UNIVERSIDADE EDUARDO MONDLANE

FACULTY OF SCIENCES
DEPARTMENT OF BIOLOGICAL SCIENCES
MASTER'S DEGREE IN BIOLOGY AND CONSERVATION ECOLOGY
MASTER'S DISSERTATION

SPACE AND HABITAT USE BY THE SABLE ANTELOPE (*Hippotragus niger*) IN THE MARROMEU COMPLEX

AGOSTINHO DE NAZARÉ MANGUEZE

Maputo, 2026

EDUARDO MONDLANE UNIVERSITY
FACULTY OF SCIENCES
DEPARTMENT OF BIOLOGICAL SCIENCES
MASTER'S PROGRAM IN BIOLOGY AND CONSERVATION ECOLOGY
MASTER'S DISSERTATION

SPACE AND HABITAT USE BY THE SABLE ANTELOPE (*Hippotragus niger*) IN THE MARROMEU COMPLEX

AGOSTINHO DE NAZARÉ MANGUEZE

Dissertation submitted to the Graduate Program in Biology and Conservation Ecology at Eduardo Mondlane University, as part of the requirements for the degree of master's in biology and Conservation Ecology.

Approved on ______________________, by:

____

Dominique Gonçalves, PhD
(Examiner: - Princeton University and GNP)

____

Prof. Dr. Almeida Guissamulo
(Presidente – DCB-UEM)

____

Prof. Dr. Valério Macandza
(Supervisor –FAEF-UEM)

____

Hugo Mabilana, PhD
(Co-supervisors – DCB-UEM)

Maputo, 2026

ACKNOWLEDGEMENTS

Special thanks go to my supervisor, Prof. Valério Macandza, for all the moral and academic support in making this research possible. My gratitude also extends to Zambeze Delta Conservation – Coutada 11 for providing data and field support for the completion of this work. I am deeply grateful to my co-supervisor, MSc. Faruk Mamugy, for his support in data analysis methods, especially in improving my skills in RStudio and geospatial data analysis techniques.

DEDICATION

To my wife, Victória da Luz Carmen Mateus Mangueze, mother of our beautiful children, for all her support throughout our life journey.

To our beloved children, Ayanda da Luz Agostinho Mangueze, Cibeli da Luz Agostinho Mangueze, and Beyan Agostinho Mangueze, for making me believe that every day there is always a special reason to live.

STATEMENT OF HONOUR

I, Agostinho de Nazaré Mangueze, hereby declare on my honour that the data presented in this work reflect the truth as observed in the field, and that this work has never been submitted, in whole or in part, for the attainment of any academic degree. It represents the result of my own research, and all sources used for scientific support are duly cited in the bibliography.

Maputo, February 2026

____

(Agostinho de Nazaré Mangueze)

ABSTRACT

The dynamics of space use and habitat selection by herbivores are influenced by the spatial and temporal heterogeneity of biotic and abiotic factors in the ecosystem. This study aimed to investigate the annual and seasonal variations in home range, habitat use, and daily movements of the sable antelope (*Hippotragus niger*) in the Marromeu Complex between 2017 and 2021, using GPS-UHF collars. Location data were collected from three adult females over approximately three years. Home range analysis was performed using the Adaptive Local Convex Hull (a-LoCoH) method to calculate the 50% and 95% isopleths, representing the core and total home range areas, respectively. For habitat use, Johnson's (1980) methodology was applied, with field data collection and calculation of selection ratios to identify habitat preferences related to variables such as grass height, shrub and tree cover, and presence or absence of termite mounds. Annual home ranges were relatively small, representing some of the smallest recorded for the species in Africa to date, likely reflecting high resource availability and relatively high population density. While no distinct differences were recorded in seasonal home range sizes, home range overlap was smaller during the dry season, suggesting more patchy distribution of food and water availability. Habitat use varied across years and seasons, with sable antelope generally showing a preference for grassland, flooded grassland, and shrubland vegetation. These spatial behaviour patterns emphasize the importance of considering temporal and spatial variability in resource availability, habitat conditions, and space use for the conservation of the species in the Marromeu Complex.

Keywords: Sable antelope, home range, habitat use, seasonal variations, Marromeu Complex.

RESUMO

A dinâmica do uso do espaço e da selecção de habitat por herbívoros é influenciada pela heterogeneidade espacial e temporal de factores bióticos e abióticos no ecossistema. Este estudo teve como objectivo investigar as variações anuais e sazonais da área de vida (*home range*), do uso do habitat e dos movimentos diários do Palapala (*Hippotragus niger*) no Complexo de Marromeu, entre 2017 e 2021, utilizando colares GPS-UHF. Os dados de localização foram recolhidos a partir de três fêmeas adultas ao longo de aproximadamente três anos. A análise da área de vida foi realizada utilizando o método *Adaptive Local Convex Hull* (a-LoCoH), para o cálculo das isópletas de 50% e 95%, representando, respectivamente, as áreas central e total da área de vida. Para o uso do habitat, aplicou-se a metodologia de Johnson (1980), com recolha de dados de campo e cálculo de rácios de selecção, de modo a identificar preferências de habitat associadas a variáveis como altura do capim, cobertura de arbustos e árvores, e presença ou ausência de termiteiros. As áreas de vida anuais foram relativamente pequenas, representando algumas das menores já registadas para a espécie em África, reflectindo provavelmente a elevada disponibilidade de recursos e a densidade populacional relativamente alta. Embora não tenham sido registadas diferenças significativas no tamanho sazonal das áreas de vida, a sobreposição das áreas de vida foi menor durante a estação seca, sugerindo uma distribuição mais irregular dos recursos alimentares e da água. O uso do habitat variou entre anos e estações, com o Palapala a apresentar, de forma geral, preferência por áreas alagadas e vegetação arbustiva. Estes padrões de comportamento espacial evidenciam a importância de considerar a variabilidade temporal e espacial na disponibilidade de recursos, nas condições do habitat e no uso do espaço para a conservação da espécie no Complexo de Marromeu.

Palavras-chave: Palapala, área de vida, deslocamentos diários, uso do habitat, variações sazonais, Complexo de Marromeu.

LIST OF TABLE

LIST FIGURES

CONTENTS

Chapter I

1. INTRODUCTION

Large herbivores inhabiting African savannas face the challenge of obtaining adequate nutrition in highly seasonal environments, exacerbated by the spatial variation of biophysical factors such as soil type, temperature, precipitation, topography, and availability of surface water (Nathan et al., 2008; Hensman et al., 2014). In these savannas, seasonality generates temporal variation in resource abundance, distribution, and foraging behavior, which manifests across a hierarchy of spatial and temporal scales. This can range from local movements within feeding patches to movements that define daily, seasonal, or annual home ranges (Bailey et al., 1996; Owen-Smith, 2002).

The home range, by definition, represents the specific area normally occupied by an animal to satisfy its needs for food, shelter, safety, and reproduction (Burt, 1943; Jewell, 1966). While habitat use refers to the selection and utilization of particular vegetation types, microhabitats, or landscape features within that area (Hall et al., 1997). Herbivores select habitats based on resource quality, forage availability, cover from predators, and other environmental factors (Fynn et al., 2014; Owen-Smith, 2002). Both home range size and habitat use are determined by the abundance, availability, and distribution of resources, as well as the landscape structure in which these resources are distributed (Jenkins, 1981; Brandt and Cresswell, 2008). Resources may vary within the home range boundaries, causing space to be concentrated in certain core areas, while other parts are visited occasionally (Owen-Smith and Cain, 2007; Owen-Smith, 2008; Macandza et al., 2012). Seasonal changes in temperature and precipitation strongly influence large herbivores through their effects on vegetation, which serves as both a food source and a determinant of habitat characteristics, including visibility, thereby affecting predator avoidance (Owen-Smith & Cain, 2007; Havemann et al., 2022).

Among populations of the same species, habitat productivity determines differences in home range size, while food availability, environmental heterogeneity, and predation influence home range size and its utilization patterns by individuals within a population (Bailey et al., 1996; Belovsky, 1991; McLoughlin and Ferguson, 2000). When certain landscape areas retain essential resources for the population, such as watercourses that sustain green forage, animals may concentrate their use of these smaller spaces during the dry season rather than dispersing when food is widely distributed (Knoop and Owen-Smith, 2006; Smith and Cain, 2007; Macandza and Mamugy, 2022). However, according to optimal foraging theory, as resources become scarce, herbivores respond by expanding their home range (Owen-Smith, 2002; Kotler et al., 2007).

According to movement ecology principles, herbivores may choose to remain in one location or move to a new habitat, varying these movements over different temporal intervals (Nathan et al., 2008). Such movements occur within a hierarchical space-time scale (Bailey et al., 1996; Owen-Smith, 2002). At daily intervals, animal movements may be influenced by resource abundance and distribution (Owen-Smith, 2013; Macandza and Mamugy, 2022). Resource abundance can result in overlapping ranges occupied during different times of the year, while scarcity may induce seasonal shifts in species' home ranges, seeking areas with higher resource density to ensure greater food acquisition rates (Owen-Smith et al., 2010).

Within the home range, habitat and resource use are complex processes involving a trade-off between forage intake and risks such as predation. Therefore, a suitable home range should contain a mix of habitats that provide necessary resources for survival, growth, and reproduction (Mysterud & Ims, 1998).

Many herbivores adapt to seasonal variability in resource availability by utilizing different habitat types (Fynn et al., 2014). In the rainy season, grasses have high nutrient content, providing high-quality forage, whereas in the dry season, leaves are rich in fibber and low in nutritional value (Rueda et al., 2008). To cope with these changes, some herbivores expand their home ranges during the dry season, while others shift their diet from preferential to more generalist feeding strategies (Rueda et al., 2008; Owen-Smith et al., 2012).

With technological advances, it has become more accessible to monitor and document wildlife movements across their home ranges in response to environmental changes. The integration of animal ecology and Global Positioning System (GPS) telemetry has allowed for more precise data on species movements. This technology enables continuous tracking of individuals without direct observer interference, minimizing disturbances to natural animal behavior (Owen-Smith, 2013).

The present study aims to evaluate the home range and habitat use of the sable antelope in the Marromeu Complex during the period 2019–2020, using data obtained from GPS collars fitted on three adult females of the species. Analysis of these data will contribute to a better understanding of sable antelope movement patterns and their response to seasonal environmental variations, supporting more effective conservation and management strategies for the species.

1.1. PROBLEM STATEMENT

Natural habitats are under increasing pressure due to climate change, which influences the availability and distribution of resources for wildlife (Alfeus, 2022). Additionally, these habitats are sensitive to anthropogenic activities that modify their structure, composition, and environmental security, directly affecting the fauna dependent on them (Alfeus, 2022). Environmental dynamics and climate variability may hinder many wild species adaptations to new ecological conditions (Parrini et al., 2016). Such changes can render ecosystems more vulnerable to disturbances, resulting in the reduction or even permanent loss of key species (Parrini et al., 2016).

The sable antelope (*Hippotragus niger*) once had a broad distribution across southern Africa. However, due to various environmental and anthropogenic pressures such as habitat loss, livestock competition, poaching, and human disturbances, its presence has been gradually reduced, currently restricted to conservation areas representing only a small fraction of its historical range (Skinner and Chimimba, 2005). Even within these protected areas, populations continue to decline. In Kruger National Park, South Africa, numbers dropped from 2,240 individuals in 1986 (Harrington et al., 1999; Grant and van der Walt, 2000) to approximately 300 in 2006 (Whyte, 2006). Similarly, in the Malilangwe Wildlife Reserve, Zimbabwe, the population declined from 197 individuals in 1994 to only 62 in 2005 (Goodman, 2009).

On the other hand, some protected areas show opposite trends. In Gorongosa National Park (GNP), Mozambique, the sable antelope population exhibited significant growth, increasing from fewer than 100 individuals in 2000 to over 750 in 2014 (Stalmans et al., 2014), surpassing the historical maximum estimate before the civil war, which was about 700 individuals (Tinley, 1977). Likewise, in Limpopo National Park, the sable antelope population grew from 25 individuals in

2001 to 30 in 2006 (Gaspar, 2011). In Mozambique's Marromeu Complex, numbers rose from ~100 individuals in 1990 to 4,800 in 2023 (Beilfuss et al., 2000; CEAGRE, 2024).

Facing seasonal variations in temperature and precipitation, many herbivores adopt differentiated foraging strategies, using distinct habitat types during rainy and dry seasons (Owen-Smith, 2008; Macandza et al., 2012; Havemann et al., 2022). While some species migrate to access seasonally functional habitats, others adjust their diet to ensure consumption of green forage throughout the year (Weber et al., 2020). For the conservation of these species, understanding how their populations respond to spatial and temporal changes in resource distribution and abundance becomes essential (Weber et al., 2020).

The sable antelope is among the most abundant species in the Marromeu Complex ecosystem, with a population exceeding 4,800 individuals (CEAGRE, 2024). However, to date, no detailed studies have been conducted on the ecology of this species within this ecosystem, particularly regarding its spatiotemporal distribution patterns and resource use. Furthermore, over the past 20 years, few studies on the ecology of the sable antelope have been conducted in Mozambique, notably the works of Gaspar (2011) in Limpopo National Park and Mamugy (2016) in Gorongosa National Park.

Besides being scarce, these studies were short-term and conducted in areas with ecological characteristics different from the extensive floodplain grasslands of the Marromeu Complex. For example, in Limpopo National Park, the study used a GPS collar that functioned for less than four months and tracked only a single herd, limiting understanding of movement patterns and habitat use throughout the year. This knowledge gap reinforces the need for more comprehensive and long-term research to understand the ecology of the sable antelope.

Given the environmental pressures, climate variations, and anthropogenic activities affecting natural habitats, it is essential to understand how the sable antelope responds to these changes in the Marromeu Complex. Thus, this study seeks to determine the extent of the home range and habitat use patterns of the sable antelope in this ecosystem, contributing to effective conservation and management strategies for the species.

1.2 JUSTIFICATION

Herbivores respond to the dynamics of environmental conditions by selecting suitable habitats and adjusting their movements within a home range (Viana et al., 2018). This habitat selection is influenced by multiple ecological factors, including the need to maximize reproductive success, ensure access to high-quality food, and minimize risks associated with predation and competition (Viana et al., 2018; Ofstad et al., 2019). Studying the spatial distribution of species provides essential information on population density, quality and availability of preferred habitats, as well as foraging patterns, which are fundamental for developing management and conservation strategies (Boitani & Fuller, 2000).

Estimating the extent, shape, and structure of species home range is a key element in understanding its behavioural ecology and ecological requirements (Kenward, 2001). Within the framework of conservation ecology, determining the area utilized by a species allows for assessing how its home range is distributed relative to available environmental resources and existing infrastructure within a protected area. Moreover, analysing the spatial distribution of a species can help estimate detection probabilities during population censuses (Ofstad et al., 2019) and identify areas of highest use over time, providing support for efficient population management.

Effective conservation and sustainable management of the sable antelope depend on detailed knowledge of its spatial distribution and the factors influencing habitat selection. The spatial representation of these data can support actions to mitigate population decline, guide the establishment of protection sanctuaries or ecological reserves, implement reintroduction programs in historically occupied areas, and direct future ecological research (Johnson et al., 2004; Rushton et al., 2004).

This study will fill a significant knowledge gap regarding the ecology of the sable antelope in the Marromeu Complex, providing valuable information on species spatiotemporal distribution. The results will contribute to a deeper understanding of habitat use patterns and seasonal movements of the sable antelope, enabling evidence-based recommendations for management and conservation plans.

2. OBJECTIVES

2.1. General Objective

- To evaluate the spatial and habitat use patterns of the sable antelope (*Hippotragus niger*) within the Marromeu Complex.

2.2. Specific Objectives

- To determine the annual and seasonal variations in the extent and location of the sable antelope's home range in the Marromeu Complex.
- To analyse the interannual and seasonal variations in habitat preference of the sable antelope in the Marromeu Complex.

3. HYPOTHESES

The dynamics of space use and habitat selection by herbivores are influenced by the spatial and temporal heterogeneity of biotic and abiotic ecosystem factors (Bailey et al., 1996). Critical factors such as temperature, precipitation, topography, and availability of surface water impose physiological constraints on species, determining the limits of their geographic distribution (Chirima et al., 2013). In this context, it is expected that animals develop space use and habitat selection strategies that minimize the adverse effects of key limiting factors (Bailey et al., 1996).

Based on this premise, the present study proposes the following hypotheses:

- **H_0:** There is no variation in the extent of the sable antelope's home range between the wet season and the dry season.
- **H_1:** During the dry season, the sable antelope expands its home range.
- **H_0:** There is no difference in habitat preference between the wet season and the dry season.
- **H_2:** During the wet season, the sable antelope shows a high preference for few habitats, whereas during the dry season it uses habitats proportionally to their availability in the landscape, without strong preference.

4. LITERATURE REVIEW

4.1. Sable Antelope (Hippotragus niger)

According to Harris (1938):

Domain: Eukaryota,

Kingdom: Animalia,

Phylum: Chordata,

Class: Mammalia,

Order: Artiodactyla,

Family: Bovidae,

Subfamily: Hippotraginae,

Genus: *Hippotragus*,

Species: *niger*.

Fig 1: *Hippotragus níger*

The sable antelope is an ungulate belonging to the family Bovidae and the order Artiodactyla (Estes and King, 2016). It has three subspecies, and in Mozambique, the subspecies *Hippotragus niger niger* occurs, being classified as Least Concern (IUCN/SSC Antelope Specialist Group, 2017). The subspecies *Hippotragus niger kirkii* and *Hippotragus niger roosevelti* are classified by the IUCN as Least Concern, whereas *Hippotragus niger variani*, known as the giant sable antelope, is considered Critically Endangered and is endemic to Angola (Estes and King, 2016).

4.2. Spatial Distribution

The sable antelope is widely distributed across the savannas of East, Central, and Southern Africa (Wilson and Stanley, 1977). Its range extends from southeastern Kenya and eastern Tanzania to Mozambique, Angola, and southern Democratic Republic of Congo, being predominantly associated with miombo woodland areas (Estes, 1993). It can be observed in various conservation units throughout its distribution. Among the locations where it is commonly sighted are Shimba Hills National Reserve in Kenya; Ruaha National Park in Tanzania; Kafue and Mweru-Wantipa National Parks in Zambia; Kazuma National Park in Zimbabwe; Kruger National Park in South Africa; and in the Marromeu Complex, Gorongosa National Park, and Limpopo

National Park in Mozambique (Estes, 1993; Skinner and Chimimba, 2005; Estes, 2012; CEAGRE, 2024).

4.3. Morphological Characteristics

The sable antelope is a medium-sized ungulate, recognized for its imposing and distinctive appearance. Its coat varies from dark brown to black, which is one of the species' most striking features (Skinner and Chimimba, 2005). They are ruminants, with adult females weighing up to approximately 220 kg and males up to 235 kg (Estes, 1991). Adult males are particularly notable for their long and robust horns, curved backward and inward in a crescent shape, which can reach up to 1.5 meters in length in some populations (Estes and King, 2016). Females are generally smaller and have shorter, thinner horns compared to males (Skinner and Chimimba, 2005).

Additionally, coat coloration may vary among individuals and populations, with some variants exhibiting contrasting spots or stripe patterns. The structure of the skull and teeth reflects their herbivorous diet, while their robust musculature is adapted for agile and swift movement across varied terrain (Skinner and Chimimba, 2005).

4.4. Social Structure and Behavior

The sable antelope is a gregarious species. Herds typically consist of between 15 and 25 individuals, although groups of up to 75 females and young are not uncommon (Estes, 1991; Estes, 1997; Skinner and Chimimba, 2005), and a group of approximately 80 individuals has been recorded in Gorongosa National Park (Stalmans et al., 2014). Herds exhibit a well-defined social structure, with a dominant female leading the group in the search for food and water (Skinner and Chimimba, 2005).

Adult males, on the other hand, are highly territorial, defending their areas and driving young males from the breeding group when they reach about 24 months of age (Bothma and van Rooyen, 2005). These young males then form small bachelor groups, staying together until they reach sufficient maturity to establish their own territories (Bothma and van Rooyen, 2005).

4.5. Reproduction

Female sable antelopes typically enter the reproductive cycle between May and July, with the peak mating period occurring in June. The mating season coincides with the dry season, during which subpopulations gather in areas where green forage is still available (Estes, 1993). According to Skinner and Chimimba (2005), adult females give birth to a single offspring after a gestation period of approximately nine months. Births mostly occur at the end of the rainy season, when grass is abundant and green.

In the first few days after birth, the female keeps the calf hidden to protect it from predators (Estes, 1993). During the mating season, males compete intensely for the right to mate with receptive females, displaying aggressive behaviours and dominance rituals. Dominant males establish territories in the most productive grazing areas to attract females, allowing subordinate males to be present only if they show submission and do not attempt to challenge for the females (Estes, 1993).

4.6. Foraging Behavior

The sable antelope primarily feeds on grasses and leaves of shrubs present in its natural habitat. Its diet is adapted to the conditions of wooded savannas and mosaic vegetation areas where the species is frequently found (Harris, 1938). Behavioural studies indicate that the sable antelope exhibits selective feeding behaviour, showing preference for certain types of vegetation, such as grasses and tender foliage, while avoiding other species that may be less nutritious or less palatable. This feeding selectivity can be influenced by factors such as resource availability, seasonality, and the nutritional quality of plants (Hensman, 2012).

Stomach content analyses conducted by Smith and Brown (2010) demonstrated that the composition of the sable antelope's diet varies according to food availability, season, and predation pressure, reflecting its capacity to adapt to environmental changes. The species prefers medium to tall grass pastures, selecting leafy and nutritious grasses. Among the most consumed species are *Panicum maximum*, *Heteropogon contortus*, and *Themeda triandra* (Macandza, 2009).

Studies suggest that the sable antelope has distinct home ranges during the rainy and dry seasons, although some overlap may occur between them (Parrini, 2006). Additionally, the species is considered highly dependent on permanent water sources, requiring daily intake and rarely moving more than 3 km from a water body (Grobler, 1981; Skinner and Chimimba, 2005). However, recent studies have shown that groups of sable antelopes in Kruger National Park travelled to water sources only every 2 to 4 days during the dry season (Rahimi and Owen-Smith, 2007; Cain et al., 2011; Macandza et al., 2012).

4.7. Preferred Habitat of the Sable Antelope

According to White and Abernethy (2009), the sable antelope is often found in wooded savanna areas, favouring habitats that offer a combination of open grasslands and dense vegetation. These environments provide adequate food resources, as well as shelter from predators and protection against adverse climatic conditions.

Recent research highlights the importance of water availability as a key factor influencing the species' habitat selection (Cain et al., 2011). Areas close to permanent water sources, such as rivers or artificial wells, are preferred, especially during the dry season. Furthermore, telemetry and movement monitoring studies indicate that the sable antelope undertakes seasonal movements in search of food and water (Skinner et al., 2005). This flexibility in habitat use allows the species to respond to environmental variations throughout the year, ensuring their survival in dynamic ecosystems.

4.8. Spatial Scales and Hierarchies of Resource Selection

The distribution of large herbivores across the landscape is influenced by various aspects of animal behaviour, ranging from individual food item choices to predator avoidance strategies, which affect habitat selection at multiple ecological levels (Shaefer and Messier, 1995; Bailey et al., 1996). Thus, the use of resources at different scales by individuals and groups may be directly linked to overall population performance.

The natural organization of selection processes described by Johnson (1980) follows a hierarchy in which first-order selection determines the species' geographic distribution, second-order selection defines the home range of individuals or groups, third-order selection involves the use of specific habitat components within that home range, and fourth-order selection pertains to the choice of food items. Higher levels control and restrict lower levels, while the lower levels provide the necessary mechanisms to explain responses at the focal level (Johnson, 1980; Bailey et al., 1996; Boyce, 2006).

4.9. Landscape Selection

The landscape is defined as a heterogeneous mosaic of landforms, vegetation types, and land uses, which can be subdivided into units relevant to large herbivores (Bailey et al., 1996). Abiotic factors, such as distance to water sources and terrain slope, are primary determinants of the large-scale distribution of these animals, acting as constraints within which biotic factors operate (Bailey et al., 1996).

At the landscape level, the arrangement of water sources strongly influences the definition of herbivores' home ranges, making proximity to water an essential criterion for understanding habitat selection (Western, 1975; Gaylard et al., 2003). During the rainy season, surface water is widely distributed across the landscape, accumulating in rivers, springs, temporary ponds, and wetlands (Gaylard et al., 2003). Changes in the distribution and availability of surface water explain the movements of herbivores between distinct regions throughout the seasons.

Studies show that herbivores respond strongly to seasonal variation in water availability and green vegetation, highlighting the influence of this resource in defining home ranges, especially in landscapes where water is scarce and unevenly distributed (Western, 1975; Powell, 2012).

The sable antelope is considered a water-dependent species, with research indicating they typically remain within a radius of 3 km from water sources (Grobler, 1981; Martin, 1983). However, more recent studies have recorded movements exceeding 7 km during periods of scarcity within the core home range (Owen-Smith and Cain, 2007). Furthermore, it has been documented that under water-restricted conditions, these antelopes can reduce the frequency of water consumption to intervals of 2 to 4 days, relying exclusively on perennial sources during the dry season (Owen-Smith and Cain, 2007; Cain et al., 2011). This longer interval between visits to water sources may allow the species to occupy regions of the landscape farther from water, where more common herbivores are less abundant (Cain et al., 2011).

4.10. Home Range Selection

Home range is defined as the area traversed by an animal over a period (i.e., month, season, year, or lifetime) while fulfilling its needs for food, shelter, safety, and reproduction (Burt, 1943; Borger et al., 2006). Hayne (1949) recognized that the biological significance of an animal's home range should include knowledge of the intensity of use in different areas, and that this knowledge changes depending on how the home range boundary is defined. He therefore proposed a method to determine the activity centre based on the number of times an animal visits a given point.

Since the concept of home range was introduced by Burt (1943), its extent has been estimated using various methods (e.g., minimum convex polygons; Local Convex Hull, adaptive kernels, and fixed kernels) (Kernohan et al., 2001). The minimum convex polygon, which connects the outermost points to define the total area of use, is the oldest and has been the most common home range estimator (Kernohan et al., 2001). For this reason, it is still used to make comparisons of home range size between different studies (Kernohan et al., 2001).

4.11. Habitat Use

A habitat is defined as the set of resources and conditions present in an area that allows the occupation, including survival and reproduction, of a given organism, being specific to each species (Hall et al., 1997). The term use refers to the amount of a resource or habitat utilized by a consumer during a fixed period (Johnson, 1980). Habitat and resource use within the home range is a complex process involving trade-offs between forage intake and risks such as predation (Mysterud and Ims, 1998; Garshelis, 2000).

For large herbivores, the structure and composition of plant species define both the habitat and the characteristics of the available food resources (Owen-Smith, 1988; Owen-Smith, 2002). Over time, herbivores may switch between different habitats to obtain these resources (Owen-Smith, 2002). In addition to forage availability, tree density and canopy cover influence habitat use by providing shade and protection against wind (Owen-Smith, 2002). Animals differ in their heat tolerance depending on coat colour and thickness, as well as their ability to regulate body temperature (Owen-Smith, 1982).

The perceived safety of herbivores also affects habitat choice (Shrader et al., 2008). In the presence of predators, herbivores avoid areas with obstacles that hinder escape or reduce visibility.

Ungulates that rely on speed to avoid predation are disadvantaged in dense vegetation, while species that use jumping as an evasion mechanism are more vulnerable in open areas (Owen-Smith, 2002). In this regard, a suitable home range should contain a combination of habitats that offer opportunities for all activities essential to reproduction and survival (Mysterud and Ims, 1998; Garshelis, 2000). For large herbivores, the structure and species composition of vegetation not only define the habitat but also determine essential characteristics, such as the available food resources (Owen-Smith, 2002).

4.12. Factors Influencing Habitat Use and Home Range Size of Large Herbivores

Large herbivores, including the sable antelope (*Hippotragus niger*), are influenced by various factors that determine their spatial use and the size of their home ranges (Owen-Smith, 2002). Understanding these factors is essential for the management and conservation of these species in their natural habitats. One of the main factors affecting the spatial use of large herbivores is the availability of food resources. According to Johnson (1980), the distribution and quality of food play a fundamental role in the habitat selection of these species, so areas with high densities of food resources tend to attract higher concentrations of herbivores (Mysterud and Ims, 1998; Smith and Brown, 2017).

Water availability also plays a crucial role in habitat selection. Areas close to water sources, whether permanent or seasonal, are preferred by herbivores due to their importance for hydration and thermoregulation (Henley, 2005). Research conducted by Smith and Jones (2017) shows that proximity to water sources significantly affects the distribution and movement patterns of these species, especially in arid or semi-arid environments.

Predation and safety-related factors also have an important role in determining the spatial use by herbivores (Shrader et al., 2008). Telemetry studies and behavioural observations, such as those by Brown et al. (2019), highlight the importance of refuge areas and dense vegetation, which help reduce predation risk and increase the survival chances of these species. Brown and Smith (2020) demonstrate that herbivores prefer areas with low predation pressure and easy access to refugees, as this reduces the risk of encounters with predators and favours their safety.

4.13. Influence of Body Size on Habitat Selection

The influence of body size on habitat selection is a key factor in herbivore ecology, with species of different sizes exhibiting distinct preferences regarding environmental characteristics. Large-bodied herbivores tend to select areas with greater availability of food resources and more open environments where they can move more easily and access large quantities of plant biomass (Riginos and Grace, 2008; Smith and Brown, 2017). Comparative analyses conducted by Smith and Brown (2017) highlight the relationship between body size and habitat preferences across various species, showing that anatomical and physiological differences directly influence the capacity to exploit different environments. Smaller species, for example, often utilize denser habitats where they find protection from predators and access to specific food resources that are not available to larger herbivores. Thus, habitat selection reflects a balance between nutritional needs, vulnerability to predation, and the limitations imposed by the morphology of each species (Smith and Brown, 2017).

4.14. Herbivore Movement

Herbivore movement is vital for survival, reproduction, and ecological interactions. Understanding movement patterns and the factors influencing them is fundamental for the management and conservation of these species. Tracking studies have shown that herbivores follow seasonal migration routes in search of food resources and suitable breeding areas, highlighting the influence of environmental variation on their movement patterns (French, 1985). Furthermore, research on movement behaviour, such as that by Johnson (1980), has analysed foraging strategies and daily movement patterns, providing insights into how herbivores optimize the use of available resources in their habitats. Environmental factors such as water availability and vegetation quality significantly influence the movement of these species, determining their trajectories and areas of greater residency. Thus, studying movement patterns is essential for implementing effective wildlife conservation and management strategies.

4.15. Daily Movement Distances

Daily movement distance is an essential component of herbivore movement behaviour, reflecting their ecological needs and survival strategies. Studies conducted by Henley (2005) analysed the average daily movement distances of herbivores in a protected area, highlighting the influence of environmental factors, such as water availability and vegetation quality, on determining these patterns. Owen-Smith and Cain (2007) specifically investigated the movement patterns of the Sable antelope, restricting their analyses to nocturnal locations to exclude excursions to water points, which could shift foraging activity to the morning period on certain days. This approach allowed the exclusion of temporary movements to resting sites or other activities that occur at different times of the day.

Additionally, research on seasonal and interannual variations in movement patterns has provided valuable insights into foraging strategies and adaptive responses of species to environmental changes. Garcia and Brown (2020) also emphasized that predation-related factors can significantly influence the distances herbivores travel daily, with some individuals adjusting their movements to minimize risks.

Understanding the daily movement patterns of large herbivores, including the Sable antelope, is fundamental for wildlife conservation, as it provides information on the ecological and behavioural needs of these species. Research by Smith and Brown (2017) identified key habitat use areas and migration corridors essential for connectivity and population survival. Furthermore, studies on the impacts of environmental changes on these patterns reinforce the importance of maintaining functional habitats and reducing movement barriers, ensuring the long-term viability of large herbivore populations.

4.16. Home Range Estimation Methods

Many methods have been developed to estimate home ranges (Getz and Wilmers, 2004). The Minimum Convex Polygon (MCP), which connects the outermost points to define the total area used, is the oldest method and was for a long time the most widely used home range estimator (Kernohan et al., 2001). However, this method can produce overestimated areas if some points fall outside the usual centres of activity. Because it was the most commonly used method in the past, it is still employed for comparing home range sizes across different studies (Kernohan et al., 2001).

The Kernel method and Local Convex Hull (LoCoH) can determine core use areas through utilization distributions (UDs). A UD evaluates the probability of an animal or group occurring at any given point (Worton, 1989; Kernohan et al., 2001). Kernel methods estimate a probability function corresponding to the UD and are generally expressed as the minimum area encompassing a fixed percentage of the UD area (Kernohan et al., 2001). Typically, 50% isopleths are used to determine core use areas, and 95% isopleths define the outer boundaries of a home range, although these values are arbitrary (Powell, 2000; Owen-Smith and Cain, 2007).

Kernel methods have a significant limitation: the inability to define hard boundaries and discontinuities within home ranges (Millspaugh et al., 2006), although these areas inherently lack fixed borders (Powell, 2000). In contrast, the Local Convex Hull (LoCoH) is a relatively new method that overcomes this limitation by allowing the representation of well-defined boundaries and excluding areas where the species was not recorded (Getz & Wilmers, 2004). Additionally, LoCoH is useful for delineating boundaries between home ranges of different groups (Getz et al., 2007) and for quantifying resource use by associating high-use areas with satellite images of corresponding resolution (Millspaugh et al., 2006; Getz et al., 2007).

The LoCoH method was developed as an alternative to the Kernel method, originally proposed by Worton (1989) and later improved by Getz and Wilmers (2004). It estimates space use distribution based on the nearest local convex curves and is widely recognized as superior to Kernel for delimiting home ranges (Getz et al., 2007).

One of its variants, the adaptive-LoCoH (a-LoCoH), adjusts the radius of the areas encompassing each convex curve, allowing the formation of smaller curves in regions of high use. Isopleths are progressively constructed by aggregating smaller convex areas into larger ones until 95% or 50% of location points are included (Getz et al., 2007). This method is particularly effective in identifying changes, interruptions, gaps, and sharp boundaries within a home range, making it a powerful tool for spatial studies in animal ecology (Getz et al., 2007).

5. Chapter II

Home range estimation and habitat selection of sable antelope (*Hippotragus niger*) in the Marromeu Complex of Mozambique

ABSTRACT

Space use and habitat selection by herbivores are driven by the spatio-temporal heterogeneity of biotic and abiotic factors. This study investigated the spatio-temporal patterns of sable antelope (*Hippotragus niger*) in the Marromeu Complex of central Mozambique, which supports one of the largest populations in Africa. Telemetry-based data were collected from three adult females over approximately three years (2018–2020) to estimate annual and seasonal variations in home range size and habitat use. Annual home ranges were small (11–19 km^2), representing some of the smallest recorded sizes across Africa to date, which is likely a result of high population density and high resource availability. While no distinct differences were recorded in seasonal home range sizes, home range overlap was smaller during the dry season, suggesting more patchy distribution of food and water availability. Habitat use varied across years and seasons, with sable antelope generally showing a preference for grassland, flooded grassland, and shrubland vegetation. These patterns highlight the importance of incorporating spatio-temporal variability into better understanding movement ecology for the species and may contribute toward species-specific conservation strategies in the Marromeu Complex. This study also provides important insights into the spatial dynamics of a recovering post-war sable antelope population, which is of both national and international importance.

Keywords: collaring, LoCoH, movement patterns, seasonal variation, spatial dynamics, ungulate

1. INTRODUCTION

Large herbivores inhabiting African savannas face the continuous challenge of acquiring adequate nutrition to sustain their metabolic functions (Owen-Smith et al., 2010). In these ecosystems, seasonal variability in biophysical factors such as temperature, precipitation, and surface water availability may lead to fluctuations in the abundance and distribution of forage resources (Nathan et al., 2008; Hensman et al., 2014). These seasonal changes influence a hierarchical process of resource selection, operating across multiple spatial scales, from the establishment of home ranges to the selection of food items in feeding stations (Johnson, 1980; Bailey et al., 1996; Owen-Smith, 2002). When vegetation is abundant and water sources are widely distributed, large herbivores tend to reduce their movements, resulting in smaller home ranges, whereas, periods of resource scarcity often compel animals to cover larger distances in search of food and water, leading to expanded home ranges (Johnson, 1980; Owen-Smith, 2002). Such seasonal variations may result in the adoption of different foraging strategies among herbivores and utilization of distinct habitat types during wet and dry seasons (Owen-Smith, 2008; Macandza et al., 2012; Havemann et al., 2022). While certain species migrate to access seasonally functional habitats, others adjust their diet to ensure the consumption of green forage throughout the year (Weeber et al., 2020). Among populations of the same species, habitat productivity largely determines differences in home range size, while food availability, environmental heterogeneity, and predation pressure influence both the size and usage patterns of home ranges within populations (Jenkins, 1981; Bailey et al., 1996; Belovsky, 1991; McLoughlin & Ferguson, 2000).

The sable antelope (*Hippotragus niger*) is a large-bodied (220–250 kg) and emblematic African herbivore, highly valued in both ecotourism and hunting industries (Skinner & Chimimba, 2005). This species occurs widely in the savanna woodlands of southern, eastern, and parts of Central Africa, with an estimated 75,000 individuals remaining in the wild (IUCN/SSC Antelope Specialist Group, 2017). While their overall population trend remains relatively stable due to increasing numbers on private lands, sable populations in some protected areas have drastically declined due to a range of environmental and anthropogenic pressures (Skinner & Chimimba, 2005; IUCN/SSC Antelope Specialist Group, 2017). For example, in South Africa's Kruger National Park, sable antelope numbers fell from 2,240 individuals in 1986 to approximately 300 by 2006 (Harrington et al., 1999; Grant & van der Walt, 2000; Whyte, 2006a), and in Zimbabwe's

Malilangwe Wildlife Reserve, the population decreased from 197 individuals in 1994 to only 62 in 2005 (Goodman, 2009). Conversely, some conservation areas show signs of recovery, such as Mozambique's Gorongosa National Park, where the population grew from fewer than 100 individuals in 2000 to over 300 in 2024 (Stalmans et al., 2014; Stalmans & Peel, 2024), and Limpopo National Park, where numbers remained relatively stable, increasing only slightly from 25 individuals in 2001 to 30 in 2006 (Whyte, 2006b). More notably, within the Marromeu Complex ecosystem, the sable antelope has displayed significant post-war population recovery from 44 individuals in 1990 (Semcer, 2018) to approximately 4,800 in 2023 (CEAGRE, 2024), representing one of the largest remaining populations in Africa.

Quantifying the spatial movements and habitat use of large herbivores can be challenging in expansive unfenced landscapes. However, the use of satellite collars enables remote monitoring of individual- or group-based movements, providing invaluable ecological data for estimating home range size and habitat use (Rahimi & Owen-Smith, 2007; Hensman et al., 2014). The application of these methodological tools, combined with advanced analytical approaches, can effectively inform species management in vast landscapes, which is particularly important for ecologically sensitive species such as the sable antelope. This species is ecologically sensitive due to its reliance on high-quality savanna habitats, selective grazing requirements, low tolerance to disturbance and habitat fragmentation (Owen-Smith & Cain, 2007; Hensman et al., 2014; Crosmary et al., 2015).

Despite major population declines in several protected areas, and their ecological sensitivity, the species remains poorly studied across their range. In Mozambique, ecological studies on sable antelope are also scarce, with the exceptions of Limpopo National Park (Gaspar, 2011) and Gorongosa National Park (Mamugy, 2016). These studies observed that sable antelope prefer habitat patches with 40–60 % vegetation cover, grass of intermediate palatability, intermediate trees, and the presence of termite mounds. It was also noted that during the dry season, herds adjust their space use by traveling long distances to access permanent water sources. However, these two areas differ ecologically from the Marromeu Complex in central Mozambique, where the predominant habitat is a floodplain grassland with year-round availability of green forage and water, adjacent to miombo woodlands. To date, no detailed studies have been conducted on the spatial ecology of sable antelope in the Marromeu Complex, despite supporting one of the largest populations in the country.

Despite major population declines in several protected areas and their ecological sensitivity, sable antelope remain poorly studied across their range. In Mozambique, ecological research on the species is limited, with notable exceptions in Limpopo National Park (Gaspar, 2011) and Gorongosa National Park (Mamugy, 2016). These studies found that sable antelope prefer habitat patches with 40–60 % vegetation cover, grass of intermediate palatability, intermediate trees, and the presence of termite mounds. During the dry season, herds adjust their space use by traveling long distances to access permanent water sources. While Limpopo differs ecologically from the Marromeu Complex, Gorongosa shares similar habitat features, including floodplain grasslands and miombo woodlands. To date, no detailed studies have been conducted on the spatial ecology of sable antelope in the Marromeu Complex, despite it supporting one of the largest populations in the country.

This study was designed to investigate sable space and habitat use in the Marromeu Complex. We hypothesize that, during the dry season, the sable antelope expands its home range, exhibiting greater extent and reduced overlap, as it travels longer distances to access water and forage that are more patchily distributed.

2. METHODS

2.1. Study Area

The Marromeu Complex, located in the Sofala Province of central Mozambique, forms the southern half of the Zambezi Delta – a Wetland of International Importance designated under the Ramsar Convention (Figure 1) (Impacto, 2012). This landscape covers an area of 10,544 km², and includes seven officially recognized conservation areas: the Marromeu National Reserve, four hunting concessions (Coutadas 10, 11, 12, and 14), and the Nhampacué and Inhamitanga Forest Reserves. The climate is tropical, with a dry season (May to October) and a wet season (November to April), and a mean annual rainfall of 1,000 1,400 mm (Beilfuss et al., 2000). This landscape supports a diversity of vegetation types ranging from miombo woodland and sand forest in the marginally higher lying west to floodplain grasslands, papyrus swamp, and palm savanna in the low-lying east (Beilfuss et al., 2000). The most abundant herbivores include African buffalo (*Syncerus caffer*), waterbuck (*Kobus ellipsiprymnus*), common reedbuck (*Redunca redunca*), and sable antelope, as well as both resident and reintroduced large carnivores (CEAGRE, 2024; Briers-Louw et al., 2024, 2025).

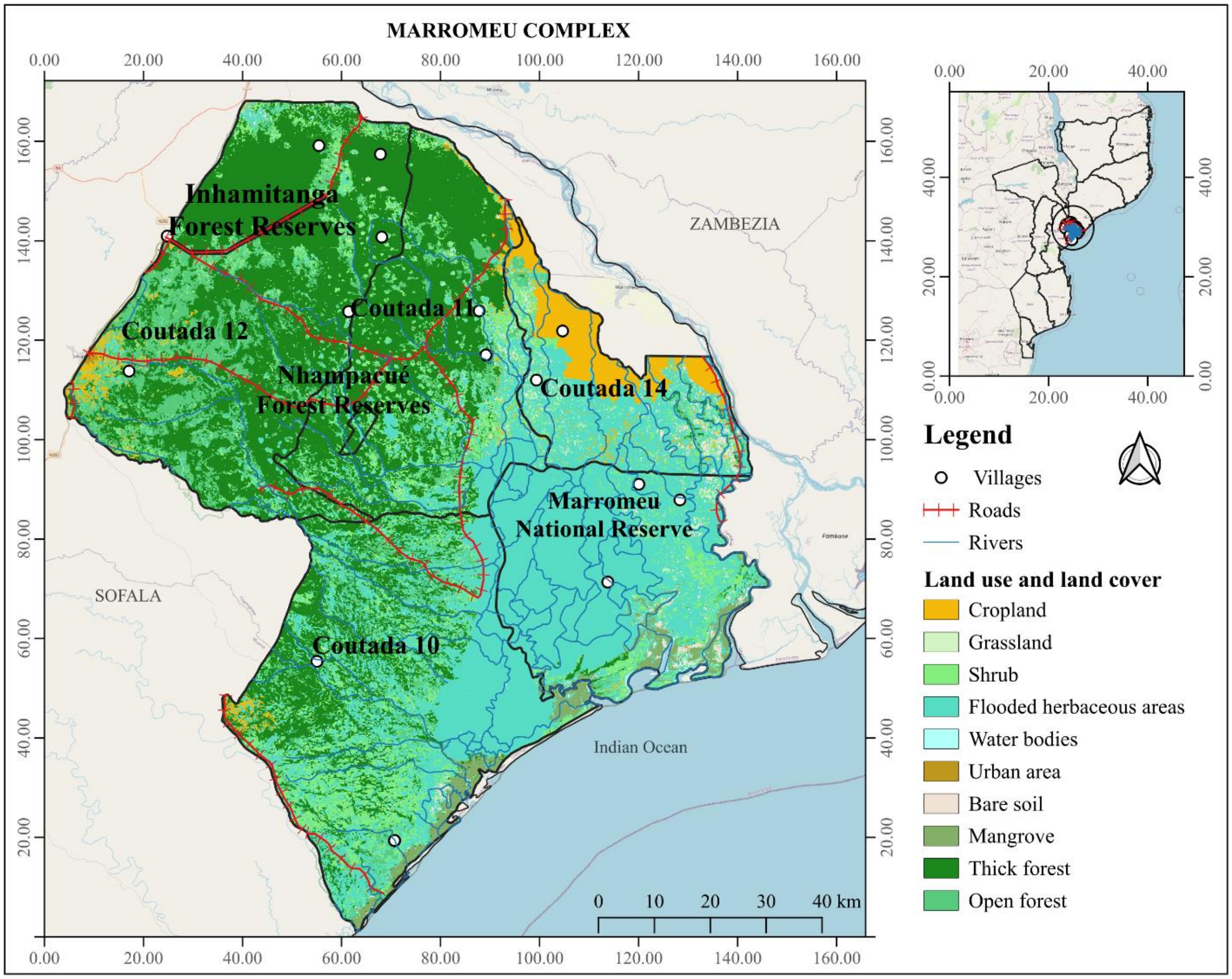

Fig 1: Location of the seven conservation areas and land use/land cover in the Marromeu Complex of central Mozambique. Source: FNDS, 2016.

3. DATA COLLECTION

To investigate space use patterns of sable antelope in the Marromeu Complex, herds were located using a helicopter, and an adult female from each herd was selected for captured. In total, three individuals were chemically immobilised by a licensed veterinarian on the same day, with herds located less than 2 km apart. Animals were fitted with GPS satellite collars, equipped with VHF transmitters from Africa Wildlife Tracking, by Zambeze Delta Safaris to monitor movements (http://www.awt.co.za). Each collared female was considered a proxy for her herd, hereafter referred to as Herds 1–3 throughout this study. Each female led a herd of 15–20 individuals. Ethical approval was granted by the Institutional Animal Care and Use Committee (IACUC #23-010), supported by a research permit from the National Administration of Conservation Areas (ANAC RP# 06/10/23). The collars transmitted GPS coordinates of herd locations via satellite uplink from December 2017 to January 2021.

GPS locations were recorded at six-hour intervals (2:00, 8:00, 14:00, and 20:00). Following Macandza et al. (2012), the 2:00 and 14:00 fixes corresponded broadly to resting periods, whereas the 8:00 and 20:00 fixes aligned with typical morning and early nocturnal foraging activity in sable antelope. Although foraging intensity may shift across seasons, these time classes provide a relatively consistent representation of active compared to inactive periods and were used primarily to ensure even temporal coverage rather than to infer fine-scale behavioural states.

4. DATA PROCESSING

To balance data completeness against analytical rigour, the dataset was trimmed to include only periods that provided complete seasonal coverage and consistent sampling effort across individuals. This resulted in a revised dataset spanning May 2018 to October 2020. The total number of GPS locations recorded per herd was: Herd 1 (n = 3,319), Herd 2 (n = 3,568), and Herd 3 (n = 3,588), with seasonal sample sizes as follows: Herd 1 (731, 707, 578, 572, 731), Herd 2 (720, 686, 723, 703, 736), and Herd 3 (730, 699, 710, 715, 734) in order: dry season 2018, wet season 2018–2019, dry season 2019, wet season 2019–2020, and dry season 2020.

GPS locations were intersected with the national vegetation map from the *Fundo Nacional de Desenvolvimento Sustentável* (FNDS, 2016; Figure 1), that used 10 m resolution Sentinel 2 imagery from ESA remote sensing data processed within Google Earth Engine. The original FNDS map contained 17 vegetation strata, but these were modified for this study. Several of the vegetation strata did not occur within the landscape and were thus excluded. The remaining strata were consolidated into broader, ecologically meaningful habitat classes to improve clarity and facilitate comparability with other studies. Specifically, closed evergreen and closed deciduous forest were merged into a single "closed forest" class; open evergreen and open deciduous forest into "open forest"; and grassland, bare soil, and crops into "grassland" (crops and bare soil occurred only as small, fractional patches in wildlife area and likely reflected abandoned settlements or remote-sensing misclassification). Both shrub and flooded herbaceous areas were retained but renamed to "shrubland" and "flooded grassland" respectively. This reclassification followed standard practice for simplifying overly detailed vegetation maps while maintaining ecological relevance.

To assess habitat preference, a random sample representing 1% of GPS locations per individual during putative foraging periods (08:00 and 20:00; see Macandza et al., 2012) was selected using a random number generator. Field-based observations were conducted at each of these 123 sampling locations, recording habitat characteristics within a 25 m radius following the methodology of Morris (1987). These variables included: (1) pasture quality, based on the nutritional value of predominant grass species and classified as low, intermediate, or high according to van Oudtshoorn (1999); (2) predominant herbaceous vegetation height, excluding emergent culms, categorised as: short (≤10 cm), medium (20–40 cm), tall (40–80 cm), and very tall (>80 cm); (3) canopy cover of trees (>2.5 m) and shrubs (<2.5 m), estimated as: 0%, 1–10%, 11–25%, and >26%; (4) tree canopy height, categorised as short (≤5 m), medium (6–10 m), or tall (>10 m); and (5) presence or absence of termite mounds. The accuracy of the revised map was also validated using ground-truthing data from these sampling points, will all locations representative of habitat reclassifications.

5. DATA ANALYSIS

Home ranges were estimated using the *tlocoh* package (Lyons et al., 2013) in RStudio (RStudio Team, 2024). The adaptive local convex hull (a-LoCoH) method was used to generate 95% (home range) and 50% (core use area) isopleths (Getz et al., 2007; Mamugy, 2016). Following Getz et al. (2007), the adaptive parameter (a) was set to the maximum nearest-neighbour distance between any two locations for each individual, ensuring that hulls were large enough to connect all locations without imposing excessive smoothing. Since the adaptive approach adjusts hull construction based on local point density, areas with dense fixes produce tighter, more detailed hulls, while sparser areas allow hulls to expand only as needed to connect points (Getz et al., 2007). This method improves spatial resolution by refining home range boundaries with increasing data, with the resulting hulls accurately reflecting used areas, while leaving genuine gaps where no fixes occurred. Consequently, a-LoCoH remains sensitive to fine-scale movement boundaries (e.g., fence or water bodies) and avoids inflating home range estimates (Getz & Wilmers, 2004; Getz et al., 2007). All home range areas were projected to the UTM Zone 36S coordinate system in QGIS v3.28.4 (QGIS Development Team, 2023), where their extents were calculated. For comparative context, ware extracted published sable antelope home range estimates from studies across Africa and used them for qualitative range-wide comparison.

Habitat selection was investigated at two of Johnson's (1980) hierarchical scales: (i) selection of home range within the landscape (second-order selection), and (ii) selection of foraging areas within the home range (third-order selection). For second-order selection, habitat use was quantified by overlaying the 95% and 50% a-LoCoH derived isopleths on the vegetation map and calculating the proportional area of each habitat type within these polygons. Habitat availability was estimated by overlaying 100% minimum convex polygons (MCPs) for each individual on the vegetation map and calculating the proportional area of each habitat type within the MCPs (Boyce, 2006). MCPs were used because they represent the maximum potential area accessible to an animal without excluding internal space. Habitat preference was then calculated as the ratio of relative use (within the 95% and 50% a-LoCoH ranges) by relative availability (within the 100% MCP ranges), where values >1 indicated preference, and <1 indicated avoidance (Manly et al., 2002). At the third-order selection level, habitat variables at 123 points within foraging areas were sampled, including grass height, tree height and cover, pasture quality, and presence of termite mounds (van Oudtshoorn, 1999). Each point was assigned to either the 95% or 50% home range isopleth, and the proportion of points failing within each habitat type was calculated for both isopleths. Binomial confidence intervals were computed in JavaStat (Boitani & Fuller, 2000) to assess differences in habitat variables between the 95% and 50% home ranges.

6. RESULTS

6.1. Home range estimation

Annual home range (95% isopleth) estimates of the three monitored herd (i.e., between 2018 and 2020) were small, ranging from 11.4 to 19.7 km2 (Fig. 2; Table 1). herd 1's home range varied between approximately 13 and 20 km², showing notable reductions and low overlap between years (46%), indicating greater range shifts. herd 2's range increased slightly from about 11 to 14 km², with moderate overlap (59%), while herd 3 maintained consistent home range sizes around 13 to 14 km², with relatively high overlap (74%), demonstrating high spatial fidelity. Core activity areas followed similar patterns, both in terms of size and overlap, with herd 3 showing the greatest size consistency, with a core area size of 3.5 km² across years and overlap (68%), and herd 1 used 3.0–5.4 km², most pronounced shift in home range location (only 16% of home range overlap) over the study period.

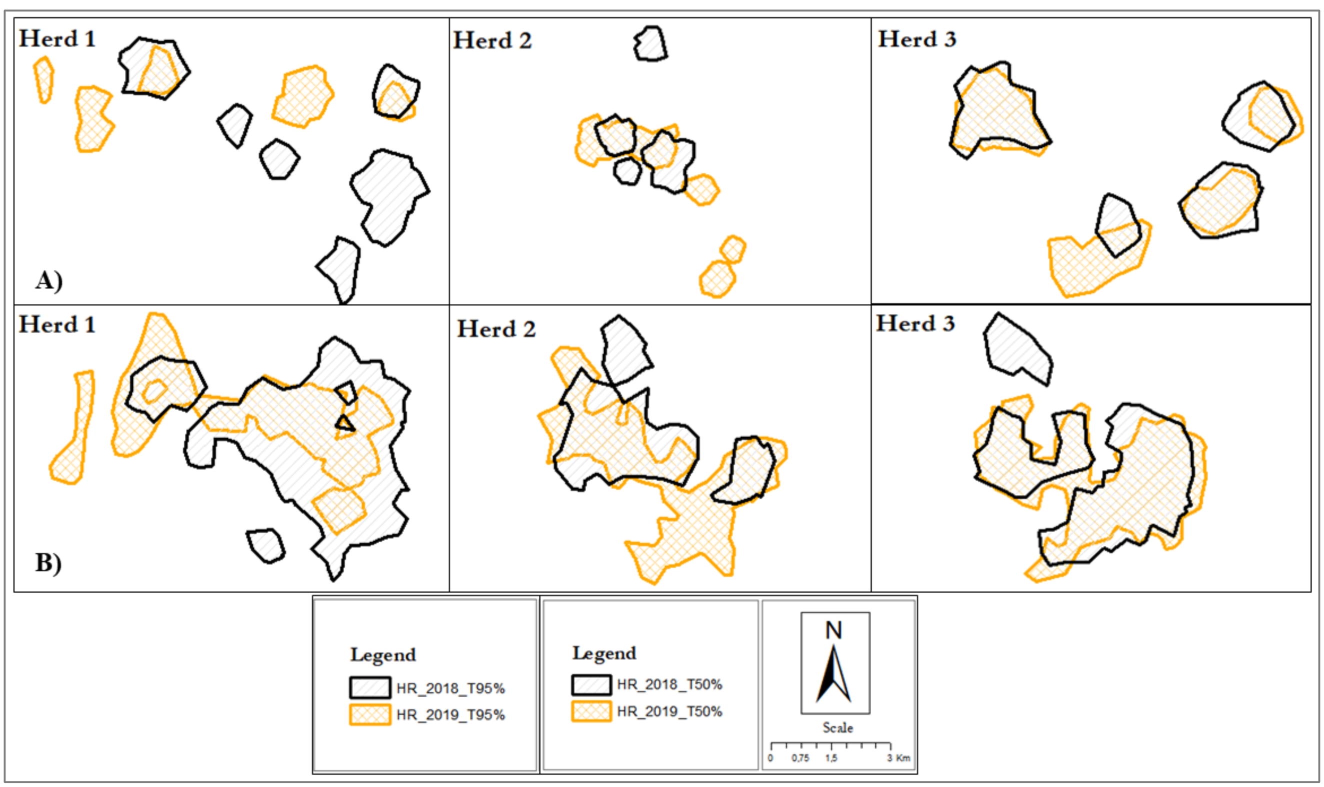

Fig 2: Home range estimation for the three herd with annual home ranges based on 95% (A) and 50% (B) isopleths. Estimates for 2018 and 2019 are indicated in black and gold respectively.

Table 1: Annual and seasonal sable antelope home range (HR) size (95% and 50% isopleths) and individual HR overlap coverage (km2) and percentage (%).

Spatial metric	Time period	95% isopleth			50% isopleth		
		Herd 1	Herd 2	Herd 3	Herd 1	Herd 2	Herd 3
HR size (km^2)	Annual (2018–2019)	19.74	11.42	13.81	5.41	2.45	3.46
	Dry 2018	16.02	9.46	11.57	3.68	2.03	2.45
	Wet 2019	13.25	7.52	9.43	3.21	2.01	1.70
	Annual (2019–2020)	13.15	13.88	13.08	3.03	3.04	3.47
	Dry 2019	4.16	7.27	7.99	1.41	1.73	1.90
	Wet 2020	10.37	9.43	10.62	2.71	1.93	2.68
	Dry 2020	7.58	4.03	7.43	1.62	0.52	1.60
HR overlap (km^2)	Annual	9.07	6.76	10.18	0.86	1.05	2.36
	Dry	6.77	1.91	4.82	N/A	0.49	0.53
	Wet	6.43	4.72	6.70	0.40	0.82	N/A
HR overlap (%)	Annual	45.98	59.22	73.76	15.94	43.10	68.18
	Dry	42.26	20.18	41.67	N/A	24.37	21.48
	Wet	48.55	62.80	71.07	12.47	40.76	N/A

Herd displayed relatively small seasonal home range sizes (95% isopleth), with low to moderate variability among individuals, ranging from 4.0 to 16.0 km² (Fig. 3; Table 1). Overall, there was no statistically significant difference in home range size between wet and dry seasons ($t = 3.84$, df = 2, $P = 0.06$). However, individual patterns varied: herd 1 showed the greatest fluctuation, with a notable decrease in home range size from 16.1 km² in the 2018 dry season to 4.2 km² in the 2019 dry season. herd 2's home range progressively decreased from 9.5 km² in 2018 to 4.0 km² in 2020. In contrast, herd 3 maintained relatively stable seasonal home ranges, varying only slightly from 11.8 km² (2018 dry season) to 7.4 km² (2020 dry season). Overall, home range size tended to decrease slightly from dry to wet seasons, though this trend was not statistically significant. Seasonal home range overlap ranged from 20–71% among individuals, with higher overlap recorded during the wet season compared to the dry season ($\chi^2 = 9.28$, df = 2, $P < 0.05$). Core area (50% isopleth) sizes followed similar trends, ranging from 0.5 to 3.7 km² among individuals. Overall, core area overlap was low (12–41%), though it could not be estimated for all individuals.

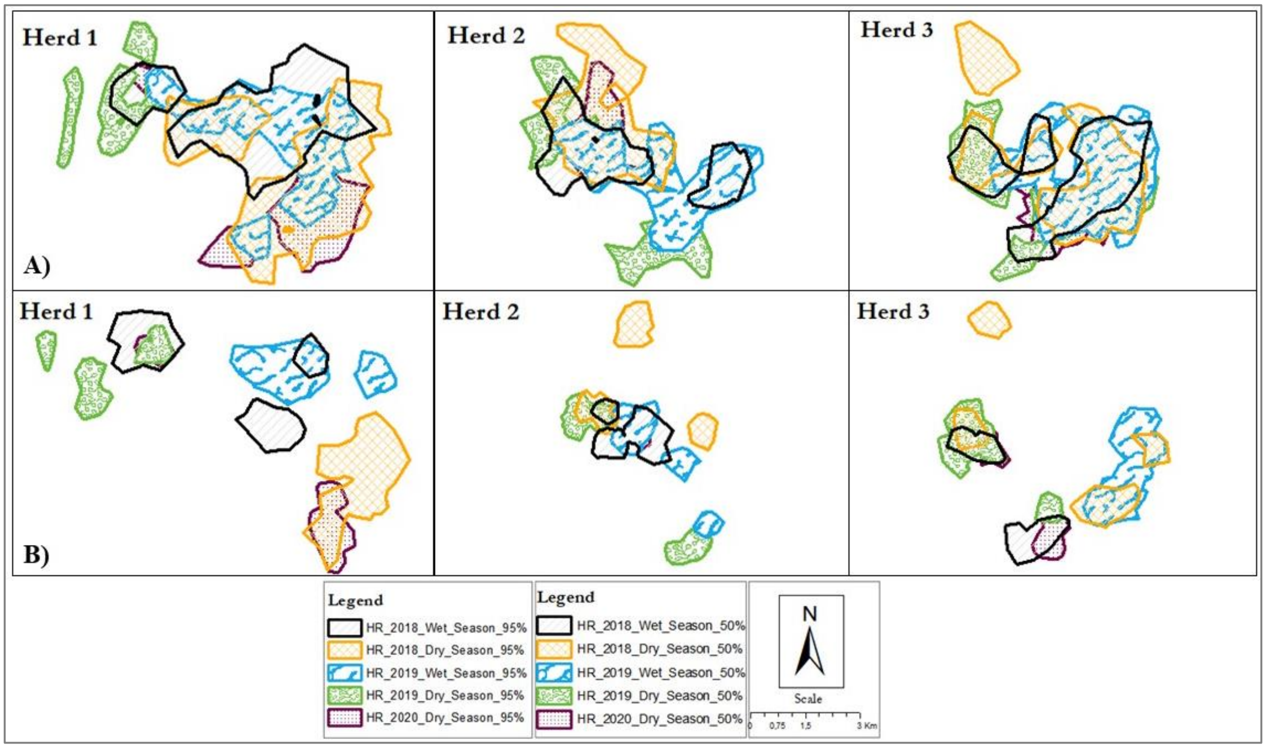

Fig 3: Seasonal variation in the home range size based on 95% (A) and 50% (B) isopleths of the three female sable antelope in the Marromeu Complex.

6.2. Habitat preference

Herd 1 consistently preferred flooded grassland, grassland, and shrubland across both the 95% home range and 50% core areas, while open and closed forest were generally avoided (Fig. 4, Table S2 and S3). Herd 2 primarily selected open forest and shrubland but showed similar use of all habitat types in 2019, indicating no clear preference that year. Notably, in 2018, shrubland was not preferred within the 50% core area. Herd 3 exhibited a pattern like herd 1, with preference for flooded grassland, grassland, and shrubland. Closed forests were generally avoided by all individuals. Overall, herd showed similar habitat preferences between wet and dry seasons, with no strong evidence of seasonal shifts in selection patterns.

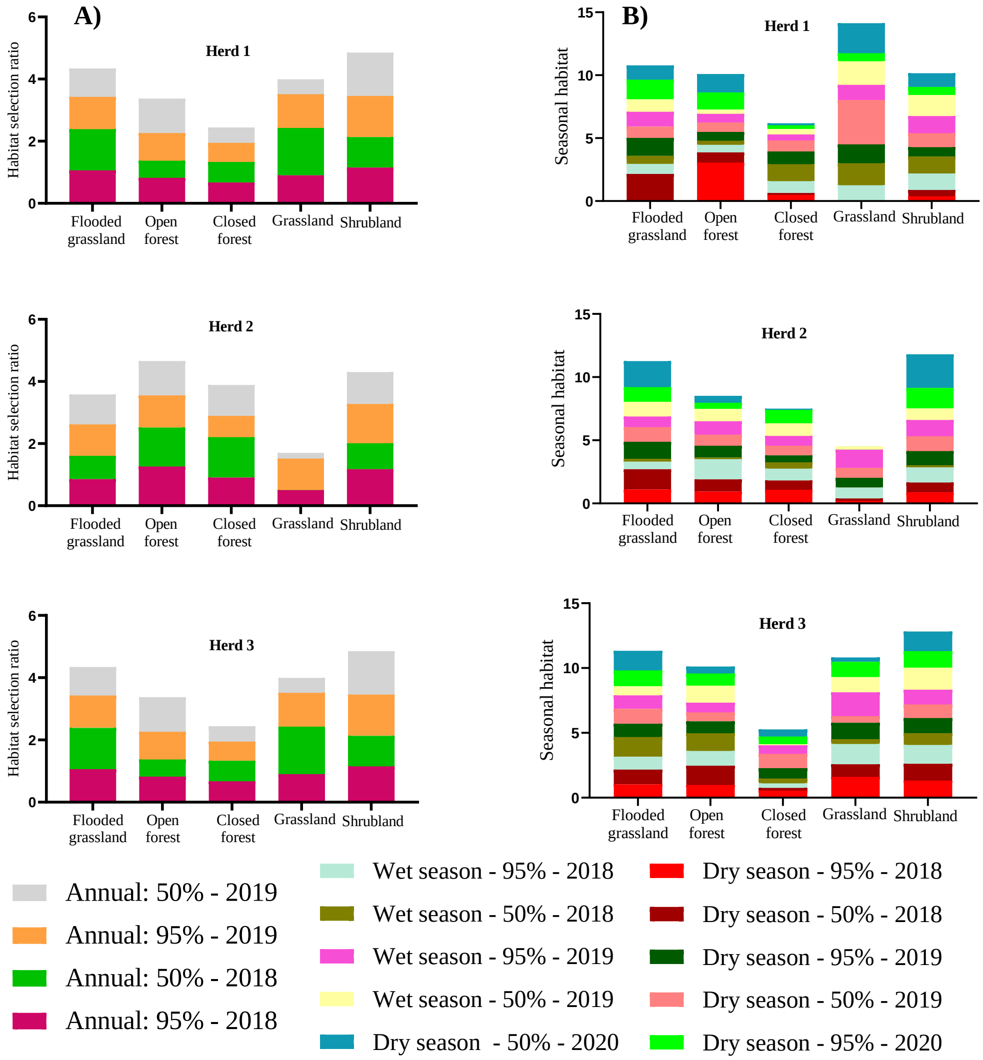

Fig 4: Habitat selection ratios for collared sable antelope between 2018 and 2019 (A); Seasonal habitat selection ratios for collared sable antelope between 2018 and 2020 (B).

6.3. Characteristics of foraging areas (microhabitats)

Intermediate-quality pasture areas dominated by *Loudetia simplex*, *Panicum coloratum*, *Cynodon* sp., and *Sporobolus africanus* were primarily foraged by herds within both the 95% and 50% home range areas. In these areas, herds preferred grasses of intermediate quality and height (40–80 cm), open habitats with less than 10% tree and shrub cover, and no presence of termite mounds.

7. DISCUSSION

Quantifying spatial dynamics of large herbivores is crucial for improving our understanding of their ecology and conservation (Macandza et al., 2012; Owen-Smith et al., 2012), particularly where populations are recovering following disturbance. This study utilized satellite collar technology to provide the first robust estimates of space use and habitat selection for sable antelope in the Marromeu Complex – an ecologically significant landscape harbouring the second largest population in the country. Our findings represent some of the smallest spatial movements of sable antelope across their range, with their habitat preference suggesting occupation of distinct ecological niches which may allow the species to thrive in the landscape. This study not only highlights key ecological traits of a recovering stronghold sable antelope population but also draws attention to the ecosystem productivity and effective long-term conservation efforts in this post-war landscape.

Estimated home range sizes in this study (11–20 km^2) were among the smallest recorded for the species to date. For instance, in Kruger National Park, annual sable antelope home range sizes were at least three times larger, ranging from 65–118 km^2 (Owen-Smith & Cain, 2007). Interestingly, in relatively similar ecosystems, sable antelope home range estimates were substantially lower in the Marromeu Complex compared to nearby Gorongosa National Park (99–182 km^2; Mamugy, 2016), and comparably lower than those found in the Okavango Delta of Botswana (21–31 km^2; Hensman et al., 2014). Our findings were most comparable to those found in Kgaswane Mountain Reserve, South Africa (15.6–19.1 km^2; Parrini 2006).

Home range size is influenced by both population density and the availability of resources. Higher population densities can lead to smaller ranges because individuals or herds share space and resources, whereas lower densities often necessitate larger ranges to satisfy nutritional and reproductive needs. Similarly, abundant and evenly distributed forage allows animals to meet their dietary requirements within smaller areas, while sparse or patchily distributed resources require longer movements, expanding the home range (Kjellander et al., 2004; van Beest et al., 2011; Augustsson et al., 2024; Balluffi-Fry et al., 2025). Both these factors could explain the small home ranges recorded in this study. In the Marromeu Complex, the relatively small home ranges recorded likely reflect a combination of moderate population density and highly productive floodplain grasslands providing year-round green forage (Beilfuss et al., 2000). The moderate levels of seasonal home range overlap are consistent with previous findings (Hensman et al., 2014; Mamugy, 2016), while the lower overlap observed during the dry season likely reflects a patchier distribution of resources, a pattern also reported in other studies (e.g., Owen-Smith & Martin, 2015).

During the dry season, sable antelope preferred flooded grassland, grassland, and shrubland, although this preference shifted to grassland, open forest, and shrubland during the wet season. The strong association with flooded grassland during the dry season may be related to dependency on regular access to drinking water and green pasture (Estes & Estes, 1974; Grobler, 1981; Skinner & Chimimba, 2005; Chirima et al., 2013). In the wet season, herds generally moved to slightly higher elevations and more diverse areas, including open forest, which might offer better grazing quality and diversity (Angassa & Baars, 2000; Sutton et al., 2002), as well as shelter from thermal extremes (Owen-Smith & Traill, 2017). In Kruger National Park, Henley (2005) observed that sable antelope prefer ecotones and areas interspersed with shrubs, due to their provision of diverse food resources, shelter, and protection from predators. Sable antelope showed preference to forage in areas with intermediate-quality grass species, and >40 cm of grass height, consistent for both home range and core areas. This coincided with a previous study where sable antelope showed strong preference for tall grasses, such as *Hyperthelia dissoluta*, at the end of dry season when these grasses maintain a high proportion of green leaves, serving as a valuable food source during resource scarcity (Hensman, 2012). The low cover of trees and shrubs (1–10%) and preference for small trees (1–5 m) support the theory that sable antelope select habitats which provide food access and protection from predators. Similar patterns of habitat selection have also been reported by other studies (Parrini, 2006; Gaspar, 2011; Mamugy, 2016), where sable antelope displayed preference for mixed forests with low shrub density and highly palatable grasses such as *Panicum maximum*, *Heteropogon contortus*, and *Themeda triandra*. The seasonal variation in habitat preference observed in our study suggests that sable antelope may be adopting a flexible habitat occupation strategy, balancing food availability, proximity to water, thermal protection, and even predation risks.

Large herbivore spatio-temporal patterns may be influenced by various environmental drivers (Hensman et al., 2014; Owen-Smith & Cain, 2007). Optimal foraging theory predicts that when resources are scarce or widely dispersed, animals tend to occupy larger areas, while in situations with greater abundance or concentration of resources, annual home ranges tend to be smaller (Harestad & Bunnell, 1979; Owen-Smith, 2002; Kotler et al., 2007). All three herds exhibited relatively small and consistent home ranges during the study period, with no major seasonal differences, suggesting sufficient forage availability throughout the year (van Beest et al., 2011). However, lower seasonal home range overlap recorded during the dry season suggests that seasonal changes may have minor influences on resource availability for sable antelope in the landscape. During the wet season, forage and surface water is widely available, while during the dry season, suitable forage and surface water become patchy across the landscape. Fire could also influence animal movement patterns and resource availability (Owen-Smith & Cain, 2007; Owen-Smith & Martin, 2015).

In the Marromeu Complex, post-wet season mosaic burns are typically used as a management tool to promote green regrowth and reduce the likelihood of intense, large-scale fires during the peak dry season. While sable antelope are known to respond spatially to fire, such as concentrating grazing in burnt areas with green growth (Parrini & Owen-Smith, 2009), this was not analysed in the present study, we encourage future studies to investigate the influence of fire on antelope spatial ecology. Another potential driver is rainfall. Precipitation during the 2019–2020 wet season was substantially lower (100–120 mm) than the region's characteristic annual average of 265 mm (INAM, 2020). Such below average rainfall may affect the regeneration of herbaceous vegetation and thus spatial heterogeneity in resource availability, which could cause an adaptive response to increased resource clumping in specific zones such as home range size reduction (Dunstone & Gorman, 1998; Makhado et al., 2020).

Furthermore, predation could also influence sable antelope spatial dynamics (Mamugy, 2016). While large carnivore densities in the Complex were relatively low during the study period (Briers-Louw et al., 2024, 2025), there has been no comprehensive predator-prey study to date. Therefore, we encourage future studies to investigate the potential effect of predators and other environmental factors such as fire on antelope spatio-temporal dynamics.

8. CONCLUSION

This study revealed that the home range and habitat use of the sable antelope in the Marromeu Complex are relatively consistent, but seasonally dynamic as influenced by resource availability. This adaptive behaviour likely enables the species to thrive and occupy distinct ecological niches across this floodplain-forest mosaic landscape. Furthermore, this study highlights the importance of the floodplains, which provide a relatively stable source of water and green pasture, essential for their survival. The Marromeu population has increased from ~100 individuals in 1990 to over 4,800 in 2023, representing ~6% of the global population (Beilfuss et al., 2010; CEAGRE, 2024; IUCN/SSC Antelope Specialist Group, 2017). Long-term spatial and demographic monitoring is critical for guiding conservation practice, including habitat protection, management of seasonal movements, and anti-poaching efforts, as well as informing policy decisions regarding floodplain conservation and sustainable land use.

9. LIMITATIONS

The main limitations of this study include the absence of an updated and comprehensive vegetation map covering the entire Marromeu Complex, which hindered detailed analysis of seasonal variations in habitat use by the Sable antelope. Although the data collected over three years are relevant, the lack of complete and up-to-date vegetation coverage of the Marromeu Complex may have limited the precision of assessments related to the structure and distribution of habitats across the landscape.

Furthermore, the short period of field data validation, especially during the dry season of 2020, may have limited the representativeness of observations and made it difficult to identify more consistent ecological patterns. The failure of the GPS collars during this critical period resulted in the loss of essential data on movement and habitat use, compromising the analysis of behavior and displacement during times of resource scarcity.

10. RECOMMENDATIONS

- Investigate the role of predation risk and competition in habitat selection by the Sable antelope, analysing the influence of the presence of large predators and other herbivores on the spatial occupation of the species.
- Conduct studies on feeding ecology and nutrition, including chemical composition analysis of the grasses and shrubs consumed, to deepen knowledge about feeding preferences and complement resource selection levels.
- Update and expand the vegetation maps of the Marromeu Complex, focusing on full area coverage and seasonal variation in habitat structure, facilitating more precise analyses of space use by this and other species.
- Implement controlled prescribed burns with the aim of maintaining pasture in early growth stages (low to medium height), increasing the nutritional value of grass in preferred foraging areas.
- Strengthen ecological monitoring with long-term data, using more durable GPS collars and remote sensing to capture interannual variations and environmental changes affecting movement and habitat use.

11. REFERENCES

- Alfeus, M. (2022). *An assessment of trends in population abundance and spatial distribution of roan antelope (Hippotragus equinus) and sable antelope (Hippotragus niger) in the greater Waterberg Plateau complex, north-central Namibia*. (M.Sc. thesis)., The University of Namibia, Windhoek, Namibia.
- Angassa, A., & Baars, R. M. T. (2000). Ecological condition of encroached and non-encroached rangelands in Borana, Ethiopia. *African Journal of Ecology*, 38, 321–328.
- Augustsson, E., Kim, H., Andrén, H., Graf, L., Kjellander, P., Widgren, S., Månsson, J., Malmsten, J., Thurfjell, H. (2024). Density-dependent dinner: wild boar overuse agricultural land at high density. *European Journal of Wildlife Research*, 70, 15.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management, 49*, 386–400. https://doi.org/10.2307/4002919
- Beilfuss, R. D., Dutton, P., & Moore, D. (2000). Land cover and land use changes in the Zambezi Delta. In J. Timberlake (Ed.), Biodiversity of the Zambezi Basin wetlands. Vol. 3: Land use change and human impacts (pp. 31–106). Biodiversity Foundation for Africa, Bulawayo and The Zambezi Society.
- Belovsky, G. E. (1991). Optimal foraging and community structure: Implications for herbivore population dynamics. *Journal of Animal Ecology, 48*, 1-10.
- Boitani, L., & Fuller, T. K. (2000). *Research techniques in animal ecology: Controversies and consequences.* Columbia University Press.
- Bothma, J. du P., & van Rooyen, N. (2005). *Ecology of desert organisms.* Springer.
- Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions, 20*, 269–276.
- Brandt, M. J., & Cresswell, W. (2008). Breeding behaviour, home range and habitat selection in Rock Firefinches *Lagonosticta sanguinodorsalis* in the wet and dry season in central Nigeria. *Ibis*, 150(3), 495-507.
- Briers-Louw, W. D., Kendon, K., Rogan, M. S., Leslie, A. J., Almeida, A., Gaynor, D., & Naude, V. N. (2024). Anthropogenic pressure limits the recovery of a postwar leopard population in central Mozambique. *Conservation Science and Practice*, e13122.

- Briers-Louw, W. D., Kendon, K., Rogan, M. S., Leslie, A. J., Bantlin, D., Evers, E., Gaynor, D., Lindsey, P., Almeida, J., & Naude, V. N. (2025). Estimated baseline density of a spotted hyaena population in a post-war landscape. *Oryx*, 1–11.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24(3), 346-352.
- Cain, J. W., Owen-Smith, N., & Macandza, V. A. (2011). The costs of drinking: Comparative water dependency of sable antelope and zebra. *Journal of Zoology,* 286, 58-67.
- CEAGRE - Centro de Estudos de Agricultura e Gestão de Recursos Naturais. (2024). *Relatório da Contagem Aérea de Fauna Bravia no Complexo de Marromeu.* Moçambique.
- Chirima, G. J., Owen-Smith, N., Erasmus, B. F., & Parrini, F. (2013). Distributional niche of relatively rare sable antelope in a South African savanna: Habitat versus biotic relationships. *Ecography, 36*(1), 68-79.
- Crosmary, W-G., Chamaillé-Jammes, S., Mtare, G., Fritz, H., & Côté, S. D. (2015). Decline of sable antelope in one of its key conservation areas: the greater Hwange ecosystem, Zimbabwe. *African Journal of Ecology*, 53, 194–205.
- Dunstone, N., & Gorman, M. L. (Eds.). (1998). *Behaviour and Ecology of Riparian Mammals*. Cambridge University Press. https://doi.org/10.1017/CBO9780511721830.
- Estes, T. H., & King, S. L. (2016). *Instruction: A models approach* (7th ed.). Pearson.
- Estes, R. D. (2012). *The behavior guide to African mammals: Including hoofed mammals, carnivores, primates* (2nd ed.). California, USA: University of California Press.
- Estes, R. D. (1991). *The behavior guide to African mammals: Including hoofed mammals, carnivores, primates*. California, USA: University of California Press.
- Estes, R. (1993). *The safari companion: A guide to watching African animals*. Chelsea Green Publishing.
- Estes, R. D., & Estes, R. K. (1974). The biology and conservation of the giant sable antelope, *Hippotragus niger variani* (Thomas, 1916). *Proc. Acad. Nat. Sci. Philadelphia*, 126, 73–104.
- Fundo Nacional de Desenvolvimento Sustentável (FNDS) (2016). *Mapa de cobertura de terra dos distritos da zona costeira de Moçambique.* Maputo, Moçambique.

- French, N. R. (1985). Herbivore overlap and competition in Kenya rangelands. *African Journal of Ecology*, 23(4), 259-268.
- Fynn, R. W. S., Chase, M., & Röder, A. (2014). Functional heterogeneity and large-herbivore seasonal habitat selection in northern Botswana. *South African Journal of Wildlife Research, 44*(1), 1–15. https://doi.org/10.3957/056.044.0101.
- Garcia, M., & Brown, J. (2020). Seasonal and inter-annual variations in foraging strategies and predation risk in herbivores. *Journal of Wildlife Ecology*, 215–230.
- Garshelis, D. L. (2000). Delusions in habitat evaluation: Measuring use, selection, and importance. In L. Boitani & T. K. Fuller (Eds.), *Research techniques in animal ecology: Controversies and consequences* (pp. 111-164). Columbia University Press.
- Gaylard, A., Owen-Smith, N., & Redfern, J. (2003). Surface water availability: Implications for heterogeneity and ecosystem processes. In J. T. du Toit, K. H. Rogers, & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity* (pp. 257–276). Washington, USA: Island Press.
- Gaspar, A. H. (2011). *Uso do habitat pela Palapala (Hippotragus niger) no Parque Nacional do Limpopo* (Trabalho de Licenciatura). Eduardo Mondlane University. Disponível em http://monografias.uem.mz/handle/123456789/202.
- Getz, W. M., Frotmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, 2, 1-11.
- Goodman, P. S. (2009). Large mammal population estimates for Malilangwe Estate: September/October 2008. *Internal Management Report*. Malilangwe Trust, Zimbabwe.
- Grant, C. C., & van der Walt, J. J. (2000). Toward an adaptive management approach for the conservation of rare antelope in the Kruger National Park-outcome of a workshop held in May 2000. *Koedoe*, 43, 103-111.
- Grobler, J. H. (1981). Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. *South African Journal of Zoology, 16*(2), 50–58. https://doi.org/10.1080/02541858.1981.11447732.
- Hall, L. S., Krausman, P. R., & Morrison, M. L. (1997). The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin, 25*(1), 173–182.

- Harestad, A. S., & Bunnell, F. L. (1979). Home range and body weight – a reevaluation. *Ecology*, 60, 389-402.
- Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R., & Funston, P. (1999). Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, 90, 69-78.
- Harris, H. (1938). The sable antelope in Southern Africa. Journal of African Zoology, 27, 145–160.
- Havemann, C. P., Retief, T. A., Collins, K., Fynn, R. W. S., Tosh, C. A., & de Bruyn, P. J. N. (2022). Home range and habitat use of roan antelope (*Hippotragus equinus*) in northern Botswana. *Journal of Arid Environments, 10*, 10-16. https://doi.org/10.1016/j.jaridenv.2021.104648.
- Henley, S. (2005). Habitat dependency and nutritional ecology of sable antelope in two regions of the Kruger National Park. *Report to South African National Parks*, Centre for African Ecology, University of the Witwatersrand, Johannesburg.
- Hensman, M. C. (2012). *Home range and resource use of sable antelope in the Okavango Delta.* MSc thesis. University of the Witwatersrand, Johannesburg, South Africa.
- Hensman, M. C., Owen-Smith, N., Parrini, F., & Bonyongo, C. M. (2014). Home range occupation and habitat use of sable antelope in the Okavango Delta region of northern Botswana. *African Journal of Ecology,* 52, 237–245. http://dx.doi.org/10.1111/aje.12111.
- INAM- Instituto Nacional de Meteorologia (2020). *Boletim Climático da Época Chuvosa 2019-2020: Avaliação das condições meteorológicas e impactos associados*. Instituto Nacional de Meteorologia, República de Moçambique.
- Impacto. (2012). *Perfil ambiental e mapeamento do uso actual da terra nos distritos da zona costeira de Moçambique*. Impacto, Maputo, Moçambique.
- IUCN/SSC Antelope Specialist Group. (2017). Hippotragus niger. The IUCN Red List of Threatened Species 2017: e.T10170A50188654. http://dx.doi.org/10.2305/IUCN.UK.2017- 2.RLTS.T10170A50188654.en
- Jenkins, S. H. (1981). Common Patterns in Home Range-Body Size Relationships of Birds and Mammals. *The American Naturalist*, 118(1), 126-128.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology, 61*(1), 65–71. https://www.jstor.org/stable/1937156.

- Balluffi-Fry, J., Majchrzak, Y. N., Peers, M. J. L., Studd, E. K., Menzies, A. K., Horne, L. G., Monk, E., Humeniuk, N., Jung, T. S., Murray, D. L., & Boutin, S. (2025). Why does animal home range size decrease with population density?. Ecology, 106(4), e70054. https://doi.org/10.1002/ecy.70054;
- Kernohan, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of space use and movements. In J. J. Millspaugh & J. M. Marzluff (Eds.), *Radio tracking and animal populations* (pp. 125–166). London, UK: Academic Press.
- Kjellander, P., Hewison, A. J. M., Liberg, O., Angibault, J. M., Bideau, E., & Cargnelutti, B. (2004). Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus L.*): a comparison of two long-term studies. *Oecologia*, 139, 478–485.
- Knoop, M-C., & Owen-Smith, N. (2006). Foraging ecology of roan antelope: key resources during critical periods. *African Journal of Ecology*, 44, 1-9.
- Kotler, B. P., Morris, D. W., & Brown, J. S. (2007). Behavioral indicators and conservation: Wielding 'the biologist's tricorder'. *Israel Journal of Ecology and Evolution, 53*(3), 237–244. https://doi.org/10.1560/IJEE.53.3.237.
- Lyons, A. J., Turner, W. C., & Getz, W. M. (2013). Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology*, 1(2), 1–14.
- Macandza, V. A., Owen-Smith, N., & Cain, J. W. (2012). Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *Journal of Zoology*, 287(3), 175–185. doi:10.1111/j.1469-7998.2012.00900.x
- Magome, D. T. (1991). *Habitat selection and the feeding ecology of the sable antelope (Hippotragus niger niger) (Harris, 1838) in Pilanesberg National Park, Bophuthatswana* (M.Sc. thesis). University of the Witwatersrand, Johannesburg, South Africa.
- Makhado, R. A., Curlewis, B. J., Luus-Powell, W. J., & Potgieter, M. J. (2020). Seasonal changes in home range among tragelaphine antelopes at Musina Nature Reserve, Limpopo Province. *African Journal of Ecology*, 58(3), 416–423. https://doi.org/10.1111/aje.12769.
- Mamugy, F. P. S. (2016). *Does predation or competition shape the home range and resource selection by sable antelope (Hippotragus niger) in the Gorongosa National Park, Mozambique?* MSc thesis. University of the Witwatersrand, Johannesburg, South Africa.

- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical design and analysis for field studies* (2nd ed.). Springer.
- Martin, R. B. (1983). *Transboundary species project: Roan, sable and tsessebe – Background study*. Report for roan, sable, and tsessebe in support of the Transboundary Mammal Project. University of Pretoria.
- Millspaugh, J. J., Nielson, R. M., McDonald, L., Marzluff, J. M., Gitzen, R. A., Rittenhouse, C. D., Hubbard, M. W., & Sherrif, S. L. (2006). Analysis of resource selection using utilization distributions. *The Journal of Wildlife Management*, 70(2), 384-395.
- Morris, D. W. (1987). Ecological scale and habitat use. *Ecology*, *68*(2), 362–369. https://doi.org/10.2307/1939267.
- McLoughlin, P. D., & Ferguson, S. H. (2000). A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, 7, 123-130.
- Mysterud, A., & Ims, R. A. (1998). Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology, 79*(4), 1435–1441.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America, 105*(49), 19052-19059. https://doi.org/10.1073/pnas.0800375105.
- Owen-Smith, N. (2002). *Adaptive herbivore ecology: From resources to populations in variable environments.* Cambridge University Press.
- Owen-Smith, N. (2008). Effects of temporal variability in resources on foraging behaviour. In H. H. T. Prins & F. van Langevelde (Eds.), *Resource ecology: Spatial and temporal dynamics of foraging* (pp. 105–120). Springer.
- Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1550), 2267–2278. https://doi.org/10.1098/rstb.2010.0095.
- Owen-Smith, N., & Cain, J. W. (2007). Indicators of adaptive response in home range utilization and movement patterns by a large mammalian herbivore. *Israel Journal of Ecology and Evolution*, 53, 423–428.

- Owen-Smith, N., Chirima, G. J., Macandza, V., & Le Roux, E. (2012). Shrinking sable antelope numbers in Kruger National Park: What is suppressing population recovery? *Animal Conservation, 15*, 195–204. https://doi.org/10.1111/j.1469-1795.2011.00504.
- Owen-Smith, N., & Martin, J. (2015). Identifying space use at foraging arena scale within the home ranges of large herbivores. *PLoS ONE*, 10, e0128821.
- Owen-Smith, N., & Traill, L. W. (2017). Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food? *Journal of Zoology*, 303, 281–290.
- Parrini, F. (2006). *Nutritional and social ecology of the sable antelope in the Magaliesberg Nature Reserve*. PhD dissertation. University of the Witwatersrand, Johannesburg, South Africa.
- Parrini, F., & Owen-Smith, N. (2009). The importance of post-fire regrowth for sable antelope in a southern African savanna. *African Journal of Ecology*, 48, 526–534.
- Powell, R. A., & Mitchell, M. S. (2012). What is a home range? *Journal of Mammalogy*, 93(4), 948–958. https://doi.org/10.1644/11-MAMM-S-177.1.
- QGIS Development Team. (2023). *QGIS Geographic Information System* (Version 3.28.4). Open Source Geospatial Foundation. https://qgis.org
- Rahimi, S., & Owen-Smith, N. (2007). Movement patterns of sable antelope in the Kruger National Park from GPS/GSM collars: a preliminary assessment. *South African Journal of Wildlife Research*, 37, 143–151.
- Riginos, C., & Grace, B. J. (2008). Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology, 89*(8), 2228–2238.
- Rueda, M., Rebollo, S., Gálvez-Bravo, L., & Escudero, A. (2008). Habitat use by large and small herbivores in a fluctuating Mediterranean ecosystem: Implications of seasonal changes. *Journal of Arid Environments, 72*(10), 1698–1708. https://doi.org/10.1016/j.jaridenv.2008.05.010.
- RStudio Team. (2024). *RStudio: Integrated development environment for R* (Version 2024.12+0.467) [Computer software]. Posit Software, PBC. https://posit.co/.
- Semcer, C. E. (2018). "The Return of the King". Property and Environment Research Center (PERC). Disponível em: https://www.perc.org/2018/12/14/the-return-of-the-king/.

- Shaefer, J. A., & Messier, F. (1995). Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography*, 18, 333-344.
- Skinner, J. D., & Chimimba, C. T. (2005). *The mammals of the southern African sub-region* (3rd ed.). Cambridge, England: Cambridge University Press.
- Smith, J., & Brown, L. (2017). Foraging patterns and habitat preferences in herbivores. *Journal of Ecology, 105*, 210–225.
- Smith, J., & Brown, P. (2010). Stomach content analysis and dietary adaptations in ungulates. *Journal of Wildlife Research, 53*, 215–230.
- Stalmans, M., & Peel, M. (2024). Aerial wildlife count of the Gorongosa National Park, Mozambique, October 2024. Gorongosa Project.
- Stalmans, M., Peel, M., & Massad, T. (2014). Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion. *Unpublished report to the Gorongosa Restoration Project*.
- Sutton, P., Maskall, J., & Thornton, I. (2002). Concentrations of major and trace elements in soil and grass at Shimba Hills National Reserve, Kenya. *Applied Geochemistry*, 17, 1003–1016.
- Tinley, K. L. (1977). *Framework of the Gorongosa Ecosystem* (PhD thesis). University of Pretoria, Pretoria, South Africa.
- Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology, 80*(4), 771–785. https://doi.org/10.1111/j.1365-2656.2011.01829.x.
- Van Oudtshoorn, F. (1999). Guide to grasses of southern Africa. Briza Publications, Pretoria, South Africa.
- Walton, J. (2001). *Satellite communication systems and technology*. Wiley.
- Weber, J., Hempson, G. P., & February, E. (2020). Large herbivore conservation in a changing world: Surface water provision and adaptability allow wildebeest to persist after collapse of long-range movements. *Global Change Biology, 26*(5), 2841–2853. https://doi.org/10.1111/gcb.15084.

- Weeber, J., Hempson, G. P., & February, E. C. (2020). Large herbivore conservation in a changing world: surface water provision and adaptability allow wildebeest to persist after collapse of long-range movements. *Global Change Biology*, 26, 2841–2853.
- Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, 13, 265-286.
- Wilson, D. E., & Stanley, H. M. (1977). Ecology and factors limiting the populations of the roan and sable antelope in South Africa. *Wildlife Monographs*, *54*, 3–11.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Journal of Ecology, 77*, 164–168.
- White, L. J. T., & Abernethy, K. A. (2009). *Savannah ecology and management: Australian perspectives and global implications*. CSIRO Publishing.
- Whyte, I. J. (2006a). *Rare antelope in the Kruger National Park: Trends, current status, and options for future management*. *Scientific Report,* South African National Parks.
- Whyte, I. J. (2006b). *An aerial census of the Shingwedzi basin area of the Parque Nacional do Limpopo: 16th–21st October, 2006* (Scientific Report No. 02/2006). South African National Parks.