermore, African mammal populations in PAs are decreasing (Caro & Scholte, 2007; Craigie *et al*., 2010) despite conservation efforts, so it is thus vital that management interventions are effective and their effect on the wildlife community understood. Scientifically verifiable assessments of species richness and community structure within PAs is an essential starting point, as results from such assessments can guide future monitoring efforts and provide the basis from which anthropogenic impacts can be assessed (O'Brien, 2008; Yoccoz *et al.*, 2001; Rocha *et al*., 2019). In addition, an understanding of species space use patterns and the anthropogenic and environmental drivers thereof can aid management in limiting negative anthropogenic impacts and optimising conservation efforts.

Malawi in south-eastern Africa lies within the Miombo woodland ecoregion which has been described as one of the world's most important ecosystems (Ribeiro *et al*., 2015). As the sixth most densely populated country in Africa (The World Bank, 2020), Malawi's PAs are now highly isolated (Happold & Happold, 1997). Nevertheless, the value of isolated PAs in conserving valuable habitat and wildlife populations can still be fundamental (Wegmann *et al.*, 2014). Majete Wildlife Reserve (MWR) in Malawi is a small, fenced reserve that experienced large-scale poaching during the second half of the 20th century. However, since 2003 numerous large mammal reintroductions have taken place and the reserve is recovering. Monitoring and understanding the system are essential for its future success and indeed before this study little was known about MWR's medium and large mammal species richness and the space use of these animals.

Species richness and community structure

A species list for MWR developed in the 1980's suggested that at least 41 medium and large mammal species (> 0.5 kg) occurred in the reserve (Martin, 2005). The camera trap study confirmed the presence of 35 medium and large mammal species (Chapter 3) which represents 85% of the listed species of the 1980's. Species richness estimators suggest that there are closer to 40 species present, indicating that some species were missed but this assessment provides a scientifically verifiable baseline measure from which future comparisons can be made.

The species that were historically present but which were undetected in this survey are Livingstone's suni (*Neotragus moschatus)*, African clawless otter (*Aonyx capensis)*, spotted-necked otter (*Hydrictis maculicollis)*, yellow-spotted rock hyrax (*Heterohyrax brucei),* banded mongoose (*Mungos mungo)* and large grey mongoose (*Herpestes ichneumann)*. Visual confirmation of the presence of suni, banded mongoose, and rock hyrax has been made in the year since the survey and sign of the presence of an otter species has been detected. The non-detection of these species in the camera trap survey is thus likely due to restricted distribution and the survey design not accounting for their specialised habitat. It is recommended that an intensive survey targeting the otter and mongoose species is undertaken to account for their presence and status in the reserve. Informed decisions can then be made on how to augment the current survey design to include the habitat of all known medium and large mammal species for future monitoring.

There was a single detection of a side-striped jackal (*Canis adustus*) along the northern border of the reserve and the most recent known sighting of this species preceding this observation was made in 2016. It is thus likely that they are present in small numbers and may be transient. With increasing settlement and land use change around MWR (Coulibaly *et al*., 2015), it is recommended that side-striped jackal be studied more closely to understand factors limiting their persistence in the reserve.

Species' relative abundance indices (RAI; derived from the camera trap capture frequencies) were used to inform community structure. The results suggest that the megaherbivore component of the community structure at MWR is not typical of Miombo woodland (Bell, 1985), with specifically elephants (*Loxodonta africana*) being underrepresented. It can thus be argued that the elephant population can be allowed to increase to levels representative of the Miombo woodland ecoregion, but their impact should be closely monitored within the confined space of this relatively small reserve. It is worth noting that both the camera trap RAI's and 2018 aerial census data suggest an underrepresentation of elephants in typical Miombo woodland community structure.

A comparison was made between the RAIs derived from camera trap capture frequencies and those derived from the 2018 aerial census to determine how well camera traps inform community structure. There was a strong relationship between the camera trap derived RAIs and the RAIs derived from the aerial census encounter rate when the outlier warthog (*Phacohoerus aethiopicus*) was removed. The use of camera trap derived RAIs is an intuitive measure, however the use of RAIs is problematic as they do not account for imperfect detection (Foster & Harmsen, 2012; Sollmann *et al*., 2013). However, these results indicate that camera traps can inform relative abundance estimates to some extent, but that camera traps perhaps provide a more accurate appraisal of encounter rates than absolute abundance. Further comparisons between RAIs derived from camera trap capture frequencies and aerial survey results need to be made at multiple sites across Africa to determine where inconsistencies lie. With more information it might be possible to discern patterns that can aid in the further development of camera trap methodology that can be used to estimate the abundance of at least some mammal species.

Ungulate space use

The ungulate space use patterns and impact of anthropogenic and environmental variables on ungulate space use was investigated (Chapter 4) by assessing landscape curvature, visibility, grass biomass, vegetation type, relative large predator abundance, fire, distance to water, distance to fence and distance to road as drivers. In this study environmental factors were found to influence ungulate space use more than anthropogenic factors. This is perhaps surprising considering the isolated nature of the reserve, and the high levels of anthropogenic land use adjacent to it. However, there were two anthropogenic factors that had a strong influence on some species, namely distance to road and notably, distance to fence. Black rhino (*Diceros bicornis*) and zebra (*Equus quagga*) space use increased with distance from the reserve fence indicating their sensitivity to anthropogenic activity bordering it. This effectively reduces the amount of core space available for these species to utilise. In addition, black rhino space use is substantially more restricted than zebra in MWR. If a management goal is for the black rhino population to increase in MWR, this is important information considering the critically endangered conservation status of black rhino (Emslie, 2020), and the varying factors contributing to their habitat suitability (Odendaal-Holmes *et al.*, 2014). With growing pressure from Malawi's expanding human population, it is recommended that remaining natural habitat on the periphery of the reserve is actively prevented from being lost to agricultural expansion and settlement so as to act as buffer areas that can maximise the effective reserve size and core area (Ewers & Didham, 2007; Herse *et al*., 2018). Elephant and impala (*Aepyceros melampus*) space use was greater close to roads, which contrasts with other studies which found these species avoiding roads attributable to human presence (Muposhi *et al.*, 2016; Gaynor *et al.,* 2018). If tourism and vehicle traffic increases in MWR, impala and elephant space use may be influenced.

Species that are strongly influenced by the presence of water in MWR are elephant, zebra, eland (T*ragelaphus oryx livingstonii)*, impala, kudu (*Tragelaphus strepsiceros*) and hippo (*Hippopotamus amphibius*). Water supplementation is commonly used in PAs, which requires careful placement to maintain vegetation heterogeneity and prevent habitat degradation (Smit *et al.*, 2007). The opening and closing of water points is a management action used to manipulate the distribution of mammals and their impacts across a landscape (Owen-Smith, 1996; Smit & Grant, 2009). Staub *et al*. (2013) suggested altering the spatio-temporal distribution of artificial water supply in MWR in order to manipulate the intensity of landscape use of elephants, thereby reducing vegetation damage. It should be borne in mind by management that the manipulation of the water supply in MWR will most likely not only influence the distribution of elephants, but also that of the other species identified to be strongly influenced by water here.

Distinct differences in the use of the identified vegetation types were detected for bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), nyala (*Tragelaphus angasii*), impala, rhino, elephant, waterbuck (*Kobus ellipsiprymnus*) and hartebeest (*Alcelaphus lichtensteinii)*, which has important implications for carrying capacity estimates of these species. When estimating optimal population numbers of a species for an area, an evaluation of habitat is essential (McLeod, 1997; Bothma *et al.*, 2004). The data here will enable management to identify the unique habitat requirements of the respective species, which will help to refine carrying capacity estimates to reflect density estimates based on suitable habitat rather than simply available space. Furthermore, the segregated use of the vegetation types by nyala and bushbuck indicated a potential competitive interaction between these species to the detriment of bushbuck (Fay & Greeff, 2008; Ehlers Smith *et al.,* 2020). It is recommended that the population size of nyala be monitored in relation to bushbuck to ensure the bushbuck population does not decline due to its use of potential suboptimal habitat necessitated by competition. Although distribution maps of nyala suggest its presence in the MWR area, there are no historic accounts of its presence in the reserve prior to their release into the reserve in 2003. Close monitoring of nyala and its effects is therefore paramount to ensure it does not jeopardise the persistence of species that were previously recorded in the area. Furthermore, it was found that the ridge-top mixed short deciduous woodland was used most by ungulates, while the high-altitude tall miombo woodland was used the least. It is suggested that vegetation monitoring focuses on the ridge-top vegetation to monitor potential vegetation damage due to the high abundance of ungulates here, which may have a knock-on effect on the ungulate community.

The influence of fire did not come up in the models as a strong driver for any species. This may be due to a mismatch between the camera trapping period and the appearance of nutrient rich green grass flushes associated with burnt patches following good rains (van Wilgen *et al.*, 2004). It may also be that other variables were involved creating complexities that were not accounted for in this study. It is recommended that a study is undertaken to unravel the dynamics of fire in MWR and its effect on mammal distribution, as other studies suggest fire has impact on mammal space use (Burkepile *et al.*, 2013; Anderson *et al*., 2016).

An association between predator presence and space use was found for only bushbuck and buffalo (*Syncerus caffer)*. This is surprising as the species making up most of the kills of lion (*Panthera leo*), hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*) in MWR are considered to be warthog, waterbuck, impala, duiker, nyala, kudu and reedbuck (*Redunca arundinum*), though bushbuck was consumed in high quantities and preferred by leopard (Briers-Louw & Leslie, 2020). Stronger associations between these preferred prey species and their predators may be masked by the relatively recent reintroduction (2011-2012; Briers-Louw *et al.*, 2019) of lion and leopard and their consequent low abundance. As predator populations increase over time in MWR, an understanding of their space use patterns would become important, as predators may then very well influence prey behaviour as has been found in other studies (Thaker *et al.*, 2011; Tambling *et al.,* 2015; Makin *et al.*, 2017)

Other potential predictors of herbivore space use are facilitation and intraguild competition between herbivores (Sinclair & Norton-Griffiths, 1982; Arsenault & Owen-Smith, 2002) as was shown through a camera trap study by Anderson *et al*. (2016). However, in order to properly understand the potential influence of these mechanisms, species-specific analysis would need to be undertaken (Anderson *et al.*, 2016) which was not possible in this study due to the number of drivers already being assessed and potential model overfitting. Furthermore, there are seasonal trade-offs between facilitation and competition, as positive facilitatory interactions in the growing season are offset by a subsequent reduction of forage in the dormant season encouraging competition between herbivores (Arsenault & Owen-Smith, 2002). This study took place during the dry season which would thus have limited the interpretation of potential results. It is recommended that future work take these factors into account.

Concluding remarks

With the importance of long term monitoring known (Margules & Pressey, 2000; Yoccoz *et al*., 2001; Cowell *et al.*, 2020) and the acceptance that camera-trapping is a repeatable method that produces comparable results between surveys (Ahumada *et al.*, 2013; Farris *et al.*, 2017; Martin *et al*., 2017), it is recommended that this study is repeated in the future. As anthropogenic pressure on the reserve boundary increases, it would be important to track species richness over time, so that the smaller elusive species are accounted for as they play an important part in sound ecosystem functioning (Ramesh & Downs, 2014). With careful replication of the survey and the potential augmentation of survey effort to account for the known undetected species, it may be possible to track relative abundance of small and rare species that are not otherwise detectable in aerial counts (Wearn & Glover-Kapfer, 2019). In addition, through replicating this study important insights can be gained into how ungulate space use changes as mammal population numbers vary. Seasonality has a strong influence on mammal space use which has been recognised through research using camera traps

(Martin *et al*., 2017; Kays *et al*., 2020). It is thus recommended that a comparative study is undertaken in the wet season as well.

In conclusion, this study has produced findings that can assist management in refining specific management actions. In doing so, the outcomes of these actions can be better predicted through improved understanding of environmental drivers in the reserve. MWR and similarly small and isolated reserves are extremely valuable in their capacity as intact natural remnants within a mosaic of converted land use. This research highlights the need for similar studies to be undertaken in other isolated PAs, which are equally unique in their ability to conserve the biodiversity characteristics of the larger landscape.

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APPENDICES

Appendix A: The quantity, location and year of large mammal reintroductions into Majete Wildlife Reserve

	Released inside the Sanctuary													Released outside the Sanctuary					
Species	**‘03**	**‘04**	**‘05**	**‘06**	**‘07**	**‘08**	**‘09**	**‘11**	**‘12**	**‘16**	**‘17**	**‘18**	**Total**	**‘08**	**‘09**	**‘10**	**‘11**	**Total**	**Grand total**
African elephant (*Loxodonta africana*)				70									**70**	64	83			**147**	**217**
Black Rhinoceros (*Diceros bicornis*)							Undisclosed										Undisclosed		
Bushpig (*Potamochoerus larvatus*)					1								**1**						**1**
Cape buffalo (*Syncerus caffer*)	120	100											**220**	86				**86**	**306**
Eland (*Tragelaphus oryx)*		20				32				25	67		**144**		25			**25**	**169**
Impala (*Aepyceros melampus*)	216									419	50		**685**	210		311		**521**	**1206**
Leopard (*Panthera pardus*)								2	4				**6**						**6**
Lichtenstein’s hartebeest (*Alcelaphus lichtensteinii*)		4		10		15	30						**59**						**59**
Lion (*Panthera leo*)									3			2	**5**						**5**
Nyala (*Tragelaphus angasii*)	6	15											**21**	38				**38**	**59**
Plains zebra (*Equus quagga*)		37	50	9		38				23	64		**221**		40			**40**	**261**
Sable antelope (*Hippotragus niger*)	100												**100**	153		99		**252**	**352**
Waterbuck (*Kobus ellipsiprymnus*)	98												**98**	198		106		**304**	**402**
Total	**540**	**176**	**50**	**89**	**1**	**85**	**30**	**2**	**7**	**467**	**181**	**2**	**1630**	**749**	**148**	**516**	**0**	**1413**	**3043**

Appendix B: The 2018 estimates of the population size of the medium and large mammals in Majete Wildlife Reserve based on aerial census results and known population numbers

Common name	2018 census total	Confidence interval
African elephant	201	± 22.22
Baboon troops	23	-
Bushbuck	106	± 11.71
Bushpig	8	-
Cape buffalo	1548	± 171.13
Common duiker	187	-
Common reedbuck	65	± 7.18
Crocodile	43	-
Eland	409	± 45.21
Greater kudu	866	± 95.73
Hippopotamus	82	-
Impala	430	± 47.53
Klipspringer	7	-
Leopard	2	-
Lichtenstein's hartebeest	76	± 8.4
Lion	3	-
Nyala	48	± 5.3
Plains zebra	572	± 63.23
Porcupine	2	-
Sable antelope	837	± 92.53
Sharpe's grysbok	44	-
Spotted hyaena	1	-
Warthog	364	± 40.24
Waterbuck	1110	± 122.71

Appendix C: Medium to large non-target species captured during the survey and their number of independent detections

Class	Species	Common name	Number of detections
Mammalia	*Otolemur crassicaudatus*	Thick-tailed galago	1
Aves	*Bucorvus leadbeateri*	Southern ground hornbill	1
	Lissotis melanogaster	Black-bellied bustard	14
	Terathopius ecaudatus	Bateleur	1
	Numida meleagris	Helmeted guineafowl	5

Appendix D: The figures for the 2018 aerial count at Majete Wildlife Reserve, and the encounter rate calculated as the total number of independent encounters per species during the census (individuals if alone, or groups when together). The count correction factors are shown which were used to correct the aerial count numbers (adjusted count)

Common name	Aerial count	Encounter rate	Count correction factor	Adjusted count
African elephant	201	50	1.05	211.05
Black rhinoceros	Undisclosed			
Bushbuck	106	93	3	318
Cape buffalo	1548	126	1.1	1702.8
Common reedbuck	65	41	3	195
Eland	409	58	1.5	613.5
Greater Kudu	866	216	1.8	1558.8
Hippopotamus	82	18	1.1	90.2
Impala	430	98	1.67	718.1
Lichtenstein's hartebeest	76	21	1.67	126.92
Nyala	48	21	2	96
Plains zebra	572	111	1.2	686.4
Sable antelope	837	193	1.33	1113.21
Warthog	364	182	2.5	910
Waterbuck	1110	328	1.67	1853.7

Appendix E: The reference scores for the comparative yield/dry weight rank method used to estimate grass biomass. The grass biomass score of one to nine was calibrated using the dry grass weight (tons/ha)

Grass biomass score	Dry grass weight (tons/ha)
1	0 - 3
2	4 - 6
3	7 - 9
4	10 - 12
5	13 - 15
6	16 - 18
7	19 - 21
8	22 - 24
9	25 - 27

Appendix F: The variance inflation factor (VIF) scores for each predictor variable which if show a value greater than five indicate collinearity

Predictor variable	**VIF score**
Distance to water	1.303034
Visibility	1.822818
Distance to fence	1.427861
Distance to road	1.227192
Landscape curvature	18.565697
Slope	18.460359
Burnt	1.493203
Vegetation type	2.015882
Grass biomass	1.77562
Predator	4.077578
Predator exc. Leopard	4.214049

Appendix G: Top-ranked models for space use (ψ) and detection (*p*) for each of the ungulates at Majete Wildlife Reserve. AICc represents the AIC value, ΔAIC is the difference in AIC values between each model and the lowest AIC model, and ΔAICc weight is the AIC model weight

Species	**Models**	**AICc**	**ΔAICc**	**ΔAICc Weight**	**Log likelihood**
African elephant	**Detection models (*p*)**				
	ψ(.),p(fence)	849.36	0	0.51	-421.59
	ψ(.),p(fence+curve)	850.87	1.51	0.24	-421.29
	Space use models (ψ)				
	ψ(biomass+road+veg+water),*p*(fence)	820.74	0	0.52	-399.52
	ψ(biomass+fence+road+veg+water),*p*(fence)	822.1	1.36	0.27	-399.02
	ψ(biomass+road+water),*p*(fence)	822.55	1.81	0.21	-404.96
Black rhino	**Detection models (*p*)**				
	ψ(.),*p*(curve)	286.64	0	0.34	-140.23
	ψ(.),*p*(curve+vis)	287.11	0.47	0.27	-139.41
	ψ(.),*p*(curve+fence)	287.27	0.63	0.24	-139.49
	Space use models (ψ)				
	ψ(fence+veg),*p*(curve)	282.32	0	0.23	-132.61
	ψ(fence+veg+vis),*p*(curve)	282.57	0.25	0.2	-131.59
	ψ(burnt+fence+veg+vis),*p*(curve)	283.02	0.7	0.16	-130.66
	ψ(fence+veg+water),*p*(curve)	283.69	1.36	0.12	-132.15
	ψ(fence+veg+water),*p*(curve)	283.84	1.52	0.11	-131.07
	ψ(fence+road+veg),*p*(curve)	284.08	1.76	0.1	-132.35
	ψ(burnt+fence+veg),*p*(curve)	284.26	1.93	0.09	-132.44
Bushbuck	**Detection models (*p*)**				
	ψ(.),*p*(vis+fence+trail)	1023.69	0	0.37	-505.53
	ψ(.),*p*(vis+fence+trail+curve)	1025.1	1.41	0.18	-505.13
	ψ(.),*p*(vis+fence)	1025.64	1.95	0.14	-508.67
	Space use models (ψ)				
	ψ(fence+preds+veg),p(vis+fence+trail)	1011.63	0	0.23	-492.59
	ψ(curve+fence+preds+veg),p(vis+fence+trail)	1012.09	0.47	0.18	-491.6
	ψ(fence+preds+road+veg),p(vis+fence+trail)	1012.42	0.79	0.16	-491.77
	ψ(preds+veg),p(vis+fence+trail)	1013.08	1.46	0.11	-494.51
	ψ(fence+preds+veg+water),p(vis+fence+trail)	1013.1	1.47	0.11	-492.1
	ψ(curve+preds+veg),p(vis+fence+trail)	1013.2	1.57	0.11	-493.37

Cape buffalo	**Detection models (*p*)**				
	ψ(.),*p*(.)	985.92	0	0.31	-490.92
	ψ(.),*p*(fence)	985.94	0.02	0.3	-489.88
	ψ(.),*p*(vis)	987.47	1.55	0.14	-490.65
	ψ(.),*p*(trail)	987.67	1.75	0.13	-489.69
	ψ(.),*p*(curve)	987.86	1.93	0.12	-490.84
	Space use models (ψ)				
	ψ(biomass+preds+road+vis),p(.)	969.32	0	0.2	-478.34
	ψ(biomass+preds+vis),p(.)	969.43	0.12	0.18	-479.49
	ψ(biomass+preds+vis+water),p(.)	970.24	0.93	0.12	-478.81
	ψ(biomass+fence+preds+vis),p(.)	970.8	1.48	0.09	-479.09
	ψ(preds+road+vis),p(.)	970.85	1.54	0.09	-480.2
	ψ(biomass+preds+road+vis+water),p(.)	970.98	1.66	0.08	-478.07
	ψ(biomass+fence+preds+road+vis),p(.)	971.02	1.7	0.08	-478.09
	ψ(preds+vis),p(.)	971.25	1.93	0.07	-481.48
	ψ(biomass+road+vis),p(.)	971.31	1.99	0.07	-480.43
Common duiker	**Detection models (*p*)**				
	ψ(.),*p*(vis+curve+fence)	1120.57	0	0.51	-555.06
	ψ(.),*p*(vis+curve)	1121.87	1.3	0.27	-556.79
	Space use models (ψ)				
	ψ(veg),p(vis+curve+fence)	1115.73	0	0.41	-548.17
	ψ(veg+water),p(vis+curve+fence)	1116.71	0.98	0.25	-547.5
	ψ(curve+veg),p(vis+curve+fence)	1117.34	1.6	0.18	-547.82
Common reedbuck	**Detection models (*p*)**				
	ψ(.),*p*(.)	321.26	0	0.39	-158.59
	ψ(.),*p*(fence)	322.77	1.51	0.18	-158.3
	ψ(.),*p*(curve)	322.77	1.51	0.18	-158.3
	Space use models (ψ)				
	ψ(.),p(.)	321.26	0	0.41	-158.59
	ψ(curve),p(.)	322.03	0.76	0.28	-157.92
	ψ(water),p(.)	323.14	1.88	0.16	-158.48
	ψ(biomass),p(.)	323.15	1.89	0.16	-158.49

Eland	**Detection models (*p*)**				
	ψ(.),*p*(.)	678.94	0	0.4	-337.43
	ψ(.),*p*(trail)	680.84	1.91	0.15	-336.27
	ψ(.),*p*(vis)	680.86	1.93	0.15	-337.34
	ψ(.),*p*(fence)	680.87	1.93	0.15	-337.34
	Space use models (ψ)				
	ψ(biomass+vis+water),p(.)	668.34	0	0.21	-328.95
	ψ(biomass+preds+vis+water),p(.)	668.34	0	0.21	-327.85
	ψ(biomass+preds+veg+vis+water),p(.)	668.73	0.39	0.17	-323.51
	ψ(biomass+veg+vis+water),p(.)	669.33	0.99	0.13	-324.97
	ψ(preds+vis+water),p(.)	669.5	1.16	0.12	-329.52
	ψ(vis+water),p(.)	669.85	1.51	0.1	-330.78
	ψ(biomass+road+vis+water),p(.)	670.17	1.84	0.08	-328.77
Hartebeest	**Detection models (*p*)**				
	ψ(.),*p*(vis+fence+trail+curve)	504.83	0	0.67	-244.99
	Space use models (ψ)				
	ψ(veg),p(vis+fence+trail+curve)	495.91	0	0.22	-235.92
	ψ(preds+veg),p(vis+fence+trail+curve)	496.34	0.43	0.18	-234.94
	ψ(fence+veg),p(vis+fence+trail+curve)	496.39	0.48	0.17	-234.97
	ψ(fence+preds+veg),p(vis+fence+trail+curve)	496.94	1.03	0.13	-234.02
	ψ(road+veg),p(vis+fence+trail+curve)	497.03	1.12	0.12	-235.29
	ψ(fence+road+veg),p(vis+fence+trail+curve)	497.56	1.65	0.1	-234.33
	ψ(preds+road+veg),p(vis+fence+trail+curve)	497.73	1.82	0.09	-234.42
Hippo	**Detection models (*p*)**				
	ψ(.),*p*(fence)	125.01	0	0.29	-59.42
	ψ(.),*p*(vis+fence+trail)	125.83	0.82	0.19	-56.6
	ψ(.),*p*(fence+vis)	126.22	1.21	0.16	-58.96
	ψ(.),*p*(fence+trail)	126.31	1.3	0.15	-57.93
	ψ(.),*p*(fence+curve)	126.52	1.51	0.13	-59.11
	Space use models (ψ)				
	ψ(fence+water),p(fence)	111.42	0	0.27	-50.48
	ψ(water),p(fence)	111.56	0.14	0.25	-51.63
	ψ(biomass+fence+water),p(fence)	112.48	1.06	0.16	-49.92
	ψ(road+water),p(fence)	113.1	1.68	0.12	-51.32
	ψ(vis+water),p(fence)	113.25	1.84	0.11	-51.4

	ψ(curve+water),p(fence)	113.3	1.88	0.1	-51.42
Impala	**Detection models (*p*)**				
	ψ(.),*p*(vis+fence+curve+trail)	834.03	0	0.55	-409.59
	ψ(.),*p*(vis+fence+curve)	834.49	0.46	0.44	-412.02
	Space use models (ψ)				
	ψ(burnt+preds+road+veg+vis+water),p(vis+fence+curve+trail)	796.53	0	0.17	-380.05
	ψ(preds+road+veg+vis+water),p(vis+fence+curve)	796.69	0.16	0.16	-381.41
	ψ(road+veg+vis+water),p(vis+fence+curve)	796.72	0.19	0.15	-382.68
	ψ(burnt+preds+road+veg+vis),p(vis+fence+curve)	797.21	0.68	0.12	-381.67
	ψ(burnt+road+veg+vis+water),p(vis+fence+curve)	797.45	0.92	0.11	-381.79
	ψ(preds+road+veg+vis),p(vis+fence+curve)	797.85	1.32	0.09	-383.24
	ψ(road+veg+vis),p(vis+fence+curve)	798.07	1.54	0.08	-384.59
	ψ(burnt+road+veg+vis),p(vis+fence+curve)	798.33	1.8	0.07	-383.49
	ψ(burnt+preds+veg+vis+water),p(vis+fence+curve)	798.47	1.95	0.06	-382.3
Kudu	**Detection models (*p*)**				
	ψ(.),*p*(trail+fence)	1428.71	0	0.43	-709.13
	ψ(.),*p*(trail+fence+vis)	1429.81	1.1	0.25	-708.59
	ψ(.),*p*(trail+fence+curve)	1430.66	1.95	0.16	-709.01
	Space use models (ψ)				
	ψ(burnt+water),p(trail+fence)	1425.94	0	0.23	-705.54
	ψ(burnt+road+water),p(trail+fence)	1426.47	0.54	0.18	-704.69
	ψ(water),p(trail+fence)	1426.98	1.04	0.14	-707.17
	ψ(curve+water),p(trail+fence)	1427.06	1.12	0.13	-706.1
	ψ(vis+water),p(trail+fence)	1427.32	1.38	0.12	-706.24
	ψ(burnt+fence+water),p(trail+fence)	1427.59	1.65	0.1	-705.24
	ψ(burnt+curve+road+water),p(trail+fence)	1427.59	1.66	0.1	-704.1
Nyala	**Detection models (*p*)**				
	ψ(.),*p*(trail+fence)	365.06	0	0.52	-177.31
	ψ(.),*p*(trail+fence+curve)	366.43	1.36	0.26	-176.9
	ψ(.),*p*(trail+fence+vis)	366.74	1.68	0.22	-177.05
	Space use models (ψ)				
		345.8	0	0.113	-162.07

Plains zebra	**Detection models (*p*)**				
	ψ(.),*p*(trail+vis+fence+curve)	910.9	0	1	-448.03
	Space use models (ψ)				
	ψ(biomass+burnt+fence+vis+water),p(trail+vis+fence+curve)	900.45	0	0.16	-437
	ψ(biomass+fence+vis+water),p(trail+vis+fence+curve)	900.85	0.4	0.13	-438.39
	ψ(fence+preds+vis+water),p(trail+vis+fence+curve)	900.9	0.45	0.13	-438.42
	ψ(fence+vis+water),p(trail+vis+fence+curve)	900.93	0.48	0.13	-439.61
	ψ(biomass+fence+preds+vis+water),p(trail+vis+fence+curve)	901.15	0.7	0.11	-437.35
	ψ(burnt+fence+vis+water),p(trail+vis+fence+curve)	901.41	0.96	0.1	-438.68
	ψ(biomass+burnt+fence+preds+vis+water),p(trail+vis+fence+curve)	901.53	1.08	0.09	-436.32
	ψ(burnt+fence+preds+vis+water),p(trail+vis+fence+curve)	902	1.55	0.07	-437.77
	ψ(curve+fence+vis+water),p(trail+vis+fence+curve)	902.35	1.9	0.06	-439.14
Sable	**Detection models (*p*)**				
	ψ(.),*p*(trail+fence)	1298.3	0	0.37	-643.93
	ψ(.),*p*(trail)	1299.99	1.69	0.16	-645.85
	Space use models (ψ)				
	ψ(road+vis),p(trail+fence)	1290.29	0	0.14	-637.72
	ψ(curve+road+vis),p(trail+fence)	1290.87	0.58	0.11	-636.89
	ψ(preds+road+vis),p(trail+fence)	1291.22	0.92	0.09	-637.06
	ψ(fence+road+vis),p(trail+fence)	1291.23	0.94	0.09	-637.07
	ψ(curve+fence+vis),p(trail+fence)	1291.29	0.99	0.09	-637.1
	ψ(curve+fence+road+vis),p(trail+fence)	1291.33	1.03	0.08	-635.97
	ψ(curve+vis),p(trail+fence)	1291.36	1.07	0.08	-638.26
	ψ(vis),p(trail+fence)	1291.4	1.1	0.08	-639.38
	ψ(fence+vis),p(trail+fence)	1291.85	1.56	0.06	-638.5
	ψ(preds+vis),p(trail+fence)	1291.86	1.56	0.06	-638.5
	ψ(preds+road+vis),p(trail+fence)	1292.13	1.83	0.06	-636.37
	ψ(curve+preds+road+vis),p(trail+fence)	1292.22	1.93	0.05	-636.42
Waterbuck	**Detection models (*p*)**				
	ψ(.),*p*(fence+trail+curve+vis)	928.2	0	0.68	-456.68
	ψ(.),*p*(fence+trail+curve)	929.77	1.57	0.31	-458.57
	Space use models (ψ)				
	ψ(road+veg+vis),p(fence+trail+curve+vis)	914.07	0	0.22	-442.59
	ψ(veg+vis),p(fence+trail+curve+vis)	914.67	0.6	0.16	-444.11
	ψ(veg+vis+water),p(fence+trail+curve+vis)	914.67	0.6	0.16	-442.89

	ψ(fence+road+veg+vis),p(fence+trail+curve+vis)	915.08	1.01	0.13	-441.86
	ψ(burnt+road+veg+vis),p(fence+trail+curve+vis)	915.15	1.08	0.13	-441.89
	ψ(road+veg+vis+water),p(fence+trail+curve+vis)	915.46	1.4	0.11	-442.05
	ψ(curve+road+veg+vis),p(fence+trail+curve+vis)	915.72	1.66	0.09	-442.18
Warthog	**Detection models (*p*)**				
	ψ(.),*p*(curve+vis)	1070.53	0	0.57	-531.12
	ψ(.),*p*(curve+vis+trail)	1072.04	1.51	0.27	-530.8
	Space use models (ψ)				
	ψ(road),p(curve+vis)	1068.72	0	0.13	-529.14
	ψ(curve+road),p(curve+vis)	1069.21	0.49	0.1	-528.29
	ψ(burnt+road),p(curve+vis)	1069.38	0.66	0.09	-528.38
	ψ(biomass+road),p(curve+vis)	1069.56	0.84	0.08	-528.46
	ψ(curve),p(curve+vis)	1069.69	0.97	0.08	-529.62
	ψ(fence+road),p(curve+vis)	1069.78	1.06	0.08	-528.58
	ψ(biomass+curve+road),p(curve+vis)	1070.02	1.3	0.07	-527.59
	ψ(preds+road),p(curve+vis)	1070.07	1.35	0.07	-528.72
	ψ(biomass+curve),p(curve+vis)	1070.4	1.68	0.06	-528.88
	ψ(road+vis),p(curve+vis)	1070.44	1.72	0.05	-528.9
	ψ(burnt+curve+road),p(curve+vis)	1070.47	1.75	0.05	-527.81
	ψ(.),*p*(curve+vis)	1070.53	1.81	0.05	-531.12
	ψ(burnt+fence+road),p(curve+vis)	1070.6	1.88	0.05	-527.88
	ψ(biomass+preds+road),p(curve+vis)	1070.69	1.97	0.05	-527.92

Appendix H: The covariate beta coefficient values and their SE, expressed as β (SE). Covariates shown to have a strong influence on a species due to their SE not crossing zero, are indicated in red. Int = intercept, Dist to road = Distance to road, Dist to fence = Distance to fence, Dist to water = Distance to water, Vis = Visibility, Curve = Landscape curvature, Predator = Relative predator abundance, Low-alt veg = Low-altitude vegetation, Med-alt veg = Medium-altitude vegetation, Ridge-top = Ridge-top vegetation and Riverine veg = Riverine vegetation

Common name	Ψ(Int)	Dist to road	Dist to fence	Dist to water	Grass biomass	Vis	Curve	Predator	Fire	Low-alt veg	Med-alt veg	Ridge-top veg	Riverine veg
Cape buffalo	0.31 (0.26)	-0.12 (0.19)		-0.03 (0.11)	0.36 (0.29)	0.87 (0.32)		0.73 (0.31)	-0.06 (0.23)				
Bushbuck	1.8 (0.55)	-0.07 (0.17)	-0.4 (0.31)	-0.02 (0.10)			-0.31 (0.33)	0.91 (0.41)	0.026 (0.16)	-1.85 (0.69)	-1.99 (0.74)	-1.22 (0.86)	-1.04 (0.94)
Common duiker	1.78 (0.55)	-0.02 (0.11)		0.08 (0.2)			-0.07 (0.23)			-0.81 (0.67)	-0.64 (0.74)	-1.24 (0.82)	-3.06 (0.98)
Eland	-0.08 (0.32)	-0.01 (0.08)		-0.69 (0.26)	0.47 (0.40)	0.87 (0.44)		0.15 (0.29)		-0.11 (0.36)	-0.26 (0.59)	0.06 (0.44)	0.32 (0.76)
African elephant	-0.17 (0.61)	-0.65 (0.28)	0.08 (0.23)	-1.12 (0.35)	0.53 (0.27)					0.86 (0.74)	1.07 (0.99)	1.04 (0.98)	8.76 (62.79)
Lichtenstein's hartebeest	-2.52 (0.84)	-0.28 (0.40)	-0.22 (0.41)				0.31 (0.7)		-0.03 (0.23)	2.57 (1.00)	3.48 (1.17)	1.61 (1.14)	1.51 (1.36)
Hippopotamous	-3.32 (2.10)	-0.05 (0.25)	1.36 (2.26)	-3.41 (1.64)	-0.16 (0.59)	-0.03 (0.21)	-0.05 (0.31)						
Impala	-1.86 (0.55)	-0.59 (0.25)		-0.34 (0.32)		0.73 (0.28)		0.15 (0.23)	0.28 (0.51)	2.72 (0.64)	1.68 (0.67)	1.86 (0.8)	1.91 (0.91)
Greater kudu	4.16 (1.59)	0.15 (0.36)	-0.03 (0.16)	-0.86 (0.4)		0.07 (0.26)	-0.07 (0.18)		-1.31 (1.65)				
Nyala	-3.05 (1.03)									2.37 (1.09)	2.16 (1.28)	2.59 (1.24)	4.5 (1.42)
Common reedbuck	-1.29 (0.26)			0.02 (0.10)	0.01 (0.10)		-0.11 (0.29)						
Black rhino	-3.07 (1.02)	-0.03 (0.15)	1.37 (0.48)	-0.08 (0.25)		0.23 (0.33)			0.21 (0.55)	2.19 (1.08)	-0.31 (1.07)	2.08 (1.25)	3.86 (1.65)
Sable antelope	1.82 (0.31)	-0.22 (0.26)	0.15 (0.26)			0.84 (0.36)	-0.15 (0.24)	0.21 (0.37)					
Warthog	3.31 (0.77)	-0.53 (0.4)	-0.04 (0.17)		-0.09 (0.25)	0.02 (0.13)	-0.24 (0.42)	0.06 (0.3)	-0.27 (0.74)				
Waterbuck	-0.47 (0.43)	-0.26 (0.26)	-0.04 (0.15)	-0.08 (0.18)		-0.67 (0.24)	0.03 (0.18)		0.08 (0.28)	1.29 (0.56)	0.71 (0.69)	3.36 (1.18)	1.61 (0.96)
Plains zebra	0.57 (0.47)		0.52 (0.23)	-0.57 (0.24)	0.21 (0.29)	0.62 (0.34)	-0.02 (0.13)	0.22 (0.25)	-0.47 (0.60)				

Appendix I: Space use covariate beta coefficient values with SE, for the variables shown to be strong drivers for species in Majete Wildlife Reserve due to their SE not crossing zero