CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences

Home Range and Habitat Preferences of Cheetahs and Lions in a Small Game Reserve in South Africa

MASTER'S THESIS

Prague 2020

Author: Maxine Piron

Chief supervisor: prof. RNDr. Pavla Hejcmanová, PhD

Second (specialist) supervisor: Dr. Lisa Graham

Declaration

I hereby declare that I have done this thesis entitled “Home Range and Habitat Preferences of Cheetahs and Lions in a Small Game Reserve in South Africa” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 14/08/2020

……………………………………

Maxine Piron

Acknowledgements

First of all, I would like to thank my supervisor prof. RNDr. Pavla Hejcmanová, PhD, who supported me and my search for my own thesis topic from the beginning. She has been a source of inspiration, continuous guidance and support throughout this research.

Secondly, I want to thank Amakhala Game Reserve and their landowners for granting access to the collected data and shapefiles, which I needed to conduct my research. I am grateful to long hours of fieldwork from the numerous members of the Amakhala Game Reserve team and for doing the data collection so thoroughly over these years. Special thanks are given to Dr. Lisa Graham, who helped me develop my research questions and giving me in-depth insight in the ecology and management of Amakhala Game Reserve, providing me with all the data and help I needed and for reviewing the paper once it was finished.

Furthermore, I would like to thank the wonderful “Leeuwenbosch family”: Steve and Kerry Maartens for all the support and providing me with a wonderful place to stay and welcoming me into their family. I want to thank Dr. William Fowlds, and his passion for wildlife and conservation, he has been a true inspiration for me.

Lastly, I want to express my gratitude to Tim Awbery and Dr. Aylin Akkaya for their continuous assistance and statistical guidance throughout my thesis.

Abstract

Understanding the ecological preferences, use of space and interactions of translocated carnivores in small, enclosed reserves is vital, however the success of translocation may fail due to interspecific conflict. Reserve managers would benefit from understanding how predators have adjusted behaviourally to the translocation site, particularly in connection to space use patterns, which influence potential for competitive interactions. An understanding of species-specific habitat use patterns in relation to competition is essential for managing protected areas to facilitate carnivore coexistence. Knowledge of predator feeding behaviour within the guild is important for managers, to assess the impact on prey populations and to detect a potential overlap within the guild in small reserves. Long-term direct observations aided by radiotracking were used to monitor four lions (*Panthera leo)* and three adult cheetahs (*Acinonyx jubatus)* in Amakhala Game Reserve to assess the home ranges, core ranges, spatial overlap, habitat preferences and prey selection for both species.

The home ranges of all individuals overlapped, the lion pride had a stable, overlapping core range throughout the whole study, the individual core ranges of the cheetahs varied annually and overlapped greatly with the lions. The female cheetah with cubs preferred valley thicket, a vegetation type completely avoided by the lions and other cheetahs. Within home- and core range, lions preferred riverine thicket, which was significantly avoided by all the cheetahs in the reserve. This could potentially be an intra-guild mechanism for minimizing intraspecific encounters with the lions. A total of 573 cheetah kills, and 532 lion kills were recorded with potential competition identified for species such as: kudu *(Tragelaphus strepsiceros)*, red hartebeest *(Alcelaphus buselaphus)* and eland *(Tragelaphus oryx)*. There was a significant preference for medium sized prey (<30 – 99 kg) for both the cheetahs and the lions in the reserve, with lions favouring adults, and cheetahs preyed more upon subadults and juveniles. This study has taken the initial steps into helping a small, fenced game reserve to understand how the lions and cheetahs in the reserve made use of space.

Key words: *Panthera leo, Acinonyx jubatus,* space use, prey selection, habitat choice

Contents

List of tables

List of figures

List of the abbreviations used in the thesis

AGR	Amakhala Game Reserve
GIS	Geographical Information Systems
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
KDE	Kernel Density Estimations
MCP	Minimum Convex Polygons
QGIS	Quantum Geographic Information System
SNP	Serengeti National Park
SA	South Africa
UD	Utilization Distribution
VHF	Very High Frequency

1. Introduction

There has been a rapid increase in small game reserves in South Africa, partly for the hunting industry and some purely as eco-tourism ventures to enhance biodiversity conservation. Many species have been reintroduced in these areas after decades of farming have led to the near eradication of all endemic wildlife. Lions *(Panthera leo)*, cheetah *(Acinonyx jubatus)* and other large predator species are introduced to attract guests and enhance the wilderness experience (Druce et al. 2004). The translocation of predators into fenced reserves is a particularly common practice in South Africa (Hayward & Hayward 2007; Hunter et al. 2007a; Lehmann et al. 2008). At least 44 lion populations can be found in smaller fenced reserves in South Africa, covering an area of 5702 km^2, and therefore expanding the free-roaming population by 500 individuals (Funston et al. 2001; Lindsey et al. 2011; Miller et al. 2013). Cheetahs have been reintroduced onto 37 South African reserves, extending the wild population by 258 individuals, covering an area of 7744 km^2 (Lindsey et al. 2011). Although the establishment of small, enclosed reserves in South Africa has reduced the human-carnivore conflict, these systems may increase the likelihood of intra-guild competition (Comley et al. 2020). Moreover, only small numbers of large predators are introduced, which can cause inbreeding problems. Populations have to be manipulated in order to create or maintain genetic diversity, requiring active management (Druce et al. 2004). Managing large carnivores in relatively small areas comes with some additional concerns. For example, lion and cheetah home ranges have been estimated to be up to 1651 km^2 (Welch et al. 2015). While small game reserves are often not bigger than 150 km^2. Furthermore, some endangered species such as cheetah can suffer consequences of interactions with other larger carnivores, like lions (Palomares & Caro 1999). This means that the co-existence of multiple carnivores in an enclosed system could be restricted by their similarities in ecological niches (e.g. dietary overlap, spatial overlap) (Comley et al. 2020).

In carnivores, patterns of resource distribution can be an influencing factor of home range size. This is often affected by habitat qualities such as food supply or access to refuges. These qualities often lead to interspecific competition over space, which can be an important factor determining the distribution of individuals within populations (Spong 2002). Habitat selection can be viewed as a hierarchical process (Johnson 1980). Within the geographical range, animals make a choice for a home range within an available area, then they select habitats where they spend most of their time in, and finally they select feeding sites within the habitats regularly used. Large carnivores are vulnerable to habitat fragmentation and understanding their processes of habitat selection and preferences is therefore crucial for the effective conservation of these emblematic species (Davidson et al. 2012). Effective conservation strategies are needed to ensure viability of carnivores in South Africa, but such strategies cannot be developed without understanding how carnivores affect each other or their prey in small reserves (Comley et al. 2020).

Thus, the objective of our study was to examine home range, home range overlap, core range, core range overlap, habitat preference and prey selection of lions and cheetahs in a small, enclosed game reserve. This could potentially expose intra-guild competition and therefore provide valuable information for management decisions.

2. Literature Review

2.1. Habitat selection principles and home range concept

Advances in animal tracking and telemetry technology have allowed the collection of data at an ever-increasing rate and accuracy. This is accompanied by the development of new methods of data analysis for interpreting space use, home ranges, and utilization (Kie et al. 2010). Here, insights are provided in the terminology relevant to ecology, habitats, home range concepts, the use of telemetry data, and basic analysing techniques.

2.1.1. What is a habitat?

The concept of habitat is a cornerstone in the management of wildlife (Krausman 1999). Imprecise terminology has prevented reliable comparisons across studies (Hall et al. 1997; Krausman 1999; Gaillard et al. 2010). In a review done by Gaillard et al. (2010) they aimed to find a general approach for studying the relationship between habitat and individual animal fitness. He reviewed and described definitions that play a role in habitat concepts.

Gaillard et al. (2010) recognized two different definitions of habitat: a niche-based definition and a resource-based definition. The resource-based ('structural') definition describes habitat as a set of physiognomically clear categories of vegetation communities. It includes trees, nests, communities or vegetation and forage resources that exist in space independent of their use or selection by an animal. Limitations of this definition are that: (1) habitat is not species-specific, it is insensitive to spatial and temporal scales and its quality to the animal is difficult to measure (Hall et al. 1997; Gaillard et al. 2010), and (2) it depends on classification of usually continuous resources or conditions into discrete categories. In the niche-based ('functional') definition the animals select resources and conditions (hence the term 'resource selection'), which will lead to a given performance or fitness. Here, habitat is defined as the suite of resources (food, shelter) and environmental conditions (abiotic and biotic) that determine the presence, survival and reproduction of a population or individual (Gaillard et al. 2010). Krausman (1999) defines habitat as the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism. It is the sum of specific resources that are needed by organisms. These resources include food, shelter, water and other factors needed by a species for survival (Hall et al. 1997; Krausman 1999), which would suggest he used the niche-based or functional definition to describe habitat. Hall et al. (1997) proposed that habitat is not the equivalent to 'habitat type' and therefore authors that intend to describe the vegetation that an animal uses, should use "vegetation association" or "vegetation type" instead. This goes in line with the structural definition of habitat described by Gaillard et al. (2010). However, these two definitions (‘structural’ and ‘functional’) of habitat correspond to different scales. On small spatial and temporal scales, animals select different structural habitats, where they choose local resources or conditions to increase their performance. When the spatial and temporal scale increases, individuals make behavioural decisions to select resources that result in survival and reproductive performances at the level of individuals and populations. Over evolutionary time these habitat choices contribute to the species niche, thus the functional habitat (Gaillard et al. 2010).

Habitat use generally refers to the way in which an individual uses the physical and biological resources in a habitat to meet its needs (Hall et al. 1997; Gaillard et al. 2010). A species may use one habitat in summer and another in winter; various activities of an animal require specific environmental components that may vary on a seasonal or yearly basis (Krausman 1999). Habitat use can be directly described from observations of how the animal interacts with habitat features. Locations obtained from GPS receivers on animals allow the establishment of more accurate and fine-scaled associations, and thus more realistic estimates of habitat use (Gaillard et al. 2010).

Habitat selection was described as a complex, hierarchical process of behavioural responses and choices (Gaillard et al. 2010), involving a series of innate and learned behavioural decisions made by an animal about what habitat it would use at different scales of the environment (Hall et al. 1997; Gaillard et al. 2010). Competition is happening because each individual is involved in intraspecific and interspecific relationships that partition the available resources within an environment. Therefore, habitat selection is an active behavioural process by an animal (Krausman 1999). Selection refers to the disproportionate use relative to the availability or occurrences of resources, which is the quantity of the resources within a specified area and period of study. It must be calculated by measuring the relationship between factor occurrence or availability and factor use (Arthur et al. 1996; Gaillard et al. 2010). Habitat preference is a consequence of habitat selection, resulting in the disproportional use of some resources over others. This is most strikingly observed when animals spend a high proportion of time in habitats that are not very abundant on the landscape. Vegetation and habitat are often terms that are misused: habitat is frequently used to describe an area that supports a particular type of vegetation. However, vegetation is a part of habitat that includes many resources like water, food, cover, precipitation, topography and other components in an area important to a species. Habitats are species-specific; manipulations of the landscape might favour the habitat of some species but will be detrimental to the habitats of others (Krausman 1999)

Johnson (1980) recognized four main hierarchical levels of selection, defined as a process in which an animal actually chooses a component. The four levels are:

- *First-order selection:* selection of physical or geographical or distribution range of a species.
- *Second-order selection:* selection of the home range of an individual or a social group within their geographic range.
- *Third-order selection*: is relating to how the habitat components within the home range are used (Krausman 1999); selection for a patch within a home range (Gaillard et al. 2010) (e.g. feeding site).
- *Fourth-order selection:* selection for a site (e.g. nest) or item (e.g. food) (Gaillard, et al., 2010); it relates to how components of a habitat are used (Krausman 1999).

These levels of selection are only landmarks belonging to a continuum from fine to very coarse spatial scales and reflect the gradient from niche to food. The spatial scales at which the analyses are performed are of prime importance when interpreting studies of habitat selection (Hall et al. 1997; Gaillard et al. 2010; Davidson et al. 2012). Habitat selection of mammals is often examined by comparing the habitat composition in the 'core area' in the 'total home range' and in the landscape. However, both the total home range and the core area can be defined in several ways (Kauhala & Auttila 2010).

2.1.2. Home range estimation

"Home range" is a standard concept in animal ecology and behaviour (Powell & Mitchell 2012). It is often defined and cited as: 'the area used by the individual in its normal activities of food gathering, mating and caring for young' (Kie et al. 2010; Tumenta et al. 2013). Occasional trips outside of the area, perhaps exploratory in nature, should not be considered as part of the home range. This does not recognise the importance of variations in the intensity of space use within a home range, nor does it specify how to delineate the boundary of the home range. Over the years, a variety of statistical methodologies have been developed with increasing complexity (Kie et al. 2010). There is no standardised way to estimate home range for an animal or group of animals, but there are numerous available methods (Gregory 2017). Researchers put energy into using the "best" method for estimating home ranges, this results in problems to compare the different methodologies used in various studies (Laver & Kelly 2008; Powell & Mitchell 2012). GPS collars could provide insights in the study of secretive mammals, allowing researchers to observe where these animals have moved. They may provide insights in what an animal perceives as 'home' and allows researchers to estimate the total use of space by an animal, which is considered to represent the animal's home range. Analyses of home ranges have been well-discussed among researchers because animals do not distribute their use of space in a statistically well-behaved pattern (Powell & Mitchell 2012). And there is much disagreement about the preferred methodology.

Home range analysis has progressed from early attempts to identify an area via minimum convex polygons (MCP) to describing them through utilization distribution (UD), like kernel density estimations (KDE) (Laver & Kelly 2008; Kie et al. 2010). MCP is a straightforward approach that involves creating a convex polygon, encompassing all of the location points gathered for the animal or group. KDE are the most commonly used utilization distribution method, and they involve a complex, nonparametric analysis of home range data. They use the location data to create a utilization distribution, which describes the probability that an animal can be found in a given location (Gregory 2017). Home ranges may differ among animals of different species or even within a species. Nonetheless, all animals use their home ranges to provide food and other resources (Powell & Mitchell 2012). Carnivore home range size varies across and within species in relation to a wide range of factors: body mass, prey availability, social interactions, habitat quality and reproductive status (Spong 2002; Bauer & Iongh 2005; Hayward & Slotow 2009; Tumenta et al. 2013).

2.1.2.1. Techniques using VHF radio collars and GPS collars

Wildlife research entered a new era when the first radio collar was fitted in the early 1960s. The technology has since evolved to allow researchers to acquire data without having to physically observe the animal. Commercial radio collars send pulse signals broadcasted in very high frequency (VHF) radio waves. Each collar or device has its own unique frequency, to identify which animal has been tracked. The transmitter fitted to the animal emits this signal, which is picked up by an antenna-receiver combination, operated by the researcher. VHF works better at relatively short ranges, and the transmitted signals are easily blocked by landforms like hills, mountains and dense vegetation. Triangulation is used to determine an animal's approximate location from afar (Johansson et al. 2016).

GPS or global positioning system technology uses satellites that send messages that can be received by a GPS device. The accuracy of GPS locations or "fixes" is currently within a few meters, depending on the GPS technology being used (Johansson et al. 2016). Recent advances in GPS technology for monitoring wildlife home ranges and movement patterns have resulted in locations that are numerous and more precise than very high frequency systems (VHF) (Walter et al. 2009). The combination of location data derived from VHF telemetry and kernel home range estimators was widely accepted prior to the advent of GPS locations. GPS-based telemetry systems have had numerous improvements in size, performance, and data transfer capabilities (Walter et al. 2009; Johansson et al. 2016). This has posed fundamental advances and challenges to the home range estimations (Kie et al. 2010). However, the cost of GPS radio collars often leads to smaller sample sizes or it may limit the desired data precision. In order to estimate home ranges, time duration between successive locations is an important factor to consider. Fix rates can be decreased to extend battery life (Walter et al. 2009), and reduce the frequency of replacements, which generally requires an anaesthetic procedure for the animal, or it can be increased to identify detailed, real-time movements (Walter et al. 2009).

Therefore, there is an obvious trade-off between increased sampling effort and decreased battery life (Kie et al. 2010). Along with these advances, researchers are challenged with understanding the proper methods to assess the home range size of different species. KDE has become the most widely accepted method of home range analysis, but it is often criticized because of errors in the proper bandwidth selection, and violation of independence assumptions (Walter et al. 2009). It also presents a problem for consistency among studies because of its multitude of possible implementations (Laver & Kelly 2008). Overall, GPS telemetry ensures the possibility of an evenly distributed sampling protocol throughout days and seasons, providing more representative samples of an animal's space use (Kie et al. 2010). Collar data, telemetry or GPS, can be enhanced with direct observations. It collects fine-scale information on animal behaviour and resource utilization. However, the limitations are that it requires time, daylight and some terrains can limit observations and the opportunistic nature of this method means that it can produce patchy or irregular datasets. Therefore, integrating a GPS collar could provide additional and continuous information and can monitor animals for a consistent time frame (Walden-Schreiner et al. 2018).

2.2. Carnivore diversity and ecology

The mammalian order Carnivora is highly diverse: it encompasses 286 different species divided over 15 families (Kingdon & Hoffman 2013; Edelman 2019). This varied array of predators, scavengers, piscivores and omnivores play keystone roles in many African habitats. Thus, species and ecological diversity varies enormously among those major animal groups (Kingdon & Hoffman 2013; Pérez-Irineo & Santos-Moreo 2013). There are eight extant families in Africa: Canidae, Mustelidae, Pinnipedia, Nandiniidae, Felidae, Viverridae, Hyaenidae and Herpestidae. This study will cover species of the family Felidae. They are morphologically a highly uniform family of hypercarnivores, meaning their diet consist of > 70 % of meat (Macdonald et al. 2010; Kingdon & Hoffman 2013) and they are highly specialised for predation with retractable claws (except cheetahs), strong forelimbs, concealing colour patterns and well-developed carnassials (Edelman 2019). The basic dental formula of the living Felidae is I $^3/_3$, C $^1/_1$, P $^3/_2$, M $^1/_1$ = 30. Skulls in small felids are rounded, while the larger felids have more elongated skulls. All species are digitigrade with five toes on the forefoot and four toes on the hindfoot. Forelimbs are being used for locomotion and for prey capture. All felids have protractile claws that are protected in a flesh sheath when retracted (Macdonald et al. 2010; Kingdon & Hoffman 2013). They have a *tapetum lucidum* within the eye that creates a superior night vision for hunting (Edelman 2019). Many conservation strategies are based on carnivorous mammals. For these strategies to be effective, they require reliable information on the population dynamics, ecological requirements of the species of interest, distribution dynamics, as well as the impact they have on their ecosystems (Pérez-Irineo & Santos-Moreo 2013).

In Africa high levels of human-carnivore conflict and habitat fragmentation, have led to human-induced carnivore mortality, causing local extinction of carnivores (Comley et al. 2020). Therefore, restricted-sized reserves are becoming increasingly common in South Africa (Hayward & Slotow 2009; Comley et al. 2020). Large carnivores have been reintroduced in these small, fenced reserves for a few reasons: first, to increase eco-tourism (Druce et al. 2004; Comley et al. 2020) second, to restore ecosystem structures and functions, and third to create metapopulations to boost population numbers (Miller et al. 2013, 2015). Many of the larger carnivores are keystone species affecting the ecosystem through top-down processes (Hayward & Slotow 2009; Comley et al. 2020). The fences prevent migration or movements during periods of food shortage, emigration and dispersal of subadults (Lehmann et al. 2008), which decreases genetic diversity. Populations must therefore be actively managed in these incomplete natural systems to maintain them (Hayward & Slotow 2009), to prevent over-utilization of resources and to ensure genetic diversity (Lehmann et al. 2008). Another consequence is that these small, enclosed reserves may increase the likelihood of carnivore intra-guild competition due to the clumping of competing carnivores into restricted spaces of the reserves (Palomares & Caro 1999; Comley et al. 2020).

2.2.1. Intra-guild competition

Competition theory proposes that effects on population dynamics are greatest when resources are limited (Creel 2001). It also suggests that carnivores should kill sympatric guild members when benefits (freeing up resources) overshadow the costs (injuries, energy expenditure) (Comley et al. 2020). Furthermore, it proposes that species that differ sufficiently in body mass do not compete (Hayward & Kerley 2008).

According to Caro & Stoner (2003) competition among carnivores can take five forms: (1) carnivores may avoid each other if they come into visual or olfactory contact, (2) active avoidance can result in shifts in habitat use, (3) exploitative competition occurs when predators share the same food resources, (4) competition may involve food stealing, and finally (5) carnivores can kill each other. These five forms can have a profound effect on the population sizes of subordinate species. Exploitative competition occurs when one species uses resources that then become unavailable to others (Comley et al. 2020), for example, geographic range, habitat and dietary preferences, and food stealing (Caro & Stoner 2003). Diets as well as habitats of sympatric carnivores often show an overlap (Palomares & Caro 1999; Hayward & Slotow 2009; Cristescu et al. 2013). However, home range overlap is a gross measure for potential of interspecific competition; species may live in different habitats despite sharing the same home range (Caro & Stoner 2003). Interference competition involves direct aggression between species (Balme et al. 2017). Competition for food has been acknowledged as a key factor in triggering intra-guild predation, as extensive dietary overlap motivates aggression among carnivores. When prey is less available, competition over food may be more important (Palomares & Caro 1999). This competition can sometimes escalate into interspecific killing, also called intra-guild predation (Palomares & Caro 1999; Creel 2001), which is the most extreme form of interference competition (Balme et al. 2017). Interspecific killing among mammalian carnivores can take two forms. It may either be symmetrical; where both species kill each other, or asymmetrical: when one species kills the other. Smaller species may kill cubs, juvenile and subadult individuals of the larger species, but in general larger species usually kill both adult and juvenile individuals of the smaller species. This is the case in lions and leopards (Palomares & Caro 1999). Both interference and exploitative competition have been recognized as important in shaping the ecological relationships of large carnivores (Hayward & Kerley 2008; Cristescu et al. 2013). Interference competition, predation or killing will affect subordinate carnivore densities (Comley et al. 2020) and can significantly alter animal behaviour and species' spatial distribution (Broekhuis et al. 2013). Prey size distributions and densities within an ecosystem can either reduce or enhance competition. In areas where suitable prey is not limited, selective predation is thought to facilitate large carnivore co-existence (Palomares & Caro 1999; Comley et al. 2020). Thus, competition between carnivores has become an important ecological factor influencing populations of subordinate carnivores. This is very important for conservation because competition among carnivores can reduce the population size of an endangered species, like cheetahs (e.g. negative relationships between densities of cheetahs and lions exist) (Palomares & Caro 1999; Hayward & Kerley 2008). The full implications of carnivores' aggressive interactions in small, enclosed, game reserves in South Africa are largely unknown (Comley et al. 2020). This study will therefore describe two important carnivore species: lion (*Panthera leo)* and cheetah *(Acinonyx jubatus)* and their interactions in small game reserves.

2.2.2. Lion *(Panthera leo)*

Lion distribution and conservation status

Lions formerly occurred across most of the African continent, their range extended outside of the African continent, through southwest Asia, and west into Europe and east to India (Kingdon & Hoffman 2013; Dolrenry et al. 2014). Over the past century, it is estimated that the lion's distribution range has been reduced by approximately 75 % (Dolrenry et al. 2014).

Large lion populations are now rare outside protected areas and the species is critically endangered in West Africa (Hunter et al. 2007a; Henschel et al. 2016), and threatened in Central Africa (Bauer & Iongh 2005; Laizer et al. 2014). Their global population has reportedly declined 43 % from 1993 to 2014 and is currently restricted to only 8 % of its historic range (Figure 1) (Belant et al. 2019). According to Dolreny et al. (2014) Kenya and Tanzania hold half of the remaining lion population in Africa. The lion is currently listed as 'vulnerable' on the IUCN (International Union for Conservation of Nature) Red List of Threatened Species and would be considered endangered if numbers were to decline by at least 50% over three lion generations (Bauer et al. 2015). This is likely to happen at the regional scale in West, Central and East Africa where many populations are either expected to disappear within the next decade, or they are already gone. Subsequently, it is a potential future reality that the intensively managed populations in southern Africa may soon supersede the iconic savanna landscapes in East Africa, as the most successful sites for lion conservation (Bauer et al. 2015).

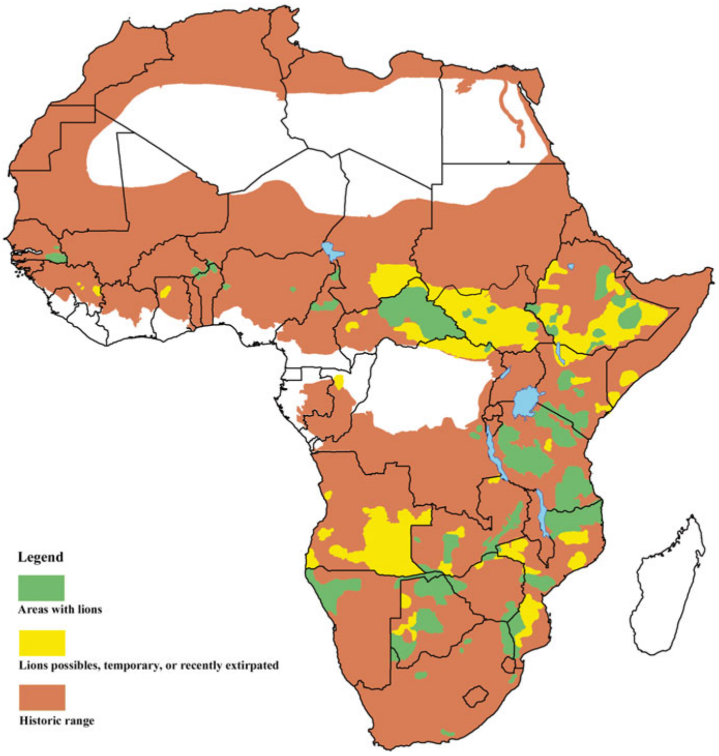


Figure 1: Historic and present distribution of the lion in Africa, green = areas with lions, yellow = possible, temporary, or recently extirpated, and orange = their historic range **(Trinkel & Angelici 2016)**.

Lion populations are shrinking as a result of multiple challenges posed by increasing human populations (Hunter et al. 2007a; Visser et al. 2009): human-wildlife conflict, habitat fragmentation, a decrease in habitat availability (Bauer & Iongh 2005; Hunter et al. 2007b; Laizer et al. 2014; Bauer et al. 2015), indiscriminate killing by humans, poorly regulated sport hunting, depletion of prey base and the demand for traditional Chinese and African medicine (Dolrenry et al. 2014; Bauer et al. 2015). Therefore, the current distribution range is very fragmented, and populations are now found in isolated enclaves. Populations today are largely restricted to protected areas and smaller reserves (Kingdon & Hoffman 2013; Dolrenry et al. 2014). Those reserves are often too small to support wide-ranging carnivores like lions and the lions are forced to utilize adjacent dispersal areas for supplementary food and other needs. This increases the chances of human-carnivore encounters and conflict, making it difficult for the two to co-exist (Laizer et al. 2014). Stock raiding often leads to the persecution of lions, this is either done by local people by poaching or poisoning, or by the authorities to remove problem animals. A high but unknown number of lions are killed each year because of the high financial value of cattle and no damage compensation system (Bauer & Iongh 2005). Options for lion management in large, unfenced areas include lion translocation, village translocation, culling or sale of problem lions and additional compensation payment. In areas where those management implementations do not work sufficiently, it creates a problem for lion populations that are at a critically low level (Bauer & Iongh 2005; Kettles & Slotow 2009).

Species restoration via translocation or reintroduction is often applied. Lion populations are not hard to re-establish. Most lions reintroduced in a game reserve in South Africa survived to reproduce and raised > 75 % of their cubs to independence. This is probable because of low densities of other predators and high density of non-migratory game (Hunter et al. 2007a). Lions in confined or small populations can lose genetic variability because of reduced gene flow, genetic drift and inbreeding (Druce et al. 2004; Hunter et al. 2007a). Even though eco-tourism is considered to offer substantial benefits by biodiversity conservation, lions incur energetic costs from the presence of tourist through an increased frequency of energetically expensive behaviour. Dense vegetation may act as a refuge for lions from tourists (Hayward & Hayward 2007).

Social behaviour and habitat use

Lions are the largest of African carnivores, with sexual dimorphism pronounced in size (Funston et al. 2001). Adult males are typically 30-50 % larger than adult females (Kingdon & Hoffman 2013). The lion is a social felid that lives in family units called prides. The prides are fission-fusion societies (Lehmann et al. 2008; Tumenta et al. 2013); the size varies from two to 18 related adult females (Tumenta et al. 2013), and most of their time is spend in smaller subgroups or alone. The females are always close genetic relatives; resident males are almost never related to the females in the pride, except in small, isolated populations. When female cubs reach sexual maturity, they will usually stay with the mother unless the father is still a member of the pride, then his female offspring will disperse. Dispersing females may establish a new pride on the edge of their natal territory, thus neighbouring prides may also be closely related (Spong 2002). When male lions are not able to disperse from stable populations, this could result in lower rescue effect for the broader metapopulations, causing an increased risk of extinction for local populations (Dolrenry et al. 2014).

As habitat generalists, lions have a very diverse habitat tolerance, ranging from semi-desert to dense woodland (Hayward & Kerley 2008; Dolrenry et al. 2014). They have been seen ranging on altitudes up to 4200 m a.s.l. (Yalden et al. 1996). When water is available, lions drink regularly, but it is not an essential habitat requirement and they are able to survive from moisture obtained from fresh carcasses (Kingdon & Hoffman 2013). Lions exhibit nocturnal (79 % of daily activity) and crepuscular activity patterns. Peak activity occurs from 02:00 to 07:00 h in the morning and 21:00 until midnight (Hayward & Slotow 2009). The largest portion of the day they spend asleep to conserve energy and resources (Kingdon & Hoffman 2013). Lions select habitats based on different factors such as protection for cubs, prey availability and cover for hunting (Druce et al. 2004; Kingdon & Hoffman 2013). Cubs begin to show signs of independence around the age of 18 months and they can survive without protection from the pride from about two years old. The ages at which lions reach sexual maturity and full size depends on the habitats and conditions they grow up in (Kingdon & Hoffman 2013).

According to Spong (2002), lions exhibit a significant preference for riverine and short-grass habitat, and a significant avoidance of acacia woodland. He also states that habitat preference ratios largely reflect prey availability in each habitat. Lion space use seems mostly driven by prey availability, which mainly varies within each habitat type.

In a research done by Broekhuis (2013) in the Okavango Delta of Botswana, lions showed significant preferences for grassland and mixed woodland habitats and spent less time in mopane and swamp than expected in the study area. Within their home ranges they preferred mixed woodland over grassland. Habitat preferences at Sabi Sands Game Reserve for lions showed significant preferences for riparian woodland and avoided grassland (Balme et al. 2017).

There are various factors that may influence lions' home range size. Large home ranges overlap extensively with those of adjacent prides, while small ranges tend to have little or no overlap (Tumenta et al. 2013; Laizer et al. 2014). Prey availability and distribution has shown to significantly affect the home range size. Depending on the size of pride, prey abundance and water availability, home and core ranges vary across different countries, protected areas and reserves. Harsher habitats require bigger home ranges (Kingdon & Hoffmann, 2013). In areas of Kgalagadi Transfrontier Park the home ranges of 14 prides varied between 266 – 4532 km^2 (Funston et al. 2001). Whilst in Serengeti National Park they would cover only an area of 20 – 500 km^2. Male and female lions both defend their territories, females defend their core area against other female groups and male lions range more widely. Territory boundaries are maintained by roaring, urine-marking and patrolling and they remain fairly constant over time, with only small changes in the core area (Kingdon & Hoffman 2013; Tumenta et al. 2013).

Diet and prey selection

Lions are highly specialized for a carnivorous foraging strategy. Their camouflaging pelage lets them approach a prey without being detected and heavily muscled limbs ensure a short, powerful burst of speed. A strangling bite immobilizes the prey (Kingdon & Hoffman 2013). Hunting is opportunistic and occurs mostly at night or in cooler daytime periods (Hayward & Kerley 2008; Kingdon & Hoffman 2013), but they have also been known to scavenge (Hopcraft et al. 2005). The strategies of a predator are forged by natural selection to maximize nutrient intake (Barnardo et al. 2020), while having a wide range of ecological constraints, such as prey density and habitat, which differs throughout their geographical distribution (Kingdon & Hoffman

2013). They are morphologically specialized to take down prey their own size or larger (Hayward & Kerley 2008; Owen-Smith & Mills 2008). Being opportunist stalk-and-ambush hunters, they rely on a combination of good cover, acceleration, body weight and occasional cooperation with other pride members to overcome their prey (Hopcraft et al. 2005). Lion typically approach their prey up to 15 m and will quickly reach their top speed of 58 km/h. This stalking behaviour is followed by a charge, grabbing or slapping the flank and dragging the prey down (Kingdon & Hoffman 2013). Group hunting allows them to kill prey larger than themselves safely and consistently (Hayward & Kerley 2008). When hunting larger animals they may leap on the back, attempting to break the animals back. There are also records of lions actively digging out prey such as common warthogs *(Phacochoerus africanus)* from shallow burrows. Prey is either consumed at the kill site or dragged away (Kingdon & Hoffman 2013).

Comley et al. (2020) analysed the scat and kill sites of lions in a small, enclosed reserve and found that lions displayed an increasing trend of prey selection preferences with increased prey size-class. When a predator kills a species more frequently than expected based on its availability then it can be considered a preferred species. However, there are many ecological, behavioural and morphological factors that could potentially influence prey capture. Vulnerability of the prey to a certain predator are influenced by body size, abundance, temporal and spatial distribution, defences and anti-predatory tactics. Environmental or ecological factors include grass/shrub cover, terrain, time of the day and moon phase (Funston et al. 2001; Comley et al. 2020). Other features that affect hunting success are hunting-group size, composition and hunting methods used (Funston et al. 2001; Hayward & Kerley 2008). In a study done near Kruger National Park by Balme et al. (2017) the most common prey for lions was buffalo (*Syncerus caffer)* (41% of kills and 63% of biomass consumed). There was no seasonal difference in the size of prey killed by lions. Funston et al. (2001) identified seven variables that they considered to have a significant independent influence on hunting success of lions in Kruger National Park: the type of hunt, wind orientation, number of adults in pride, prey species, herd size, moon brightness and grass height. The sex of the lions had no effect on the overall probability of hunting success. Hayward & Kerley (2005) conducted an analysis of 32 studies from 48 different spatial locations or temporal periods throughout the distribution of the lion and demonstrated a preference for prey species within a weight range of 190-550 kg. Gemsbok *(Oryx gazella)*, buffalo, wildebeest spp., giraffe spp. and zebra spp. were significantly preferred. However, lions often do take prey substantially smaller than this range, reflecting their dietary opportunism. Species within the preferred weight range that are not significantly preferred generally have features that reduce predation either morphologically (e.g. horns of sable antelope *Hippotragus niger*), ecologically (e.g. roan antelope *H. equinus* and sable occur at low density), or behaviourally (e.g. the large herd size and increased vigilance of eland) (Hayward & Kerley 2008; Kingdon & Hoffman 2013). For a successful daytime hunt grass of 0.4 m height was required, and hunting success increases when grasses are higher (Funston et al. 2001). Altered habitat conditions (wet- and dry season, rainfall variation) leads to changes in prey chosen (Hayward & Kerley 2008). As mentioned earlier, besides typical prey items, lions have been recorded preying on other carnivores, including spotted hyaenas (*Crocuta crocuta)*, leopards *(Panthera pardus)*, cheetahs, black-backed jackals (*Canis mesomelas)* and many other smaller species (Kingdon & Hoffman 2013).

2.2.3. Cheetah *(Acinonyx jubatus)*

Cheetah distribution and conservation status

Cheetahs were historically found across most of the African continent and southern Asia (Welch et al. 2015; Vebber et al. 2020), occurring over a wide range of habitats (Welch et al. 2015). There has been a dramatic decline over the past century, from 100,000 individuals in 1900 to 12,000 in 1995 (Houser et al. 2009), now existing within just 9% of their former distribution range (Durant 1998; Vebber et al. 2020). Namibia and Botswana are believed to have the largest existing free-ranging populations in the world (Figure 2) (Vebber et al. 2020). With a decreasing population trend, cheetahs are listed as ‘vulnerable’ on the IUCN Red List of Threatened Species, with only an estimated 7100 adult and subadult individuals left (Welch et al. 2015; Durant et al. 2016; Weise et al. 2017). Most populations (91 %) contain less than 200 individuals. Both Weise et al. (2017) and Durant et al. (2017) recommended a revision of the cheetah’s threat status suggesting up-listing the species to ‘endangered’.

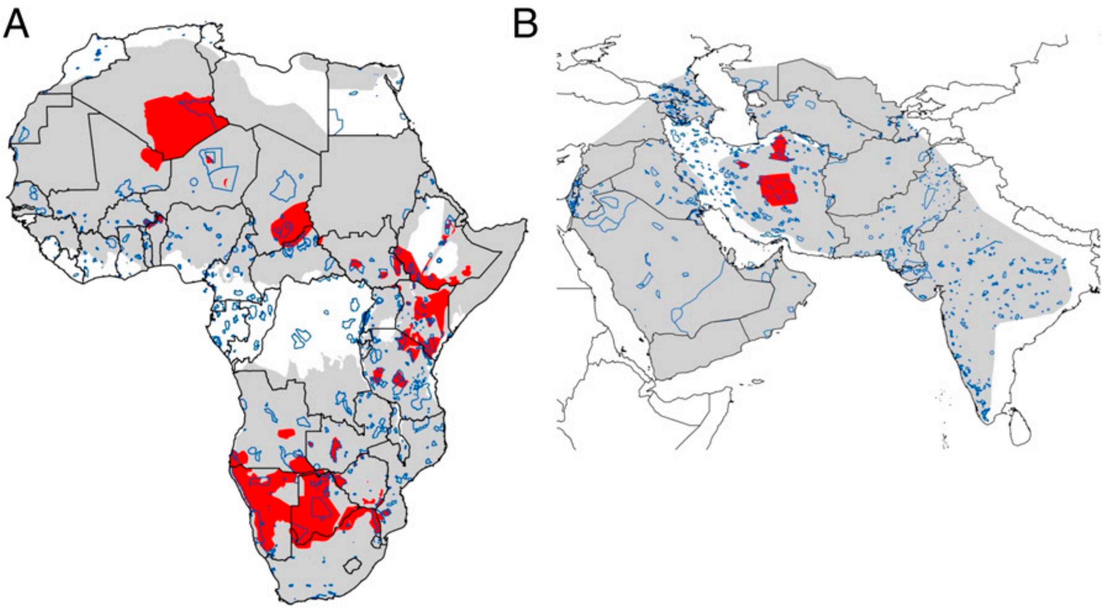


Figure 2: Known cheetah distribution in (A) Africa and (B) Asia. Grey is historical range, red is range where cheetahs are known to be resident, blue are the boundaries of protected areas (Durant et al. 2016).

Two key reasons for the decline in cheetah populations are human-wildlife conflict outside of protected areas, and their status as subordinate predators to lions, spotted hyena and leopards when they are living inside protected, fenced areas (Vebber et al. 2020). Outside of protected areas, cheetahs have been observed to have large home ranges, which increase their contact with humans and human settlements (Welch et al. 2015). The species thus has to overcome challenges like prey loss caused by overhunting and bushmeat harvesting, habitat loss, fragmentation and illegal trade (Welch et al. 2015; Durant et al. 2016). Some populations are to be expected to be in decline due to poorly managed protected areas. Such declines are likely to go undetected because of the survey and monitoring effort required, particularly for a wide-ranging and elusive species like the cheetah (Durant et al. 2016). Consequently, the establishment of fenced protected areas may present one of the greatest tools for the continuing survival of cheetahs. As mentioned earlier these enclosed systems require careful management because natural processes such as emigration, immigration and out-breeding cannot normally take place (Welch et al. 2015). However, inside protected areas they face threats like kleptoparasitism, intra-guild competition, disease and human interference (Hayward & Kerley 2008).

Social behaviour and habitat use

Home range sizes in cheetahs have shown large variation and vary greatly with vegetation type, prey density, sex, social grouping, age of cubs (Houser et al. 2009), migration of prey, size of area, human-wildlife conflict and the presence of apex predators (Welch et al. 2015). Home range estimates for cheetah range from 11 km^2 in Matusadona National Park in Zimbabwe (Purchase & du Toit 2001) to over 1651 km^2 in Namibia (Welch et al. 2015). These studies were conducted in conservation areas, where cheetahs are protected from human persecution but often subjected to high rates of intra-guild competition and kleptoparastism from lion and spotted hyena (Houser et al. 2009). Cheetahs may lose up to 12 % of kills to kleptoparasites (Hayward et al. 2006). According to different studies, the home ranges of male cheetahs are considerably smaller than that of the females. This is not often seen in carnivores and there are multiple possible explanations. In Kruger National Park and in Serengeti National Park, male cheetahs had smaller home ranges, but they were overlapping with multiple female territories (Broomhall et al. 2003). In another study conducted in a smaller enclosed reserve, by Welch et al. (2015) all female cheetahs were contracepted, which could be a possible reason for a smaller home range in males because no females came into oestrus. If females don’t come into oestrus it can affect their interactions with other male cheetahs. However, this theory has not been proven.

Cheetahs are able to tolerate a relatively wide range of environmental conditions, indicated by their large historical geographical range (Purchase & du Toit 2001) as seen in Figure 2. They are known as predators with a preference for open plains habitats, with early reports stating that they are savanna specialists, requiring open habitats to chase down prey at high speed. However, recently studies have indicated that cheetahs are utilising a wide range of habitat and denser vegetation for rearing cubs (Bissett & Bernard 2007; Houser et al. 2009; Welch et al. 2015). Females generally select areas of thicker vegetation than males, possibly for hiding their cubs from predators and from kleptoparisitsm. However, both males and females used the thickest vegetation equally (Welch et al. 2015). A study done by Broekhuis (2013) found significant cheetah habitat preference for grassland and woodland than would be expected within the study area. Within their home ranges they preferred grassland over woodland. They were found closer to lions in mixed woodlands, which suggests that when cheetahs are in more densely vegetated habitats they either cannot detect lions or do not feel the need to avoid them. Therefore, denser habitats may be a relatively safe refuge for cheetahs as the reduced visibility is likely to reduce detection.

Female cheetahs are solitary, unless dependent cubs accompany her. Male cheetahs can either be solitary or form a stable coalition. Coalitions generally exist of two to five unrelated or related males. Male roaming behaviour can be categorized in two groups: resistant males, who defend small territories possibly based on access to resources such as females, and floaters, who roam over vast areas that they do not defend. It is believed that cheetahs use a 'time-share approach'. This means that territories and home ranges can overlap but interactions are minimized by olfactory communication. Male territorial behaviour includes scent-marking (urinating and defecating) on marking posts (termite mounds, logs or trees). If males do encounter each other it can either be passive or acutely aggressive (Broekhuis et al. 2019). Coalitions have a number of benefits like improved territory acquisition-and defence and increased foraging efficiency. However, group living male cheetahs will catch larger prey and will be more visible, therefore they will attract more scavengers (Hunter et al. 2007a). Cheetahs exhibit a diurnal, crepuscular activity pattern with 62 % of activity occurring during the day, mainly occurring around dusk. Cheetahs were significantly more active between 16:00 and 17:00 and in the four hours between 18:00 and 21:00, they also showed peak activity from 9:00 until 11:00 (Hayward & Slotow 2009). Cheetahs are sometimes nocturnally active despite the threat from more dominant predators, possibly to avoid heat stress (Hetem et al. 2019).

Cheetahs have been described to be a 'refugial species'. They may adjust their behaviour, for example, habitat use or anti-predator behaviours such as vigilance, in response to changing levels of risk (Broekhuis et al. 2013). A response can be either reactive or predicative. A reactive response to risk is based on an animals' knowledge of actual, real-time risk. A predictive response is based on a pre-emptive response to a potential risk, this is driven by previous knowledge of the competitors or predators' whereabouts (Broekhuis et al. 2013; Balme et al. 2017). Due to their smaller body size and solitary nature, cheetahs are subordinate to the larger and more social lion (Durant 1998; Broekhuis et al. 2013). In Serengeti National Park, cheetahs lose 10-12 % of their kills to behaviourally dominant scavengers, and lions and spotted hyenas have been known to kill 73 % of dependent cheetah cubs. These agonistic interactions between cheetahs and larger carnivores can seriously impact the long-term viability of cheetah populations (Hunter et al. 2007a; Broekhuis et al. 2013). According to Broekhuis (2013) cheetahs did not consistently avoid habitats and areas with a high likelihood of encountering lions or spotted hyenas (predictive response), but instead they adjusted their behaviour in short-term presence of lion risk (reactive response). Thus, they tend not to avoid areas with a high likelihood of encountering lions, but rather react to the immediate presence of lions (Balme et al. 2017).

Diet and prey selection

According to Kingdon (2013) cheetahs do most of their hunting during the early hours of the morning and late afternoon, largely to avoid competition with other larger predators. Thus, it may help them reduce kleptoparasitism and interference from lions and spotted hyenas (Palomares & Caro 1999). They are the fastest living land mammals with speeds of up to 112 km/h, made possible by their highly flexible spine. The former wide distribution range of cheetah suggests it is capable of killing a wide range of prey species. It has been reported to catch hares (*Lepus* spp.) from 2 kg to zebras weighing up to 279 kg. Hunting group size varies from solitary individuals, to females with cubs and coalitions of territorial males. Larger groups have higher hunting success rate (Hayward et al. 2006).

Hayward (2006) analysed 19 published studies covering 3909 cheetah kills of 58 prey species. He concluded that cheetah preferentially preys upon medium-sized prey (23-56 kg). Five species are significantly preferred: blesbok (*Damaliscus pygargus phillipsi)*, impala *(Aepyceros melampus)*, springbok *(Antidorcas marsupialis)*, Thomson's gazelles (*Eudorcas thomsonii)* and Grant's gazelles *(Nanger granti)*. In contrast to lions that select prey based upon its body mass, cheetah select prey based on its abundance. However, there is still substantial overlap in the diets of the two predator species (Hayward et al. 2006). In another study done by Bissett and Bernard

(2007), where the vegetation of the study area resembles the vegetation in this study, species that were killed most often were: kudu, springbok, grey duiker *(Sylvicapra grimmia),* impala and harnessed bushbuck *(Tragelaphus scriptus)*. Knowing what prey species are needed and preferred will help to increase the density of cheetahs and will be useful for further conservation strategies, especially in small, fenced game reserves.

3. Aims of the Thesis

In South Africa, many game reserves are small, fenced and managed. This means that individuals cannot naturally disperse, as they would if they were free-roaming animals. Research and monitoring animals in small, fenced reserves could detect potential intra-guild competition of predators over a certain resource, for example, if they prefer the same vegetation types, if there is sufficient prey available or if they are eating the same prey species. All the above could provide valuable information for management implications of having lions and cheetahs on a small, enclosed reserve.

The aims and goals in this study are focused on only a small number of individuals within Amakhala Game Reserve and can therefore not be generalized for other, larger, game reserves. The fundamental goal of this thesis was to investigate the home ranges, habitat preference and feeding behaviour of cheetahs and lions within Amakhala Game Reserve. Based on these results potential interspecies competition may be exposed between these large carnivores. Thus, the outcome of this study may be inferred as having implications for wildlife management in the selected reserve. In order to make these implications, we have set three aims. First, we aimed to determine the home and core ranges and the spatial overlap of lions and cheetahs in the study area. Second, we aimed to determine the habitat preference of lions and cheetahs in the reserve. Lastly, we aimed to determine the prey selection and potential overlap in prey species of cheetahs and lions in the study area. Based on these aims we have set up four research questions:

1. Is there any intraspecies and interspecies spatial overlap in the core ranges of cheetahs and lions in Amakhala Game Reserve?
2. Does the interspecies and intraspecies spatial overlap in the core ranges between cheetahs and lions in Amakhala Game Reserve vary annually?
3. Is there a difference in habitat preference of cheetahs and lions in Amakhala Game Reserve?
4. Is there a difference in prey selection for lions and cheetahs in Amakhala Game Reserve?

4. Material and methods

4.1. Study area

This study was conducted at Amakhala Game Reserve (AGR) (26°2′–26° 11′E, and 33°30′–33° 36′S) an 8,500 ha, fully fenced reserve which lies approximately 90 km northeast of Port Elizabeth in the Eastern Cape province of South Africa (Figure 3). The reserve is located in an Albany thicket region. The reserve has a long history of goat farming that has transformed the area to open grassland with patches of thicket and blue bush *(Pteronia incana)* invasion on parts of its degraded land (Zengeni & Kakembo 2017). Amakhala was formed in 1999 where it began as a conservation venture that converted farmland into game land (Zengeni et al. 2016; Zengeni & Kakembo 2017). It has been extended by the acquisition of adjacent farms and the co-operation of surrounding owners: this has led to fences being removed between neighbouring farms. Various wildlife that would have been found in the area were again introduced, including lions, cheetahs, leopard, elephants *(Loxodonta africana)*, various antelope species and other mammals, to ensure conservation of animal and plant species.

AGR is semi-arid with an average mean annual rainfall of 533 mm within a range of 298 mm (2019) and 788 mm (2015). Mean summer minimum and maximum temperatures range from 16 to 30 °C, while winter minimum and maximum temperatures range between 5 and 22 °C, respectively (Zengeni, et al., 2016). AGR consists of a Northern section and a more Southern main reserve intersected by a main road. Both sections are fully fenced. This study focuses on the main reserve (60.09 km^2) and it includes the Bushman's River that goes through the northeast part of the main reserve, which is partially dried out. Furthermore, the main reserve includes 32 water access points (2019), of which 9 are artificial (man-made dams and reservoirs), and 23 natural pans and waterholes. Some of the water access points may have been empty for a certain amount of time during the study period.

4.1.1. Vegetation types in the study area

The Albany district in the Eastern Cape province of South Africa is rich in history both in terms of natural and geological features, but also in the complex narrative of human influence that has characterised the landscape. It is primarily known for the Thicket biome, which is characterized by spekboom *(Portulacaria afra)*, euphorbia and aloe species. The majority of the vegetation on AGR today has been shaped to a large extent by historical human influences, such as beef and dairy farming, angora goats and the cultivation of crops. This reserve encompasses a stretch of rolling hills, grassy plains and the Bushman's River. AGR is divided into eight vegetation types (Figure 3), which resembles other biomes, but they are not strictly true representations of those biomes, e.g. savanna. The determination of plant species and the vegetation types is done by Amakhala Ecology Unit based on the book "The vegetation of South Africa, Lesotho and Swaziland" written by Mucina and Rutherford (2006) (Hoare et al. 2006).

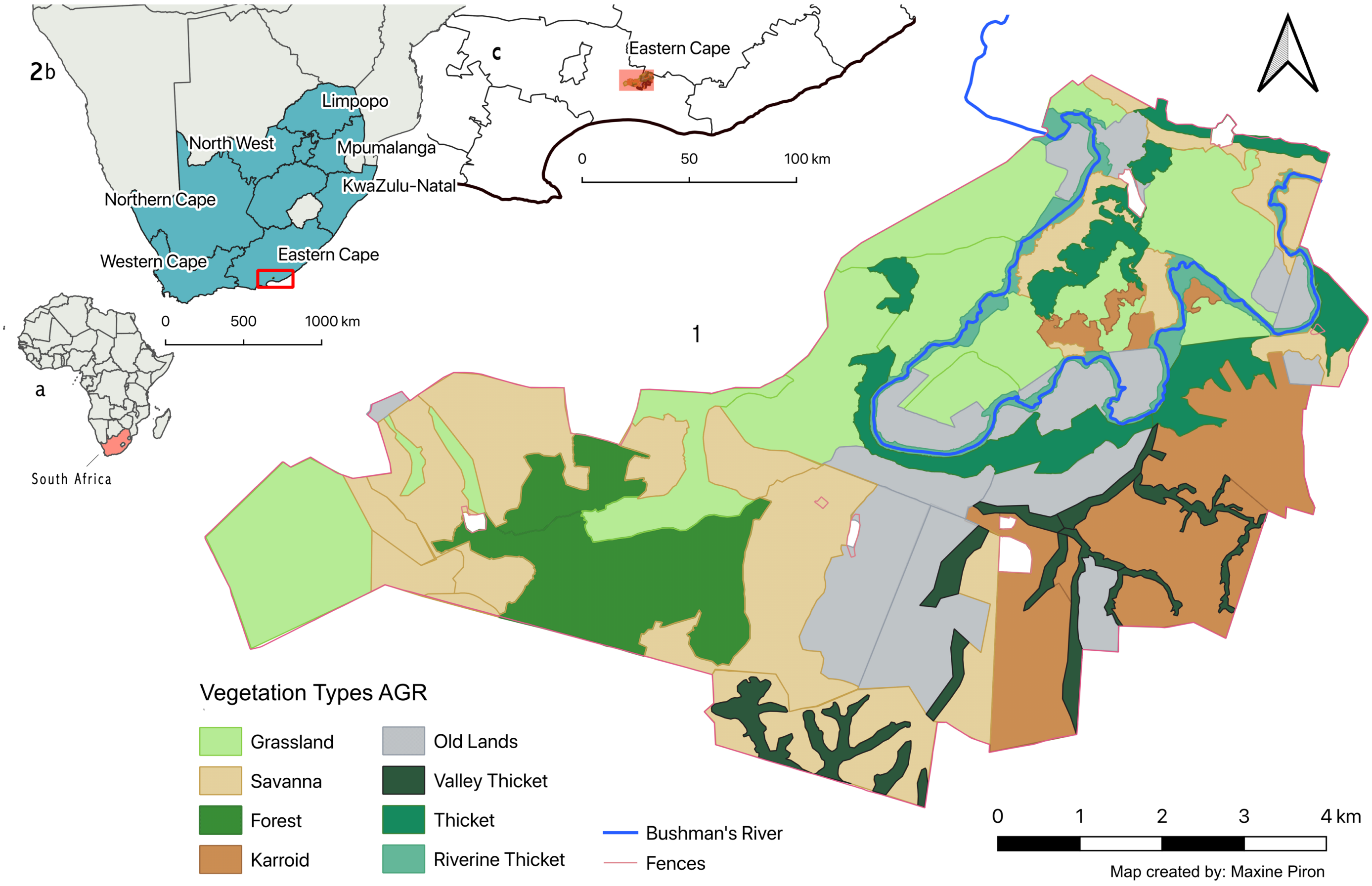


Figure 3: Vegetation types on Amakhala Game Reserve (1), located in the Eastern Cape province (2c), in South Africa (2a, 2b).

Table 1: The area (km^2) and percentage of each vegetation type at the main reserve of AGR.

Vegetation Type	Area (km^2)	%
Forest	5.20	8.72 %
Grasslands	14.81	24.84 %
Karroid	7.78	13.05 %
Old Lands	8.98	15.06 %
Riverine Thicket	2.19	3.67 %
Savanna	14.05	23.58 %
Thicket	3.98	6.68 %
Valley Thicket	2.62	4.40 %
Total	**59.60**	**100 %**

The total area within the main exterior fence is 60.09 km^2, of which 59.60 km^2 (Table 1) is determined as vegetation type, the remaining 0.49 km^2 are lodges within the interior fences.

Forest

This stretch of the Albany Coastal Belt is found in the southwestern section of AGR with sandy substrates of the Nanaga Formation. It is colloquially referred to as the "dune forest." Common species include *Zanthoxylum capense, Pterocelastrus tricuspidatus, Canthium inerme, Gymnosporia nemorosa, Brachylaena discolour* and *Diospyros dichrophylla*. It contains a grass layer that is lacking in other thicket vegetation types. Dominant grasses are *Panicum coloratum, Digitaria eriantha, Eragrostis curvula* and *Tristachya leucothrix.* It is also referred to as mesic thicket.

Grassland

The grasslands found on AGR have typically been cleared in the past for farming and now provide forage for grazing species. Generally, an area is classified as grassland if it contains less than 30% tree cover. The lower lying grassland areas, typically on clay and alluvial sediments are dominated by *Themeda triandra, Eragrostis curvula, Digitaria eriantha* and *Cynodon dactylon.* At altitudes above 400 m *Themeda triandra, Heteropogon contortus, Eragrostis curvula, Brachiaria serriata, Sporobolus africanus,* and *Tristachya leucothri* are common. *Rhus longispina* and *Acacia karroo* are the dominant tree species found in the grassland areas.

Old lands

Old lands were used for cultivating crops and are in various stages of rehabilitation. In the early stages of succession, they are dominated by ephemeral weedy species such as horseweed (*Conyza scabrida),* coastal galenia *(Galenia pubescens)* and common saltwort (*Salsola kali*).

Karroid

The high percentage of succulents is characteristic as a major diagnostic feature, in particular *Portulacaria afra,* which acts as an indicator species, as well as the dominant species. Other indicator species are *Crassula muscosa* and *C. perforate*, *Schotia afra, Carissa bispinosa, Pappea capensis, Euclea undulata, Sideroxylon inerme* and Aloe spp*.* It generally occurs on slopes subject to direct radiation from the sun, and therefore dominates north-facing slopes.

Riverine Thicket

This vegetation type encompasses the riparian margin of the Bushman's River. The indicator species are *Combretum caffrum, Salix mucronata, Acacia caffa, A. karroo, Celtis africana, Rhus lancea* and *Plumbago auriculata.*

Savanna

The term savanna is used to loosely describe any area on AGR with a tree cover ranging from 30 % to 70 %. *Acaicia karroo* is by far the most common tree species found in savanna vegetation types and can totally dominate some areas. Other common species include *Diospyros dichrophylla, Rhus pyroides, R. lucida, Olea europaea, Euclea undulata, E. natalensis* and *Scutia myrtina*. The dominant perennial grasses are *Themeda triandra, Eragrostis curvula, Digitaria eriantha* and *Tristachya leucothri*.

Albany Thicket

The Albany Thicket Biome is part of a poorly defined global Subtropical Thicket Biome, characterised by subtropical, semi-xeric conditions. It consists of various major vegetation types, and a wide variety of plant communities. This poses a challenge for researchers to describe it (Hoare et al. 2006). On AGR the vegetation of the Albany

Thicket Biome is described as a dense, woody, semi-succulent and thorny vegetation type of an average height of 2 - 3 m.

Valley Thicket

Valley thicket is also referred to as Woody Subtropical Thicket and generally occurs on the south facing areas or slopes where direct radiation from the sun is reduced. The absence of succulents *Portulacaria afra* and *Crassula* spp. differentiate it from the Xeric Thicket. Species characteristic to Valley Thicket are *Euphorbia triangularis, Olea europaea, Ptaeroxylon obliquum, Cassine aethiopica, Scutia myrtina* and *Cussonia spicata*.

4.1.2. Studied animals

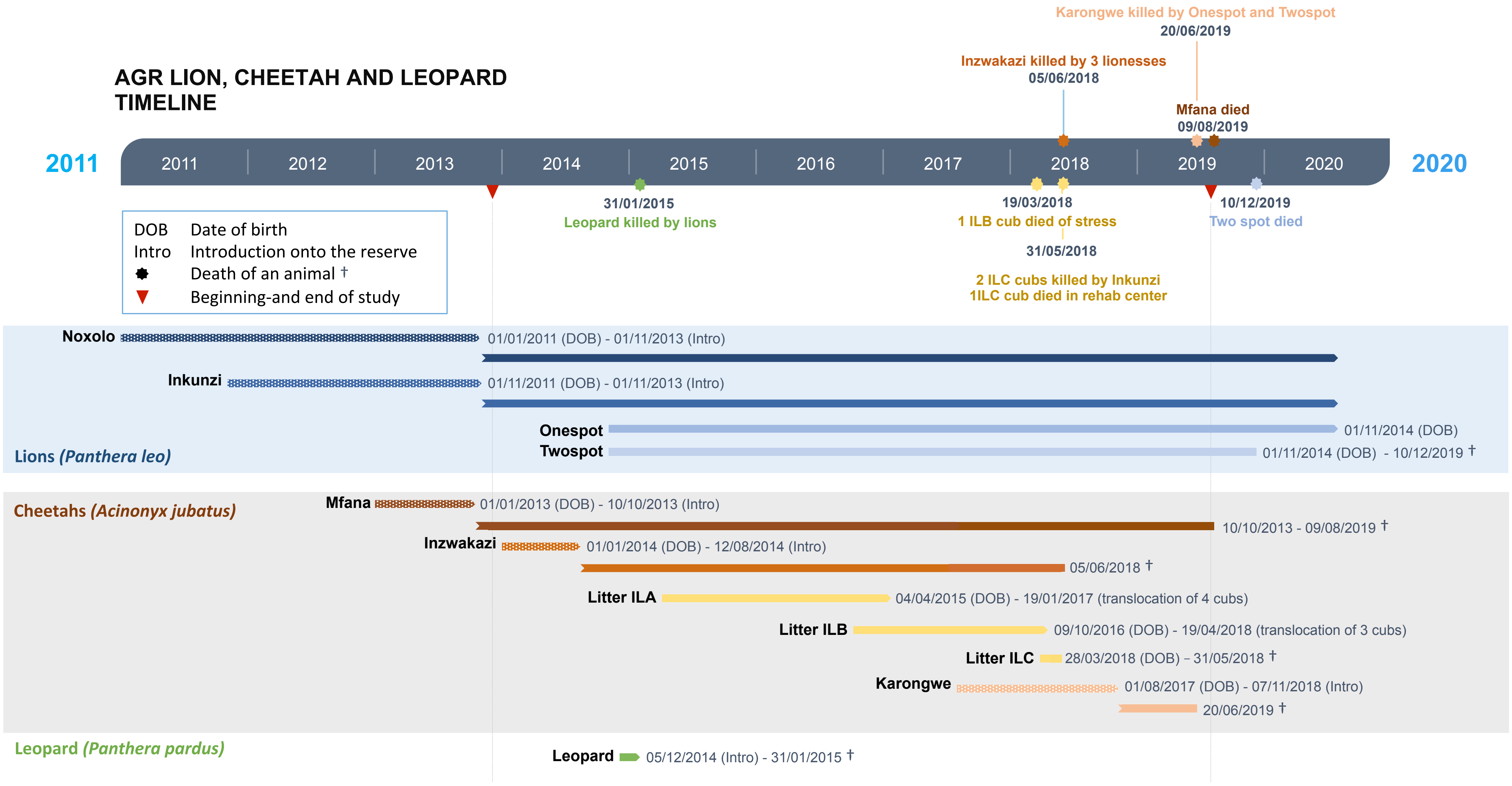
Between October 2013 and August 2019, there were a total of two adult lions: Inkunzi (male) and Noxolo (female) and a total of three adult cheetahs: Mfana (male), Inzwakazi (female) and Karongwe (female) introduced. The two lions had one litter consisting of two females (Onespot and Twospot), and the cheetahs: Inzwakazi and Mfana had a total of three litters (ILA, ILB and ILC) during the study period (Figure 4). Two leopards were also introduced during the study period. One got attacked by the lions two months post introduction and died in a boma two days later. Both leopards will not be considered in the study due to the short amount of release and therefore a lack of data.

Lions in the study area

There were four individual lions during the study period in the study area. In November 2013 Noxolo (female) and Inkunzi (male) were introduced. They came from two different game reserves, were placed in a boma together at AGR and were released onto the reserve one month later. One year later, in November 2014 they had their first litter together. Two female cubs were born: Onespot and Twospot (Figure 4). For management purposes and to prevent inbreeding was Noxolo contracepted on the 6th of August 2015 with Deslorelin after having received her first litter. Inkunzi got a vasectomy 6th of February 2018 and Onespot and Twospot were also contracepted with Deslorelin on the 21st of October 2016. Deslorelin as a contraceptive has been successfully used in other wild carnivores, it blocks the hormone GnRH (Gonadotropin-releasing hormone), and under this method the individual does not have an oestrus cycle. It involves anaesthetizing the lioness (Kettles & Slotow 2009). Twospot escaped and died on the 10th of December 2019.

Cheetahs in the study area

There were three adult cheetahs introduced in the study area between 2013 and 2019 (Figure 4). Mfana (male) got introduced 10th of October 2013 after being placed in a boma for a month. Inzwakazi (female) was introduced by hard release in August 2014. Mfana and Inzwakazi produced three litters together (ILA, ILB, ILC) between the years 2015 and 2018 with a total of eleven cubs (five females, six males). Therefore, Inzwakazi was either pregnant or had dependent cubs during most of the study. Mean time between successive progeny was 544.5 ± 13.44 SD days. Seven out of 11 cubs were successfully translocated and released in other game reserves and national parks. One cub of the ILB litter died because of stress and broken metacarpals, Inkunzi and Noxolo killed two cubs of the ILC litter, this was five days prior to the killing of Inzwakazi in June 2018 by the lionesses. The remaining ILC cub was taken to a wildlife rehabilitation centre where it died one week later. In order to create some genetic diversity and to replace Inzwakazi, Karongwe (female) was introduced in November 2018 but the lion offspring (Onespot and Twospot) killed her eight months later. Mfana died in August 2019 because of an anaesthetic complication due to an underlying heart condition during his last collar change procedure.



Timeline created by: Maxine Piron

Figure 4: Lion, cheetah and leopard timeline at Amakhala Game Reserve (2011 – 2019), during the study period (01/11/2013 – 01/08/2019), where the full lines represent animals that were present on the reserve, and dotted lines represent animals that were not introduced on the reserve yet.

4.2. Data collection

4.2.1. Field observations

Sighting and location data were collected on key species at AGR for the purpose of gathering information on animals that are not commonly seen in the reserve and to make future management decisions. The information collected includes: the species, date, time, the grid reference, type of sighting and the person who recorded the sighting. Each main grid (525m x 530 m) is divided into a sub grid of nine smaller squares for accuracy. The type of a sighting could either be: visual, spoor, scat, den or carcass. The AGR Ecology Unit collected handwritten latitude-longitude sightings (locations/ datapoints) for every lion and cheetah almost twice daily during the whole study period. Sightings were reported within a sub grid size of 175 m x 176.67 m. AGR hosts several eco-tourism lodges that operate photosafaris and game drives. Therefore, opportunistic sightings and direct observations were also recorded and reported by rangers or field guides on morning (7:00–10:00)-and evening (16:00–19:00) game drives. The times of the game drives may vary according to season. If the cheetahs and lions were not opportunistically seen, the Ecology Unit used telemetry to locate them. However, when the animals were not seen directly, due to dense vegetation, triangulation assisted with a VHF receiver narrowed their location down within the grid size. There were a few occasions when animals were not seen or found some days and therefore did not have a recorded location for that particular day. Other parameters recorded were: date and time, location, condition of the animal and vegetation categories.

All adult, introduced animals in this study (Inkunzi, Noxolo, Mfana, Inzwakazi and Karongwe) had VHF collars made by African Wildlife Tracking (AWT cc, Pretoria, South Africa). Different sizes were provided for different species. Inkunzi (male lion) had the same collar but with GPS capability. During the whole period of the study he had three collar changes. The first collar after release gave readings every four hours, which gave approximately six locations daily. The first collar was changed in November 2015 and the second collar gave four readings daily. The GPS of the second collar stopped working in November 2017 and was only removed and changed in February 2018. Between August 2017 and November 2017, the collar was set to give one reading a day. The third and last collar was set to four readings a day and failed in October 2019. This explains why the fixes for Inkunzi are not consistent over different years. However, alongside his GPS fixes he still was tracked by the Ecology Unit and recorded by rangers during game drives, also providing location data. Noxolo's (female lion) collar was changed twice during the study period (July 2017 and August 2019). Onespot and Twospots (lion offspring) independent location data collection started at the end of August 2016 (24/08/2016). They both did not have a collar, but they were monitored by direct observations by the Ecology Unit and by rangers on game drives.

All adult, introduced cheetahs also had collar changes. Mfana had collar changes in August 2016 and July 2017. Inzwakazi had one collar change in September 2016. The litters ILA had independent recordings from 26/06/2015 until 07/02/2017 and so did the ILB litter from 30/11/2016 until 10/04/2018. The ILC litter did not have individual data because the mother died two months post giving birth.

4.2.2. Vegetation data

Habitats were grouped into eight major vegetation types as described in paragraph 4.1.1. Vegetation types in the study area were: (1) forest, (2) grassland, (3) karroid, (4) old lands, (5) riverine thicket, (6) savanna, (7) thicket and (8) valley thicket (Table 1, Figure 3). The determination of each vegetation type was based on the habitat evaluation described by Bothma and du Toit (2016). All habitat fixes (82) were plotted onto a basemap and hand-digitalized to create a layer for each vegetation type in QGIS. The vegetation map does not fully account for minor variations in vegetation cover. These layers were used to determine habitat preferences for each predator species.

4.2.3. Prey data

All kill data is gathered by direct observations. Cheetah kill data used for analysis in this study was recorded from 04/11/2013 until 29/07/2019 and lion kill data was collected from 25/12/2013 until 29/07/2019. The Ecology Unit collected this data during monitoring sessions and reports from rangers during early morning and late afternoon tourist game drives. The following information was recorded when a kill was found: date, time, which predator made the kill, which prey species got killed, age of the prey species (adult > 24 months, subadult < 24 months, juvenile < 12 months), sex of the prey, longitude and latitude and extra notes. The prey species for the lions and cheetahs in AGR are found under Appendix 1.

Increase of fullness or "belly scores" were also recorded to enable the allocation of missed kills using substantial increases in abdomen as an indicator of a kill having taken place. This was a subjective score ranging from one, which was an empty stomach, to five, being a full stomach. This scoring system gives an indication of the size of prey species caught when carcasses were not found. However, small kills would not necessarily have been accounted for from the belly scores.

An annual game count was done every year to calculate the carrying capacity of herbivores. The Ecology Unit of AGR did an annual aerial survey and vehicle counts by driving every road in the reserve while counting all the predetermined animals. Species they included in the annual game count were: aardvark (*Orycteropus afer)*, blesbok, buffalo, cape bushbuck *(Tragelaphus sylvaticus)*, cheetah, common duiker *(Sylvicapra grimmia)*, eland, elephant, gemsbok*,* giraffe *(Giraffa camelopardalis)*, red hartebeest, hippopotamus (*Hippopotamus amphibius)*, impala, black-backed jackal, kudu, lion, ostrich *(Struthio camelus)*, mountain reedbuck (*Redunca fulvorufula)*, springbok, warthog, waterbuck (*Kobus ellipsiprymnus),* black wildebeest (*Connochaetes gnou)* and Burchell's zebra (*Equus quagga burchellii*). In these game counts the sums of: adult females, adult males, unsexed adults, total adults, subadult males, subadult females, unsexed subadults, total subadults, juvenile females, juvenile males, unsexed juveniles, total juveniles and total individuals were collected. This count method was not chosen for its accuracy but rather for its ability to show trends in the prey population numbers over the years. Therefore, no abundance estimations were calculated from this data. Smaller, solitary species may be underrepresented when using this method.

4.3. Data analyses

For each individual and for each species the 95 % home ranges and the 50 % core ranges were assessed annually. Then, it was investigated if there was any annual, spatial overlap between the core and home ranges of the individuals. Third, the general habitat preference was determined for each individual within the core range (50 %) and over the whole area (100 %) for each year. Finally, it was examined which prey was eaten most often, and which prey weight category was preferred by each species.

4.3.1. Statistical methods and software

Various software packages were used to analyse the above-described data. All data were entered into different spreadsheets and Excel (Version 16.37) was used for managing and organizing all the datasets. Spatial data usually require a geographic information system, and in this study, QGIS (Quantum Geographic Information System, version 3.10.2 – A Coruna, Boston, USA) was used, which is a free and open-source program. In this study the location sightings do not extend outside of one respective UTM (Universal Transverse Mercator) zone (UTM zone 35S). Therefore, all analyses were done in this projection. The R environment (R Core Team 2015, version 1.3.959, Boston, USA) and BCO Statistica 13 package (TIBCO Software Inc., Palo Alto, USA) were used for statistical analyses and determining home- and core ranges for each individual.

Home range and core range

VHF sighting data and direct observations were recorded daily over the study period (November 2013 – July 2019). The mean annual number of datapoints for each individual can be found in Table 2. It was chosen to include all the recorded datapoints per individual to increase the accuracy of the home- and core range estimation for each animal.

To determine the home and core ranges of each individual the package *adehabitatHR* (Calenge 2006) in the R statistical environment (R Core Team 2015) was used (Balme et al. 2017). With 95 % kernel being used as the estimate of home range and the 50 % kernel as an estimate of core range. Most studies define home range as the smallest area containing 95 % of the distribution, excluding occasional sallies outside their normal range (Druce et al. 2004). The reference bandwidth (H_{ref}) was used as smoothing factor of the kernel as suggested by the ad hoc default of the software (Balme et al. 2017). This gave an output of the home and core ranges per animal per year and the total home and core ranges for the entire study period of each animal. The home and core ranges were subsequently clipped to the park boundary in the cases where kernel utilization distribution exceeded the park boundary. These outcomes were plotted in QGIS to detect and calculate the spatial overlap among individuals (intraspecies overlap) and between individuals (interspecies overlap). In order to estimate if there was a significant difference in the core range sizes of cheetahs and lions, the non-parametric Wilcoxon Rank-Sum Test was used in the statistical R environment (version 1.3.959).

Table 2: Total number of datapoints in the study period and annual mean number of datapoints per year per individual lion and cheetah.

Species	Individual	Year	Total number of datapoints	Mean annual datapoints	SD
Lion	Inkunzi	2013 – 2019	6685	955	939.94
	Noxolo	2013 – 2019	2277	325	149.49
	Onespot	2016 – 2019	1071	267.8	142.08
	Twospot	2016 – 2019	1162	290.5	136.53
Cheetah	Mfana	2013 – 2019	1714	244.9	93.84
	Inzwakazi	2013 – 2018	1374	274.8	131.2
	Karongwe	2018 – 2019	293	146.5	79.9
	ILA	2015 – 2017	493	196.7	69.69
	ILB	2016 – 2018	558	186	202.72
	ILC	2018	18	18	-

Spatial overlap

Lion and cheetah home ranges and territories may overlap, but each individual maintains a core area where most activities are undertaken. An intersection of the home ranges and core ranges was made in QGIS to estimate if there was any interspecies or intraspecies spatial overlap. The overlap between two individuals was calculated in km^2 using QGIS. Then, each proportion of overlap was calculated, using the home range overlap equation as adapted by Welch et al. (2015) using dyads and pair-wise combinations:

$$\%\ \text{Overlap} = \frac{2 \times overlap}{area_A + area_B} \times 100$$

where *area* represents the home range or core range of individual A and B, and where *overlap* signifies the total overlap between individual A and B (Poole 1995; Cristescu et al. 2013; Welch et al. 2015). This allows for the area of overlap to be perceived as a proportion of the total home range or core range.

In order to estimate the overlap between both species (lions and cheetahs) the total area occupied by all the lions, cheetahs and lion offspring per year was used, as illustrated in Table 7. Merging the polygons for all the individuals of a certain species, per year, together in QGIS created the areas described this table.

Habitat preferences

In order to determine in what vegetation type the lions and cheetahs spend most of their time, the vegetation map of AGR has been used. These layers were used to determine availability of each vegetation type in each individual core range, defined as the proportion of the core range composed of each vegetation type (Spong 2002). The availability of habitats was constant during the study period and each observation of an animal represented an independent choice taken from the pool of available habitats (Arthur et al. 1996). From the data collected during individual encounters, the habitat preference of lions and cheetahs was calculated as the proportion of all data points that fell in each vegetation type (Spong 2002). The vegetation types at each location datapoint were compared with the vegetation types available within AGR and within the core range. To detect whether each species used the vegetation types in accordance to their availability, the Ivlev's electivity index (E) was used:

$$\text{E} = \frac{(p - q)}{(p + q)}$$

where p is the proportion of habitat used and q is the proportion of habitat available. It has values ranging from –1 to 1. Avoidance of a habitat occurred when p was less than q ($E < 0$) and habitat preference took place when p was greater than q ($E > 0$), 0 indicates that the habitat was used according to its availability (Broekhuis et al. 2013; Balme et al. 2017). The Ivlev's indices were calculated for the core range (50 %) and for the total area (100 %) of each animal per year.

To test whether cheetahs and lions selected for a specific vegetation type in the total area, data distribution, i.e. normality, of the indices was tested using the Kolmogorov-Smirnov test. Furthermore, (1) to test the difference between species, Generalized Linear Models (GLM) were used with Ivlev's index as dependent variable and interaction "species*vegetation type" as predictor. (2) To test the difference between species in selection for each vegetation type, separate t-tests were used. (3) To test the difference among individuals within a species, Generalized Linear Models (GLM) for each species separately was used with Ivlev's index as dependent variable and interaction "individual*vegetation type" as predictor. For the 50 % core range the data was not normally distributed. However, there were sufficient numbers of independent cases in the analysis and therefore parametric tests were used. (1) To test the difference between species, GLM was used again, with Ivlev's index as a dependent variable and "vegetation type*species" as a predictor. (2) To test the difference between species in selection for each vegetation type, separate t-tests were used for each vegetation type. (3) To test the difference among individuals within a species, separate ANOVAs were used, with Ivlev's index as dependent variable and interaction "individual*vegetation" as predictor. All analyses on habitat preferences were performed in the TIBCO Statistica 13 package (TIBCO Software Inc., Palo Alto, USA).

Prey selection

Due to the opportunistic nature and group hunting strategies in the lions, the lion kill data was divided in seven groups by who made the kill: Inkunzi, Noxolo, Inkunzi and Noxolo, Noxolo offspring, core female pride, pride, or unknown. Because of the small sample size of individual kills by the offspring it was decided to put Onespot and Twospots individual kills and the kills they made together under one group: 'Noxolo offspring'. 'Core female pride' means a kill was made by all the female lions together. The category 'pride' relates to all four lions together at the kill site, however, it was not always specified who made the actual kill. 'Unknown' was assigned when a kill was found surrounded with lion tracks, but the lion that made the kill was not identified. The cheetahs all hunted solitarily at AGR and each individual had individual kill recordings: Mfana, Inzwakazi, Karongwe. There were also independent recordings for the ILA and ILB litter. The term ‘cheetah in the main reserve’ was used when they were hunting together. During the collection of the data the term ‘unknown prey’ was sometimes used, this is an observed increase in the fullness in the animal, allowing the researchers to determine if the predator had fed. However, there was no visual recording of the killing or there was no carcass found, and therefore this data was not included in the analyses but, it was used for the descriptive part of the prey selection results. The term ‘unknown prey’ was also used when predators were on a kill, but the kill could not be identified due to tall grasses, thicket or when only bones were left.

Kills were assigned to one of four size classes: small (< 30 kg), medium (31 – 99 kg), large (100 – 199 kg) and very large (> 200 kg). Estimates from adult male and female prey bodymass were taken from Kingdon at al. (2013), Radloff et al. (2004), and Hayward (2007). In the absence of growth curves for all prey species, male and female adult mass was multiplied by 0.7 to approximate subadult mass. The juvenile mass was estimated by taking the average of the male and female adult mass and multiplying it by 0.3 (Balme et al. 2017). The annual game count data was also categorized in those four classes. However, smaller kills may have been underrepresented due to the opportunistic nature of the data collection during the day (Radloff & du Toit 2004).

Due to overdispersion of the data (the variance is not equal to the mean), the Quasi-Poisson Regression in R statistical environment (R Core Team 2015, version 1.3.959, Boston, USA) was used. This was used to determine if there was a preference for a certain weight category for cheetahs and for lions. In this analysis the response variable was ‘count’, the predictor variables were ‘category’ and ‘year’ and as an offset the ‘game count data’ was used. Game counts were included as exposure in the model since it differed between years. To detect whether there was an association between species and prey category, another Quasi-Poisson Regression was used, with ‘count’ as response variable, ‘weight category’ and ‘predator’ as predictor variable, and again the game count data was used as offset.

5. Results

5.1. Home range estimations

The home and core range calculations were done for four adult lions, three adult cheetahs and three cheetah litters in Amakhala Game Reserve. This gave an output of the home ranges and core ranges per animal per year (2013 – 2019) and the total home ranges and core ranges per animal over the entire study period. Furthermore, individual overlaps were calculated annually for the home ranges (95 %) and core ranges (50 %).

5.1.1. Lion home and core ranges

Individual lion home range estimations ranged from 31.94 km^2 to 53.55 km^2 (Table 3) for the whole duration of the study. Lions generally used the North East side of Amakhala Game Reserve, but spread out almost over the full area (60.09 km^2), with exception of the southwest area of the reserve (Figure 5). Core ranges varied between 7.13 km^2 and 14.76 km^2 (Table 3). There was a big increase in home range and core range sizes after introduction in 2013 of Inkunzi and Noxolo in contrast with the end of the study in 2019. After release in 2013, Inkunzi had a home range size of 2.58 km^2 that expanded to 55.91 km^2 in 2018. Over a seven-year period his home range increased, with a mean of 34.13 ± 19.47 SD km^2, and his core range enlarged from 0.52 km^2 to 12.74 km^2 in 2019, with a mean of 8.67 ± 5.30 SD km^2. The collective mean core range for all the lions (n = 4) for the whole study period encompassed an area of 11.49 ± 3.66 SD km^2 and the mean home range covered an area of 46.24 ± 10.14 SD km^2 , calculated using the estimates in Table 3.

Table 3: Lion individual core ranges (50 %) and home ranges (95 %) in km^2 over the whole study period, calculated by the total number of datapoints for each animal. Including the mean and standard deviation (SD) per individual lion in between years.

Individual	n_{years}	**Nr. of datapoints**	**Area (km^2) 50 %**			**Area (km^2) 95 %**		
			50 % CR	Mean	SD	95 % CR	Mean	SD
Inkunzi	7	6685	7.13	8.67	5.30	31.94	34.13	19.47
Noxolo	7	2277	9.80	9.82	6.40	46.14	33.79	21.22
Onespot	4	1071	14.26	14.7	4.11	53.33	48.71	12.65
Twospot	4	1162	14.76	15.28	3.96	53.55	48.81	12.25

Table 4: Lion individual core ranges (50 %) and home ranges (95 %) in km^2 for each year. Rows coloured in grey are home and core ranges that do not account for a full year. Numbers in bold indicate that there were less than 60 datapoints.

Individual	**Year**	**Number of datapoints**	**Area (km^2) 50 %**	**Area (km^2) 95 %**
Inkunzi	2013	80	0.53	2.58
Inkunzi	2014	2626	4.83	22.34
Inkunzi	2015	1089	5.33	22.36
Inkunzi	2016	1768	9.15	34.99
Inkunzi	2017	528	13.04	49.73
Inkunzi	2018	386	15.04	55.91
Inkunzi	2019	208	12.74	50.98
Noxolo	2013	**18**	0.86	3.28
Noxolo	2014	401	5.76	20.64
Noxolo	2015	405	4.79	18.88
Noxolo	2016	361	8.82	29.01
Noxolo	2017	434	15.42	51.77
Noxolo	2018	414	17.05	57.26
Noxolo	2019	244	16.09	55.69
Onespot	2016	98	8.99	30.23
Onespot	2017	399	14.87	51.46
Onespot	2018	370	18.64	58.52
Onespot	2019	204	16.31	54.62
Twospot	2016	97	9.85	30.98
Twospot	2017	400	14.91	51.41
Twospot	2018	371	18.78	58.64
Twospot	2019	294	17.56	54.21

5.1.2. Cheetah home and core ranges

Cheetah individual home ranges varied from 56.84 km^2 to 60.09 km^2, and therefore covered almost the whole area (Figure 5). The core ranges varied in size from 20.29 km^2 to 37.14 km^2 (Table 5). Individual annual home ranges and core ranges did not differ that much over the years, female adult cheetahs had bigger core ranges than the male adult cheetah (Table 6). According to Spong et al. (2002) there should be at least 60 datapoints used to estimate a home range. The litter ILC was therefore not taken into account because it had only 18 datapoints over its whole study period. The entire core range for all the cheetahs and litters together, excluding litter ILC (n = 5) for the whole study period covered a mean area of 28.13 ± 6.85 SD km^2, and the mean home range covered an area of 59.68 ± 0.34 SD km^2, calculated using the estimates in Table 5.

Table 5: Adult cheetah (Mfana, Inzwakazi, Karongwe) and cheetah litters (ILA, ILB, ILC) individual core ranges (50 %) and home ranges (95 %) in km^2 over the whole study period, calculated by the total number of datapoints for each animal. Including the mean and standard deviation (SD) per individual cheetah in between years. Numbers in bold indicate that there were less than 60 datapoints.

Individual	**n_{years}**	**Nr. of datapoints**	**Area (km^2) 50 %**			**Area (km^2) 95 %**		
			50 % CR	Mean	SD	95 % CR	Mean	SD
Mfana	7	1714	20.29	23.67	4.22	59.94	59.70	1.74
Inzwakazi	5	1374	30.22	21.85	7.29	59.49	56.84	4.10
Karongwe	2	293	37.14	27.77	3.47	60.09	60.09	0
ILA	3	493	22.30	21.55	6.12	59.62	58.22	2.49
ILB	2	558	30.71	21.92	9.85	59.24	50.88	13.29
ILC	1	**18**	6.51	-	-	24.18	-	-

Table 6: Adult cheetah (Mfana, Inzwakazi, Karongwe) and cheetah litters (ILA, ILB, ILC) individual core ranges (50 %) and home ranges (95 %) in km^2 for each year. Rows coloured in grey are home and core ranges that do not account for a full year. Numbers in bold indicate that there were less than 60 datapoints.

Individual	Year	Number of datapoints	Area (km^2) 50 %	Area (km^2) 95 %
Mfana	2013	87	25.75	59.94
Mfana	2014	397	25.63	59.82
Mfana	2015	230	18.04	60.08
Mfana	2016	252	23.67	55.20
Mfana	2017	275	20.55	59.64
Mfana	2018	278	26.41	59.70
Mfana	2019	195	15.69	59.30
Inzwakazi	2014	173	13.12	50.12
Inzwakazi	2015	397	20.67	55.59
Inzwakazi	2016	232	26.09	59.87
Inzwakazi	2017	430	32.92	59.25
Inzwakazi	2018	142	21.85	59.22
Karongwe	2018	90	25.31	60.09
Karongwe	2019	203	30.22	60.09
ILA	2015	208	15.13	55.35
ILA	2016	260	27.31	59.83
ILA	2017	122	22.21	59.47
ILB	2016	**23**	13.69	35.57
ILB	2017	413	32.83	59.30
ILB	2018	122	19.24	57.78
ILC	2018	**18**	6.51	24.18

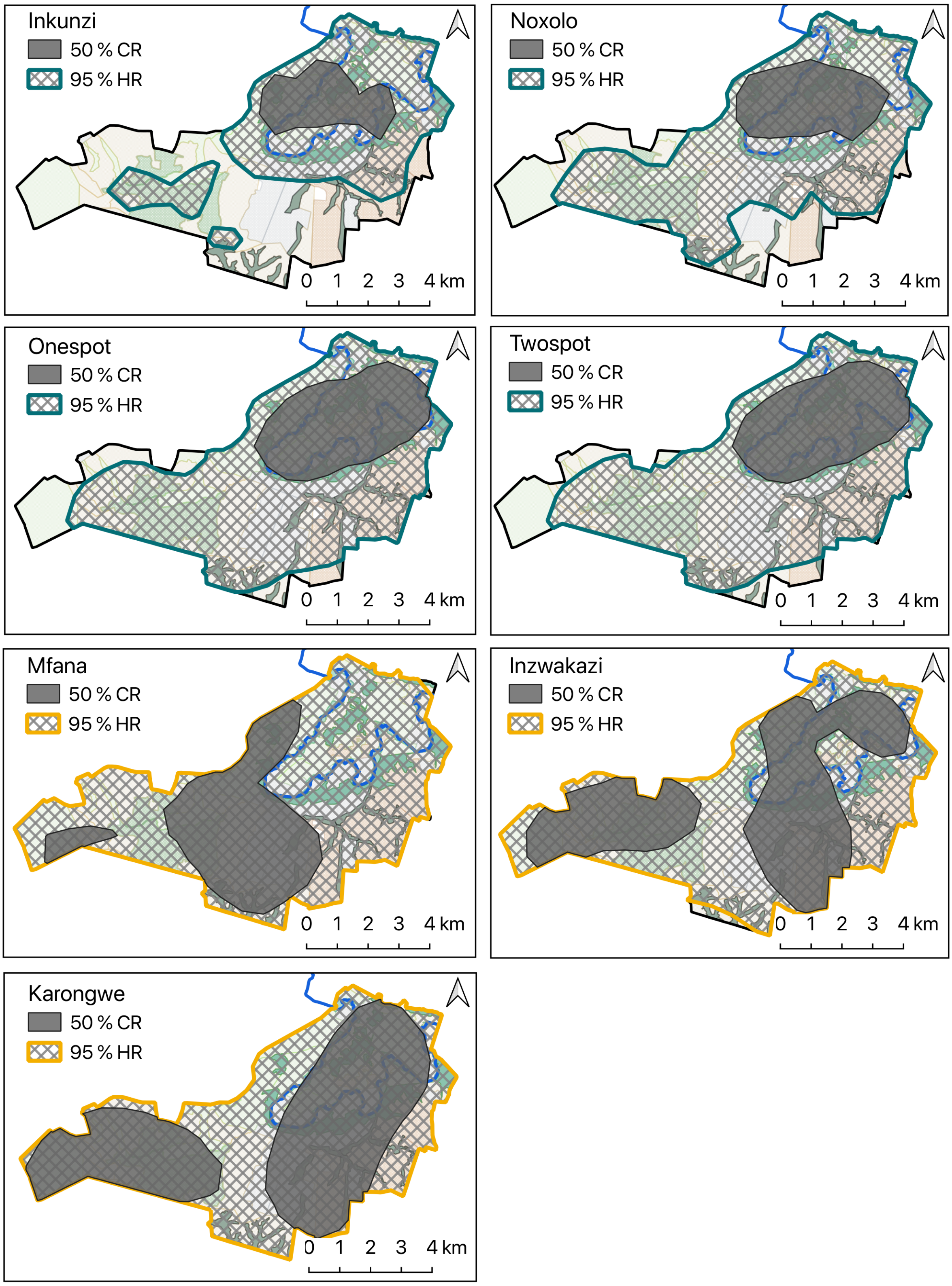


Figure 5: Home ranges (95 % HR) in crossed hatch and core ranges (50 % CR) in grey, for adult lions (n = 4) with a blue outline and for adult cheetahs (n = 3) with yellow outline, in AGR for the total duration of the study period, as described in **Table 3** and **Table 5**.

5.1.3. Spatial overlap

In comparison with the lions, cheetah home ranges in AGR covered the total area of the reserve. Therefore, it was almost inevitable that the home ranges of the cheetahs overlapped with the home ranges of the lions. There was a significant difference between the size of the core ranges of the lions and the size of the core ranges of the cheetahs ($W = 42$, $p = 0.001$) (Table 7).

Table 7: The total core and home ranges in km^2 per species per year. Where n_{ind} indicates the total animals used to estimate the core and home ranges for that particular year, lion offspring are the areas of Onespot and Twospot together, and cheetah estimates includes the present adults and litters for that year. Rows coloured in grey are home and core ranges that do not account for a full year.

Species	n_{ind}	**Year**	**Area (km^2) 50 %**	**Area (km^2) 95 %**
Lions	2	2013	0.92	3.99
Lions	2	2014	6.09	22.39
Lions	2	2015	5.73	22.43
Lions	4	2016	12.94	36.92
Lions	4	2017	16.21	51.94
Lions	4	2018	21.16	58.69
Lions	4	2019	20.30	56.55
Mean lions	-	2013 – 2019	11.91 ± 7.48 SD	36.13 ± 20.76 SD
Lion offspring	2	2016	9.95	30.98
Lion offspring	2	2017	15.02	51.48
Lion offspring	2	2018	19.11	58.69
Lion offspring	2	2019	17.66	54.76
Mean lion offspring	-	2016 – 2019	15.44 ± 4.03 SD	48.98 ± 12.36 SD
Cheetahs	2	2014	38.63	60.09
Cheetahs	3	2015	35.72	60.09
Cheetahs	4	2016	33.67	59.92
Cheetahs	4	2017	52.24	60.09
Cheetahs	4	2018	42.42	60.09
Cheetahs	2	2019	39.68	60.09
Mean cheetahs			40.39 ± 6.56 SD	60.06 ± 0.07 SD

Intraspecies overlap: lions

The lions in the study area showed a big overlap in home ranges and core ranges throughout the whole period of study. Noxolo and Inkunzi had a mean core range overlap of 86.48 % ± 8.19 % SD and had a mean home range overlap of 90.55 % ± 11.58 % SD. Onespot and Twospot shared almost the whole core range with a mean of 96.71 % ± 2.04 % SD and a mean home range overlap of 99.46 ± 0.53 % SD (Table 8).

Table 8: Percentage of core range (50 %) and home range (95 %) overlap of each dyad calculated using the overlap equation from Welch et al. (2015). Results show the percentage overlap between each pair-wise combination of two individual lions. INK = Inkunzi, NOX = Noxolo, 1SP = Onespot, 2SP = Twospot and CUBS are Onespot and Twospot together.

	Year	INK & NOX	NOX & CUBS	INK & CUBS	1SP & 2SP
50 % CR	2013	67.55	-	-	-
	2014	85.06	-	-	-
	2015	86.62	-	-	-
	2016	86.48	72.13	65.66	94.36
	2017	88.99	94.13	91.88	98.86
	2018	93.73	82.96	78.00	97.90
	2019	86.19	81.45	68.69	95.72
95 % HR	2013	65.53	-	-	-
	2014	95.81	-	-	-
	2015	91.27	-	-	-
	2016	88.97	95.28	88.62	98.74
	2017	98.05	99.45	98.23	99.91
	2018	98.70	98.77	97.57	99.81
	2019	95.55	97.64	93.08	99.37

Intraspecies overlap: cheetahs

Cheetah home ranges covered almost the whole area of AGR, therefore the home range overlap among cheetahs was always more than 74 %. The core range overlaps for the cheetahs varied strongly between years. In the year 2016 there was a relatively high core range overlap between all the cheetahs, with a mean of 68.13 % ± 13.12 % SD. In the year 2017 the same individuals had a mean overlap of 47.66 % ± 27.05 % SD (Table 9). The total mean core range overlap between Inzwakazi and Mfana was 33.12 % ± 26.24 % SD, however in the year 2016 there was a high overlap of 72.59 % between the two individuals. Inzwakazi had a mean core range overlap of 67.89 ± 18.46 % SD with her ILA litter and a mean core range overlap of 75.17 % ± 21.52 % SD with her ILB litter.

Table 9: Percentage of core range (50 %) and home range (95 %) overlap of each dyad calculated using the overlap equation from Welch et al. (2015). Results show the percentage overlap between each pair-wise combination of two individual cheetahs or cheetah litters. MF = Mfana, INZ = Inzwakazi, ILA = litter A, ILB = litter B, lLC = litter C, KAR = Karongwe.

	Year	**MF & INZ**	**MF & ILA**	**INZ & ILA**	**MF & ILB**	**INZ & ILB**	**ILA & ILB**	**MF & KAR**
50% CR	2014	0.66	-	-	-	-	-	-
	2015	21.54	19.34	69.39	-	-	-	-
	2016	72.59	79.33	85.56	62.40	55.67	53.18	-
	2017	35.27	19.81	48.72	34.88	98.27	49.00	-
	2018	35.53	-	-	41.79	71.56	-	44.15
	2019	-	-	-	-	-	-	27.19
95% HR	2014	90.69	-	-	-	-	-	-
	2015	96.10	95.87	97.22	-	-	-	-
	2016	95.94	95.97	99.88	78.37	74.54	74.57	-
	2017	98.93	99.52	98.79	98.96	99.96	98.83	-
	2018	98.97	-	-	97.72	98.74		99.67
	2019	-	-	-	-	-	-	99.34

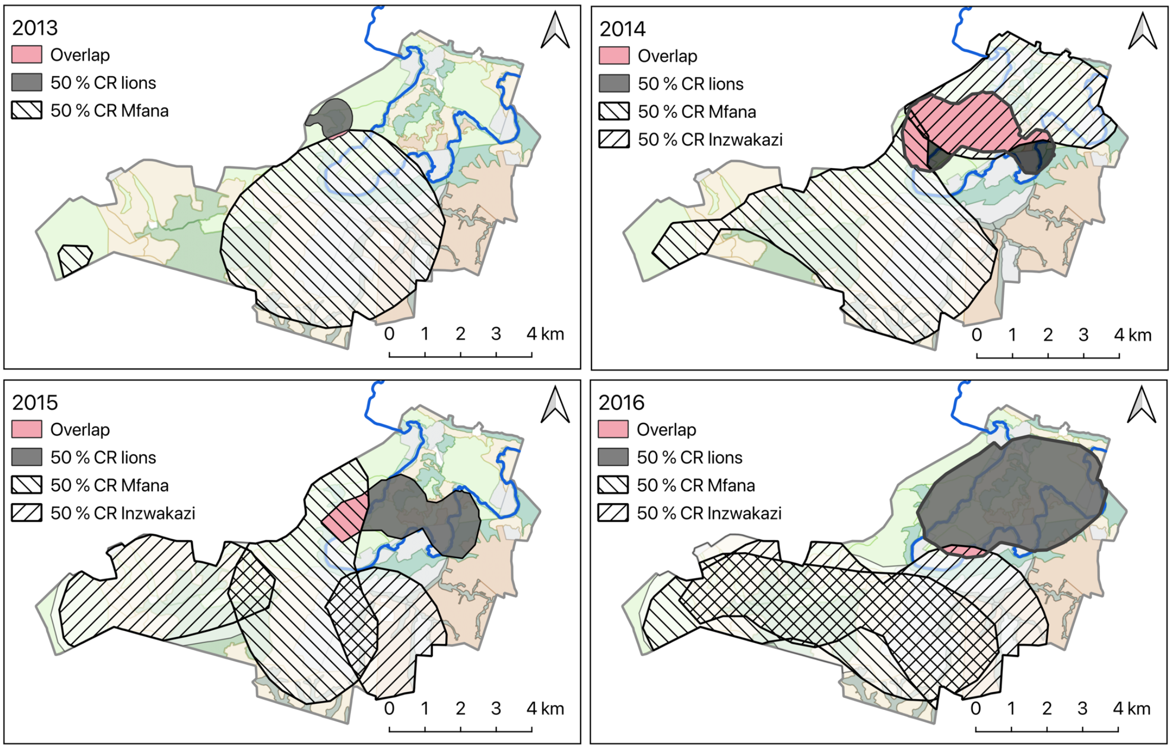


Figure 6: Core range (CR) overlap (pink) between the lions (n = 4) and the individual cheetahs (Mfana, Inzwakazi) for the years 2013 to 2016 at AGR.

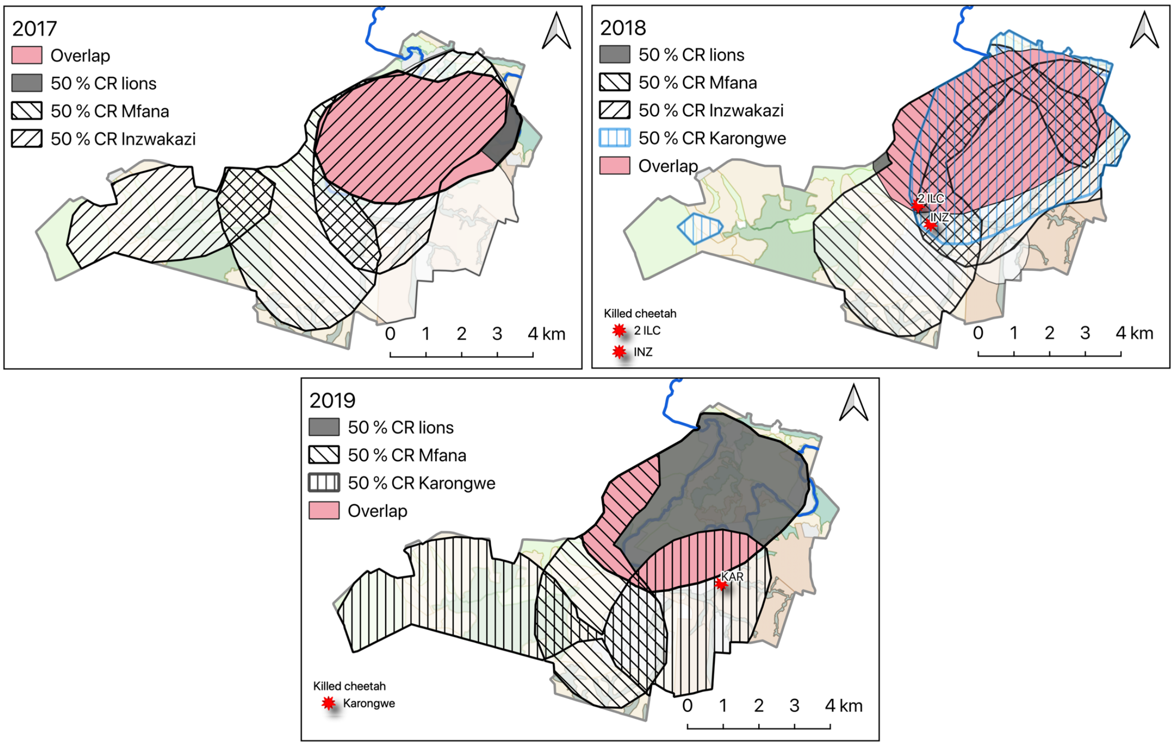


Figure 7: Core range overlap (pink) between the lions (n = 4) and the individual cheetahs (Mfana, Inzwakazi, Karongwe) between the years 2016 and 2019 at AGR. The red star indicates that this particular cheetah was killed at that location by the lions.

Interspecies overlap

The cheetahs showed little to no core range overlap with the lions in 2013, 2015 and 2016. In the year 2014 Inzwakazi was released and that year she showed an overlap of 43.93 % with the lions (Table 10). Inzwakazi's core range changed over the years but showed a big increase in overlap with the lions towards the year 2018, this is also the year she was killed. ILA and ILB cubs both had no overlap with the core ranges of the lions in their first year of existence in contrast to the ILC cubs that had an overlap of 9.08 %. All of the killed cheetahs were close to the lion core range of that particular year (Figure 7).

Table 10: Percentage core range (50 %) overlap of each dyad calculated using the overlap equation from Welch et al. (2015). Results show the percentage overlap between each pair-wise combination of lions (Inkunzi, Noxolo, Onespot and Twospot) and individual cheetahs and cheetah litters over the different years. Percentages marked in bold are the years this individual cheetah was killed by the lions.

Year	Lions	Mfana	Inzwakazi	Cheetahs	ILA	ILB	ILC	Karongwe
2013	Lions	0.34	-	-	-	-	-	-
2014	Lions	5.51	43.93	22.20	-	-	-	-
2015	Lions	8.96	0.00	5.14	0.00	-	-	-
2016	Lions	0.00	1.53	1.28	0.00	0.00	-	-
2017	Lions	22.57	58.80	42.20	31.06	59.78	-	-
2018	Lions	50.85	**69.33**	66.04	-	76.23	**9.08**	80.84
2019	Lions	19.26	-	23.93	-	-	-	**15.22**

5.2. Habitat preference

Habitat preferences were estimated in order to detect if there was a significant preference for a certain vegetation type, based on the Ivlev's indices. Here, the habitat preferences for the adult lions (n = 4) and adult cheetahs (n = 3) are described, in the whole area (100 %), as well as the habitat preferences in the core range (50 %).

5.2.1. Lion habitat preferences

Over the whole area (100 %) the individual lions' vegetation preference did not differ significantly among individuals, thus all the individuals had the same selection for each vegetation type as illustrated in Figure 8. However, there was a significant difference between the choices of vegetation (*F* = 9.905, *df* = 31, *p* < 0.001) selected by the lions. Lions showed a preference for riverine thicket, grassland, and thicket and showed avoidance towards valley thicket, forest, karroid and savanna. Old lands was preferred by the lion offspring (Onespot and Twospot) but avoided by Inkunzi and Noxolo during the whole study period.

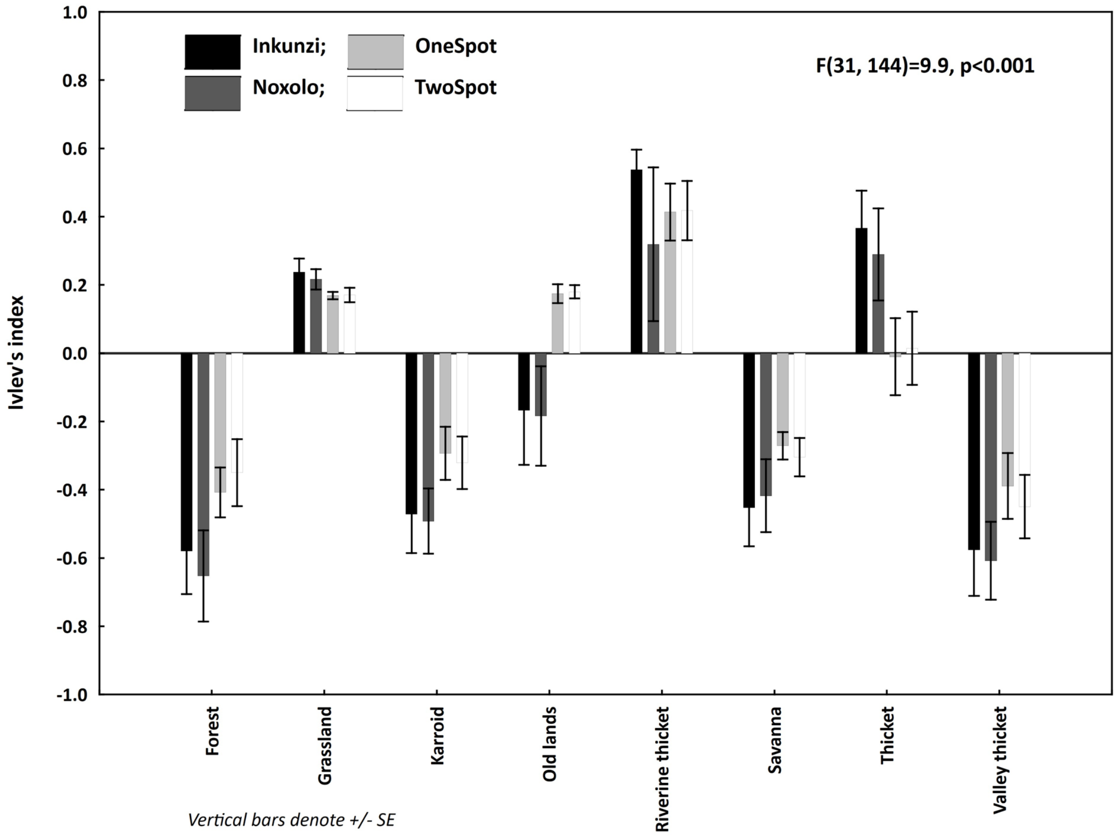


Figure 8: Habitat selection for individual lions (n = 4) in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period over the whole area (100 %).

The habitat preferences in the core range (50 %) of the lions showed different preferences in comparison with the habitat selection in the whole area. The vegetation type forest was not present in the core range, and therefore not included in the graph (Figure 9). There were no significant differences among individuals for a particular vegetation type (p > 0.05). However, Onespot and Twospot did prefer old lands more than Noxolo and Inkunzi, and they showed avoidance behaviour towards thicket in their core ranges. All of the lions had valley thicket present in the core area but showed 100 % avoidance towards it (Figure 9).

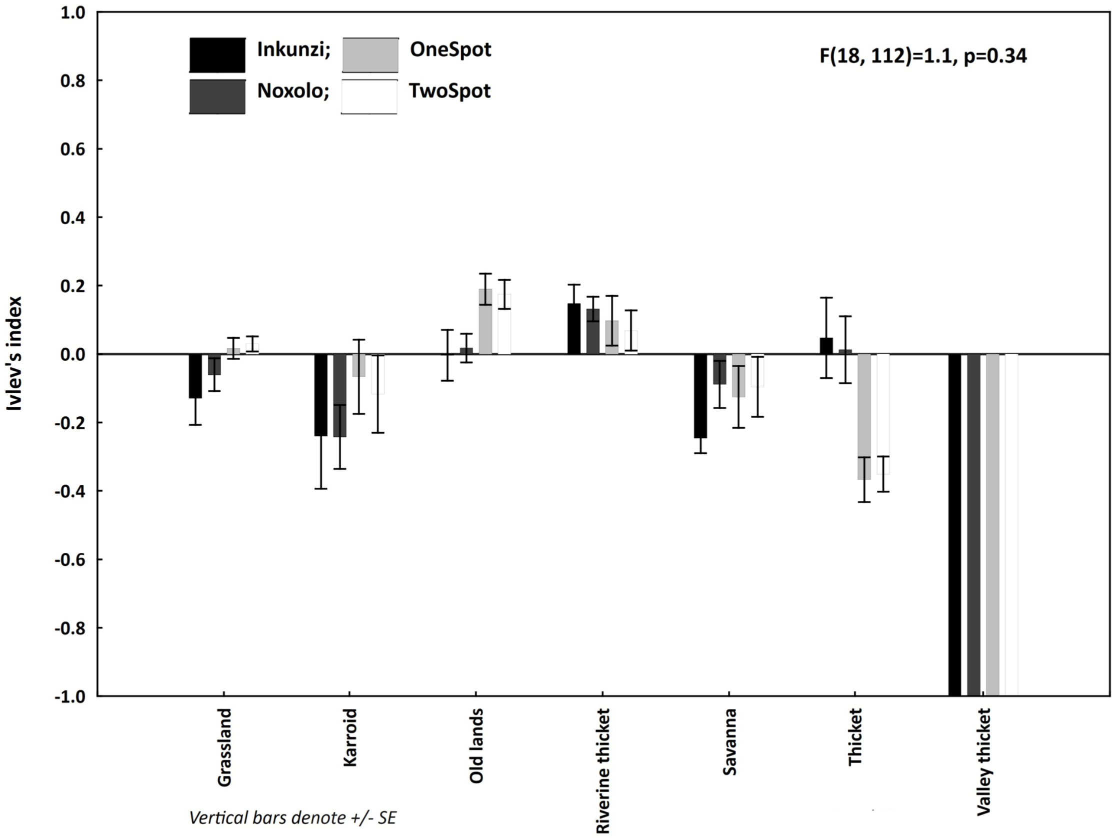


Figure 9: Habitat selection for individual lions (n = 4) in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period in the core range (50 %).

5.2.2. Cheetah habitat preferences

All the cheetahs (n = 3) in the whole study area (100 %) had the same selection for six out of the eight vegetation types at AGR. They did however have an individual significant preference in two vegetation types: savanna (*F* = 4.294, *df* = 2, *p* = 0.041) and 'old lands' (*F* = 9.329, *df* = 2, *p* = 0.004). Mfana had a preference for old lands, whereas Inzwakazi and Karongwe showed avoidance behaviour towards old lands. Mfana and Karongwe both showed preferences towards the savanna vegetation, whereas Inzwakazi tended to avoid the savanna region (Figure 10). There was a significant difference in between each vegetation type (*F* = 0.328, *df* = 23, *p* < 001).

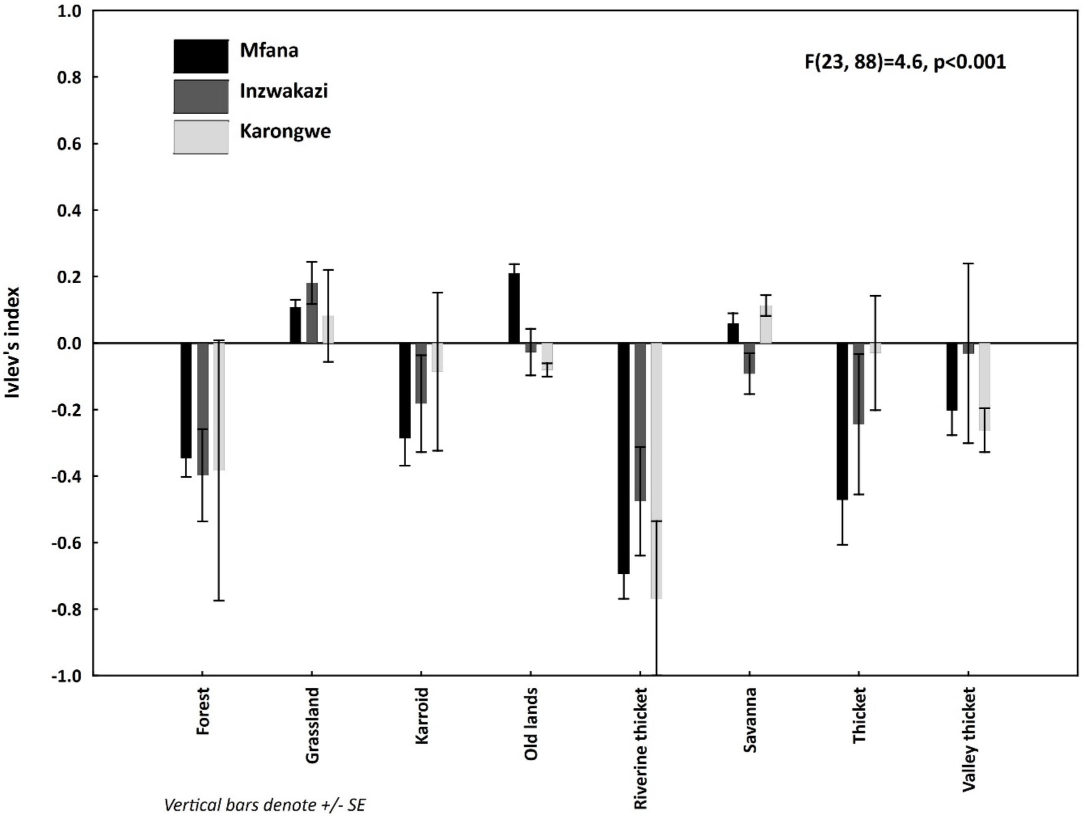


Figure 10: Habitat selection for individual cheetahs (n = 3) in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period over the whole area (100 %).

The vegetation selection for the cheetahs in the core area (50 %) was in line with the selection in the whole area. In the core area, Inzwakazi showed a significant preference for valley thicket in comparison with the other individuals (*F* = 7.639, *df* = 2, *p* = 0.009). Karongwe had a significant preference for savanna (*F* = 4.723, *df* = 2, *p* = 0.033), and Mfana showed significantly more preference to old lands in his core range (*F* = 8.732, *df* = 2, *p* = 0.005) in contrast to the other two cheetahs (Figure 11). In both the home ranges and the core ranges there was a clear avoidance towards 'riverine thicket' for all the cheetahs.

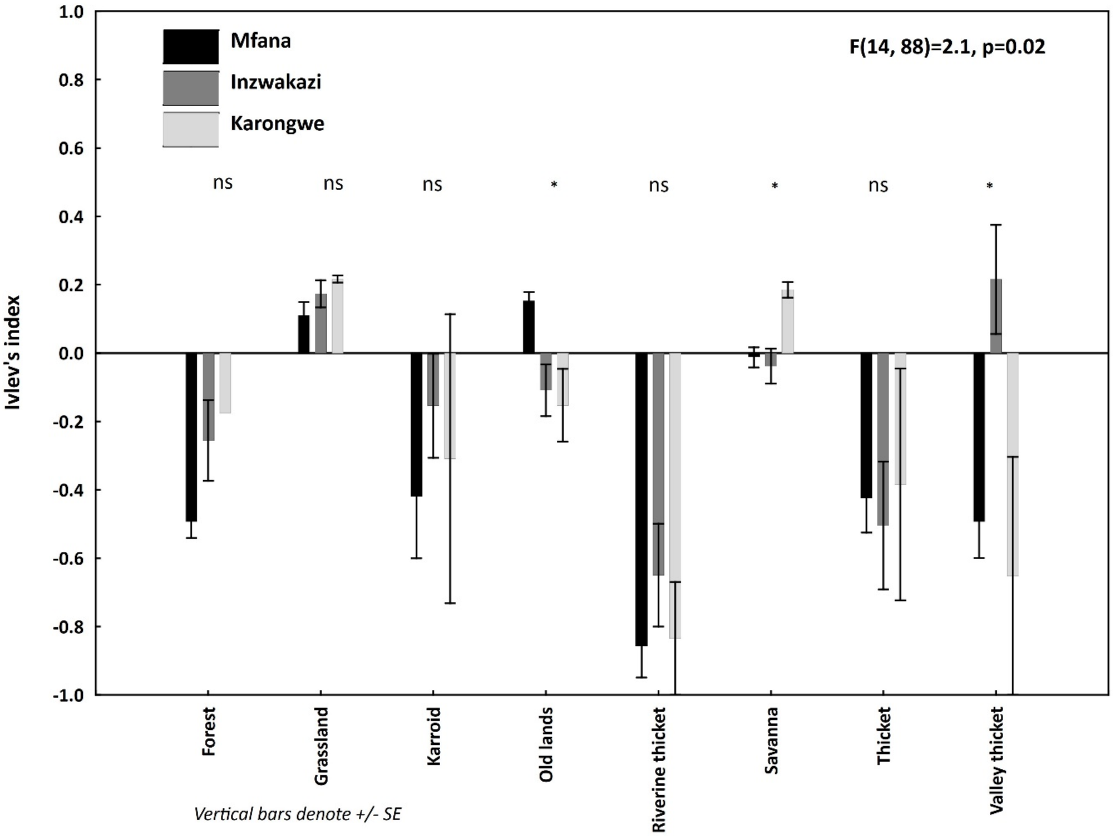


Figure 11: Habitat selection for individual cheetahs (n = 3) in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period for the core ranges (50 %) of each individual, where ns = not significant, and * = p < 0.05.

5.2.3. Interspecies habitat preference

Lions and cheetahs showed a significant difference in selection for six out of eight vegetation types for the whole area in AGR as illustrated in Figure 12. There was a significant difference in selection of grassland (*t* = 2.398, *df* = 34, *P* = 0.022), karroid (*t* = -2.312, *df* = 34, *P* = 0.037), riverine thicket (*t* = 9.332, *df* = 34, *P* < 0.001), savanna (*t* = -5.683, *df* = 34, *P* < 0.001), thicket (*t* =4.474, *df* = 34, *P* < 0.001) and valley thicket (*t* = -3.454, *df* = 34, *P* < 0.002). The lions' vegetation preference is cohesive for all the individuals, whereas the cheetahs do show different preferences for different vegetation types (Figure 8, Figure 10).

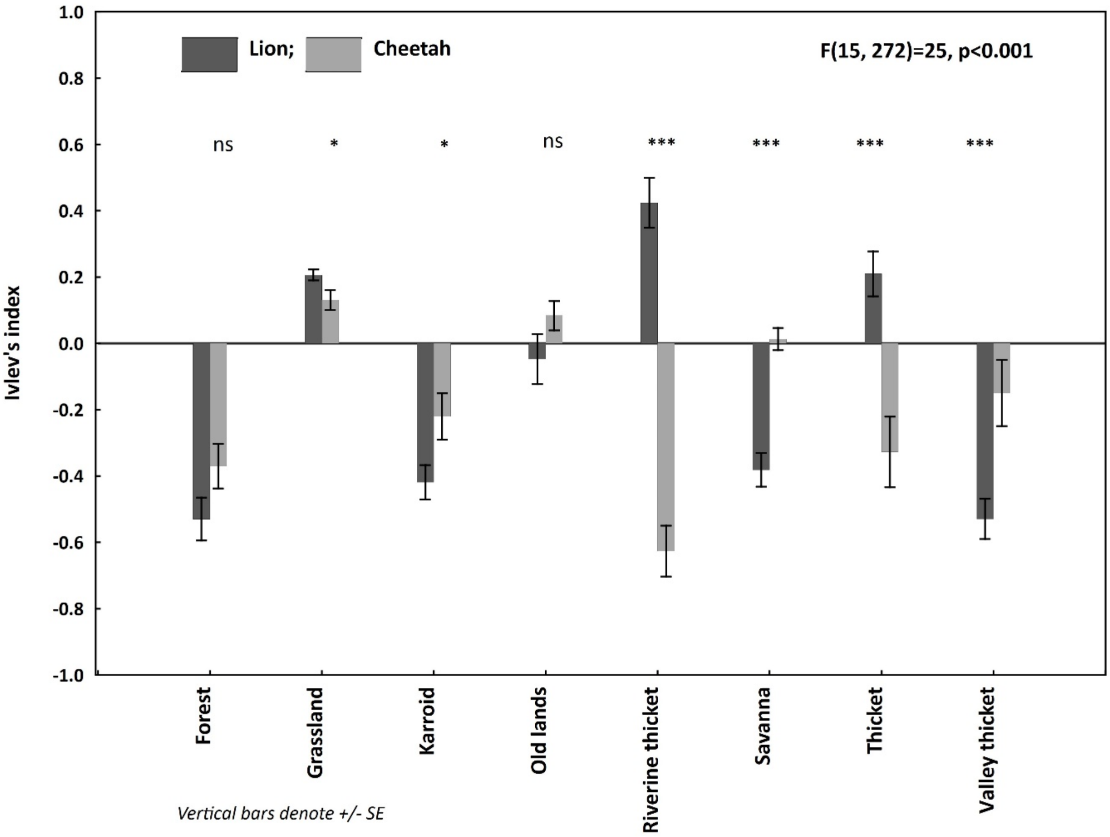


Figure 12: Habitat selections for lions (n = 4) in dark grey and cheetahs (n = 3) in light grey in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period over the whole area (100 %). Where * = p < 0.05, *** p < 0.001 and ns = no significance.

The vegetation preference in the core area (50 %) of lions and cheetahs differed significantly for grassland (*t* = -4.478*, df* = 35*, p* < 0.001), riverine thicket (*t* = 13.948*, df* = 30*, p* < 0.001), savanna (*t* = -3.058*, df* = 32*, p* = 0.004), thicket (*t* = 3.147*, df* = 33*, p* = 0.003) and valley thicket (*t* = -3.935*, df* = 18*, p* < 0.001) (Figure 13).

Overall, cheetahs had a clear avoidance for riverine thicket, thicket and forest in the whole area, as well as in their core ranges. Lions avoided valley thicket and forest in the whole area and in the core range.

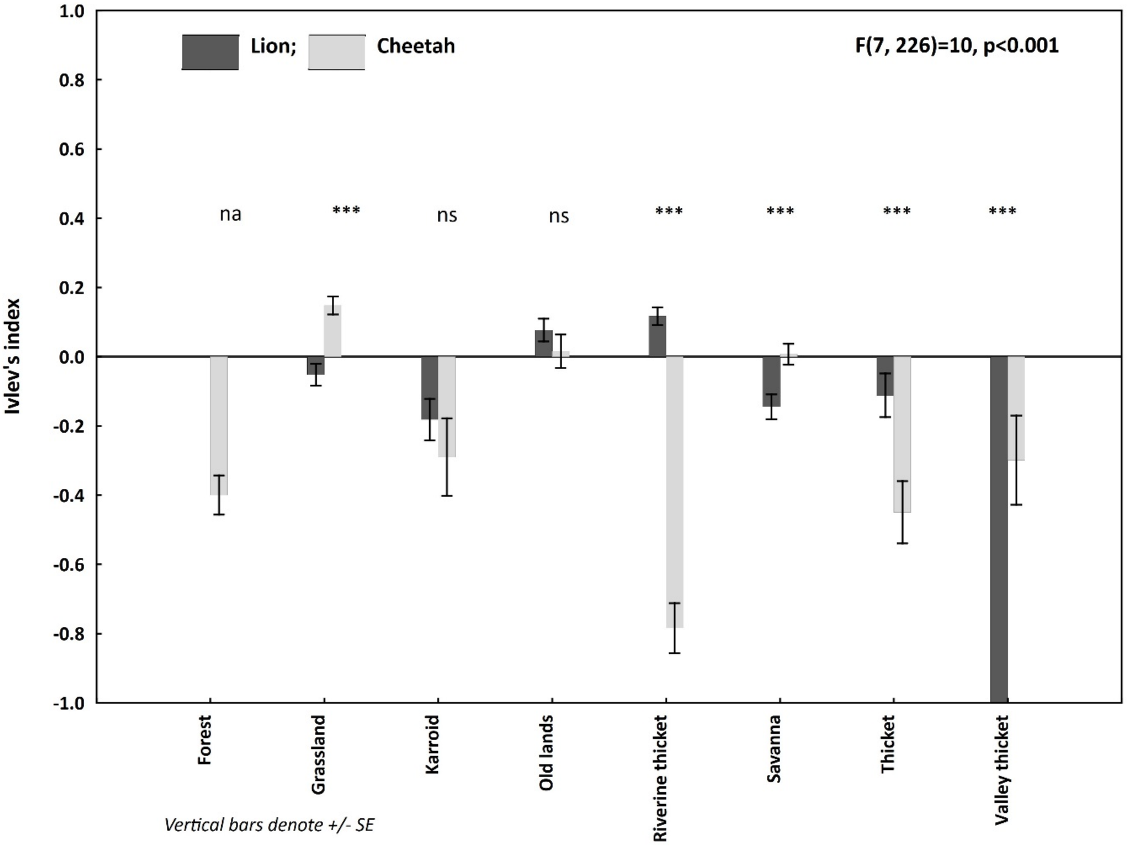


Figure 13: Habitat selections for lions (n = 4) in dark grey and cheetahs (n = 3) in light grey in AGR using the Ivlev's index for preference or avoidance. Values < 0 indicate that a vegetation type was avoided, and > 0 indicate that there is a preference. The analysis was done for the whole study period in each species' core area (50 %). Where: *** p < 0.001, ns = no significance, na = not available.

5.3. Prey selection

Due to the small sample size of the individuals, these results focused on the prey selection per species instead of looking at the different selection between each individual.

5.3.1. Lion prey selection

There was a total of 532 kills made and recorded over the entire six-year period. For 97 % (n = 513) of the kills made, the individual predator was identified and therefore only these were used in the study. Inkunzi made 11.1 % (n = 57) of the kills, Noxolo made 26.7 % (n = 137) of the kills and Noxolo and Inkunzi made 22.2 % (n = 114) of the kills together. Noxolo's offspring (Onespot and Twospot together and individually) killed 6.6 % (n = 34) of the recorded kills, while the core female pride (Noxolo plus offspring) made 11.3 % (n = 58) of the kills over a four-year period. For 22 % (n = 113) of the kills it was recorded that the whole pride was present but the exact individual who made the kill was not always identified. These results include the observed increase of fullness of the animals. Collectively the lions were recorded to make a mean of 7.78 ± 0.97 SD kills per month, ranging from 6.8 ± 1.79 SD in August and 6.8 ± 2.28 SD kills in October to a total of 10 ± 1.89 SD kills in April.

For 452 (85 %) of the kills the prey species was identified. The lions preyed upon 21 species: five of those compromised 82.1 % (n = 371) of all kills found (Figure 14), demonstrating warthog (42.3 %, n = 191), black wildebeest (21 %, n = 95), kudu (6.4 %, n = 29), red hartebeest (6.4 %, n = 29) and eland (6 %, n = 27) as the most highly predated species by the lions. Adult prey made up 65 % (n = 296) of the identified kills, subadult prey 12.61 % (n = 57), and juveniles 21.90 % (n = 99) (Figure 14).

5.3.2. Cheetah prey selection

Over the six-year study period, cheetahs made a total of 573 kills. Mfana, the male cheetah, made with 46.9 % (n = 269) of the kills, Inzwakazi, the female cheetah made 43.3 % of the kills (n = 248). Karongwe the other adult cheetah, who was in the reserve for less than a year, had 4.54 % (n = 26) of the kills. The ILA cheetah litter was recorded making 1.05 % of the kills (n = 6), and the ILB litter made 2.97 % (n = 17). When the cheetah that made the kill was not identified it fell under the category ‘cheetah in the main reserve’ and collectively these made up 1.22 % of the kills (n = 7). These results include the increased fullness observations. Individually, Inzwakazi had made a mean of 5.39 ± 2.9 SD kills per month, Mfana had a mean of 3.89 ± 1.86 SD kills per month and Karongwe had a mean of 3.25 ± 1.16 kills per month. Together, the cheetahs killed a mean of 8.29 ± 2.2 SD animals per month over a six-year period. Values ranged from a mean of 4.5 ± 2.43 kills in June to a mean of 12.17 ± 7.03 SD kills in November.

The cheetahs preyed upon 18 different species. In 384 (67 %) of the 573 kills the prey species were identified, and six prey species accounted for 75.78 % (n = 291) of the kills. Impala kills made up the largest percentage of all cheetah kills with 21.88 % (n = 84), kudu 19.79 % (n= 76), red hartebeest 12.24 % (n = 47), blesbok 8.59 % (n = 33), common duiker 7.03 % (n = 27) and black wildebeest (n = 24). Cheetahs collectively killed mostly juveniles (48.70 %, n = 187); adult prey animals represented a percentage of 35.16 % (n = 135) and subadult prey accounted for 16.15 % (n = 62) of the kills (Figure 14).

5.3.3. Interspecies prey selection

In total 26 prey species were identified from observations (Appendix 1). Lions fed on 21 different species and cheetahs on 18. The five most selected prey species for lions and the six most selected for prey species by cheetahs are displayed in Figure 14. Here, the results show that all age categories of warthog were highly consumed by the lions, in contrary to the cheetahs, which mostly killed juveniles and subadults warthogs. Cheetahs were most likely to kill the juveniles and subadults of larger species, for example black wildebeest, eland, red hartebeest, in comparison with the lions who mostly consumed the adults of these species. Furthermore, impala, blesbok and common duiker were eaten often by the cheetahs but almost never by the lions.

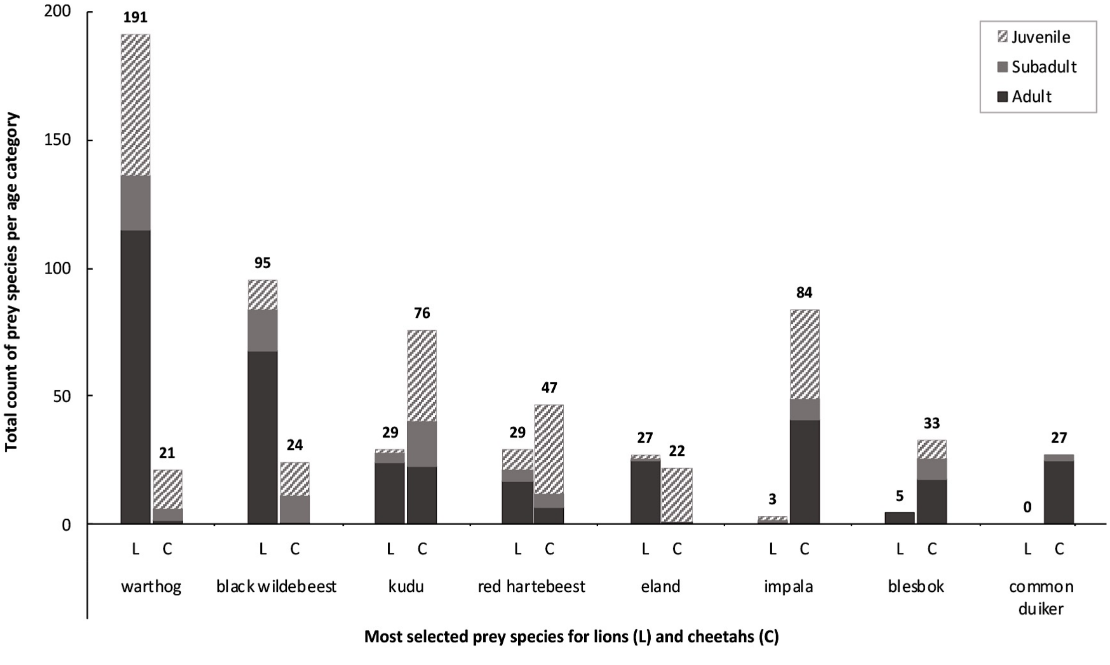


Figure 14: Most selected prey species and their age category for lions (warthog, black wildebeest, kudu, red hartebeest and eland (n = 371) and cheetahs (impala, kudu, red hartebeest, blesbok, common duiker and black wildebeest (n = 291) from 2013 – 2019.

Most of the kills found were made in the grassland vegetation (Figure 15). Open habitats like: savanna, old lands and grassland were mostly used for the hunting by both species. Forest, valley thicket and thicket were not used as much by either one of the predators. Lions did hunt observantly more in riverine thicket in comparison with the cheetahs. Open habitats like grassland, savanna and old lands represented 63.48 % of the total vegetation of AGR and, forest, valley thicket and thicket account for 19.8 % of the total vegetation of AGR.

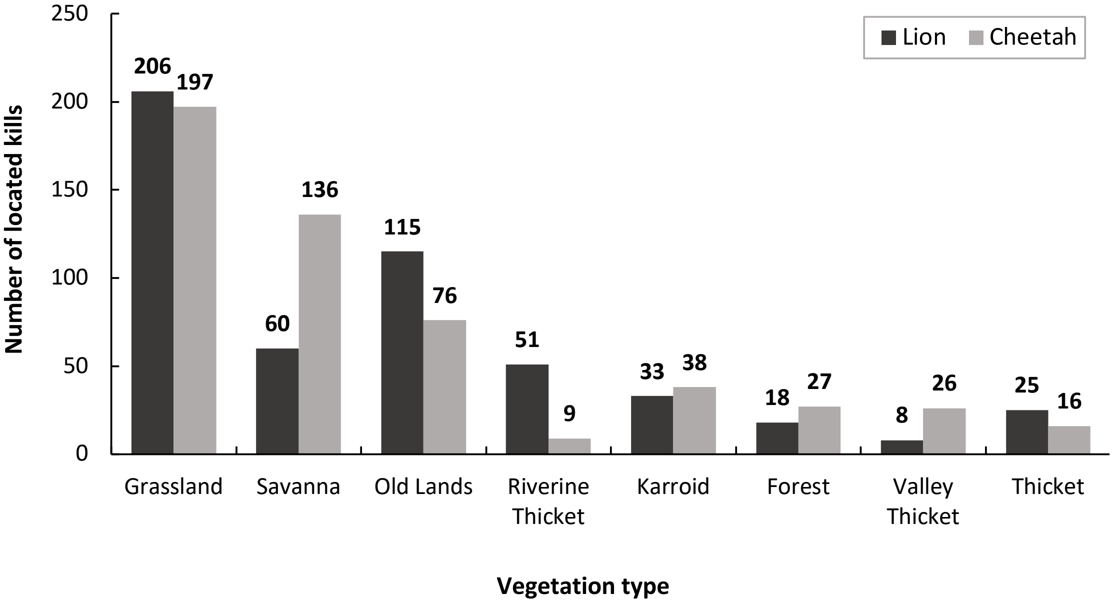


Figure 15: Located and recorded kills in each vegetation type (n = 8) over the whole study period (2013 – 2019) for lions in dark grey (n = 4) and cheetahs in light grey (n = 6). Lions had a total number of 516 located kills and cheetahs had 525 located kills.

5.3.4. Weight category preference

Because of the nature of the data (categorical) the outcomes from the quasipoisson regression are relative to the category small sized prey and to the year 2014. Thus, the outcome in Figure 16 plots the average annual kills for each prey category and the results show whether the lions or the cheetahs were less or more likely to go for a certain weight category, relative to the small sized prey.

Interspecies weight category preference

The output of the GLMS showed that, when looking for the interactions between prey weight category and species, medium sized prey was preferred by both lions and cheetahs (*t* = 2.167, *p* = 0.038*)*. They were both significantly less likely to go for very large prey (*t* = -2.964*, p* = 0.006) or large sized prey (*t* = -2.836*, p* = 0.008*)* in comparison to small sized prey*.* However, the lions would significantly prey more upon the very large prey (*t* = 2.725, *p* = 0.01) in comparison to the cheetahs. There was no significant difference for selection of medium-and large prey, when both species were compared to one another.

Intraspecies weight category preference

The lions would significantly go more for a medium sized prey over a small sized prey (*t* = 3.602, *p* = 0.004), but there was no significant difference for the selection between large size, and very large sized prey. Thus, they were not significantly more likely, or less likely to go for large or very large sized prey over the small sized prey (Figure 16). For the lions there was no significant increase when the variable 'year' was taken into consideration. However, in the year 2016 there was a 45 % (*t* = 1.92*,* p = 0.078*)* increase in the kill count in comparison with the year 2014 (Figure 17).

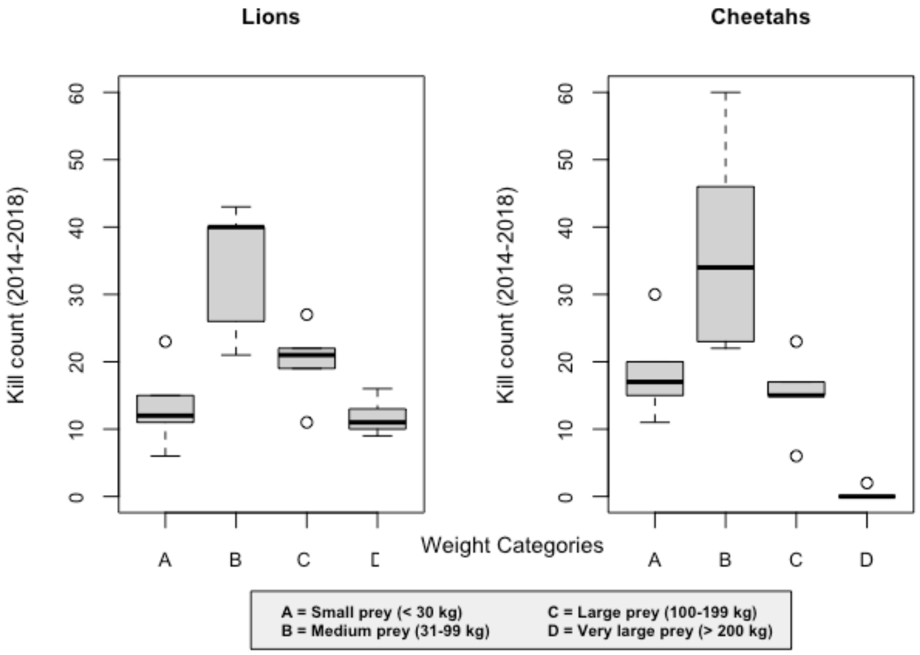


Figure 16: The average of annual kill counts from 2014 – 2018, for each weight category for the lions and cheetahs in AGR.

Cheetahs would significantly prey more upon medium sized prey compared to large sized prey (*t* = 4.918*, p* > 0.001), and compared to small sized prey (*t =* 2.754, *p =* 0.017). They were significantly less likely to prey upon a very large prey, compared to the small sized prey *(t* = -3.806, *p* = 0.002) and also compared to large sized prey (*t* = -3.670, *p* = 0.003). The GLM showed that in 2017 there was significant (*t* = 3.176*, p* = 0.008*)* increase of 101 % in the kill count compared to the year 2014 (Figure 17).

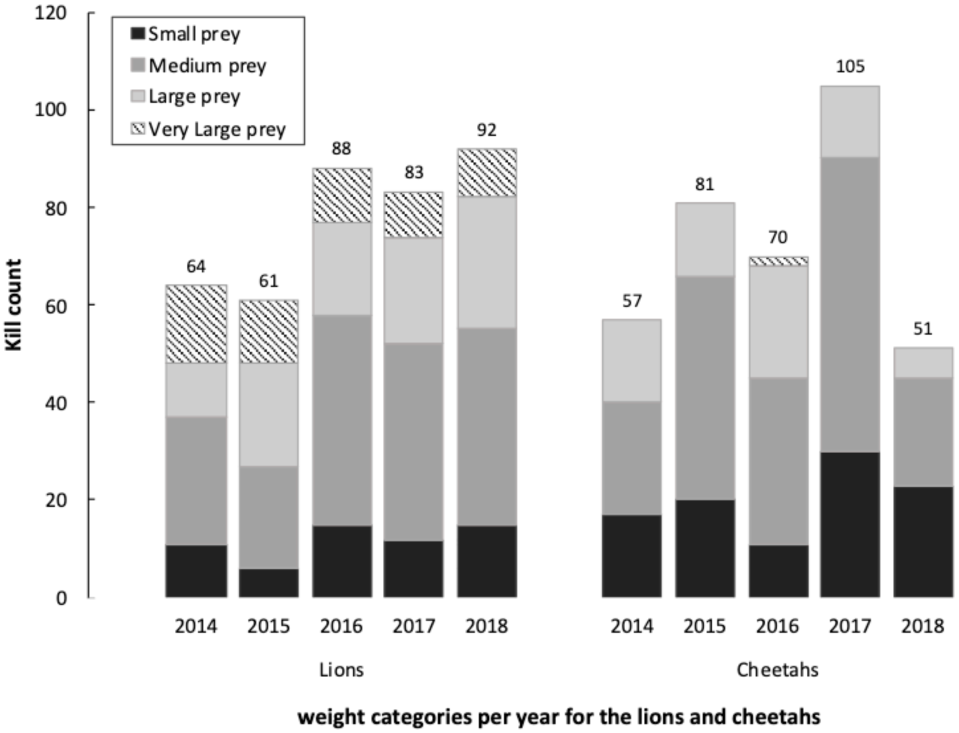


Figure 17: The kill count of lions and cheetahs per year (2014 – 2018) per weight category.

If all other variables remained constant, there was 154 % increased chance that the lions would prey upon a medium sized prey and 46 % increased chance of preying upon a large sized prey in comparison with the small sized prey. There was 9 % decreased chance it would go for the very large prey over the small prey. The cheetahs had 98 % increased chance of choosing a medium sized prey over a small sized prey, and they had a 17.7 % and 9.8 % decreased chance of going for a large or very large prey.

6. Discussion

For carnivore translocations and reintroductions, caution and careful management may be required (Palomares & Caro 1999). Attempts to translocate top predators to fenced reserves may fail if the predators do not behaviourally adjust to the reintroduction site. On these small reserves, wildlife managers are potentially faced with increased interspecific competition and intra-guild predation between large predators (Bissett & Bernard 2007). It could potentially influence local extinction risks for the smaller species within the guild (Palomares & Caro 1999; Cristescu et al. 2013). Even at high resource abundance and a low predator rate, the confined space increases the likelihood of predators encountering each other, heightening the risk of interference competition (Cristescu et al. 2013). Therefore, reserve managers would benefit from understanding how predators have adjusted behaviourally to the relocation site.

To potentially detect the driving force of the intra-guild predation at Amakhala Game Reserve, we compared the space use, spatial overlap, habitat preference and prey selection to describe possible competition over some resources by the lions and cheetahs at AGR.

6.1. Home range, core range and spatial overlap

Lions and cheetahs home ranges and core ranges in the reserve

The home range size (46.24 ± 10.14 SD km^2) and core range (11.49 ± 3.66 SD km^2) of the lions in AGR were similar to the home- and core ranges estimated by Spong (2002). His mean core area for five free-roaming prides was 11.7 ± 8.6 SD km^2, and the home range covered a mean area of 52.4 ± 26.3 km^2 in the 1000 km^2 Selous Game Reserve in Tanzania. This indicates that even when they have larger areas available, lions still have a relatively small home- and core ranges. Therefore, depending on prey density, lion could be adequately housed on reserves smaller than 100 km^2 as stated by Druce et al. (2004). However, other studies have demonstrated bigger home and core range estimates (Funston et al. 2001; Bauer & Iongh 2005; Loveridge et al. 2009). Inconsistent methodologies, pride size variation, available area, physical barriers, intra- and interspecific competition, and available resources are among the factors that constrain comparisons of home ranges of different studies (Spong 2002; Druce et al. 2004; Davidson et al. 2012; Laizer et al. 2014). The results show that Noxolo, the adult female lion on AGR, had a bigger home range than the male lion, Inkunzi. This contradicts several studies which state that male lions have bigger home ranges than females (Loveridge et al. 2009; Tumenta et al. 2013; Laizer et al. 2014). Inkunzi's smaller home range could be explained by the fact that he had more fixes obtained from his GPS collar, and therefore had a more accurate home range estimation compared to the other lions. However, in the year 2018 Inkunzi had 386 data points and a core range of 15.04 km^2 and home range of 55.91 km^2, while Noxolo had 414 datapoints and a bigger core range of 17.05 km^2 and a home range of 57.26 km^2. Suggesting that the male lion in AGR had a smaller home and core range than the female lions in this reserve. This could be due to the fact that he was the only male lion in the reserve and therefore, did not have to compete with other male lions.

It was found that the AGR lion home ranges did not completely cover the whole reserve, which suggest that lions where satisfying their needs within the reserve. This was further emphasized with the relatively small and stable core range the lions had annually (Druce et al. 2004). Cheetah on the contrary, are known to have larger home ranges (Broomhall et al. 2003; Houser et al. 2009; Welch et al. 2015) and they covered the whole area of the reserve (60.06 km^2 ± 0.07 SD km^2). This was further demonstrated by the fact that their space use in relation to the core ranges varied greatly annually as illustrated in Figure 6. This is particularly true for Inzwakazi's core range locations which changed almost each year. Mfana, the male cheetah had a mean core range of 20.29 ± 4.22 SD km^2 and Inkzwakazi's had a mean core range of 30.22 ± 7.29 SD km^2. When compared to other private reserves in the Eastern Cape province the core ranges were bigger than in Kwandwe Private Game Reserve where the cheetahs had an average core area of 9.4 km^2 (Bissett & Bernard 2007) and showed a similar core range of 23.3 km^2 to the cheetahs in Shamwari Game Reserve (Cristescu et al. 2013).

Interspecies and intraspecies spatial overlap

To investigate whether there was any interspecies and intraspecies spatial overlap in the core range, the overlap equation by Welch (2015) was used. The results found that the lion core ranges overlapped greatly and consistently over the years, as would be expected from a pride of lions. The cheetahs on the contrary showed less intraspecific overlap in the core ranges and there was a big difference between the years. In the year 2016 there was notably a higher intraspecies core range overlap than other years, and no interspecies overlap. This could be due to the fact that Inzwakazi had two litters to take care of during that time period and could potentially be an intra-guild mechanism for avoiding interspecific encounters with the lions. However, home range overlap is a gross measure for potential of interspecific competition, species may live in different habitats despite sharing the same home range (Caro & Stoner 2003).

When taken a closer look to Inzwakazi and her three litters it can concluded that during most of the study period, there were cubs and subadults on the conservancy to consider. This could greatly affect her space use in the reserve. In 2014, the year of Inzwakazi's introduction, she showed a lot of overlap with the lions (43.93 %). When she had her first litter in 2015, her core range, as well as the core range of the ILA litter showed no overlap with the lions and she was showing a high preference towards the valley thicket vegetation. When having her second litter in 2016 the overlap with the lions increased to 1.53 %. From the year 2017, her overlap with the lions showed a steep increase to 58.80 %. Furthermore, in 2018, she had her third and last litter but the overlap with the lions increased drastically to 69.33 %. The increase in the lion core ranges in 2017 (16.21 km^2) and in 2018 (21.16 km^2), the increase in Inzwakazi's core range in 2017 (32.92 km^2), and the high overlap in 2017 and 2018 resulted in her death, and the death of her young cubs in 2018. Karongwe also showed a high overlap of 80.84 % with the lions in 2017, in 2018 her overlap decreased to only 15.22 %. However, she was killed in her core range in close proximity to the overlap area and the lion core range. We can only speculate for the drivers of inzwakazi's movement towards the lions and therefore having an increased overlap in 2017 and 2018. There could have potentially be competition over the space used or prey species consumed. According to Miller et al. (2013) reproductive control of female lions could lead to fragmentation of the pride, which can cause shifts in predator-prey relationships and intraguild dynamics. The three female lions were all contracepted, suggesting that having no dependent cubs could have increased their roaming behaviour and therefore, there would have been a higher chance of intra-guild predation. Palomares and Caro (1999) stated that predator avoidance increases fitness. Therefore, a potential explanation could be that with the increase in home ranges of the lions over the years, it became harder for the cheetahs to avoid interactions with the lions. All the cheetahs killed were in close proximity of the core ranges of the lions.

Limitations

Due to the nature of the data it was difficult to make a comparable, accurate, total home range estimate for each individual or species over the whole study period (October 2013 – August 2019) at AGR. The reason for this is that: (1) there were only a small number of individuals to consider, (2) different periods of availability of each individual in the study area, (3) the home range calculations done did sometimes not account for a full year, and (4) inconsistency in collected location data points. To reduce bias the home- and core ranges were calculated annually, to compare the present individuals for that particular year. Besides Inkunzi's GPS fixes, all the location datapoints were recorded during the day, which could underestimate the lions' movement and kills made during the night. On some days there were up to four sightings for one individual and other days there were none, indicating the inconsistency of data sampling. Kernel density estimation is a commonly used method for estimating 95 % home ranges and 50 % core ranges utilization distribution (Broekhuis et al. 2013; Balme et al. 2017; Gregory 2017). By estimating the home ranges annually, the home ranges and core ranges do provide an accurate indication of the area each individual used. However, it should be taken into consideration that there could have been an overestimation of home and core ranges due to oversmoothing the bandwidth by H_{ref} (Walter et al. 2009).

6.2. Differences in habitat selection

The fact that the animal has its home range where it does, is itself indicative that the animal has already made a selection (Johnson 1980). Due to the eco-tourism, key species like lions and cheetah are kept within fencing, and therefore they are limited to a certain area, with a determined habitat. Therefore, it was decided to investigate the preference for a certain vegetation type for each individual in the total available area (100 %) and in the core range (50 %). The analogous situation appears in selection of prey, where the presence of an animal at its feeding site suggests that it selected that site in part because of the food items available there (Johnson, 1980). However, several factors other than absolute availability may constrain resource use and selection and the results strictly give an indication of the vegetation type preferred by each individual and does not account for other biotic factors such as predation pressure, competition, risks of diseases and human disturbances which can all obviously affect animal behaviour and performance (Gaillard et al. 2010). Even if different carnivores were to use similar habitats, temporal variation in space use may decrease risk of encounters (Hayward & Slotow 2009; Cristescu et al. 2013). Because of the absence of spatial/habitat information for prey, it was not possible to map the distribution of prey on the landscape (Cristescu et al. 2013), which could have given valuable insights into the selection for a certain habitat.

Habitat preferences for lions

The lions at AGR collectively preferred the riverine thicket and grassland vegetation more than other habitat types at the 3rd order habitat selection (selection for locations within the core range). Lions are considered to be opportunistic stalk-and-ambush hunters that use vegetation cover to be more successful hunters where vegetation is dense (Funston et al. 2001; Davidson et al. 2012). Therefore, they might select for habitats where they can ambush their prey (Hopcraft et al. 2005; Davidson et al. 2012), like riverine thicket. However, most of the kills in this study were found in the grassland vegetation type. This could explain an alternative scenario that lions prefer to be located in the dense vegetation adjoining grassland and old land areas, from where they can remain concealed, while observing potential prey. However, Funston (2001) found that lions had the same chance of hunting success in open, moderate and dense bush areas. He did discover that there was a linear relationship with grass height and hunting success. This indicates that lions are more likely to successfully hunt when the grass is higher, thus, when they are less detectable by prey species. Lions in other reserves used different kinds of habitats (Spong 2002; Broekhuis et al. 2013; Balme et al. 2017), therefore it seems that lions possess a considerable degree of behavioural plasticity and respond to the prevalent ecological conditions. Davidson et al. (2013) found that habitat selection is influenced by distance to water for most herbivores. Hence predators have a greater chance of encountering prey in areas surrounding water holes (Davidson et al. 2012), this would suggest that habitat selection within the core range is largely influenced by prey abundance and availability (Spong 2002; Broomhall et al. 2003). The results in this study also show that lions choose areas where prey is easier to catch (riverine thicket) and also prefer areas where prey densities are highest (Hopcraft et al. 2005). Thus, the lions at AGR prefer both denser habitats like riverine thicket and thicket, and open habitats like grassland. Therefore, both the stalk-and-ambush theory, and the prey abundance and availability theory could be potential explanations of why the lions at AGR preferred these vegetation types, both strategies could have increased the success of hunting.

Habitat preference for cheetahs

The individual variation in preference for a certain habitat at AGR is higher in cheetahs than it is with the lions, probably because they are solitary species, each with an individual preference within the reserve and due to different driving factors. Since there were only two long-term cheetahs of different sexes to consider in this study, they should not be generalized. Additionally, there are many factors that an animal must consider when choosing a certain habitat, such as sex, protection of cubs, territorial behaviour, prey preference, intra-guild predation and others, and it is not solely vegetation type that is a driver for selection of habitat. These factors will not be equal drivers for each cheetah.

The cheetahs within AGR appeared to show a preference for grassland within their core areas and home ranges, and clear avoidance towards thicket, riverine thicket, karroid and forest. The valley thicket vegetation was significantly preferred by Inzwakazi, the female cheetah with three litters, compared to the other two cheetahs in the reserve. This could have possibly been to avoid interaction with the lions, a way to hide her cubs and seek shelter while denning, or it could also be an individual preference. The selection of intermediately dense vegetation could be associated with the steeper slopes of the valley thicket vegetation allowing for concealment and improved visibility over the surrounding area (Welch et al. 2015). Owen-Smith and Mills (2008) concluded that cheetahs are limited in their distribution due to aggressive interference competition from lions, rather than selecting habitats for prey availability (Owen-Smith & Mills 2008). It could be that they spent time in vegetation close to the treeline in order to not be detected by prey species and to avoid interactions with the lions, and then use their running speed by bursting from the cover and capturing prey on the grassland (Purchase & du Toit 2001). Bissett and Bernard (2007) highlighted the adaptability of cheetahs by showing that they can hunt successfully in very dense thicket vegetation (Bissett & Bernard 2007; Welch et al. 2015).

Interspecies habitat difference

The results in this study show that the different patterns of vegetation used by the lions and the cheetahs resulted in a significant difference in preference for vegetations like riverine thicket, thicket, savanna, grassland and valley thicket. In the total area of the reserve there is a clear significant difference in riverine thicket and thicket vegetation, where lions highly prefer the riverine thicket and thicket vegetation in contrast to the cheetahs that highly avoid these two vegetation types. This spatial avoidance is believed to be one of the main mechanisms by which these carnivores minimize competitive interactions (Broekhuis et al. 2013). Forest and karroid were both avoided by the lions and the cheetahs. Possibly there is only a limited number of prey available in these areas, but without having the abundance of each prey species in each habitat, this cannot be concluded. The lions' vegetation preference is cohesive for all the individuals, where the individual cheetahs do show different preferences for different vegetation types. However, the low number of individuals in this study might explain this trend and therefore it should not be generalized.

6.3. Prey selection

Lions at Amakhala Game Reserve

Hayward and Kerley (2005) found that lions selected prey species preferentially within a mass range of 190 – 550 kg, but no adjustments were made for a potential under-recording of smaller prey species. These analyses were done for many reserves with big lion populations, hunting sometimes in groups of ten lions, killing small elephants up to 2500 kg (Hayward & Kerley 2005; Owen-Smith & Mills 2008). Whereas a single male will refrain from killing large species such as giraffe(Lehmann et al. 2008). Also, Balme et al. (2017) stated that lions selected large and very large prey. In contrast to what was expected, this study has found that lions at AGR significantly selected for medium sized prey (31-99 kg). A reason for this could be that there were only two lions to consider the first two years of the study, resulting in catching smaller prey than a larger pride normally would be capable of. Another factor that might have affected the preference for medium sized prey, is that warthog made up 42.3 % of all identified killed prey species. Adult warthogs weigh between 55 kg – 69 kg, subadults weigh between 40 kg – 55 kg and juveniles weigh up to 20 kg. Therefore, the adults and subadults were classified under medium sized prey and this has resulted in a high medium prey count.

In studies elsewhere, buffalo were shown to be the numerically predominant prey of lions (Hayward & Kerley 2005; Lehmann et al. 2008; Balme et al. 2017; Barnardo et al. 2020). In AGR there were only three buffalos present in the main reserve, this could indicate that the lions selected for prey species that were more abundant than buffalos, such as warthog. On the contrary, zebras are frequently preferred by lions (Purchase & du Toit 2001). The lions at AGR actually showed a lower selection for zebras than would be expected. This study only recorded a total of 15 zebra kills over a six-year study period. However, there were sufficient amounts of zebras available within AGR, with a yearly mean of 151.20 ± 28.50 SD individuals. This confirms the lions' selection for medium sized prey species over large, and very large prey species by the lions.

Cheetahs at Amakhala Game Reserve

Cheetahs are known to kill a wide variety of prey species, but tend to end up specializing in one prey species in an area (Purchase & du Toit 2001). This contradicts the results in this study where six prey species made up 75.78 % of the cheetah diet in AGR, the cheetahs consumed mostly impala, kudu, red hartebeest, blesbok, common duiker, and eland. In Matusadona National Park in Zimbabwe, the main prey for cheetahs was impala, which was abundant and resident throughout the year (Hayward et al. 2006; Bissett & Bernard 2007). In other studies cheetahs often show a high preference for Thomson's gazelle and springbok (Lehmann et al. 2008). At AGR Thomson's gazelle have not been introduced and there is only a low number of springbok available in the reserve and thus, cheetahs consumed prey species that were more abundant in AGR, like impala and kudu. Hayward et al. (2006) found that the preferred weight range for cheetahs is 23 kg – 56 kg, this result is in line with the preference for medium sized prey in AGR.

The majority of kills in the reserve were made by Mfana and Inzwakazi. This can be explained by the fact they were both in the reserve for more than four years in comparison to Karongwe, who was only in the reserve for eight months. The cheetah kills per month ranged from 4.5 ± 2.43 kills in June and 12.17 ± 7.03 SD kills in November. There were never more than two actively hunting adult cheetah present during the study period. Therefore, the difference in kills per month can be possibly explained by the longer daylight hours in November, and therefore a higher chance of monitoring staff observing the kills or carcasses.

Potential for intraspecies overlap

Prey species were not consumed in equal proportions by the predators, with 82.1 % of the diet of lions consisting of five different prey species and 75.78 % of the diet of cheetahs consisting of six prey species. Out of the 21 prey species hunted by lions and 18 hunted by cheetahs, there was an overlap of 13 prey species. Kudu, red hartebeest, and eland were selected for the most by the two predator species. When there was large prey (black wildebeest, kudu, red hartebeest) the cheetahs selected mostly for juveniles and subadults, while the lions consumed the larger adults.

Cheetah did not appear to alter their diet in response to lions. Despite substantial overlap in the range of prey sizes killed, cheetahs killed more juvenile prey in species that were also killed by the lions, however this difference was not significant.

Lions selecting medium-sized prey, could be a potential for intra-guild predation and could have resulted in interactions between the two species. According to Radlolf and Du Toit (2004), lions prey typically upon proportionally larger prey (Radloff & du Toit 2004; Hayward et al. 2006), and would therefore not compete directly with smaller predators for most prey species (Hayward & Slotow 2009). However, the results in this study show that there is a potential for competition over larger species like black wildebeest, kudu, red hartebeest and eland, which are four of the most selected for prey species by the lions and cheetahs. Selecting for the same prey species could increase the chance of intra-guild competition. However, interspecific temporal avoidance has been documented in several guilds that include felids (Hayward & Slotow 2009; Cristescu et al. 2013). Cheetahs can avoid lions and potential interactions by hunting and being active during the day and being stationary when lions are active (Hayward et al. 2006). The results in this study suggest that cheetahs prefer prey species that offer minimal injury risk like smaller species (common duiker and impala), and the subadults and juveniles of horned species (kudu, black wildebeest, red hartebeest and eland). Cheetahs may also choose smaller species to reduce the risk for kleptoparasitsm without the risk of losing too much food (Lehmann et al. 2008). Cheetahs choosing smaller and juvenile prey could minimize the substantial overlap in the diet of the cheetahs and lions in AGR and therefore, the potential for interspecies competition.

The species that lions and cheetahs select for mostly have a great impact on prey populations and it is therefore important for management purposes to know if a prey species in the reserve is depleted (Welch et al. 2015). Some animals are stocked in very low numbers (nyala *Tragelaphus angassi*, bushbuck, common duiker, mountain reedbuck and springbok) but these species were sometimes found in cheetah kills. Cheetah could have actively selected for those animals, but it could also be an opportunistic hunt. However, these prey species are easy to overlook on an annual game count and could therefore be underrepresented.

The majority of the kills were found in grassland, savanna and old lands, which are all areas that provide greater visibility for the predator and for prey species when trying to avoid predation, although this advantage may be reduced during the night (Hayward et al. 2007). Grassland, savanna and old lands account for 63.48 % of the available area in AGR and therefore it was expected to find more kills in vegetation types that were more available. However, these results must be interpreted with caution, because of the small area, there were different vegetation types close to each other. Therefore, a hunt could have started in one vegetation type, but the carcass may have found in another vegetation type, where the prey species went to seek shelter. Forest, valley thicket and thicket only account for 19.8 % of the total vegetation and were not used as much by either one of the predators. Therefore, it is not surprising that there were only a limited number of kills found in these vegetation types. This might be due to a visibility bias because it is more difficult to see animals and kills in these areas. Lions using more riverine thicket is expected because it was their preferred habitat.

Limitations

The prey selection analysis in this study involved several adjustments to suppress the bias against the data collected and to statistically test whether the species selected for a certain weight category. The reliability of this data is impacted by the fact that there was no data available on prey occurrence or density by each habitat type, so there were no prey abundance estimates to detect the actual preference according to availability for each species or individual. Therefore, the results could not be compared with most of the other studies that uses various indexes to measure preference for a certain species. Because of the opportunistic data collection done by rangers, guides and ecologists there is likely to be bias in the determination of prey species, the prey species age and sex. Due to the monitoring hours of the reserve team, there are likely to be some gaps in data, particularly in terms of missed kills especially during the night. These incidental observations are biased towards larger prey, because they are more likely to be detected. However, this bias against smaller animals is generally reduced by undercounting small prey species in ground or aerial counts. Annual aerial and ground game counts were used to calculate the carrying capacity but does not predict the population estimates for each prey species. The methods used were sufficient to locate most of the kills but were biased in favour of larger and adult prey.

6.4. Management suggestions

The results have shown that there is spatial and dietary overlap between the cheetahs and lions in AGR. Therefore, it would be advisable to only host one of the two predator species on a small, fenced game reserve. If fences could be removed within geographically contiguous areas to increase the size of some areas, then it would presumably reduce the management intensity. However, the extent of human habitation and infrastructure in South Africa would only allow a relatively small proportion of the various reserves to connect (Lindsey et al. 2011). Therefore, the reserve must manage a fenced area to make it as natural as possible and must enhance populations of prey. The results in this study suggest that AGR can support a small lion pride, however they have to be constantly monitored and managed to ensure genetic diversity and that they do not have a negative impact on the prey population. Cheetah on the other hand require large areas for its reintroduction and conservation of the species, particularly in the presence of competing predators. Very small subpopulations require frequent augmentation to prevent inbreeding and to support larger subpopuations (Miller et al. 2013). It is important that managers bear in mind the potential cascade effects that lions may have on other predators and/or keystone species on smaller reserves. For example, very few small reserves with lions seem to be able to sustain reasonable numbers of the more threatened predators such as cheetahs (Lehmann et al. 2008). Further research in AGR could provide valuable insights in why vegetation types like karroid and forest are avoided by both the lions and the cheetahs in the reserve.

The AGR lions killed a total of 532 prey species and the cheetahs made a total of 573 kills during the whole study period. Therefore, from the results obtained in this study, it is clear that a small number of predators can kill substantial numbers of prey species. However, the data is incomplete, making it difficult to fully understand the patterns and full extend of the impact of the predators. A small reserve must ensure that the preferred prey base is large enough to sustain lion and cheetah populations. Therefore, it is advisable to calculate the abundance of the prey species and to increase the overnight kill observations, in order to make better estimations of what species each predator prefers. The information obtained from these studies could prove very valuable to other small reserves that want to stock predators or already have stocked predators. Restocking less abundant species like springbok that is preferred by cheetahs (Hayward et al. 2006; Bissett & Bernard 2007) and avoided by lions (Hayward & Kerley 2005), could potentially decrease the intraspecific prey selection.

7. Conclusions

This study has taken the initial steps into helping a small, fenced game reserve to understand how the lions and cheetahs in the reserve are making use of space by analysing the spatial distribution, habitat preferences and the prey species available to them on the reserve. It has also highlighted what further information is needed to answer the questions better and to inform management further.

The outcome of our results show that cheetah and lion home ranges almost fully overlapped, and the intraspecies core range overlap varied across different years. There also was also a significant difference in habitat preference for lions and cheetahs in six out of eight different vegetation types in the total area. This could potentially indicate that even though both species have large overlapping areas, they mitigate competition or conflict by using different habitats in these areas. Furthermore, both the cheetahs and lions in Amakhala Game Reserve significantly preferred medium sized prey over small sized prey, and there was also an overlap in the most selected for prey species of lions and cheetahs. It can therefore be concluded that the current small numbers of individuals may cope with interspecies competition by avoidance mechanisms, but the killing of the cheetah females (Inzwakazi and Karongwe) and its offspring in the last years, suggest that the co-habiting of these carnivores in the reserve could have narrow limits.

It must be kept in mind that this is a case study, and results may not be universal across other small reserves. It is hoped that this thesis provided valuable insights on the management issues related to having different key-predators in a small, enclosed reserve. Further investigations are needed to determine how habitat influences interactions between sympatric carnivores. The small size of many of these reserves might increase the intensity of competition between cheetahs and other large carnivores. The intra-guild mechanisms of reintroduced carnivores' coexistence should be studied across enclosed systems of different sizes, hosting varying carnivores within the guild to ensure long time survival of an endangered species such as cheetah.

References

Arthur SM, Manly BFJ, Mcdonald LL, Garner GW. 1996. Assessing habitat selection when availability changes. Ecological society of America **77**:215–227.

Balme GA, Pitman RT, Robinson HS, Miller JRB, Funston PJ, Hunter LTB. 2017. Leopard distribution and abundance is unaffected by interference competition with lions. Behavioral Ecology **28**:1348–1358.

Barnardo T, Tambling CJ, Davies AB, Klein-Snakenborg S, Asner GP, le Roux E, Cromsigt JPGM, Druce DJ, Kerley GIH. 2020. Opportunistic feeding by lions: non-preferred prey comprise an important part of lion diets in a habitat where preferred prey are abundant. Mammal Research **65**:235–243.

Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, Macdonald DW, Packer C. 2015. Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. Proceedings of the National Academy of Sciences of the United States of America **112**:1–6.

Bauer H, Iongh HH. 2005. Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. African Journal of Ecology **43**:208–214.

Belant JL, Bled F, Mkasanga IJ, Wilton CM, Mwampeta SB, Beyer DE, Mwakilema W, Fyumagwa R. 2019. Track surveys do not provide accurate or precise lion density estimates in Serengeti. Global Ecology and Conservation **19**:1–6.

Bissett C, Bernard RTF. 2007. Habitat selection and feeding ecology of the cheetah (Acinonyx jubatus) in thicket vegetation: Is the cheetah a savanna specialist? Journal of Zoology **271**:310–317.

Broekhuis F, Cozzi G, Valeix M, Mcnutt JW, Macdonald DW. 2013. Risk avoidance in sympatric large carnivores: Reactive or predictive? Journal of Animal Ecology **82**:1098–1105.

Broekhuis F, Madsen EK, Klaassen B. 2019. Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. Animal Conservation **22**:404–416.

Broomhall LS, Mills MGL, du Toit JT. 2003. Home range and habitat use by cheetahs (Acinonyx jubatus) in the Kruger National Park. Journal of Zoology **261**:119–128.

Caro TM, Stoner CJ. 2003. The potential for interspecific competition among African carnivores. Biological Conservation **110**:67–75.

Comley J, Joubert CJ, Mgqatsa N, Parker DM. 2020. Do spotted hyaenas outcompete the big cats in a small, enclosed system in South Africa? Journal of Zoology 1-9.

Creel S. 2001. Four Factors Modifying the Effect of Competition on Carnivore Population Dynamics as Illustrated by African Wild Dogs. Conservation Biology **15**:271–274.

Cristescu B, Bernard RTF, Krause J. 2013. Partitioning of space, habitat, and timing of activity by large felids in an enclosed South African system. Journal of Ethology **31**:285–298.

Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ, Madzikanda H, Macdonald DW. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. Journal of Mammalogy **93**:677–685.

Dolrenry S, Stenglein J, Hazzah L, Lutz RS, Frank L. 2014. A metapopulation approach to African lion (Panthera leo) conservation. PLoS ONE **9**:1–9.

Druce D, Genis H, Braak J, Greatwood S, Delsink A, Kettles R, Hunter L, Slotow R. 2004. Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. Koedoe **47**:103–118.

Durant SM. 1998. Competition refuges and coexistence: An example from Serengeti carnivores. Journal of Animal Ecology **67**:370–386.

Durant SM et al. 2016. The global decline of cheetah Acinonyx jubatus and what it means for conservation. Proceedings of the National Academy of Sciences of the United States of America **114**:528–533.

Edelman AJ. 2019. Carnivora. Pages 1–9 in J. Vonk and T. Shackelford, editors. Encyclopedia of Animal Cognition and Behavior. Springer Nature, Switzerland.

Funston PJ, Mills MGL, Biggs HC. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology **253**:419–431.

Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, van Moorter B. 2010. Habitat-performance relationships: Finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2255–2265.

Gregory T. 2017. Home Range Estimation. Pages 1-4 in Fuentes A, editor. The International Encyclopedia of Primatology. John Wiley & Sons, Hoboken.

Hall LS, Krausman PR, Morrison ML. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin **25**:173–182.

Hayward MW et al. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: An assessment. Oryx **41**:205–214.

Hayward MW, Hayward GJ. 2007. Activity patterns of reintroduced lion Panthera leo and spotted hyaena Crocuta crocuta in the Addo Elephant National Park, South Africa. African Journal of Ecology **45**:135–141.

Hayward MW, Hofmeyr M, O’Brien J, Kerley GIH. 2006. Prey preferences of the cheetah (Acinonyx jubatus) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? Journal of Zoology **270**:615–627.

Hayward MW, Kerley GIH. 2005. Prey preferences of the lion (Panthera leo). Journal of Zoology **267**:309–322.

Hayward MW, Kerley GIH. 2008. Prey preferences and dietary overlap amongst Africa’s large predators. African Journal of Wildlife Research **38**:93–108.

Hayward MW, Slotow R. 2009. Temporal Partitioning of Activity in Large African carnivores: Tests of Multiple Hypotheses. African Journal of Wildlife Research **39**:109–125.

Henschel P, Petracca LS, Hunter LTB, Kiki M, Sewadé C, Tehou A, Robinson HS. 2016. Determinants of Distribution Patterns and Management Needs in a Critically

Endangered lion Panthera leo population. Frontiers in Ecology and Evolution **4**:1–14.

Hetem RS, Mitchell D, de Witt BA, Fick LG, Maloney SK, Meyer LCR, Fuller A. 2019. Body temperature, activity patterns and hunting in free-living cheetah: biologging reveals new insights. Integrative Zoology **14**:30–47.

Hoare DB et al. 2006. Albany Thicket Biome. Pages 540–567 in L. Mucina and M. C. Rutherford, editors. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Hopcraft G, Sinclair ARE, Packer C. 2005. Planning for success Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559–566.

Houser AM, Somers MJ, Boast LK. 2009. Home range use of free-ranging cheetah on farm and conservation land in Botswana. African Journal of Wildlife Research **39**:11–22.

Hunter JS, Durant SM, Caro TM. 2007a. To flee or not to flee: Predator avoidance by cheetahs at kills. Behavioral Ecology and Sociobiology **61**:1033–1042.

Hunter LTB, Pretorius K, Carlisle LC, Rickelton M, Walker C, Slotow R, Skinner JD. 2007b. Restoring lions Panthera leo to northern KwaZulu-Natal, South Africa: Short-term biological and technical success but equivocal long-term conservation. Oryx **41**:196–204.

Johansson O, Simms A, McCarthy T. 2016. From VHF to Satellite GPS Collars: Advancements in Snow Leopard Telemetry. Pages 355–365 in T. McCarthy and D. Mallon, editors. Snow Leopards: Biodiversity of the World: Conservation from Genes to Landscapes. Elsevier, San Diego.

Johnson DH. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology **61**:65–71.

Kauhala K, Auttila M. 2010. Estimating habitat selection of badgers - A test between different methods. Folia Zoologica **59**:16–25.

Kettles R, Slotow R. 2009. Management of free-ranging lions on an enclosed game reserve. African Journal of Wildlife Research **39**:23–33.

Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, Mitchell MS, Gaillard JM, Moorcroft PR. 2010. The home-range concept: Are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2221–2231.

Kingdon J, Hoffman M. 2013. Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsburry Publishing, London.

Krausman PR. 1999. Some Basic Principles of Habitat Use. Pages 85–90 in K. Launchbaugh, J. Mosley, and K. Sanders, editors. Grazing Behavior of Livestock and Wildlife. University of Idaho Forest, Wildlife and Range Experiment Station.

Laizer H, Tarimo TMC, Kisui B. 2014. Home range and movement patterns of lions (Panthera leo) in Tarangire National Park, Tanzania. American Journal of Research Communication **2**:44–58.

Laver PN, Kelly MJ. 2008. A Critical Review of Home Range Studies. Journal of Wildlife Management **72**:290–298.

Lehmann MB, Funston PJ, Owen CR, Slotow R. 2008. Feeding behaviour of lions (Panthera leo) on a small reserve. African Journal of Wildlife Research **38**:66–78.

Lindsey P, Tambling CJ, Brummer R, Davies-Mostert H, Hayward M, Marnewick K, Parker D. 2011. Minimum prey and area requirements of the vulnerable cheetah acinonyx jubatus: Implications for reintroduction and management of the species in South Africa. Oryx **45**:587–599.

Loveridge AJ, Valeix M, Davidson Z, Murindagomo F, Fritz H, MacDonald DW. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography **32**:953–962.

Macdonald DW, Loveridge AJ, Nowell K. 2010. Dramatis personae: an introduction to the wild felids. Pages 3–57 in D. W. Macdonald and A. J. Loveridge, editors. Biology and Conservation of Wild Felids. Oxford University Press, New York.

Miller SM et al. 2013. Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. South African Journal of Wildlife Research **43**:138–154.

Miller SM, Harper CK, Bloomer P, Hofmeyr J, Funston PJ. 2015. Fenced and fragmented: Conservation value of managed metapopulations. PLoS ONE **10**:1–16.

Owen-Smith N, Mills MGL. 2008. Predator-prey size relationships in an African large-mammal food web. Journal of Animal Ecology **77**:173–183.

Palomares F, Caro TM. 1999. Interspecific Killing among Mammalian Carnivores. The American Naturalist **153**:492–508.

Pérez-Irineo G, Santos-Moreo A. 2013. Trends in research on terrestrial species of the order carnivora. Mastozoologia Neoptropcial **20**:113–121.

Poole KG. 1995. Spatial organization of a lynx population. Canadian Journal of Zoology **73**:632–641.

Powell RA, Mitchell MS. 2012. What is a home range? Journal of Mammalogy **93**:948–958.

Purchase GK, du Toit JT. 2001. The use of space and prey by cheetahs in Matusadona National Park, Zimbabwe. African Journal of Wildlife Research **30**:139–144.

Radloff FGT, du Toit JT. 2004. Large predators and their prey in a southern African savanna: A predator's size determines its prey size range. Journal of Animal Ecology **73**:410–423.

Spong G. 2002. Space use in lions, Panthera leo, in the Selous Game Reserve: Social and ecological factors. Behavioral Ecology and Sociobiology **52**:303–307.

Trinkel M, Angelici FM. 2016. The Decline in the Lion Population in Africa and Possible Mitigation Measures. Pages 45–68 in F. M. Angelici, editor. Problematic Wildlife: A Cross-Disciplinary Approach. Springer, Rome.

Tumenta PN, van't Zelfde M, Croes BM, Buij R, Funston PJ, Udo de Haes HA, de Iongh HH. 2013. Changes in lion (Panthera leo) home range size in Waza National Park, Cameroon. Mammalian Biology **78**:461–469.

Vebber L, Noack J, Heyns L, Rodenwoldt D, Edwards S. 2020. Rehabilitated cheetahs exhibit similar prey selection behaviour to their wild counterparts: A case study of prey selection by rehabilitated cheetah released into an enclosed reserve in north-central Namibia. Namibian Journal of Environment **4**:13–19.

Visser H, Muller L, Tumenta P, Buij R, de Iongh H. 2009. Factors affecting lion (Panthera leo) home range, movement and diet in Waza National Park, Cameroon. Journal of Zoology **300**:131–142.

Walden-Schreiner C, Leung YF, Kuhn T, Newburger T. 2018. Integrating direct observation and GPS tracking to monitor animal behavior for resource management. Environmental Monitoring and Assessment **190**:1–15.

Walter WD, Fischer JW, Baruch-Mordo S, Vercauteren KC. 2009. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. Pages 249–268 in O. Krejcar, editor. Modern Telemetry. InTech, Rijeka.

Weise FJ et al. 2017. The distribution and numbers of cheetah (Acinonyx jubatus) in southern Africa. PeerJ:1–29.

Welch RJ, Bissett C, Perry TW, Parker DM. 2015. Somewhere to hide: Home range and habitat selection of cheetahs in an arid, enclosed system. Journal of Arid Environments **114**:91–99.

Yalden DW, Largen MJ, Kock D, Hillman JC. 1996. Catalogue of the mammals of Ethiopia and Eritrea. 7. revised checklist, zoogeography and conservation. Tropical Zoology **9**:73–164.

Zengeni R, Kakembo V. 2017. 13C and 15N isotope ratios in Leptosols of thicket ecosystems in South Africa. Geoderma Regional **11**:113–122.

Zengeni R, Kakembo V, Nkongolo N. 2016. Soil carbon dioxide effluxes from different vegetation environments in semi-arid Eastern Cape, South Africa. African Journal of Range and Forage Science **33**:111–118.

Appendices

List of the Appendices:

Appendix 1: Prey Species List for Lions and Cheetahs at AGR

Appendix 1: Prey Species List for Lions and Cheetahs at AGR

Order	Family	Species	Scientific Name	Lion	Cheetah
Artiodactyla	Bovidae	Black Wildebeest	*Connochaetes gnou*	Yes	Yes
Artiodactyla	Bovidae	Blesbok	*Damaliscus pygargus phillipsi*	Yes	Yes
Artiodactyla	Bovidae	Buffalo	*Syncerus caffer*	No	No
Artiodactyla	Bovidae	Cape bushbuck	*Tragelaphus sylvaticus*	Yes	Yes
Artiodactyla	Bovidae	Common duiker	*Sylvicapra grimmia*	No	Yes
Artiodactyla	Bovidae	Eland	*Tragelaphus oryx*	Yes	Yes
Artiodactyla	Bovidae	Gemsbok	*Oryx gazella*	Yes	Yes
Artiodactyla	Bovidae	Impala	*Aepyceros melampus*	Yes	Yes
Artiodactyla	Bovidae	Kudu	*Tragelaphus strepsiceros*	Yes	Yes
Artiodactyla	Bovidae	Mountain reedbuck	*Redunca fulvorufula*	No	Yes
Artiodactyla	Bovidae	Nyala	*Tragelaphus angasii*	No	Yes
Artiodactyla	Bovidae	Red hartebeest	*Alcelaphus buselaphus*	Yes	Yes
Artiodactyla	Bovidae	Springbok	*Antidorcas marsupialis*	Yes	Yes
Artiodactyla	Bovidae	Waterbuck	*Kobus ellipsiprymnus*	Yes	Yes
Artiodactyla	Giraffidae	Giraffe	*Giraffa camelopardalis*	Yes	No
Artiodactyla	Hippopotamidae	Hippopotamus	*Hippopotamus amphibius*	No	No
Artiodactyla	Suidae	Bushpig	*Potamochoerus larvatus*	Yes	No
Artiodactyla	Suidae	Warthog	*Phacochoerus africanus*	Yes	Yes
Carnivora	Canidae	Black-backed jackal	*Canis mesomelas*	Yes	No
Carnivora	Felidae	Caracal	*Caracal caracal*	No	No
Carnivora	Felidae	Cheetah	*Aciconyx jubatus*	Yes	No
Carnivora	Felidae	Leopard	*Panthera pardus*	Yes	No
Carnivora	Felidae	Serval	*Leptailurus serval*	No	No
Carnivora	Herpestidae	Yellow mongoose	*Cynictis penicillata*	No	No
Carnivora	Hyaenidae	Brown hyena	*Hyaena brunnea*	No	No
Lagomorpha	Leporidae	Scrubhare	*Lepus saxatilis*	No	Yes
Perissodactyla	Rhinocerotidae	White rhinoceros	*Ceratotherium simum*	No	No
Perissodactyla	Equidae	Burchell's zebra	*Equus quagga burchellii*	Yes	Yes
Primates	Cercopithecidae	Chacma baboon	*Papio ursinus*	No	No
Primates	Cercopithecidae	Vervet monkey	*Chlorocebus pygerythrus*	No	No
Proboscidea	Elephantidae	African elephant	*Loxodonta Africana*	No	No
Rodentia	Hysticidae	Porcupine	*Hystix cristata*	Yes	No
Rodentia	Pedetidae	Southern African springhare	*Pedetes capensis*	Yes	No
Tubulidentata	Orycteropodidae	Aardvark	*Orycteropus afer*	Yes	No
Galliformes	Phasianidae	Red-necked spurfowl	*Pternistis afer*	No	Yes
Struthioniformes	Struthionidae	Ostrich	*Struthio camelus*	Yes	Yes
Total				**21**	**18**