Cheetah *Acinonyx jubatus* behaviour and resource use in response to other African large carnivores

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Declaration

I, Kristina Lee Cornhill, s217036759, in accordance with Rule G5.6.3, hereby declare that the above-mentioned thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

SIGNATURE:

Kristina Cornhill

Table of Contents

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Abstract

Competition occurs between species for shared resources. Subordinate species employ resource selection to shift their resource use away from that of dominant species in order to avoid the negative consequences of competition. Only in Africa is the post-Pleistocene large carnivore guild intact, consisting of lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus,* and African wild dogs *Lycaon pictus.* Therefore, only in Africa can we explore how large carnivores co-exist with one another in a diverse community. Cheetahs are a subordinate member of the large carnivore guild due to their small stature and solitary nature. However, we still do not fully understand how competition shapes cheetah behaviour and resource use. I used cheetahs as a model subordinate predator to determine the behavioural responses and resource selection of cheetah in response to assumed competition from other large carnivores. I experimentally explored the behavioural response of cheetah to large carnivore scent sources (scats) and their presence at cheetah scent-marking sites to test for avoidance of such cues. Moreover, using unplanned experiments based on the resource use of cheetahs in the absence and then presence of lions (assessing space and time use by cheetah) and African wild dogs (assessing prey use by both species), I evaluated resource selection by cheetahs as a way to reduce competition with these large carnivores. In addition, I measured spatial and temporal partitioning between cheetahs and all four large carnivores at camera trap sites. Finally, I assessed whether cheetahs responded to competitors using a long term proactive response or a short term reactive response. I found that all four of the other large carnivores in the guild shaped cheetahs resource use, however, all did so on different axes in accordance with the niche complementarity hypothesis. Lions and spotted hyenas were avoided through time, African wild dogs through space and prey use, and lions and leopards on the spatiotemporal axis. Moreover, I show that cheetahs utilize a reactive response to competition that allows them to avoid risk while still obtaining necessary resources.

Keywords

Resource partitioning; interference competition; exploitative competition; Carnivora; reactive response

CHAPTER 1

General Introduction

The guild of large predators in Africa, comprising lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus,* remains intact (Vanak *et al.*, 2013), and sympatric across much of these species ranges. The persistence of these predators in Africa, despite population declines, is in contrast to the losses experienced in this guild on the other continents (Van Valkenburgh *et al.*, 2016). Opportunities to develop an understanding of how a complete guild of large terrestrial predators co-exists and use resources is therefore limited to the African continent. Furthermore, there is a necessity for such studies given the further decline in populations of these species across the globe (Ripple *et al.*, 2014). Competition theory provides the framework in which to develop these studies since these predators are largely sympatric and share resources. Given that competition theory focusses on resource use, there is also an applied aspect to this approach, as it provides knowledge of the resource requirements needed for the persistence of these large predators and, therefore, their conservation management (Hayward *et al.*, 2007a).

Cheetahs are mainly solitary and one of the smallest large predators in Africa so maybe at risk of being dominated by their fellow guild members (Durant, 1998; Bissett & Bernard, 2007; Hayward & Kerley, 2008; Hayward & Slotow, 2009; Cozzi *et al.*, 2012; Broekhuis *et al.*, 2013; Cristescu, Bernard & Krause, 2013; Vanak *et al.*, 2013; Broekhuis *et al.*, 2014; Bissett *et al.*, 2015; Cusack *et al.*, 2015; Swanson *et al.*, 2016; Dröge *et al.*, 2017; Broekhuis, 2018), and thus at risk of the costs of competitive interactions. Therefore, cheetahs can serve as a useful focal species to explore competitive interactions among the guild of large predators in Africa. This thesis explores this opportunity, by assessing the behavioural response of cheetahs to other large predators, spatiotemporal responses of cheetahs to the other large predators and the overlap in resource use between cheetahs and African wild dogs.

Competition

Species that depend on the same resources, regardless of their phylogenetic background or geographical location, are grouped into guilds (e.g. trees, plankton, carnivores) (Simberloff & Dayan, 1991). The environmental conditions where a species is able to survive, due to the presence of all required resources, is called its fundamental niche (Austin & Margules, 1990; Pearman *et al.*, 2007). However, when members of the same guild live sympatrically, they compete for common resources. When the costs of competition are taken into account, a species may shift its resource use to avoid competitive interactions, and thus occupies its realized niche (Case & Gilpin, 1974; Pianka, 1974; Austin & Margules, 1990; Wauters *et al.*, 2002).

The principle of competitive exclusion states that two species cannot occupy the same niche or exclusion (local extinction) will occur (Hardin, 1960). Therefore, in order for species to coexist, one or both species must incur an evolutionary or behavioural shift (Pianka, 1974; Schoener, 1974). This is known as niche differentiation, one mechanism of which is resource partitioning (Aarssen, 1984). A species' niche is made up of multiple dimensions, although for competition there are three main axes: space, time and food (Pianka, 1974). Resource partitioning occurs when species separate themselves along the axis of a resource (e.g. select for different sized prey or are active at different times) (Schoener, 1974). However, for species to co-exist, partitioning doesn't have to occur along all of the dimensions of overlap (Vieira & Port, 2007). As long as there is dissimilarity along one common axis, resource utilization may be sufficiently different to allow for coexistence between the species (Schoener, 1974).

Competition between species takes on two forms: interference and exploitative competition (Birch, 1957). Interference competition involves direct behavioural encounters that free up resources from one species to the other (e.g. killing, harassment, poisoning, kleptoparasitism, etc. of the subdominant species). Exploitative competition occurs when one species consumes a limiting resource, reducing the availability of that resource for the other species. Niche theory assumes that access to common, limiting resources is the main force behind competition (Case & Gilpin, 1974). However, interference competition can be costly as well, as direct encounters can result in death or injury for the subordinate species (Palomares & Caro, 1999). In addition, there are costs associated with avoiding direct encounters through the use of time and energy (Case & Gilpin, 1974).

The effects of interference competition can mimic anti-predator responses such as risk avoidance (Laundré, Hernández & Ripple, 2010). However, the probability of encountering a predator or competitor is not evenly distributed across time nor space (Brown, Laundré & Gurung, 1999). Therefore, when avoiding a competitor, a species can invoke a proactive or reactive response. A proactive response is a long-term response, typically involving prior knowledge of the dominant competitor's space and time use, and using this to avoid risky areas or times (Creel, 2018). A reactive response is a short-term response to the immediate risk of encountering a predator or competitor (Creel, 2018). Fleeing is a characteristic reactive response to a dominant competitor. In the trade-off between resource attainment and competition, a proactive response evokes a higher nutritional/energetic cost, whereas, a reactive response has a higher stress cost (Creel, 2018) and a higher potential for injury if "fleeing" from the compeititor.

Without the addition or removal of a species from a community and a measure of population responses, the effects of competition can be hard to definitively quantify (Harrington *et al.*, 2009). However, utilizing a landscape of fear approach allows us to model risk across niche axes to assess possible competition (Laundré *et al.*, 2010). A landscape of fear can be created by modelling known risk (predator usage) or by manipulating risk. One can manipulate risk through changes in habitat (e.g. increasing visibility) (Jacob & Brown, 2000) or through manipulating cues of predator presence (e.g. adding the scent of a predator) (Shrader *et al.*, 2008). Therefore, by using a landscape of fear and assessing shifts in resource use, we are able to at least infer the relationship between competitors that would be otherwise difficult.

Large Carnivores

Carnivores compete with one another in a multitude of ways, including through intraguild predation, kleptoparasitism and reduced access to prey species due to the consumption of prey. Interference competition through intraguild predation within the predator guild is not uncommon, as they are specifically adapted for killing other species (Palomares & Caro, 1999). However, consumption of the victim is rarely seen as an outcome of intraguild predation among large mammalian carnivores, and the killer benefits from less competition over "freed resources" or by removing a threat to their young as opposed to energetic gains (Case & Gilpin, 1974; Palomares & Caro, 1999). Kleptoparasitism is another way that predators competitively acquire resources from one another. Kleptoparasitism occurs when a kill is stolen from its hunter and consumed by another predator. The original hunter stolen from experiences negative consequences of increased energetic expenditure of the hunt without the benefit of the meal (Scantlebury *et al.*, 2014) and, potentially, injuries from the direct encounter with the displacing predator. In contrast, the kleptoparasite gains the meal without the full cost of hunting it. Additionally, dominant predators can reduce access to prey through exploitative competition (Kortello, Hurd & Murray, 2007; Clements, 2012) or, through interference competition by monopolizing prey-rich times or places through a proactive avoidance response of a competitor (Dröge *et al.*, 2017).

Large carnivores are critical to the ecosystem as they structure communities by controlling smaller predators through competition and herbivores through predation (Ripple *et al.*, 2014). Nevertheless, carnivores are vulnerable to extinction due to their low population densities, slow reproductive rates, large ranges and pressures places on them by humans (Dalerum *et al.*, 2009; Ripple *et al.*, 2014). Given this vulnerability, carnivore populations have been on the decline since the Pleistocene. During the Pleistocene, the large carnivore guild was much more species-rich than it is today and an average of 6-7 species were sympatric with one another (Van Valkenburgh *et al.*, 2016). At present day, only 21% of the world's land area retains its large carnivore guild

(Ripple *et al.*, 2014) and only in Africa is an intact guild still in place (Dalerum *et al.*, 2009; Van Valkenburgh *et al.*, 2016).

In Africa, there are currently seven species occupying the large carnivore guild (Table 1.1). Of these seven species, five may occur sympatrically, across much of their range, including African wild dogs, cheetahs, lions, leopards, and spotted hyenas (Vanak *et al.*, 2013). All five species have undergone range contractions and experience varying levels of local extinction probability or population declines. The vulnerability of all five species can be mainly attributed to habitat loss or fragmentation and human persecution (Ripple *et al.*, 2014).

Carnivores are frequently in conflict with human populations, as they are not only a threat to human safety, but often prey upon livestock, threatening the livelihoods of humans (Marker, 2000). Moreover, with human populations increasing, habitat is being converted from natural "wild" landscapes to those for human use (e.g. farming, industrial or urbanization) (Lindsey *et al.*, 2011; Ripple *et al.*, 2014). The expansion of the human population puts further pressure on carnivore populations not only from direct persecution or habitat loss, but also through prey depletion (Ripple *et al.*, 2014). Therefore, across their range, African carnivores are typically being relegated into smaller fragmented areas, often inside fenced game reserves (Lindsey *et al.*, 2011).

Tourism is a major source of revenue for some African countries (e.g. South Africa) (Lindsey *et al.*, 2007). Studies have found that tourists are drawn to reserves for sighting of charismatic animals such as carnivores and other members of the Big 5 (Lindsey *et al.*, 2007; Maciejewski & Kerley, 2014). But carnivores naturally occur at low densities, which is not conducive to tourism, as it decreases the likelihood of sightings. Therefore, managers often tend to keep carnivores stocked at above sustainable densities to increase sightings, especially on private reserves that rely solely on ecotourism revenue (Bissett & Bernard, 2011; Clements, Cumming & Kerley, 2016a). Thus, even though large carnivores in Africa have co-evolved, these artificially high densities may lead to increased competition between the carnivores for resources (Darnell *et al.*, 2014). Additionally, in fenced reserves competition can be further exacerbated by the inability to move freely due to the constraints of predator-proof

Table 1.1: Large carnivores (> 15 kg) extant in Africa, with their species and common names, mass, IUCN status, population trend, population size and the percentage of their historical range that they currently occupy. Body mass and percent historical range currently occupied from Ray et al. (2005). The IUCN status, population trend and estimated population sizes from the IUCN Red List of Threatened Species with the specific citations listed in the footnotes. IUCN Status in increasing threatened order: Least Concerned (LC), Near Threatened (NT), Vulnerable (VU) and Endangered (EN).

Species	Common Name	Mass (kg)	IUCN		Population Size	% of Historical Range
			Status	Trend		
Canidae						
Lycaon pictus	African wild dog	20-34	EN[a]	Decreasing	1,409	10
Felidae						
Acinonyx jubatus	Cheetah	35-65	EN[b]	Stable	7,500-10,000	17
Panthera leo	Lion	120-180	VU[c]	Decreasing	23,000-39,000	17
Panthera pardus	Leopard	30-60	VU[d]	Decreasing	Unknown	65
Hyaenidae						
Crocuta crocuta	Spotted hyena	46-70	LC[e]	Decreasing	Unknown	73
Parahyaena brunnea	Brown hyena	28-47	NT[f]	Stable	4,365-10,111	62
Hyaena hyaena	Striped hyena	26-41	NT[g]	Decreasing	5,000-9,999	62

[a](Woodroffe & Sillero-Zubiri, 2012), [b](Durant *et al.*, 2015), [c](Bauer *et al.*, 2016), [d](Stein *et al.*, 2016), [e](Bohm & Honer, 2015), [f](Wiesel, 2015), [g](AbiSaid & Dloniak, 2015).

fencing (Hayward *et al.*, 2009; Ferreira & Hofmeyr, 2014; Rostro-García, Kamler & Hunter, 2015).

Cheetah

Cheetahs are one of the smaller large carnivores present in Africa. They are solitary mammals, except for some adult males who form coalitions of normally two or three siblings, and mothers with dependent offspring (Caro & Collins, 1987). Females are polyestrous, meaning that they can mate throughout the year (Laurenson, Caro & Borner, 1992; Wielebnowski & Brown, 1998). On average a female gives birth to her first litter at two years old (Kelly *et al.*, 1998), after a 93 day gestation period (Laurenson *et al.*, 1992), with 2-5 cubs being born (Mills & Mills, 2017). Cubs remain with their mothers until independence at an average age of 17 months (Kelly *et al.*, 1998), but only 4.8% of cubs born reached independence in the Serengeti (Laurenson, 1994). The average adult life span is 5.7 years in Kruger National Park (Kelly *et al.*, 1998).

Although the IUCN lists the global cheetah population as stable with a Vulnerable status (Durant *et al.*, 2015), recent papers by cheetah experts disagree (Durant *et al.*, 2017; Weise *et al.*, 2017). One paper on global cheetah population trends states that only 7,044 cheetahs are estimated to live in Africa (4,097 in southern Africa) across only 13% of the cheetah's historical range (Durant *et al.*, 2017). The second paper suggests a population size of only 3,577 cheetahs in southern Africa (Weise *et al.*, 2017). Additionally, the authors of both papers suggest up-listing cheetahs from vulnerable to endangered status due to decreasing populations across their range (Durant *et al.*, 2017; Weise *et al.*, 2017). In 2017, approximate 1200 wild cheetahs occurred in South Africa, with 300-450 free roaming individuals along the Botswana and Zimbabwe borders, 412 in Kruger National Park, 82 in the Kgalagadi Transfrontier Park and the rest occurring in small fenced reserves (Buk *et al.*, 2018). These small fenced reserves form a metapopulation with 50 reserves in five clusters containing 314 cheetahs (Buk *et al.*, 2018). Although across their range the majority of cheetahs are free-roaming individuals (i.e. are not fenced in reserves) (Durant *et al.*, 2017), the cheetahs inside fenced reserves in South Africa's metapopulation are the only increasing population known at present (Buk *et al.*, 2018).

Cheetahs are known to suffer from the negative effects of competition, including the extreme of death, as studies cite upwards of 55% of adult mortalities being attributed to large predators (Hunter, 1998; Mills & Mills, 2017). Additionally, the majority of cheetah cub mortality was caused by carnivores, this comprising 73.2% of cub mortality in the Serengeti (Laurenson, 1994) and 84.2% in the Kalahari (Mills & Mills, 2017). It is noteworthy that Mills and Mills (2017) suggest that smaller carnivores, not just large carnivores contribute to cheetah cub mortality. Cheetahs also suffer from kleptoparasitism, with 6.1% of kills in the Kalahari (Mills & Mills, 2017), 13% in the Maasai Mara (Broekhuis, Thuo & Hayward, 2018) and 14% in Kruger National Park (Mills & Biggs, 1993) being lost to other large predators.

Many studies (Durant, 1998; Bissett & Bernard, 2007; Hayward & Kerley, 2008; Hayward & Slotow, 2009; Cozzi *et al.*, 2012; Broekhuis *et al.*, 2013; Cristescu, Bernard & Krause, 2013; Vanak *et al.*, 2013; Broekhuis *et al.*, 2014; Bissett *et al.*, 2015; Cusack *et al.*, 2015; Swanson *et al.*, 2016; Dröge *et al.*, 2017; Broekhuis, 2018) have focused on how cheetahs use resource partitioning to reduce competition with the other large African carnivores, with varying results being reported. On the temporal axis, cheetahs may show temporal avoidance of other predators (Bissett & Bernard, 2007; Hayward & Slotow, 2009; Dröge *et al.*, 2017), with one study suggesting that cheetahs decrease their nocturnal activities in reserves with lions (Bissett *et al.*, 2015). In contrast, other studies documented cheetah activity throughout the 24 hour period, and with optimal foraging as opposed to predator avoidance hypothesized to be driving hunting on moonlit nights (Cozzi *et al.*, 2012; Broekhuis *et al.*, 2014). On the spatial dimension, cheetahs have been reported to seek refuge from high predator use areas (Durant, 1998) but may also show extensive overlap in their space use (Hunter, 1998; Cristescu *et al.*, 2013). Alternatively, cheetahs have shown no large scale displacement from competitors, avoiding competitors through differences in fine scale habitat selection (Bissett & Bernard, 2007; Cristescu *et al.*, 2013; Vanak *et al.*, 2013) or spatiotemporal avoidance (Broekhuis *et al.*, 2013; Vanak *et al.*, 2013; Swanson *et al.*, 2016).

Additionally, cheetahs experience overlap in prey preferences with all other large predators (Radloff & Du Toit, 2004; Hayward & Kerley, 2008; Clements, Tambling & Kerley, 2016b; Vogel, Somers & Venter, 2019). All cheetahs experience high dietary overlap with leopards and African wild dogs (Vogel *et al.*, 2019), however, male coalitions are also thought to experience high dietary overlap with lions (Broekhuis *et al.*, 2018).

Research Approach

The best way to study the effects of competition on cheetah behaviour would have been to have replicated areas with cheetahs present but no other carnivores, and systematically add and remove the other carnivores, while controlling for environmental factors (Harrington *et al.*, 2009) and monitoring cheetahs resource use and demographic responses. However, in reality, this experimental set-up is not possible. Therefore, I chose to use data from multiple reserves that contained varying densities of large carnivores in different guild compositions, including the absence of some species. This allowed me to partially approximate the abovementioned experimental design, without having to manipulate populations. Opportunities to replicate this approach across multiple reserves are, however, rare. Additionally, as all study reserves are located in close proximity, I was able to control for major variation in the environmental factors such as rainfall, temperature and major biome types. I was able to use these opportunities to assess the behavioural responses of cheetahs to other large predators in two reserves, space use of cheetahs in response to the re-introduction of lions in one reserve and overlap in resource use between cheetahs and African wild dogs in one reserve.

Study Sites

My fieldwork was conducted in the northern section of South Africa’s KwaZulu-Natal Province. The region is characterized as humid and subtropical with two distinct seasons: the warm, dry winter (April – September) and the wet, hot summer (October –

March) (Schulze, 1965). The average rainfall is 550 mm with the majority falling during the summer months (Schulze, 1965). Mean monthly temperatures range from 19 – 33°C, with July being the coolest month and January the hottest (Schulze, 1965). Land use consists of protected areas/reserves, community, mining and farming (Balme, Slotow & Hunter, 2010; Rathzel, Cock & Uzzell, 2018). Numerous reserves are located in this region including those owned privately, those managed by the provincial government and iSimangaliso, which is a World Heritage site. All reserves are surrounded by electrified game fences. My study makes use of four reserves: Hluhluwe-iMfolozi Park (HiP), Manyoni Private Game Reserve (Manyoni), Phinda Private Game Reserve (Phinda) and uMkhuze Game Reserve (uMkhuze) (Figure 1.1, Table 4.1).

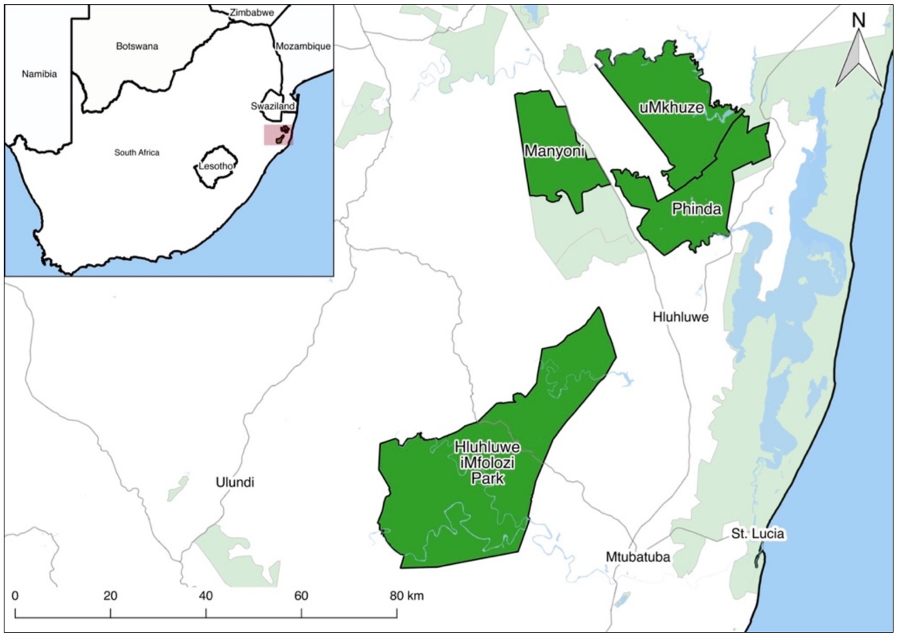

Figure 1.1: Map of reserves studied in the Kwa-Zulu Natal province of South Africa. The study site reserves included uMkhuze Game Reserve (uMkhuze), Manyoni Private Game Reserve (Manyoni), Phinda Private Game Reserve (Phinda) and Hluhluwe-iMfolozi Park.

Historically, wildlife species were heavily persecuted outside of reserves in this region, with populations becoming locally extirpated in the 1930s for cheetahs and

African wild dogs and 1940s for lions (Pringle, 1977). Re-introductions of species took place at different times in the different reserves. Spotted hyena and leopard populations persisted, although they were also extensively hunted (Somers *et al.*, 2017). Brown hyenas are rare in the area (Eaton, 1976). Many other smaller carnivores are present including black-backed jackal, *Canis mesomelas*, side-striped jackal, *Canis adustus*, caracal, *Caracal caracal*, serval, *Felis serval*, aardwolf, *Proteles* cristatus, honey badger, *Mellivora capensis*, striped polecat, *Ictonyx striatus*, large-spotted genet, *Genetta tigrina*, and several mongoose species (Pringle, 1977; Whateley & Brooks, 1983; Somers *et al.*, 2017).

Hluhluwe – iMfolozi Park (HiP)

HiP is a state-managed game reserve proclaimed in 1895, with an area of 900 km^2. The habitat ranges from open grasslands to thickets and closed Acacia and broad-leaved woodlands (Howison *et al.*, 2017). This heterogeneity is explained by the strong elevation and rainfall gradient in the park, with the northern Hluhluwe being hillier and with higher rainfall than the southern iMfolozi section. There are three main rivers within the park: the Hluhluwe, Black iMfolozi and White iMfolozi rivers, and the two sections (Hluhluwe and iMfolozi) are separated by a public road. HiP currently houses an intact large carnivore guild made up of populations of African wild dogs, cheetahs, lions, leopards and spotted hyenas. Lions were re-introduced in 1965 and African wild dogs in 1981 (Somers *et al.*, 2017). A total of 64 cheetahs were initially re-introduced over a four year period starting in 1965 (Rowe-Rowe, 1992; Somers *et al.*, 2017), but after a population decline to 13 individuals, a supplementation of 22 more individuals took place starting in 1994 (Marker-Kraus, 1996).

Manyoni Private Game Reserve

Manyoni, previously called Zululand Rhino Reserve, was formed when 17 landowners dropped their fences to form one game reserve. The 230 km^2 game reserve was founded in 2009 to support the World Wildlife Foundation (WWF)'s black rhino range expansion project. The reserve is open savanna thornveld to bushveld with riverine woodlands (Chapman & Balme, 2010). There is an altitude gradient of 130 – 437 m above sea level (masl), with the lowest point occurring along the Msunduze river (Odendaal-Holmes, Marshal & Parrini, 2014). Leopards persisted in Manyoni (Chapman & Balme, 2010) and cheetahs were re-introduced starting in 2009 (V. van der Merwe, Endangered Wildlife Trust, personal communications, April 2016). In 2011, lions re-introductions started (C. Kelly, Wildlife ACT, personal communications, April 2016) and African wild dogs in 2014 (Vogel *et al.*, 2018). Brown hyenas occur within the reserve in small numbers and spotted hyenas are rare (D. Antrobus, Manyoni, personal communication, March 2018).

Phinda Private Game Reserve

Phinda was established in 1990 and is now a 233 km^2 private game reserve. The habitat is mainly broad-leafed woodlands with grasslands and wooded grasslands mixed in (Balme *et al.*, 2010). Phinda has an elevation gradient of 4 – 201 masl, however, 95% of the reserve is below 100 masl (Hunter, 1998). There are two main rivers within the reserve, the Mzinene and the Munyawana, and the Ubombo mountain range runs through the southwest of the reserve. Leopards and spotted hyenas were never extirpated from Phinda (Hunter, 1998), and African wild dogs do not normally occur, however, they occasionally enter via the shared fence with uMkhuze (Rostro-García *et al.*, 2015). Cheetahs and lions were re-introduced in 1992 (Hunter, 1998).

uMkhuze Game Reserve

uMkhuze is a 400 km^2 state-managed reserve that was founded in 1912 and became part of the iSimangaliso Wetlands Park, World Heritage Site in 1999. Like the neighbouring Phinda, the habitat is mainly broad-leafed woodland with some open and wooded grassland (Balme *et al.*, 2010). The north and eastern border of the reserve is the Mkuze river, the Msunduzi river is in the south, and the western border extends along the Lebombo Mountains. The altitude varies from 30 – 480 masl on a gradient from the southeast to the northwest (Goodman, 1990). Leopards and spotted hyenas have always occurred within the reserve. Cheetahs were re-introduced starting in 1965, however, the population did not persist (Rowe-Rowe, 1992), and a second re-introduction was undertaken in 2006 (C. Kelly, Wildlife ACT, personal communications, April 2016). African wild dogs were initially re-introduced in 2005, however, the population was not viable and was removed in 2008 (C. Kelly, Wildlife ACT, personal communications, June 2016), and re-introductions occurred again in 2010 (Vogel *et al.*, 2018). Lions were re-introduced in 2013 (C. Kelly, Wildlife ACT, personal communications, April 2016).

Aim of Thesis

My thesis aims to assess the response of cheetahs to competing members of the guild of large carnivores. Although competition between predators in Africa has been studied previously, we still do not fully understand how the intact guild shapes cheetah niche use. Additionally, aspects of exploitative competition have never been explored, and only the inferred responses of competition have been reported, not the direct effects. In order to address this, I looked into three resources that cheetahs experience competition over, including space, time and prey, using both direct and indirect methods. My thesis consists of six chapters including four data chapters that have been written as independent scientific manuscripts, accordingly, some material is repeated between the chapters. Chapter One provides the background information necessary to understand competition and my study. Chapters Two through Five are my data chapters, briefly described below, and Chapter Six synthesizes my data chapters providing general conclusions and the broader implications of my study.

In Chapter Two, I assess how cheetah behaviour at scent-marking sites is changed by the presence of other large carnivores and their scent-marks. I wanted to know if intraguild communication was occurring at these scent-marking sites and if large carnivores are interrupting cheetah communication. I provide competing hypotheses for whether intraguild or intraspecific communication is the focus, whether cheetahs are avoiding other large carnivores, and whether intraspecific communication or predator avoidance is more important. Additionally, I offer predictions for avoidance based on predator body size and time of day.

In Chapter Three, I look at the response of cheetahs to lion re-introductions. I wanted to directly investigate how cheetah space and habitat use change depending on lion presence/absence. I develop hypotheses depending on whether the response of cheetah is random, proactive or reactive. Furthermore, I predict that cheetah sex and season will both influence the strength of the response.

Chapter Four evaluates resource partitioning utilized by cheetahs to reduce competition through both space and time. I sought to determine how cheetahs separate themselves in space and time from other members of the large carnivore guild, and whether they employ different strategies for different species. I hypothesize that cheetahs should avoid all competitors on at least one of three axes: spatial, temporal or spatiotemporal.

In the final data chapter, Chapter Five, I focus on the potential for competition between the two subordinate members of the large carnivore guild. I wanted to determine whether African wild dogs were limiting cheetahs’ access to shared prey resources, given their high overlap in preferred prey species. I lay out competing hypotheses to determine whether competition is occurring or not. Moreover, I predict that if competition is occurring, cheetah prey use should become more generalized than when competition is not occurring when assuming prey depletion.

CHAPTER 2

Predators Affect Cheetah Behaviour at Scent-Marking Sites

INTRODUCTION

Some mammals use scent-marking to convey information about their reproductive and social status to other individuals in their population, as well as to mark their territories (Gosling, 1982; Rodgers *et al.*, 2015; Allen, Gunther & Wilmers, 2017; Wachter *et al.*, 2017; Wikenros *et al.*, 2017). This form of communication is reliable as the information remains long after the individual has left, making it ideal for solitary carnivores (Cornhill & Kerley, in press). However, scent-marking information is not exclusive to intraspecific communication but can be accessed by individuals of other species. Therefore, it is appropriate that studies have started to look at the role of scent-marking on a community level (Li *et al.*, 2013; Allen *et al.*, 2015, 2017; Harmsen, Sanchez & Foster, 2016).

Studies have shown that prey species alter their behaviour in response to predator scent-marks (Apfelbach *et al.*, 2005; Monclús, Rödel & Von Holst, 2006; Shrader *et al.*, 2008; Bytheway, Carthey & Banks, 2013; Zöttl *et al.*, 2013). This has also been shown for mesocarnivores in response to apex predators (Allen *et al.*, 2017; Wikenros *et al.*, 2017; Haswell *et al.*, 2018). Specifically, competitively inferior individuals are found to increase the time spent accessing dominant individuals' scent-marks to gain information on the marker, while heightening defence behaviours (Apfelbach *et al.*, 2005).

Cheetahs, *Acinonyx jubatus*, are solitary carnivores who are slender, built for speed (Durant, 2000a), and often found to be competitively subordinate to other members of the large carnivore guild (Laurenson, 1994; Durant, 1998; Hunter, 1998; Durant, 2000a, 2000b; Hunter, Durant & Caro, 2007a; Broekhuis *et al.*, 2013; Cristescu *et al.*, 2013; Vanak *et al.*, 2013; Bissett *et al.*, 2015; Swanson *et al.*, 2016). A main source of cheetah cub mortality is attributed to carnivores (Laurenson, 1994; Mills &

Mills, 2017) and adults are also killed by predators (Hunter, 1998). Moreover, cheetahs suffer kleptoparasitism, losing up to 11% of their kills to other large carnivores (Hunter *et al.*, 2007a). Many studies have investigated resource partitioning by cheetahs as an adaptive response to reduce the impacts of competition (Durant, 1998; Hunter, Durant & Caro, 2007b; Cristescu *et al.*, 2013; Bissett *et al.*, 2015). Cheetahs have been found to avoid other large carnivores by seeking out areas of refuge (Durant, 1998), as well as relying on fine-scale avoidance behaviours and tactics (Broekhuis *et al.*, 2013; Vanak *et al.*, 2013; Swanson *et al.*, 2016).

Cheetahs have been shown to move away from the vocalizations of lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta* (Durant, 2000a, 2000b), however, the role of olfactory communication within the large carnivore guild in Africa has yet to be examined. Cheetahs use trees, termite mounds and man-made objects that are conspicuous on the landscape to scent-mark (Eaton, 1970; Marnewick, Bothma & Verdoorn, 2006; Marker, Fabiano & Nghikembua, 2008; Walker *et al.*, 2016; Wachter *et al.*, 2017). Males regularly visit these scent-marking sites to signal dominance status and mark their territories or to gather information on the dominant male(s) in the area, whereas females visit to signal estrous (Cornhill & Kerley, in press). Moreover, carnivores in Africa are known to countermark each other at leopard scent-marking sites (Apps, Rafiq & Mcnutt, in press), but what about at cheetah scent-marking sites? Here, I aim to explore whether scent-marking sites are used solely by cheetahs for intraspecific communication, or by multiple large carnivores for intraguild communication. Moreover, whether the presence of another large carnivore affects the behaviour of cheetahs at these scent-marking sites. Specifically, my questions are:

1) Does intraguild or intraspecific communication occur at scent-marking sites?
    a. If intraguild communication occurs, I would expect to find other large carnivores visiting sites as often as cheetahs.
    b. If intraspecific communication is the main function of scent-marking sites, I would expect other large carnivores to visit at random, far less often than cheetahs.
2) Are cheetahs threatened by large carnivores being near scent-marking sites?

    a. If cheetahs are threatened, they should avoid the sites when other large carnivores are present in the area (Durant, 2000b). This avoidance will lead to an increase in the visitation interval to the site.
    b. If cheetahs are not threatened by other large carnivores, carnivore presence should have no affect on cheetah visitation to scent-marking sites. However, cheetahs should increase their duration of stay, as they will be collecting the information provided by the other species' scent (Apfelbach *et al.*, 2005).

3) If avoidance of other large carnivores occurs, is intraspecific communication or predator avoidance more important to cheetahs?
    a. If intraspecific communication is more important than predator avoidance, then cheetahs should scent-mark at the site, despite clues as to the occurrence of other large predators.
    b. If predator avoidance is more important than intraspecific communication, cheetahs should forgo scent-marking at the scent-marking site when there are clues as to the occurrence of other large predators, in order to spend less time at the site.
4) Does the identity of the large carnivore visiting the scent-marking site matter?
    a. Responses of cheetahs to clues as to the occurrence of other large predators at scent-marking sites should vary depending on the species of the other large predator (e.g. by body size) (Durant, 2000b).
5) Does the time of day affect cheetahs use of scent-marking sites, given the increased activity of other large carnivores at night (Hayward & Slotow, 2009)?
    a. If predator avoidance is important, I predict that cheetahs will mainly visit the sites during the day.

METHODS

Study Sites

I conducted this study in two protected areas in the KwaZulu-Natal Province of South Africa (Figure 2.1). Hluhluwe-iMfolozi Park (HiP) is a 900 km^2, state managed reserve that houses an intact large carnivore guild including cheetahs, lions, leopards, *Panthera pardus*, spotted hyenas and African wild dogs (Somers *et al.*, 2017). Phinda Private Game Reserve (Phinda), is a 233 km^2 privately owned game reserve located 15.3 km northeast of HiP. Phinda currently supports four of the five large carnivore species, excluding African wild dogs, although these do occur occasionally, having entered via a shared fence line with uMkhuze Game Reserve (C. Sholto-Douglas, &Beyond, personal communications, June 2017). During the course of this study, only five cheetahs were present in HiP, four females and a male (D. Druce, EKZNW, personal communications, July 2016), and in Phinda, 27 individuals of known sex and rank occupied the reserve. The social rank of cheetahs in Phinda is known through intensive monitoring of cheetahs space use and interactions between individuals (C. Sholto-Douglas, &Beyond, personal communications, June 2017).

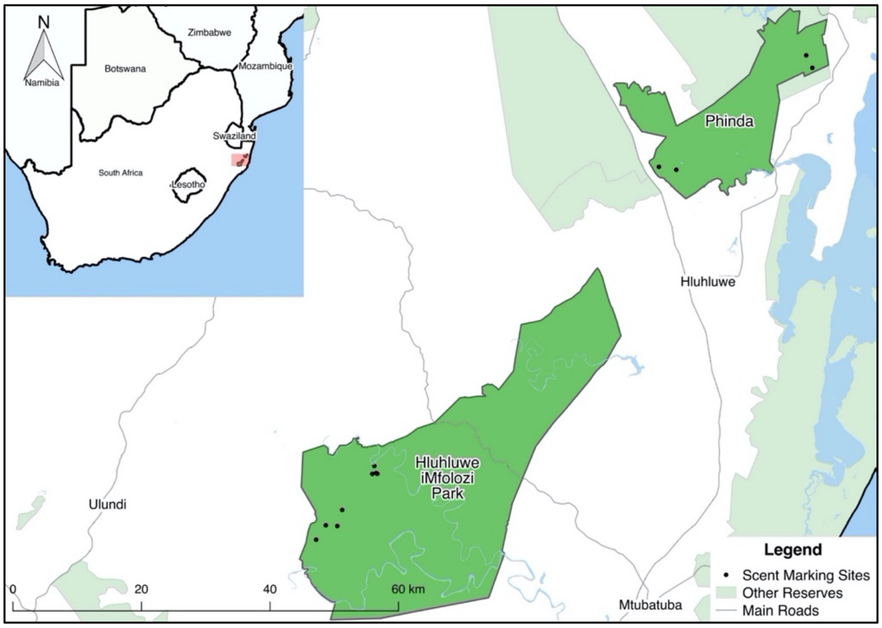

Figure 2.1: Map of camera trap sites located in Hluhluwe-iMfolozi Park (N = 8) and Phinda Private Game Reserve (N = 4) in KwaZulu Natal, South Africa.

Data Collection

I located scent-marking sites used by cheetahs in both reserves between July 2016 and May 2018. I identified eight sites in HiP and four in Phinda and set up video recording camera traps to capture behaviour (Figure 2.1). All sites were located in open habitats along either a road or a well-defined game path. At each site, one camera-trap was positioned to face the scent-marking site, attached to either a nearby tree or a metal stake. The cameras were Bushnell Trophy Cam's (Bushnell Corporation) taking one minute videos, with a one second trigger delay, and no sound in HiP, and Browning Recon Force Camera's (Browning Arms Company) taking 20 second videos inclusive of sound, with a one second trigger delay, in Phinda. Eleven of the 12 sites consisted of various tree species, one of which had a large termite mound at the base, and the final site was the ledge of an inactive quarry. The sites within each reserve ranged from 200 m to 25.4 km apart. All sites were visited at least once a month to service the cameras.

Behavioural Responses to Large Carnivore Cues

In order to explore cheetah behavioural responses to the presence of other large carnivores, I provided scat of these species at the scent-marking sites and monitored cheetahs use through video recordings. I opportunistically collected fresh large carnivore scat from sightings of other predator species, confirming which species deposited the sample. The entire scat was collected and placed inside a small bucket at the scent-marking site. The bucket was secured to the tree at about 50 cm above the ground, ensuring clear visibility in the videos. Containing the scat in a bucket allowed me to remove it entirely, as per the experimental design. Scats were not placed at the quarry site due to the inability to secure the sample. Each time a scat was placed I used a new bucket and wore gloves to minimize human scent. I only placed a scat at a site if I had video confirmation that a cheetah had used the site, and if I had not placed a scat at the site in the previous two weeks. The scats were removed after five days to ensure freshness (Haswell *et al.*, 2018), and I replaced the scat if a cheetah had not visited the site while the scat was present. If the collected scat could not be used right away, it was frozen inside a sealed plastic bag to retain its freshness (Bytheway *et al.*, 2013). I randomly selected which predator scat would be placed at the site from the scats available using a random number generator in Excel (ver. 16, Microsoft Office).

Ethical Note

The Nelson Mandela University Research Ethics Committee: Animal approved all methods used in the study (A16-SCI-ZOO-006), as did park management in both HiP (E/5119/02) and Phinda.

Video Processing

Cheetahs visits to the scent-marking site often occurred over several videos that I grouped into one event. I performed scan samples at five second intervals (Altmann, 1974) for each visit, recording the behaviour that occurred. Scan sampling was used, as opposed to continuous sampling, as there were gaps of time that I could not account for the cheetah's behaviour (e.g. between videos). The behaviours were grouped into four categories: scent-marking, sniffing, vigilance and other (Table 2.1).

For recorded visits (videos) of other large carnivore species (lion, leopard, spotted hyena or African wild dog) to the scent-marking sites, I noted whether they scent-marked or not, defined as at least one individual undertaking at least one scent-marking behaviour while at the site.

I classified cheetah visits into three groups based on their sex and rank: females, dominant males and submissive males, subsequently referred to as the “cheetah class”. Cheetahs were individually identified using their unique spot patterns (Marnewick *et al.*, 2006) and identification kits supplied by the parks. In addition, I classified all of the videos depending on who the previous visitor was to the site; a cheetah or another predator, referred to as “previous visitor”. If the previous visitor was one of the other large carnivore species, I further classified the data depending on whether it was a “predator video” or a “predator scent”. The “predator video” group included all captures of cheetah where a predator had been captured at that site since another cheetah. The

Table 2.1: Ethogram of cheetah behaviour when visiting scent-marking sites, taken from Cornhill and Kerley (in press).

Type	Behaviour	Description
Scent-Marking	Defecating	Depositing feces. A specific posture is undertaken by cheetah whereby they bend their knees and assume a distinct position. This behaviour was assigned if the posture was assumed.
	Rubbing	Rubbing their cheek or body on a tree trunk, ground or other objects.
	Scrapping	Raking their hind feet through the substrate or on the tree.
	Scratching	Intentional raking or gripping onto the tree trunk with their front claws.
	Urinating	Depositing urine at the scent-marking site. Posture is upright, on all fours. For males, this included their tail being upright, perpendicular to the ground.
Sniffing	Sniffing	Nose next to object, with chest moving inward and outwards consistent with a sniffing movement.
Vigilance	Vigilance	Head upright looking out into surroundings, the body could be in any position.
Other	Grooming	Cleaning, licking or washing oneself in any position.
	Laying Down	Laying horizontal on the ground off of their feet with their head down.
	Moving	Walking or climbing a tree.
	Vocalizing	Making audible sounds such as calls. Obvious even without sound by the sharp movement of the stomach and mouth.

"predator scent" group included all captures of cheetah where a predator scent-mark was present, either naturally placed by the predator or placed by myself. When a scent-mark was placed by a predator, the following cheetah visit was categorized as both "predator video" and "predator scent". The first cheetah visit to a site following the placement of the camera or after a camera failure was omitted from the analyzes, as I could not identify the previous visitor(s). As I was interested in the change in cheetah behaviour in response to other large predators, I only looked cheetah presence and not cheetah absence.

Statistical Analysis

R (ver. 3.4.3, R Core) was used to perform all analyses, as well as to create all figures. For mixed-effect models, I used QQ and residual fitted plots to ensure that assumptions were met, and performed a square-root transformation to normalize the data if needed.

Time of Day

I categorized the time of day as dawn, day, dusk and night, based on the time of day and amount of light present in the video. I calculated a kernel density plot using the overlap package to visualize the data (Meredith & Ridout, 2016). I calculated the proportion of cheetah visits that occurred during the day and night. In order to test if cheetahs visited sites more during the day or night than expected, I calculated the proportion of the 24 hour period that day and night occurred. I compared the proportion of day visits by cheetahs to the night visits using a chi-squared test to determine if they preferred one time period over the other. I also compared day and night visits to the expected time portion to determine if they used the time period more than expected. I calculated the proportions of visits by other large carnivore species that occurred during the day and night.

Duration of Stay

From the time stamp on the video, I calculated the duration that the cheetah remained at the scent-marking site. When looking at the time spent at a scent-marking site by cheetahs I was only interested in the influence of olfactory communication, not predator presence, therefore, I only selected previous visitor data that was cheetahs or "predator-scent", omitting the "predator-video" data. I ran two generalized linear mixed-effect models to determine any differences in the duration of stay using the lme4 package (Bates *et al.*, 2015). The model included duration as the response variable, transformed for normality, and cheetah class in an interaction term with previous visitor (cheetah versus "predator-scent") as the fixed effects. The other predator portion of the previous visitor term ("predator-scent") was modelled in two ways: with all other predators grouped together regardless of the species (cheetah versus "predator-scent") and with all other predators separated out by species (cheetah versus lion-scent versus leopard-scent versus spotted hyena-scent versus African wild dog-scent). I selected the best model using lowest Akaike information criteria corrected for small sample sizes (AICc) (Burnham & Anderson, 1998). In addition, the models included cheetah ID and site ID nested in reserve as random effects. I obtained pairwise p-values using the lmerTest package using the Kenward-Rogers method, as it handles small sample sizes better (Kuznetsova, Brockhoff & Christensen, 2017).

Visitation Interval

I calculated the interval that cheetahs took to return to a scent-marking site by measuring the time between subsequent visits of the same individual. I only calculated the interval if the camera had remained active the entire time between visits. When analyzing the frequency data, I was interested in what factors affect the cheetahs decision to visit the scent-marking site (e.g. predator presence in the area). Therefore, the previous visitor data consisted of cheetah versus "predator-video", omitting the "predator-scent" data. I again ran linear mixed-effect models with visitation interval transformed for normality as the response variable. Cheetah class and the previous visitor were the fixed effects in an interaction term, with cheetah ID and site ID nested in reserve as the random effects. Again, two models were run with predator portion of the previous visitor as all predators combined versus all predators separated to species level, and the best model was selected by lowest AICc. I estimated p-values using the Kenward-Rogers method.

Scent-Marking Frequency

For each video, I noted whether a cheetah scent-marked or not in a binary response, defined as undertaking at least one of the scent-marking behaviours noted in Table 2.1. If multiple individuals were present (e.g. a coalition), only one member needed to scent-mark for this behaviour to be noted. I only used the “predator-scent” category for the predator visitor data, as, I was interested in whether olfactory communication, as opposed to predator presence, changed the cheetahs behaviour. I tested the data using a generalized linear mixed-effect model with a binomial distribution. The response variable was the binomial scent-marking data, with cheetah class and previous visitor (cheetah versus “predator-scent”) as the fixed effects. I again ran two models separating out and grouping the predator portion of the previous visitor term by different predator species, selecting the best model by AICc. Cheetah ID and site ID nested in reserve formed the random variables.

Time Allocation

Finally, I calculated the behaviour data into proportions of time to remove bias caused by differences in the time spent at the site. I only used the predator data from the “predator-scent” category, as I was interested in the effects of olfactory communication, not just predator presence. I ran two linear mixed-effect models, the first separating out the “predator-scent” portion of the previous visitor term by species and the second grouping all other predators. The response variable was the behaviour data, with cheetah class and previous visitor (cheetah versus “predator-scent) as the fixed effects in an interaction term. I selected the best model using AICc. The random effects were cheetah ID and site ID nested in reserve and I obtained p-values using the Kenward-Rogers method.

RESULTS

Cheetahs visited the scent-marking sites on 590 occasions in 2920 days of camera trapping. Of those occasions, 404 cheetahs recorded visits (videos) were usable for this study. I removed all visits by males where a female was the previous visitor, as male cheetah behaviour is known to change in response to female visitation (Cornhill & Kerley, in press) and I did not have sufficient data for comparing the response of a male to a female cheetah visiting when a large predator had also been present. In addition, a female cheetah never visited a scent-marking site following a recorded visit of one of the other large carnivore species or when a predator's scent-mark was present. Moreover, submissive males only visited once while a predator scent-mark was present at a scent-marking site, as a result, I removed both groups (submissive males and females) from the analysis. This left me with only dominant male cheetah data (N = 2 cheetah groups) and forced me to remove the cheetah class fixed-effect variable from the models.

Other larger predators visited scent-marking sites on 35 occasions, 34 of which were usable for this study. One was not used as the camera failed after the predator visited. During seven visits predators left their scent-mark at the sites, including two urinations by leopards, lions climbing the scent-marking tree three times, a spotted hyena rolling beneath the scent-marking tree in cheetah scat and a leopard rubbing on the scent-marking tree. I placed scat at scent-marking sites an additional 14 times yielding 14 data points (Table 2.2). I was unable to separate out male versus female visits/scats of other predators due to a small sample size.

Time of Day

All cheetahs visits, regardless of sex, rank or previous visitor, were used for the time of day analysis (N = 590). Cheetahs visited the scent-marking sites at all times of the day (Figure 2.2). Contrary to predictions, 48.0% of cheetah visits were during the night, significantly more than the 37.6% that occurred during the day (χ = 12.18, $P < 0.001$).

But neither time period had more visits than expected (day: (χ = 0.07, P = 0.8, night: (χ = 0.25, P = 0.6). Other predators mainly visited the sites during the night, 79% of visits.

Table 2.2: Sample size for the number of videos containing a predator and the number of scent-marks left either naturally by the predator or artificially placed by researchers.

Predator	Number of Videos	Number of Scent-Marks		
		Natural	Artificial	Total
Lion	10	3	2	5
Leopard	4	3	7	10
Spotted Hyena	16	1	0	1
African Wild Dog	4	0	5	5
Total	34	7	14	21

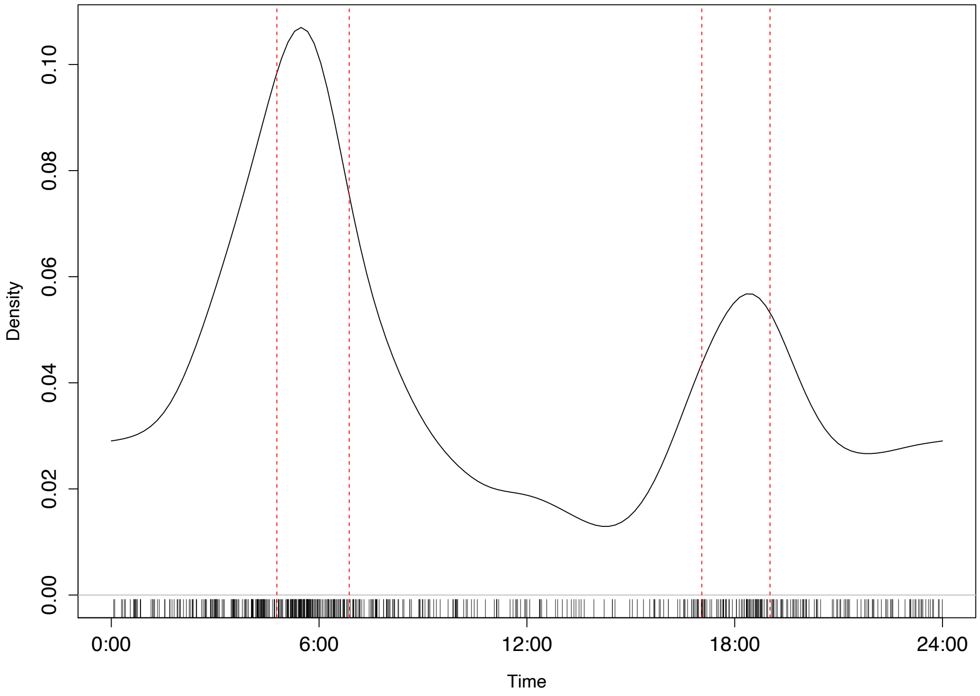

Figure 2.2: Density plot showing the time of day that cheetahs visited scent-marking sites. The vertical dotted red lines denote the earliest and latest sunrise and sunset times throughout the year, the small vertical black bars on the x-axis represent each individual visit.

Duration of Stay

I chose to omit five data points from the duration of stay analysis as they appeared irregular. During four of these five points, the cheetah remained at the scent-marking site, resting in the shade for over two hours. On the final occasion, a cycling event in HiP took place near a scent-marking tree that was beside the road, causing an abnormal number of vehicles to go past the site. While the cars were passing by, the dominant male cheetah in the area sat on the scent-marking tree watching the vehicles for over 20 minutes.

The model for the duration of stay performed better with all species of other predators grouped together (Appendix: Table A2.1). Cheetahs spent similar amounts of time at the site regardless of the presence of another predator’s scent-mark (t = -1.8, P = 0.069) (Figure 2.3).

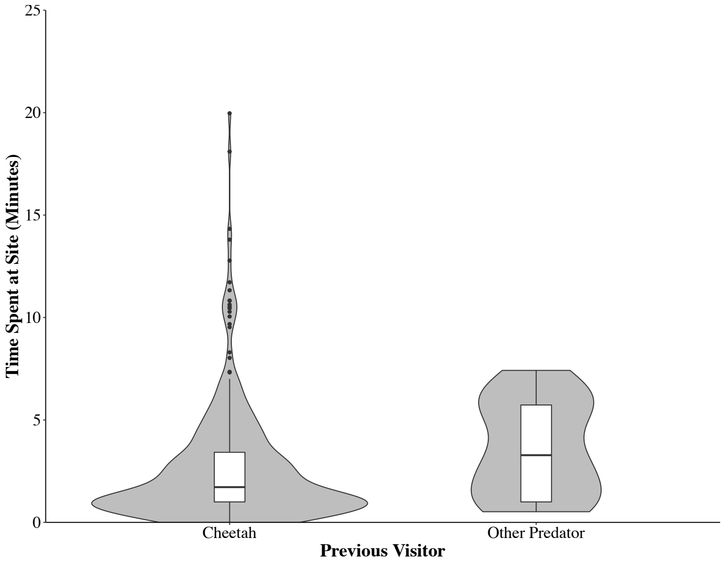

Figure 2.3: Duration of stay (minutes) at a scent-marking site by cheetahs depending on the previous visitor (other predator species vs cheetah) leaving a scent-mark at the site.

Intervals Between Visits

For the visitation interval, the model performed best when other predator species were separated out (Appendix: Table A2.1). Cheetahs took longer to return to a site when a lion or leopard was the previous visitor to the site, as opposed to a cheetah (lion: t = -3.9, df = 310, P < 0.001, leopard: t = -3.3, df = 310, P = 0.01) (Figure 2.4, Appendix: Table A2.2).

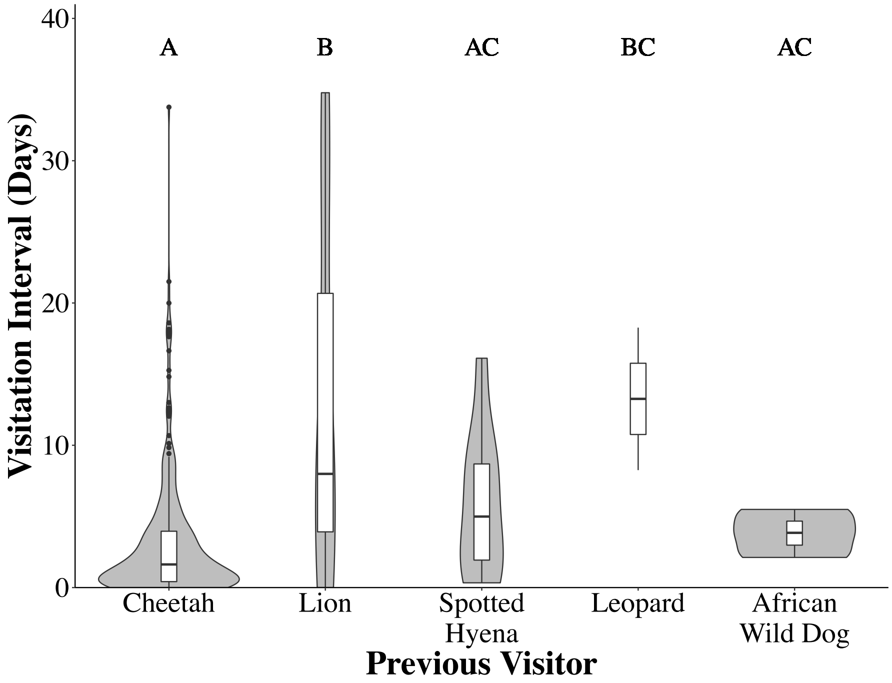

Figure 2.4: The visitation interval (days) for cheetahs returning to a scent-marking site depending on the previous visitor to the site. Letters indicate significant differences between species (P < 0.05).

Scent-marking Frequency

For this analysis, predator species grouped together performed better (Appendix: Table A2.1). Cheetahs did not change the frequency in which they scent-marked irrespective of whether a cheetah (63%) or another predator (81%) was the previous visitor to scent-mark at the site (z = 1.2, P = 0.3).

Time Allocation During Visits

The time allocation model performed best when other predator species were grouped into one predator response (Appendix: Table A2.1). When the previous visitor to the site was a cheetah, cheetahs spent the majority of their time at scent-marking sites performing other behaviours. Cheetahs performed other behaviours 18.0% more than sniffing (t = -4.73, df = 1486, P < 0.001) (Figure 2.5, Appendix: Table A2.3). They also spent 18.7% more time sniffing than being vigilant (t = -2.38, df = 1486, P = 0.017), and 18.4% more time being vigilant than scent-marking (t = -4.36, df = 1486, P < 0.001). When a predators scent-mark was present at the site, cheetahs spent 25% more time sniffing than when the previous visitor was a cheetah (t = -2.97, df = 1486, P = 0.003). This meant that they spent 57.6% more time sniffing than scent-marking in response to another predators' scent (t = -2.08, df = 1486, P < 0.038).

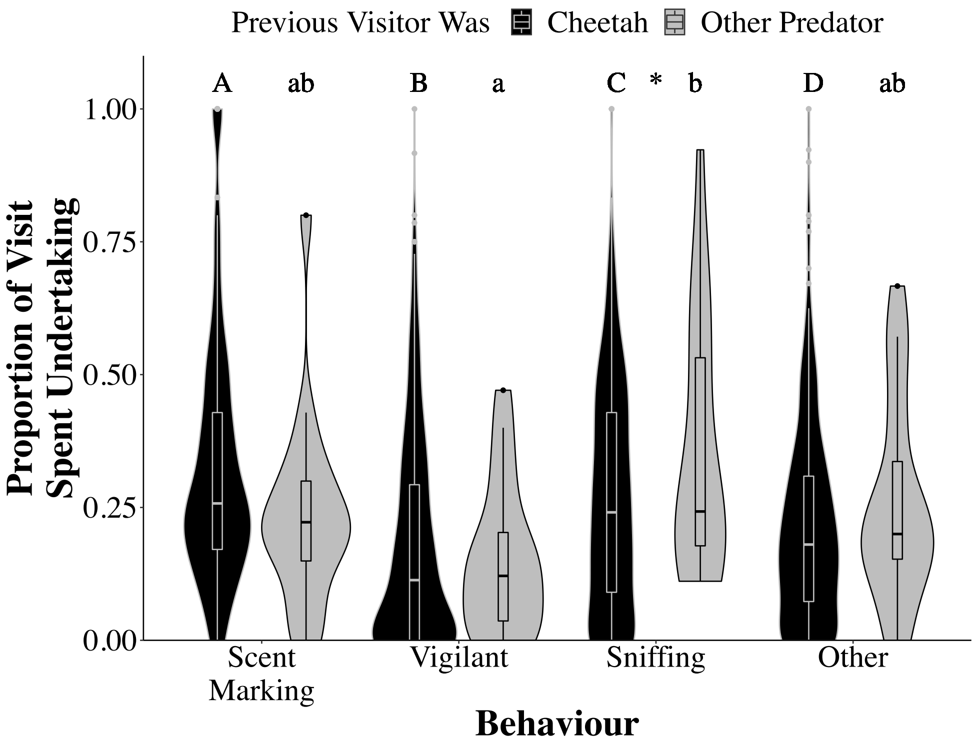

Figure 2.5: Time allocation of behaviours at scent-marking sites depending on the previous visitor (other predator species vs cheetah) to scent-mark at the site. Letters indicate significant differences between behaviours for the same previous visitor, capitals for cheetah and lowercase for other predators (P < 0.05). * indicates significant differences in the proportion of time spent on the behaviour between cheetah and other predators being the previous visitor (P < 0.05).

DISCUSSION

This chapter shows the negative impacts other large carnivores have on cheetahs as they can use interference competition to block intraspecific communication. Cornhill and Kerley (in press) showed the significance of scent-marking sites for cheetah behaviour and communication. However, I was able to show that other large carnivores can impede this communication, as female cheetah did not visit a scent-marking site following predator activity. This means that large carnivores were potentially blocking a female cheetahs ability to signal estrous, and moreover, potentially inhibiting cheetahs reproduction. It is possible, that cheetahs are able to maintain communication by having multiple scent-marking sites within their home range and even several fairly close together, as this will allow cheetahs to avoid interference competition while still communicating. I found that cheetahs did use scent-marking sites that were located close together, in particular in HiP there were three sites in a 0.45 km^2 area, and this redundancy can be explained by interference competition.

My results support the idea that intraguild communication is not the primary role of scent-marking sites. The fact that other large carnivores visited scent-marking sites much less than male cheetahs indicated that they were not visiting cheetah scent-marking sites in order to countermark or gain information on a cheetah. I did note visiting leopards urinated twice on the scent-marking tree, so it is possible that they were opportunistically communicating, but not outright searching for the sites. However, large carnivores visited (36 occasions) near as often as female cheetahs (43 occasions, Cornhill and Kerley, in press), showcasing the potential for inhibiting reproductive signalling but without more data this can only be seen as incidental effect.

I found support for the hypotheses that cheetahs responded to cues of the presence of other large carnivores and tried to avoid them, but that intraspecific communication was also important. As predicted, cheetahs took longer to return to a scent-marking site following a video showing that a carnivore was present in the area, specifically lions and leopards. It is thought that cheetahs took longer to return to a site, in order to avoid interactions with these larger of the large carnivores (Broekhuis *et al.*, 2013). However, once a cheetah visited a site, they spent the same amount of time at the site regardless of the previous visitor. Cheetahs spent longer sniffing when large carnivore scents were present, but scent-marking occurred in the same frequency of visits. This shows that although cheetahs were curious about the source of the scent-mark, and potentially threatened, it was still important for them to communicate with other cheetahs. However, during the study, there was one instance where a pack of African wild dogs arrived at a scent-marking site when a cheetah was present. From the video, I saw that they had a short stand-off (stood staring at each other for 40 seconds) before both species left the site and the cheetahs did not scent-mark during this visit. This suggests that the actual presence of a competitor causes more of a threat than the presence of a competitor's scent-mark, and forces cheetahs to abandon communication, in order to move away from the threat, as demonstrated by Durant (2000b).

I found support for my hypothesis that the predator species would matter to cheetah behaviour. When looking at the interval in which cheetahs returned to sites, previous visits by lions and leopards produced a longer delay. Whether this is a body size response, species-specific response, response to felids, or something else cannot be distinguished from the available data.

I did not find the predicted nocturnal avoidance of scent-marking sites, with cheetahs visiting the sites throughout a 24 hour period and the majority of visits happening in the dark. This result allowed me to reject my hypothesis that cheetahs would visit sites more during the day in order to avoid the nocturnal activity patterns of other large carnivores. This suggests that cheetahs at scent-marking sites were not using temporal resource partitioning as a way to avoid interference competition from other large carnivores as suggested by Hayward and Slotow (2009) but possible use temporal partitioning as a way to avoid interactions during other activities (e.g. hunting). My results are further supported by Broekhuis *et al.* (2019) who documented that the majority of visits by cheetahs to scent-marking sites in the Maasai Mara occurred at night.

Although I tried to control for predators being present in the vicinity of the scent-marking sites including video captures of them, this is not exhaustive. A predator could have been in the area and walked immediately behind, or out of camera range. I was unable to control for this and recommend that future studies make use of spatial data (i.e. GPS collar data) to control for predator presence. In addition, studies have shown that the freshness of a scent-mark varies considerably over time, as does the affect of the scent-mark on the receiver (Bytheway *et al.*, 2013). I, therefore, suggest that future studies include freshness of scent-marks as a variable in their analysis, or conduct a pilot study looking into the effects. Unfortunately, due to the small sample size, I was unable to include this variable in the analysis. I do feel, however, that the use of five days old as a cut-off was reasonable as scent-marks are intended to last for a long time and other studies successfully demonstrated responses to scent-marks used longer durations (Shrader *et al.*, 2008; Wikenros *et al.*, 2017).

In conclusion, by showing that large carnivores can limit a cheetah's access to scent-marking sites, they can thereby block, or at least delay, biologically important intraspecific communication. Moreover, Cornhill and Kerley (in press) showcased the potential for scent-marking sites to be used as a tool to monitor cheetah populations. However, I have shown that the utility of this is affected by the presence of other large carnivores. Not only will managers need to control for the presence of other large carnivores, I caution against studies comparing across reserves with different compositions of carnivore guild.

CHAPTER 3

Cheetah Space Use Before and After Lion Re-introductions: A Reactive Response

INTRODUCTION

Cheetahs, *Acinonyx jubatus*, in South Africa occur mainly in fenced reserves (Buk *et al.*, 2018). Reserves with predator-proof fencing often experience higher levels of competition, as they constrain movements of animals (Ferreira & Hofmeyr, 2014). In addition, tourism, which is often a driving force behind these reserves (Lindsey *et al.*, 2007), favours stocking charismatic animals, such as predators, in higher than 'normal' densities to increase sighting opportunities (Maciejewski & Kerley, 2014). When such species are competing, this may lead to subordinate species suffering excessive competition. Cheetahs are frequently subjected to competition, mainly from lions, *Panthera leo,* but also from spotted hyenas, *Crocuta crocuta,* and leopards, *Panthera pardus* (Durant, 2000b; Mills & Mills, 2017). Lions kill cheetahs of all ages (Hunter, 1998), and are a main source of cheetah cub mortality (Laurenson, 1994). Additionally, cheetahs suffer from kleptoparasitism by other predators (Hunter, Durant, & Caro, 2007).

Species only occur under certain environmental conditions, that are genetically and physiologically determined, and provide them with the resources necessary to survive and reproduce, this is called their fundamental niche (Austin & Margules, 1990; Swart *et al.*, 1994; Pearman *et al.*, 2007). A niche can be based around any resource that they require including space, time or food. As most species live in a community, competition between species occur for the available resources. The portion of the species niche that they occupy after constraints from interspecific competition is called their realized niche (Pearman *et al.*, 2007).

Competition can occur either directly, through interference, or indirectly, by exploiting a shared limiting resource (Case & Gilpin, 1974; Pianka, 1974; Crooks & van Vuren, 1995). For subordinate predators, the consequences of competition can be extreme, resulting in death (Holt & Polis, 1997). An animal's response to a competitor or predator has been postulated to be either proactive or reactive (Creel, 2018). A proactive response allows individuals to use knowledge of the environment to make long-term decisions and avoid potentially risky areas or times. Knowledge on a predators use of the environment is commonly referred to as a landscape of fear (Laundré *et al.*, 2010). This has been demonstrated in Africa where prey species avoid areas used by their common predators (Thaker *et al.*, 2011). Alternatively, a reactive response is the short-term avoidance of an immediate threat of a competitor/predator being present and allows for extensive overlap in space, while avoiding direct interaction. Cougars, *Puma concolor,* show extensive overlap of their home ranges with wolves, *Canis lupus*, but avoid areas recently used by wolves (Kortello *et al.*, 2007).

Studies investigating how cheetahs and lions co-exist in spatial terms show both proactive and reactive responses. Cheetah home ranges but not core areas showed overlap with lion home range and core areas (Hunter, 1998; Cristescu, Bernard, & Krause, 2013), supporting a proactive response. A proactive response was also demonstrated when cheetahs sought refuge away from high lion use areas (Durant, 1998). Alternatively, cheetahs were located further from lions than expected at random, even though both species had high space use overlap, suggesting a reactive response (Broekhuis *et al.*, 2013). Durant (2000b) found that cheetahs moved away from lion and spotted hyena vocalizations, also suggesting a reactive response. At the habitat level, Rostro-García, Kamler, & Hunter (2015) suggested that female cheetahs selected for closed habitat, presumably using the vegetative to avoid detection by lions (reactive), whereas male coalitions selected areas with lower lion densities (proactive), suggesting a difference in response depending on the sex of the cheetah. However, all these studies look at the inferred response of cheetahs to lion competition, not the effects of the presence or absence of lions in the system. Here I investigate how lions affect cheetah space use following the re-introduction of lions into cheetah habitat which previously had no lions. This unplanned experiment provides the opportunity to explore how lions shape the space which cheetah use. In addition, I will be able to directly investigate whether a cheetah's response to lion competition is reactive or proactive.

My questions relate to whether cheetahs employ a proactive or reactive response to competitive risk posed by lions. Additionally, I provide predictions relating to environmental factors and the demographic class that the cheetah belongs too. My hypothesis and predictions specifically are:

1. If cheetahs employ a proactive response to lion risk, they should shift their space use to avoid lions overall (Durant, 1998).
    a. Cheetah home ranges and core areas will contract following the re-introduction of lions, as they will try to seek refuge from lions, occupying space that lions do not.
    b. This contraction will cause a decrease in the overlap of core areas, but cheetahs will experience some overlap in home ranges due to limitations of reserve size.
    c. Cheetahs will change their habitat selection to avoid habitats selected by lions.
2. If cheetahs employ a reactive response to lion risk, cheetahs should not shift their space use but should avoid interactions with lions (Broekhuis *et al.*, 2013).
    a. Cheetah's home ranges and core areas will not change in size or distribution following the re-introduction of lions, as they are not reacting to the long-term risk of encountering a lion.
    b. The cheetah's habitat use will go unchanged following lion re-introductions.
    c. Cheetahs should avoid the immediate risk of encountering a lion by being located further than expected from lions at any given time.
3. If cheetahs do not employ a reactive or proactive response to lions, I should not see a shift in their space use, nor avoid interactions.
    a. Cheetah home ranges and core areas remain unchanged.

   b. Cheetah habitat selection will be unchanged.
   c. Cheetah locations will be randomly located compared to lion locations.
4. Cheetah space use should be a function of the season (Van Orsdol, Hanby & Bygott, 1985) and sex of the cheetah (Broomhall, Mills & du Toit, 2003).
   a. The winter period should yield smaller home ranges and higher overlap, as prey should be concentrated at water sources and less widespread, meaning that predators will have to cover a smaller area to find prey.
   b. Females should respond more strongly than males to lion presence, as they would potentially have cubs present who are more vulnerable to predation. Additionally, females should have larger home ranges than males (Hunter, 1998; Bissett & Bernard, 2007).

METHODS

Study Area

uMkhuze Game Reserve, hereafter uMkhuze, is located in northern KwaZulu-Natal (KZN), South Africa (Figure 3.1). The area has two distinct seasons, characterized by a hot, wet summer (October - March) and a cool, dry winter (April – September). The annual average rainfall is 550 mm, with mean temperatures ranging from 19°C to 33°C (Balme *et al.*, 2010). The 395 km^2 is state managed by Ezemvelo KZN Wildlife (EKZNW) but also forms part of the iSimangaliso Wetland Park World Heritage Site. Scott-Shaw and Escott (2011) mapped out vegetation types in uMkhuze following Mucina and Rutherford's (2006) descriptions of the different vegetation types. uMkhuze has seven vegetation types, representing three biomes, including Western Maputaland Clay Bushveld (WMCB), Makatini Clay Thicket (MCT), Southern Lebombo Bushveld (SLB), Lowveld Riverine Forest (LRF), Western Maputaland Sandy Bushveld (WMSB), Maputaland Coastal Thicket (MLCT) and Sand Forest (SF) (Table 3.1).

Predator populations throughout KZN declined under heavy hunting pressure in the 1800s and early 1900s, with cheetah and lion populations being locally extirpated by

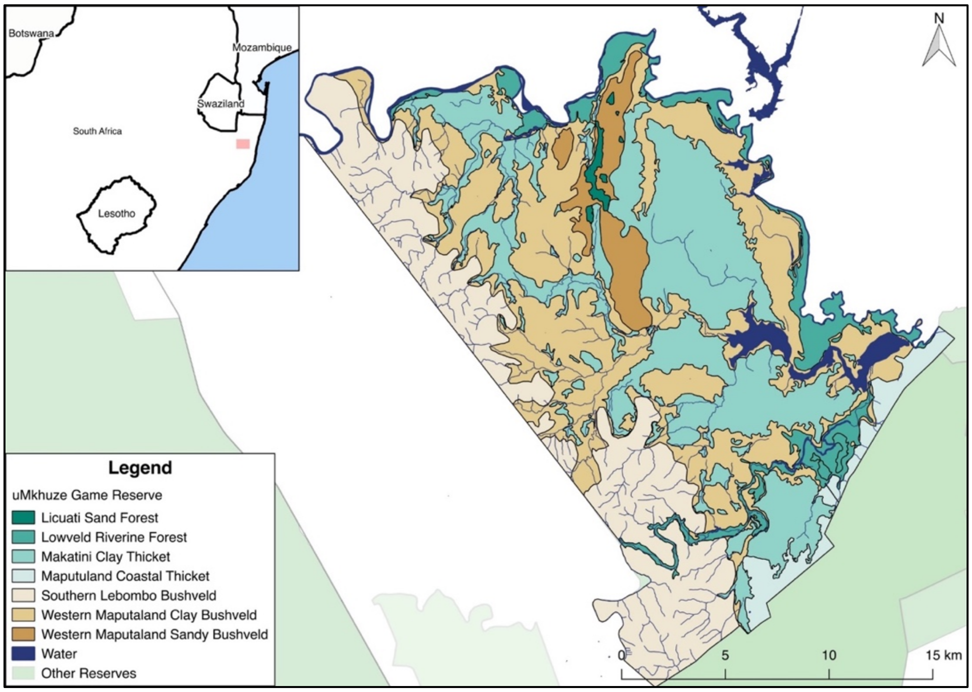

Figure 3.1: Map showing the location of the study site, uMkhuze Game Reserve, and the vegetation units present, as mapped by Scott-Shaw and Escott (2011).

the 1930s and 1940s, respectively (Pringle, 1977). Cheetahs were re-introduced to uMkhuze in 2006 and the population has since fluctuated between 4-18 individuals (Church, 2016). Four lions were re-introduced in 2013, with population sizes increasing to a peak of 18 in 2016 (Church, 2016). Other large predators present over the study period included African wild dogs, *Lycaon pictus*, leopards, and spotted hyenas (Church, 2016).

Data Collection

From December 2006 till March 2018 a total of 30 adult cheetahs were tracked (Table 3.2) including six two-male coalitions of which four of these coalitions had a member die and the surviving males were then tracked on their own. Both collared and un-collared cheetahs were present over the years, with EKZNW placing all collars either prior to the

Table 3.1: Summary of vegetation types occurring in uMkhuze Game Reserve following Mucina and Rutherford (2006).

Biome	**Vegetation Type**	**Description**	**Area (km^2)**	**% of Park**
Savanna	Western Maputaland Clay Bushveld	Mainly short compound woodlands and wooded grasslands	131	33.2
Savanna	Makatini Clay Thicket	Mainly short simple-leaved bushland Thicket up to 10m Dense shrub layer	113	28.6
Savanna	Southern Lebombo Bushveld	Open Bushveld	90	22.8
Savanna	Western Maputaland Sandy Bushveld	Mainly short simple-leaved bushland Mixed with woodlands and wooded grasslands	17	4.3
Forest	Lowveld Riverine Forest	Tall dense forest along water Well developed dense shrub layer	29	7.3
Forest	Sand Forest	Dense thickets Tall canopied forest Developed shrub layer	2	0.5
Indian Ocean Coastal Belt	Maputaland Coastal Thicket	Pockets of dense forest Separated by non-forest plant communities	13	3.3

Table 3.2: Summary of individual cheetah tracked in uMkhuze Game Reserve between December 2006 and March 2018, either without (unshaded) or with lions present (shaded). MCF9 was present both before and after lions were re-introduced, so her data are listed as the number of fixes or seasons before and after lions.

Cheetah ID	Sex	First Season Active	Last Season Active	Collared	Number of Seasons	Number of Fixes	Lions Active
MCF1	Female	Summer 2006	Winter 2008	Yes	4	317	No
MCF2	Female	Summer 2006	Summer 2008	Yes	5	348	No
MCM1&2	Male	Summer 2006	Summer 2008	Yes	5	357	No
MCF4	Female	Summer 2006	Winter 2008	Yes	4	305	No
MCF3	Female	Summer 2006	Winter 2012	Yes	12	408	No
MCF8	Female	Summer 2007	Winter 2011	Yes	8	25	No
MCM3&4	Male	Winter 2008	Summer 2011	Yes	8	492	No
MCM5	Male	Winter 2009	Winter 2009	No	1	32	No
MCF7	Female	Summer 2009	Winter 2012	Yes	6	248	No
MCF6	Female	Summer 2009	Summer 2010	Yes	3	145	No
MCM6&7	Male	Winter 2010	Winter 2013	Yes	7	251	No
MCF10	Female	Winter 2012	Winter 2016	No	9	25	Yes
MCF9	Female	Winter 2012	Summer 2015	Yes	3/5	96/392	No/Yes
MCM9	Male	Summer 2012	Winter 2013	No	2	5	No
MCF11	Female	Winter 2013	Summer 2017	Yes	10	252	Yes
MCF12	Female	Winter 2013	Summer 2016	No	8	6	Yes
MCM10	Male	Summer 2013	Summer 2017	No	9	79	Yes
MCM11&12	Male	Summer 2014	Winter 2016	Yes	4	68	Yes
MCM13	Male	Summer 2014	Summer 2015	No	3	8	Yes
MCM19	Male	Winter 2015	Summer 2016	No	2	10	Yes
MCF13	Female	Summer 2015	Summer 2017	Yes	5	103	Yes
MCM17&18	Male	Winter 2016	Summer 2017	Yes	4	303	Yes
MCM22	Male	Summer 2017	Summer 2017	Yes	1	30	Yes
MCM23&24	Male	Summer 2017	Summer 2017	Yes	1	38	Yes

release of the cheetah, or opportunistically for animals present in the reserve. Cheetah collars were equipped with very high frequency (VHF) transmitters and motions sensors that signal mortality, resting or moving signals differentiated by the frequency of the beeps. Monitoring of priority species, such as cheetahs, occurred almost every day of the year by EKZNW staff, researchers, or Wildlife ACT. Cheetah location data were collected on 2238 days in the field in one of four ways: 1) opportunistic sightings of collared/uncollared cheetah. 2) sightings of cheetah tracked with telemetry. 3) triangulations and 4) sightings of cheetah submitted with GPS points and pictures for confirmation of the individual. Cheetahs were identified by their unique spot patterns, and were compared to an identification kit (Marnewick *et al.*, 2006). Triangulations were only taken if the collar was sending a resting signal. Then two GPS points were taken, each with a bearing in the direction of the signal of the collar. The inter-bearing angle needed to be at least 50° and the point where the bearings intercept was calculated in Microsoft Excel (2018).

I categorized the location data by individual, year and season. The seasons were summer: October 1st of one year to March 31st of the next, and winter: April 1st to September 30th of the same year, based on well-defined wet and dry periods in KZN (Balme *et al.*, 2010). I defined a season of data to be the points collected for each individual cheetah during a six month season (Table 3.2) to control for variations in habitat and prey movements that occur between the seasons (Hunter, 1998).

Nine lions, including five females and four males, were collared with GPS/Satellite equipped collars on their release into uMkhuze between November 2013 and March 2018 (Table 3.3). Location data were collected at intervals varying from every 15 minutes to every four hours.

Ethical Note

The parks’ ecologists and conservation managers undertook the placement of all collars for monitoring purposes that would inform management decisions. This study serves as a secondary use of the location data and the Nelson Mandela University Research Ethics Committee: Animal approved the use of data (A16-SCI-ZOO-017).

Table 3.3: Summary of individual lions tracked in uMkhuze Game Reserve between November 2013 and March 2018, reflecting the seasonal samples and number of fixes available.

Lion ID	Sex	First Season Active	Last Season Active	Number of Seasons	Number of Fixes
MLF1	Female	Summer 2013	Winter 2017	8	4495
MLF3	Female	Summer 2013	Winter 2017	8	3490
MLM1	Male	Summer 2013	Winter 2014	2	7539
MLM3	Male	Summer 2013	Winter 2014	2	4838
MLF4	Female	Winter 2014	Summer 2016	6	12028
MLM7	Male	Winter 2016	Summer 2017	4	1297
MLM8	Male	Winter 2016	Summer 2017	4	1730
MLF13	Female	Summer 2017	Summer 2017	1	113

Statistical Analysis

I conducted all statistical analysis in R (ver. 3.4.3, R Core Team). All mapping and spatial analysis was conducted in QGIS (ver. 2.18.15, QGIS Development Team).

Space Use

I used the adehabitatHR package (Calenge & Fortmann-Roe, 2019) to calculate space use by cheetahs. I measured space use using utilisation distributions (UD), as this considers the relative amount of time an animal spends in each place (Seaman & Powell, 1996) and is less affected by outliers or unused space (Harris *et al.*, 1990). Specifically, I used the href version of the UD function, as the majority of data was collected using VHF technology. Both the core area (50% of points) and home range (95% of points) (Poole, 1995) polygons were calculated. I graphed the polygon area by the number of points used to determine the polygon to visual an asymptote. Any polygons based on less than 50 locations were removed, as this was where I visually assessed the asymptote to be reached. Additionally, less than fifty data points are considered insufficient for estimating calculated home range or core area of animals

(Seaman *et al.*, 1999; Cristescu *et al.*, 2013). The constructed UD polygons were clipped by the boundary of the reserve in QGIS, and a new, final, area was calculated, which I used for all further analysis.

I ran generalized mixed-effect models in R using the lme4 package (Bates *et al.*, 2019) for the home ranges and core areas separately and used the core area or home range size as the response variable. The fixed effects were lion presence/absence, cheetah sex and season. I used cheetah ID as a random variable to control for repeated sampling of individuals across the years. I ranked models according to the lowest Akaike information criterion corrected for small sample size (AICc)(Burnham & Anderson, 1998)(Appendix: Table A3.4). The drop1 function was used to test the significance of each fixed effect (Kuznetsova, Brockhoff & Christensen, 2019).

Overlap

I calculated home ranges and core areas for lions as described above for cheetahs. Only one location point per 24 hours were selected, to avoid autocorrelation between points, as the lion collars provided up to 96 locations per 24 hours (Rooney, Wolfe & Hayden, 1998). I randomly selected one data point, using the data table function in R, during the diurnal period for each 24 hour period to match the cheetah data.

I measured the overlap between cheetahs and lions space use in QGIS using home range and core area polygons: I selected all lions active during a 6 month period and merged all polygons into one general lion area for each period. Then I selected all cheetahs active during the same period and intersected each cheetah polygon with the general lion area. I calculated the proportion of overlap as the area of intersection divided by the individual cheetah's area (Poole, 1995). This was done for both space use distributions (core areas and home ranges) across all the years and seasons. I used a Wilcoxon Rank Sum test to determine any differences between the percentage of overlap of the home range and core areas.

Interaction

I conducted a dynamic interaction analysis for all pairs of cheetah and lion data points following methods described by Kortello *et al.* (2007). The actual observed distance, hereafter actual distance, was calculated as all available paired points of lions and cheetahs taken within two hours of each other. The expected distance was calculated using all cheetah pairing not used for the actual distance. For the expected data I again used a randomly selected point for lions during each day to match sampling effort. The straight-line distance between the two points was calculated and I used Wilcoxon Rank Sum tests to assess the differences across sexes and seasons. In instances where the actual distance was closer than expected, this was classified as attraction, if they were equal they were randomly distributed, and if the actual distance was larger, I categorized it as avoidance (Poole, 1995). For this to hold true, I have assumed that cheetahs are able to detect lions over varying distances, habitat and densities.

Habitat Availability and Use

To calculate habitat preferences in the presence and absence of lions, I used all cheetah and lion data points. I separated out the cheetah points based on the sex, season and lion presence/absence. The proportion of points in each habitat type was calculated by overlaying the GPS points with the habitat types in QGIS. I then calculated habitat selection, using the following equation, $D = \frac{r-p}{r+p-2rp}$, where r represents the observed proportion of points in each habitat type and p represents the expected proportion of points in each habitat type (Jacobs, 1974). Therefore, habitat selection, D, is constrained to values between -1 and 1, where $D > 0$ ($r > p$) indicated preference and $D < 0$ ($r < p$) indicated avoidance (Jacobs, 1974). I used chi-squared tests to evaluate the differences between observed and expected proportions. The expected habitat was calculated as the availability of each habitat within the park for lions as well as cheetah before lions were re-introduced. For cheetah habitat use after the introduction of lions, the expected habitat was the observed habitat use before lions were present.

RESULTS

In total, I had 4343 cheetah data points that were usable for this study including 3029 before lions were present and 1314 after lion re-introduction. In addition, I had 41 seasonal home range or core areas (i.e. Table 3.2) that had sufficient data to estimate space use for cheetah, including 29 before lions were re-introduced, and 12 after (Table 3.4). I also had 1816 lion GPS points that were used, including 15 seasonal home range or core areas (i.e. Table 3.3) for lion space use estimates (summer: 7, winter: 8).

Table 3.4: Sample size used for cheetah home range analysis by sex, season and lion presence.

	Males		Females	
	Summer	Winter	Summer	Winter
Before Lions	5	5	10	9
After Lions	2	2	5	3

Space Use

Cheetahs (n = 41 seasonal units) did not change the size of their home range (reporting mean ± SE, before: 202.3 ± 79.7 km^2 vs after: 200.5 ± 57.8 km^2, P = 1.0, Figure 3.2) nor core area (before: 55.9 ± 30.7 km^2 vs after: 53.2 ± 29.1 km^2, P = 0.7, Figure 3.3) following the re-introduction of lions. The home range model performed best when lion presence was excluded (Appendix: Table A3.4). Females and males had similar sized home ranges (P = 0.3) and core areas (P = 0.2). Additionally, cheetahs winter and summer home ranges (P = 0.3) and core areas (P = 0.3) did not differ.

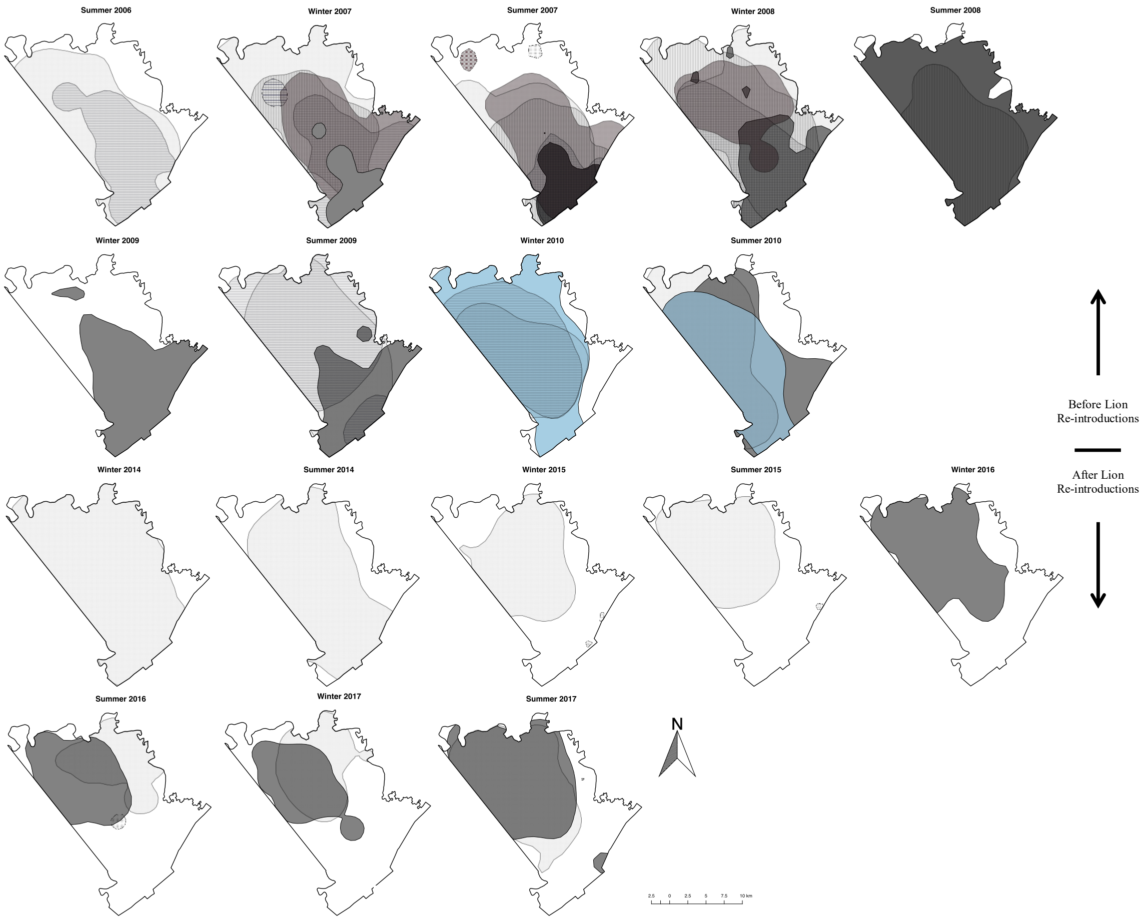

Figure 3.2: Male (solid) and female (textured) cheetahs home ranges in uMkhuze. . Each colour of polygon is for an individual cheetah. The top two rows refer to cheetah home range areas before lions were re-introduced and the bottom two row refer to after lions were re-introduced.

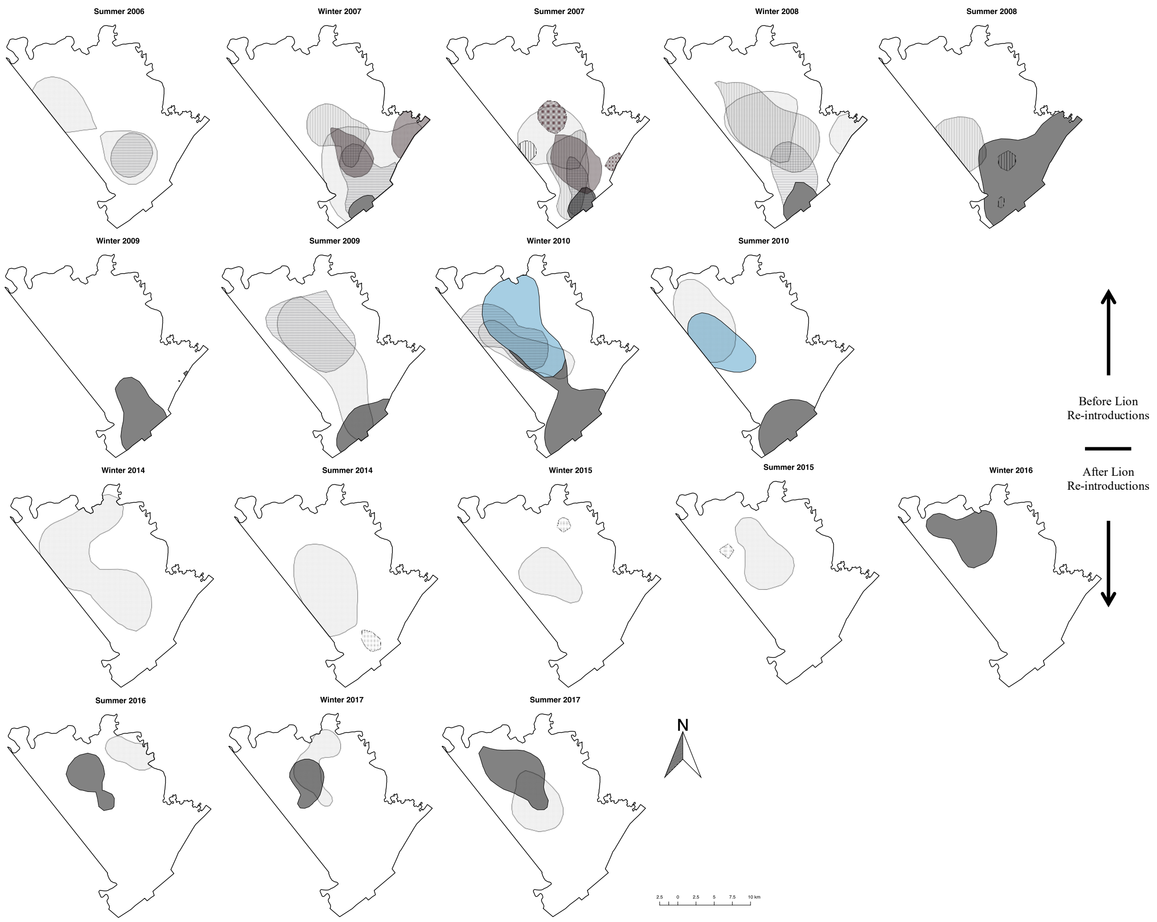

Figure 3.3: Maps of the core areas used by male (solid) and female (textured) cheetahs in uMkhuze. Each colour of polygon is for an individual cheetah. The top two rows refer to cheetah core use areas before lions were re-introduced and the bottom two row refer to after lions were re-introduced.

Overlap

Cheetahs space use overlap with lions did not differ when separate out by sex of the cheetah (Wilcoxon Rank Sum Tests: $P > 0.6$) nor season (Wilcoxon Rank Sum Tests: $P > 0.3$). Therefore, I combined both sexes and seasons for the overlap analysis ($n = 10$) (Figure 3.4). Cheetahs home range overlap with lions, 81.3 ± 15.0%, was larger than the core area overlap, 52.6 ± 32.8% ($W = 20$, $P = 0.02$).

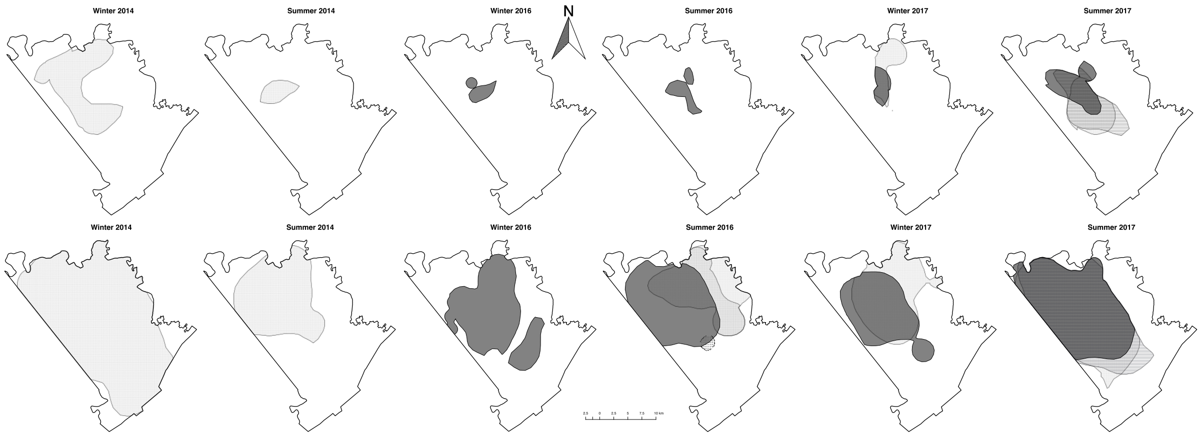

Figure 3.4: Area of overlap between male (solid) and female (textured) cheetahs with lions for both their core areas (top row) and home ranges (bottom row) in uMkhuze (n = 10 seasonal units).

Interaction

Overall, I found cheetahs were (n = 619) located further from lions than expected at random (W = 595600000, $P < 0.001$). In addition, this distance changed depending on the sex of the cheetahs, and the season, pooled across all years (Figure 3.5). During both seasons, female cheetahs were located further than expected from lions (winter: W = 60998000, $P < 0.001$, summer: W = 3808000, P = 0.002), but males were only located further from lions than expected in the summer (W = 25663000, $P < 0.001$).

Habitat Use

Habitat use did not differ between seasons (Wilcoxon Rank Sum Test: $P > 0.2$) nor sexes (Wilcoxon Rank Sum Test: $P > 0.05$), so they were combined for this analysis. I differentiate cheetah habitat use by the presence (n = 3029) and absence (n = 1314) of lions (Figure 3.6).

Using Jacob's Index, lions selected strongly for WMCB ($\chi^2 = 10.5$, P = 0.001) and MCT ($\chi^2 = 4.2$, P = 0.04). Cheetahs used WMCB relative to its abundance before lions were re-introduced ($\chi^2 = 3.0$, P = 0.08), but used it significantly more after the re-introductions ($\chi^2 = 43.5$, $P < 0.0001$). On the other hand, cheetahs selected against

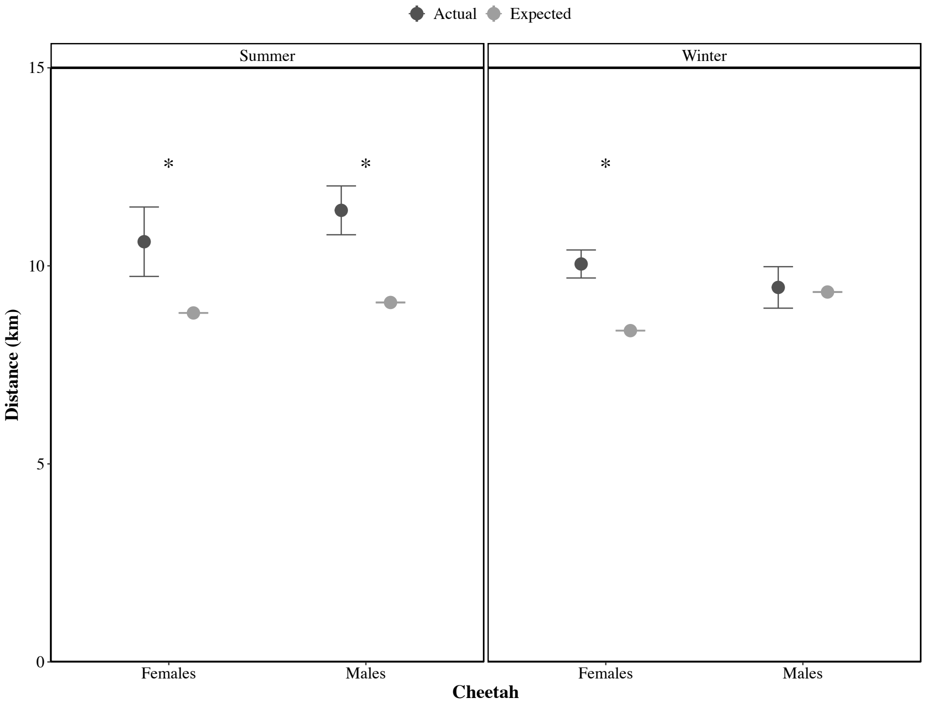

Figure 3.5: Actual distance (km) of a cheetah from a lion versus the expected distance for both sexes (female and male) and seasons (winter and summer). A star indicates significant differences between the two distances (P < 0.002).

MCT before lions ($\chi^2 = 51.0$, $P < 0.0001$) and their use of the habitat did not change following the re-introductions ($\chi^2 = 0.22$, $P = 0.6$). Similarly, for LRF, cheetahs selected strongly against this habitat before lions ($\chi^2 = 76.8$, $P < 0.0001$), this persisting following the re-introduction ($\chi^2 = 2.1$, $P = 0.1$), while lions used the habitat relative to its abundance ($\chi^2 = 0.72$, $P = 0.4$). The SLB was selected for by lions ($\chi^2 = 73.9$, $P < 0.0001$), used relative to its abundance by cheetahs before lions ($\chi^2 = 0.77$, $P = 0.4$) and selected against after lion re-introductions ($\chi^2 = 50.3$, $P < 0.0001$). Lions which selected for WMSB ($\chi^2 = 13.1$, $P = 0.0003$) used this habitat type significantly more than expected by cheetahs following the re-introductions ($\chi^2 = 50.4$, $P < 0.0001$). MLCT was selected for by cheetahs before lion re-introductions ($\chi^2 = 42.9$, $P < 0.0001$) but used the habitat significantly less following re-introductions ($\chi^2 = 101.8$, $P < 0.0001$), similar to lions who used it relative to its abundance ($\chi^2 = 0.69$, $P = 0.4$). SF was selected against by lions (χ^2 = 6.7, P = 0.0096) and cheetahs before lions (χ^2 = 15.3, P < 0.0001) but used more often by cheetahs following re-introductions (χ^2 = 23.2, P < 0.0001).

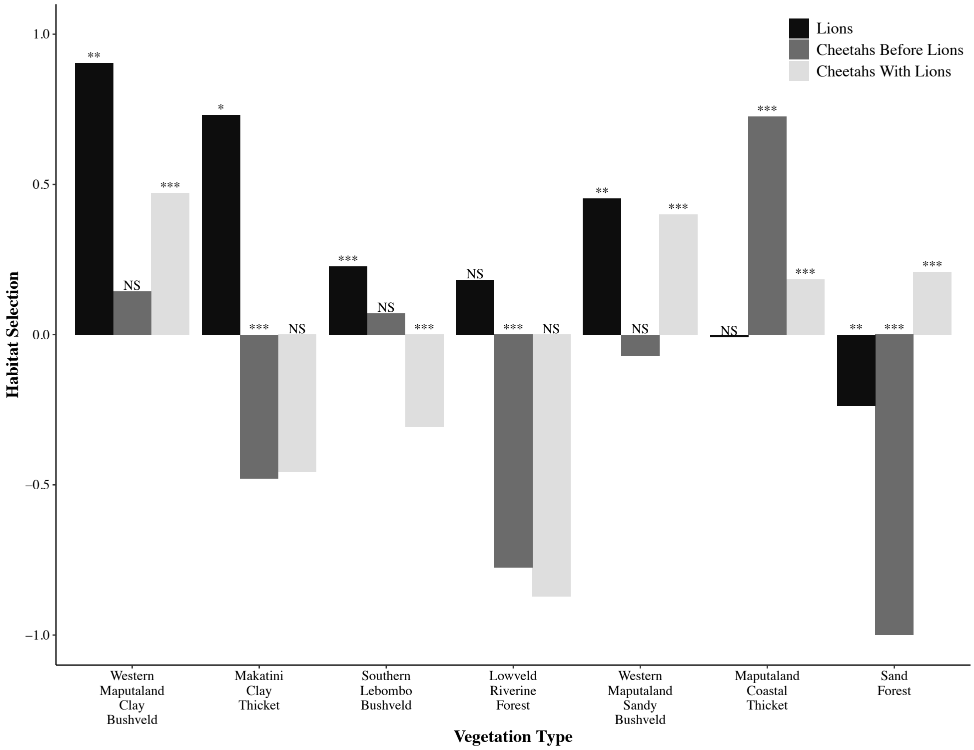

Figure 3.6: Jacob's index of habitat selection for lions and cheetahs both before and after lion re-introductions in uMkhuze for different vegetation types. The habitats are ordered relative to their decreasing abundance within the park. Where habitat selection differed from expected is noted above each bar, NS P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

DISCUSSION

My unique opportunity to compare the space use of cheetahs before and after the re-introduction of lions has provided useful information with regard to competition between these species. The data supports my hypothesis that cheetahs will employ a reactive and not a proactive response to lion competition in all aspects tested. This finding conforms to that of Broekhuis et al. (2013), who found cheetahs to have high spatial overlap with lions, avoiding only the immediate risk of encountering them.

For my broad hypotheses on general cheetah space use, I found mixed support. Specifically, I did not find support for my hypothesis that seasons would influence space usage. However, during 10 out of the 12 years studied, uMkhuze received below average rainfall (Church, 2016), suggesting that the summers were not as wet as they had been historically, and that water, and in return, prey would not have been as dispersed. I also did not find support for my hypothesis that the sex of the cheetah influenced space use. I was, however, unable to control for factors such as denning by females that could have skewed my data. Other studies indicate that females occupy larger areas than males (Bissett & Bernard, 2007), but denning females cover much smaller areas (Durant, 1998), and the average of all females could appear similar to males.

The space use analysis supported a reactive response by cheetahs. Cheetahs home range and core areas did not change in size following the introduction of lions, and they experienced high overlap with lion space use. These results allow us to reject hypotheses about a proactive response. Additionally, cheetahs mainly used Western Maputaland clay and sandy bushveld, both described as mixed woodlands/wooded grasslands (Table 3.1). Cheetahs did this irrespective of the fact the lions also selected for these habitat types, showing no proactive avoidance, and this result was supported by previous studies that also found cheetahs made use of similar mixed habitats regardless of the lions usage (Hunter, 1998; Broekhuis et al., 2013; Rostro-García, Kamler, & Hunter, 2015). Cheetahs selected for the Maputaland coastal thicket and lions used it relative to is abundance, however, this habitat only occurs along the southeastern fence line, which is shared with Phinda Private Game Reserve. This reserve also has a cheetah population (Rostro-García *et al.*, 2015) and I speculate that cheetahs were not using this habitat type to avoid lions but were trying to communicate with cheetahs in the neighbouring reserve. Finally, I found that the cheetahs were located further from lions than expected at random, suggesting a short-term avoidance, or reactive response, to lion presence. Additionally, I did not find this for males in the winter, however, I predicted that the males would be less affected by lions and that cheetahs would be less spread out in the winter, a result which supports my hypotheses.

Although lions are thought to be a major competitor/predator to cheetahs (Durant, 2000a), there are other members of the large carnivore guild that were present in the study area and potentially played a role in intraguild competition. However, I was not able to control for these factors, as fine-scale data on population sizes and movements was not available. In addition, my study had a small sample size that did not allow me to further separate out females with cubs from those without, as well as singleton versus coalitions, which could potentially influence results. Nonetheless, by demonstrating that lions did not displace cheetahs in uMkhuze, I have provided beneficial information to managers of reserves looking to re-introduce cheetahs. By employing a reactive response to lions, even in a small, fenced reserve, cheetahs are able to trade-off the negative effects of competition while still obtaining the necessary resources.

CHAPTER 4

Resource Partitioning Between Cheetah and Other African Large Carnivores

INTRODUCTION

Species that occur sympatrically, and are members of the same guild, typically compete for common resources (Schoener, 1983). Within the carnivore guild, competition or predation have been documented as important interactions defining the community structure, going as far as being responsible for the decline of subordinate species populations (Palomares & Caro, 1999; Caro & Stoner, 2003). Competition between species occurs in one of two forms; exploitative competition, where one species reduces the availability of a resource for another, or interference competition, where one species behaviorally impacts another's ability to use a shared resource through direct interactions (ie. harassment, kleptoparasitism, predation, etc.) (Carothers & Jaksić, 1984). Niche differentiation, however, allows species to co-exist, one mechanism of which is resource partitioning along consumable (e.g. food) or non-consumable axes (e.g. space and time) (Harrington *et al.*, 2009). For resource partitioning to be effective, species require environmental heterogeneity and a difference in their abilities to utilize the resources present (Ziv *et al.*, 1993; Wauters *et al.*, 2002). Competitors must separate themselves by at least one resource axis, meaning that a high overlap in one niche dimension can be compensated for by low overlap in another, as stated in the niche complementarity hypothesis (Vieira & Port, 2007). In addition, several theories, including game or interference competition theory, suggest that dominant predators should be unrestricted with their resource use, matching that of their common prey, whereas subordinate predators should partition their resource use trading off acquisition and risk (Vanak *et al.*, 2013; Palomares *et al.*, 2016).

Resource partitioning has become a common theme in community and conservation ecology. Mink, *Neovison vison*, become active during the day when otters, *Lutra lutra*, or polecats, *Mustela putoris,*(both of which are largely nocturnal) are present but remained nocturnal when these species are absent (Harrington *et al.*, 2009). Arboreal mammals (*Macaca silenus, Macaca radiata, Semnopithecus johnii,* and *Ratufa indica*) in the Western Ghats use vertical stratification to co-exist, occupying different heights within the forest canopy (Sushma & Singh, 2006). Ocelots, *Leopardus pardalis*, and bobcats, *Lynx rufus*, where they co-occur avoided each other through differences in microhabitats (Horne *et al.*, 2009), as did cougars, *Puma concolor*, and jaguars, *Panthera onca* (Palomares *et al.*, 2016). Moreover, studies have looked at multiple axes simultaneously, including in Brazil where fox species (*Cerdocyon thous* and *Psedalopex gymnocercus*) had low overlap in activity patterns, moderate habitat overlaps, but had no differences in their prey use (Vieira & Port, 2007). In South Africa, black-backed jackals, *Canis mesomelas*, dominated over Cape foxes, *Vulpes chama*, separating across multiple axes (space, time and diet), but bat-eared foxes, *Otocyon megalotis*, which overlapped considerably with jackals in space and time, only separated out by diet (Kamler *et al.*, 2012). These examples highlight the importance of resource partitioning in the community structuring of predators.

Africa is home to the last remaining intact large carnivore guild, consisting of lions, *Panthera leo,* leopards, *Panthera pardus,* spotted hyenas, *Crocuta crocuta,* cheetahs, *Acinonyx jubatus,* African wild dogs, *Lycaon pictus,* brown hyenas, *Parahyaena brunnea*, and striped hyenas, *Hyaena hyaena*, with the first five being sympatric across most of their range (Vanak *et al.*, 2013). All seven species are declining, driven mainly by habitat loss and fragmentation, as well as human persecution (Ripple *et al.*, 2014). Across their ranges, these carnivores are increasingly being relegated to smaller areas, and in South Africa they occur in fenced game reserves, with fences increasing across Africa (Packer *et al.*, 2013), creating artificially high densities which in turn may cause an increase in competition (Darnell *et al.*, 2014). Cheetahs, known to be a subordinate member of this guild due to their small build and largely solitary nature, have received considerable attention regarding possible resource partitioning to allow their co-existence (Durant, 1998; Cozzi *et al.*, 2012; Broekhuis *et al.*, 2013; Vanak *et al.*, 2013; Bissett *et al.*, 2015; Swanson *et al.*, 2016; Dröge *et al.*, 2017). Traditionally, cheetahs were classified spatially as open savanna specialists, as most studies came out of the Serengeti (Caro, 1994; Laurenson, 1994; Durant, 1998), but later work in other landscapes shows that cheetahs use wooded areas effectively (Hunter, 1998; Broomhall *et al.*, 2003; Broekhuis *et al.*, 2013; Rostro-García *et al.*, 2015). In addition, cheetahs were classified as diurnal/crepuscular (Durant, 1998; Hayward & Slotow, 2009), until studies demonstrated nocturnal behaviour on moonlit nights (Cozzi *et al.*, 2012; Broekhuis *et al.*, 2014). These studies, and the variability in cheetah resource use, highlight the potential for greater overlap in resource usage between cheetahs and other large carnivores than previously suggested. However, attempts to resolve the effects of dominant competitors on cheetah behaviour did not take the entire guild into account (Durant, 1998; Vanak *et al.*, 2013; Swanson *et al.*, 2016; Dröge *et al.*, 2017). The one study that looked at the intact guild only looked at temporal partitioning (Hayward & Slotow, 2009).

In this study, I aim to determine what factors, if any, cheetah use to separate themselves across space and time from other members of the large carnivore guild (lions, leopards, spotted hyenas and African wild dogs). Using camera trap data, I analyze resource partitioning across three axes: spatial, temporal or spatiotemporal. Spatial partitioning is when a species avoid habitats/sites that other competitors visit. Temporal partitioning occurs when a species is active at different times to its competitors, and the spatiotemporal partitioning is the avoidance of habitats sites only when, and shortly after, a competitor is present (Niedballa *et al.*, 2019). In addition, I explore factors such as prey availability and habitat characteristics affects on resource use, where possible, as these also influence cheetah behaviour (Vanak *et al.*, 2013). Overall, I hypothesize that cheetahs should avoid each of the other large predator species across at least one of the three axes, thereby selecting for less risky areas/times, as competitive interactions between cheetah sand other carnivores can result in death (Palomares & Caro, 1999). Additionally, I hypothesize that cheetahs should align their activity patterns and space use with their commonly utilized prey species. Specifically, with respect to the spatiotemporal analysis, I predict that cheetahs will avoid sites (camera traps) shortly after other large carnivores have visited the site (Broekhuis *et al.*, 2013). For the spatial analysis, I predict that cheetahs should utilize sites not/less utilized by other predators (Durant, 1998) and avoid extra-large bodied prey that are too large for them to catch (Clements *et al.*, 2014), but which are attractive to larger predators (Vanak *et al.*, 2013). However, cheetahs should be positively associated with their commonly-utilized prey species (Vanak *et al.*, 2013) and open habitat, that is perceived to be less risky (le Roux, Kerley & Cromsigt, 2018) and which allows for their cursorial hunting style (Makin, Chamaillé-Jammes & Shrader, 2017). For my temporal analysis, I predict that cheetahs activity patterns should be mainly crepuscular (Hayward & Slotow, 2009). Additionally, I expect a high overlap in activity with commonly-utilized prey species and other crepuscular predators (e.g. African wild dogs) and a low overlap with nocturnal predators (e.g. lions, leopards and spotted hyenas) (Hayward & Slotow, 2009).

METHODS

Study Area

This study was conducted in four protected areas, in close proximity to one another in the KwaZulu-Natal Province of South Africa, including two state-managed and two private reserves (Figure 4.1, Table 4.1). The state-managed reserves are Hluhluwe-iMfolozi Park (HiP) and uMkhuze Game Reserve (uMkhuze), and the privately-owned reserves are Phinda Private Game Reserve (Phinda) and Manyoni Private Game Reserve (Manyoni). The region is characterized as hot, humid and subtropical with two distinct seasons: a dry winter from April – September, and a wet hot summer from October – March (Balme, Hunter & Slotow, 2007). HiP ranges from open grassland to closed woodland (le Roux *et al.*, 2018). Manyoni is open savannah thornveld and bushveld (Chapman & Balme, 2010). Phinda and uMkhuze are mainly thickets interspersed with grass and shrubland (Miller *et al.*, 2018). Currently, three out of the four reserves house an intact large carnivore guild (cheetah, lion, leopard, spotted hyena and African wild dogs). Phinda does not have African wild dogs, but occasionally individuals break through the shared fence with uMkhuze. Manyoni has a population of brown hyenas (N = 2), but due to their low number, they were not considered in this study.

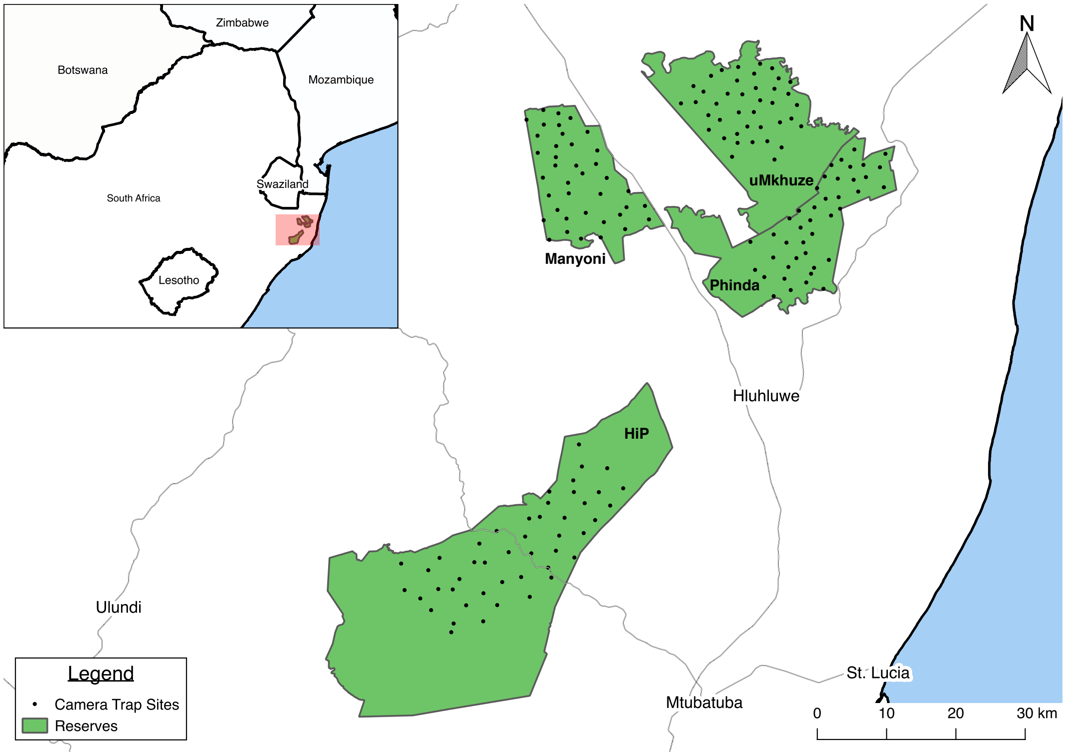

Figure 4.1: Map of the reserves (green) used for this study in KwaZulu-Natal, South Africa, with the black dots representing camera trap sites: HiP (N = 46), Manyoni (N = 39), Phinda (N = 42) and uMkhuze (N = 40).

Data Collection

Panthera, a non-government organization, conducts camera trap surveys throughout reserves in KwaZulu-Natal to obtain population estimates of leopards, as well as capturing images of the other mammals. I used these images for my analyses (Appendix: Table 4.1). I recognize a possible bias in the data, as traps were specifically located at sites commonly visited by leopards (Miller *et al.*, 2018), however, the surveys covered most of the area of all reserves, with the exception of hunting blocks and

Table 4.1: Reserve statistics including the size of the reserve (km^2), size of the area surveyed (km^2), number of sites, the density of camera sites (by reserve size/by survey area), the years that each reserve was surveys and the predators present in the reserves.

Reserve	Size (km^2)	Size Surveyed (km^2)	# of Sites	Camera Density (Sites per km^2)	Years Surveyed				Predators Present				
					2013	2014	2015	2016	Cheetah	Lion	Leopard	Spotted Hyena	African Wild Dog
HiP	900	417	46	0.05/0.11	✓	✓	✓	✓	✓	✓	✓	✓	✓
Manyoni	233	205	39	0.17/0.19			✓		✓	✓	✓	✓	✓
Phinda	233	226	42	0.18/0.19		✓		✓	✓	✓	✓	✓	During 2016 Survey
uMkhuze	395	166	40	0.10/0.24	✓	✓	✓	✓	✓	✓	✓	✓	✓

wilderness areas. Given the broad coverage and the fact that all carnivore species present were regularly captured in each survey, the data were considered appropriate to use for my study. In addition, this is a comparative study assessing point-specific spatial and temporal activity of the focal species.

Since 2013, cameras were set up in each reserve for approximately six weeks, either once each year or every alternate year (Miller *et al.*, 2018). Each camera station consisted of two cameras, normally on opposite sides of the road, pointing towards each other, as per Panthera protocols (Miller *et al.*, 2018). For each capture, the camera recorded the time and date, and researchers, staff or volunteers identified the species photographed with all identifications checked by an expert. Camera sites were not always active for the entire sampling period due to various reasons (e.g. animal interference), so data were collected on the days the cameras were active, to give a measure of effort per site (Swanson *et al.*, 2016). In HiP, the majority of camera trap sites used in 2013 were different from the sites used during subsequent years. Due to very low capture rates and sampling efforts, the 26 sites surveyed only in 2013 were therefore omitted from this study.

During 2017, I measured vegetation openness or visibility at each camera site, to represent perceived predation risk (le Roux *et al.*, 2018). I used a 1.6 m Nudds' density board, that was marked into 20 cm sections (Nudds, 1977). I positioned my eye level at approximately 80 cm height (an estimate of cheetah eye height), as visibility differs depending on the vantage point (Henley, 2001). The visibility was measured in the four Cardinal and the four primary Inter-Cardinal directions based on compass headings, at the center point between the two cameras. The distance at which approximately half of each 20 cm section was blocked by vegetation (Nudds, 1977) was noted in meter intervals for all eight directions. I was the observer for all sites to keep biases consistent. The final visibility value used was an averaged distance per site.

Ethical Note

I used non-invasive methods for data collection and no animals were manipulated or handled in the process.

Statistical Analysis

I conducted all statistical analysis in R (ver. 3.4.3, R Core Team) and all mapping and spatial analysis was conducted in QGIS (ver. 2.18.15, QGIS Development Team).

Spatiotemporal Analysis

I analyzed the data to determine any spatiotemporal avoidance of other predators by cheetah following the linear regression methods described by Niedballa et al. (2019). To do this, I determined the time interval between images of cheetahs and other predators at a site, regardless of whether the cheetah was the first or second visitor. Following Niedballa et al. (2019)'s methodology, cheetahs were my primary species, A, and the other predators were my secondary species, B. Therefore, I ended up with time intervals for AB, the time between a photograph of species A, followed by B, and for BA, the time difference between a photograph of species B followed by A. I then fit a generalized linear mixed-effect model using the lme4 package (Bates *et al.*, 2015). The time interval was the response variable with the order of species (AB or BA) as the fixed-effect. I also included site ID nested in reserve as a random variable to control for pseudoreplication across sites. The data failed normality assumptions as assessed by the Shapiro-Wilk test, so the response variable was log transformed. I ran the model separately with lion, leopard, spotted hyena and African wild dog as the secondary species. The linear model estimates the difference in the time interval between AB and BA, with a positive estimate showing avoidance and a negative estimate showing attraction (Niedballa *et al.*, 2019).

Spatial Analysis

For the spatial analysis, I analyzed the data by camera trap site (N = 167) to try to determine spatial avoidance or overlap among the cheetahs and the other carnivores. Due to low capture rates of cheetahs, data for all years were combined. When I had multiple consecutive captures of a species at a camera trap site, I defined independence as 30 minutes between photos (Si, Kays & Ding, 2014). Additionally, I calculated prey abundance using a relative abundance index (RAI), defined as the number of independent prey captures (30 minutes between photos) per 100 trap days (Miller *et al.*, 2018). I grouped prey species into four categories based on their average adult female mass (Owen-Smith & Mills, 2008) with the masses from Owen-Smith (1988): small (< 25 kg), medium (25 – 99 kg), large (100 – 350 kg) and extra-large (> 350 kg) (Balme *et al.*, 2017). All prey categories were used as I have hypotheses based on cheetah prey preferences as well as those of other carnivores. Commonly utilized prey by cheetah is defined as small, medium bodied prey, and large bodied prey given that coalitions were present in the reserves (Clements *et al.*, 2014; Broekhuis *et al.*, 2018). I assessed spatial avoidance in two ways to look at different underlying processes: the presence/absence of cheetah at camera trap sites as a binomial response, as well as the abundance of cheetah captures in a truncated response (Swanson *et al.*, 2016).

I used a binomial response to identify presence/absence, where zero indicated no captures at a camera trap site and one indicated at least one capture. I calculated a binomial response for all predator species and prey body size categories. I classified visibility into a binomial response based on quantiles into high (≥ 50th quantile) and low (< 50th quantile) visibility sites. I fit the data using a generalized linear mixed-effect model with a binomial response variable: cheetah presence/absence. The presence/absence of lion, leopard, spotted hyena, African wild dog and small, medium, large and extra-large bodied prey were fixed effects, along with visibility. I included the trapping effort and camera trap site ID nested in reserve as a random variable to control the different number of days sampled and pseudoreplication.

To identify factors affecting cheetah abundance I used a truncated model, selecting sites that had a minimum of one cheetah capture (Swanson *et al.*, 2016). Once again, I ran a generalized linear mixed-effect model using the Poisson family with cheetah abundance (all captures summed per camera trap site) as the response variable. Lion, leopard, spotted hyena and African wild dog abundance were used as fixed effects, as was visibility and prey RAI per size class. Camera trap site ID nested in reserve and trap effort were used as random variables.

I determined the relative importance of predators on cheetahs by assessing the analysis of deviance for different models. The models included a null model (no fixed effects), a model with only visibility and prey covariates, models with visibility, prey and one predator species, and the full model containing visibility, prey and all predators. The analysis of deviance was calculated using the model deviance and the formula: $\frac{Null\ Model - Model\ Being\ Tested}{Null\ Model - Full\ Model}$ (Swanson *et al.*, 2016).

Temporal Analysis

To test for temporal avoidance or overlap of cheetahs with other carnivores and prey species, I calculated activity patterns for all species and measured the overlap between cheetahs and all other species using the overlap package (Meredith & Ridout, 2016). Using a kernel density plot, I calculated activity patterns for all predators and prey categories using all camera trap photos from all sites and reserves (Miller *et al.*, 2018). I did not test for differences between reserves due to the small sample size of cheetah captures per reserve. I determined the overlap in activity patterns between cheetahs and all other species using the non-parametric estimator for the coefficient of overlap (D4) (Miller *et al.*, 2018). An overlap value of 0 indicates no overlap and 1 is an entire overlap of activity patterns by the two species (Ridout & Linkie, 2009). I used a Kolmogorov-Smirnov test to determine overlap significant (Hayward & Slotow, 2009).

RESULTS

In total 167 camera trap sites were surveyed for a total of 18,578 days with 214 captures of cheetahs (128 independent captures at 56 sites), 1055 captures of lions (648 independent captures at 129 sites), 1547 captures of leopards (1337 independent captures at 146 sites), 2346 captures of spotted hyenas (1923 independent captures at 139 sites) and 659 captures of African wild dogs (278 independent captures at 83 sites).

Spatiotemporal Partitioning

There was a total of 43 captures of cheetahs after lions, 61 after leopards, 64 after spotted hyenas and 8 after African wild dogs. Additionally, there were 36 captures of lions after cheetahs, 55 leopards, 53 spotted hyenas and 6 African wild dogs. Cheetahs showed a non-significant spatiotemporal relationship towards lions, leopards, spotted hyenas and African wild dogs (Appendix: Table A4.2).

Spatial Partitioning

The variance in cheetah presence at camera trap sites was explained equally by prey availability/habitat and predator presence (Table 4.2). African wild dog presence alone explained a quarter of the additional deviance (Table 4.2) and was a significant predictor of cheetah presence exhibiting a negative relationship ($z = -2.49$, $P = 0.015$) (Figure 4.2F, Appendix: Table A4.3). All other factors (visibility, small, large, and extra large bodied prey, lions, leopards and spotted hyenas) had non-significant relationships. Lions, leopards and spotted hyenas explained the least additional deviance (Table 4.2), (Figure 4.2G, H, I, Appendix: Table A4.3).

The variance in cheetah abundance at camera trap sites was slightly over 50% explained by prey RAI and visibility (Table 4.2). Cheetah abundance was significantly positively associated with the RAI of large bodied prey ($z = 3.208$, $P = 0.001$) (Figure 4.3D). Lion abundance explained an additional 21% of the variation, but cheetah abundance experienced a non-significant relationship (Figure 4.3G, Appendix: Table A4.4). Spotted hyena occurrence explained 16.5 % of the additional variation in cheetah abundance, but displayed a non-significant relationship (Figure 4.3I, Appendix: Table A4.4). Leopard and African wild dog abundances explained relatively little additional variance in cheetah abundance (Table 4.2), and were not significant factors in cheetah abundance (Figure 4.3H, F, Appendix: Table A4.4).

Table 4.2: Analysis of deviance (ANODEV) for models of presence and abundance of cheetahs at camera trap sites. The incremental change is the explanatory power of each predator species alone and all together compared to the model of only habitat and prey.

	Presence		Abundance	
Model	ANODEV (%)	Incremental Change	ANODEV (%)	Incremental Change
Null	0.0	-	0.0	-
Habitat + Prey	50.2	-	53.2	-
Habitat + Prey + Lions	55.9	5.7	74.8	21.6
Habitat + Prey + Spotted Hyenas	60.4	10.2	69.8	16.5
Habitat + Prey + Leopards	63.3	13.1	57.6	4.3
Habitat + Prey + African Wild Dogs	76.3	26.1	57.6	4.3
Full	100.0	49.8	100.0	46.8

Temporal Partitioning

All predator and prey species' activity patterns indicated activity throughout the 24-hour period, with peaks at different times (Figure 4.4). Cheetah activity peaked at dawn with a smaller peak in activity at dusk (Figure 4.4A), as did African wild dogs (Figure 4.4F). Small-bodied prey activity peaked during the crepuscular periods (Figure 4.4B), whereas medium- and large-bodied prey activity levels peaked during the day (Figure 4.4C, D). Extra-large bodied prey had the highest activity at dusk (Figure 4.4E). Lions, leopards and spotted hyenas activity levels peaked at night (Figure 4.4G, H, I).

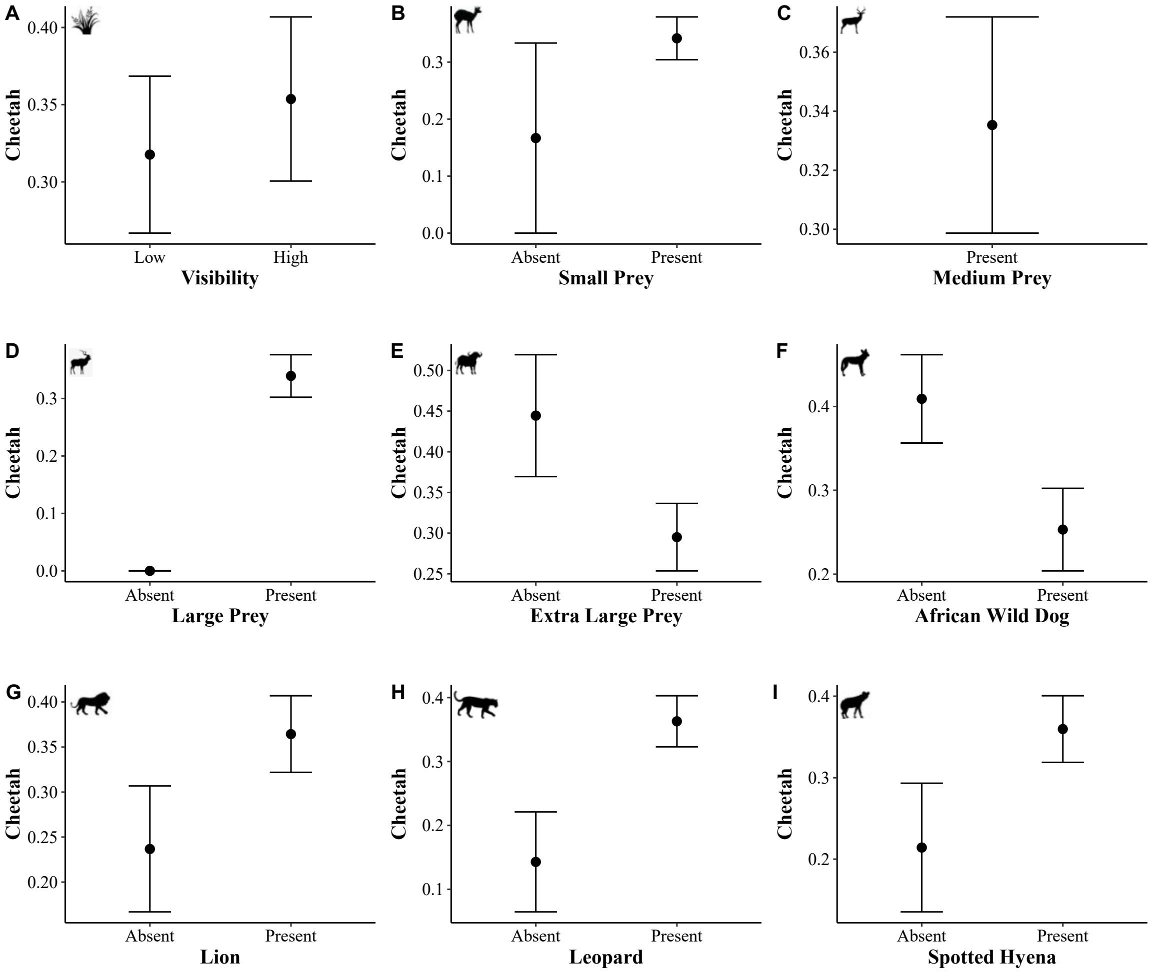

Figure 4.2: Presence of cheetahs at camera trap sites depending on environmental factors including habitat visibility, prey visitation and intraguild predators. The factors are visibility (A), small prey (B), medium prey (C), large prey (D), extra-large prey (E), African wild dogs (F), lions (G), leopards (H) and spotted hyenas (I). The y-axis is a scale of cheetah presence with zero indicating absence and one indicates presence.

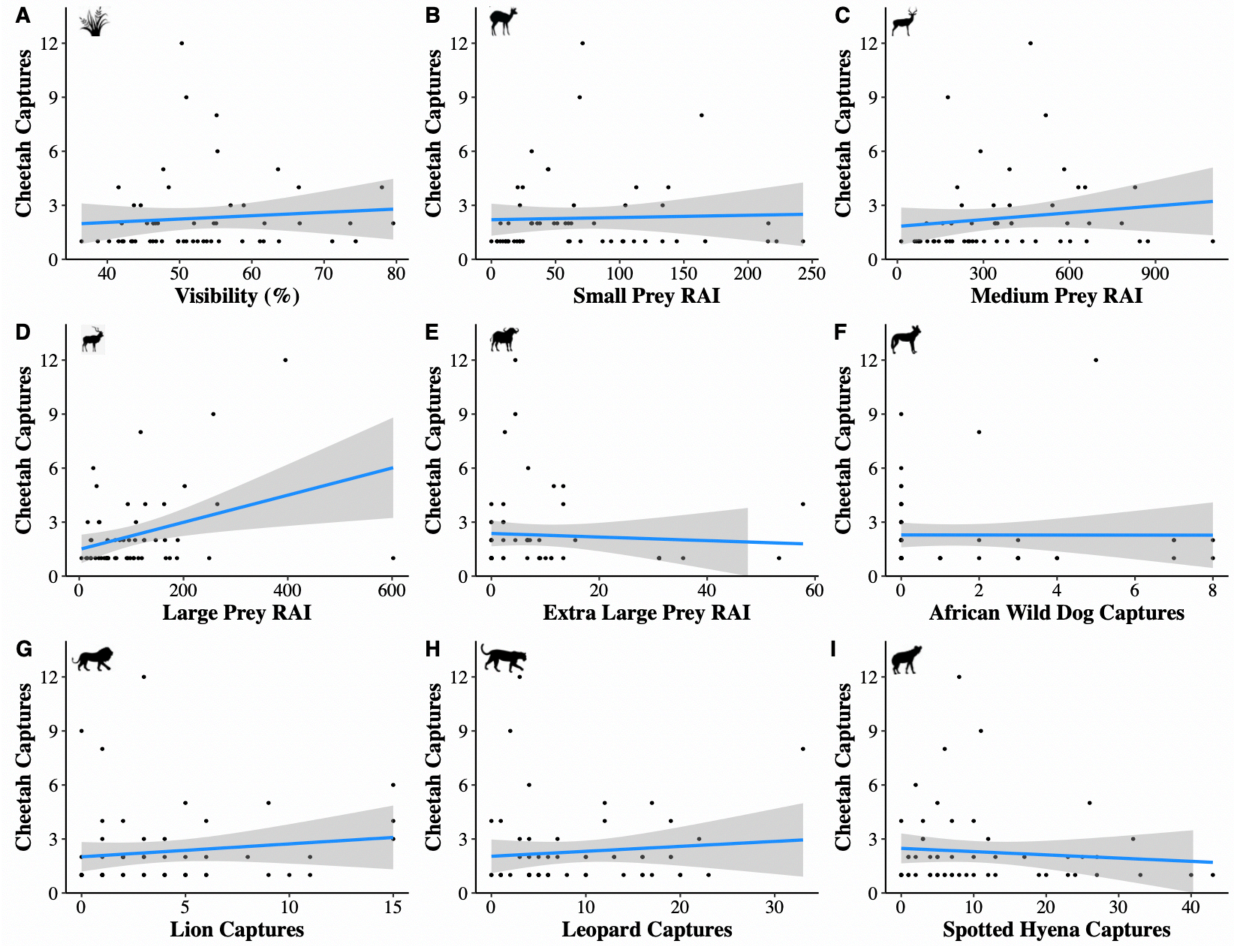

Figure 4.3: Cheetah abundance at camera trap sites in response to environmental factors including habitat visibility, prey visitation and other predators. The factors are visibility (A), small prey (B), medium prey (C), large prey (D), extra-large prey (E), African wild dogs (F), lions (G), leopards (H), spotted hyenas (I). Visibility is a measure of percent, openness and prey factors are a relative abundance index (RAI) as opposed to the absolute abundance rates.

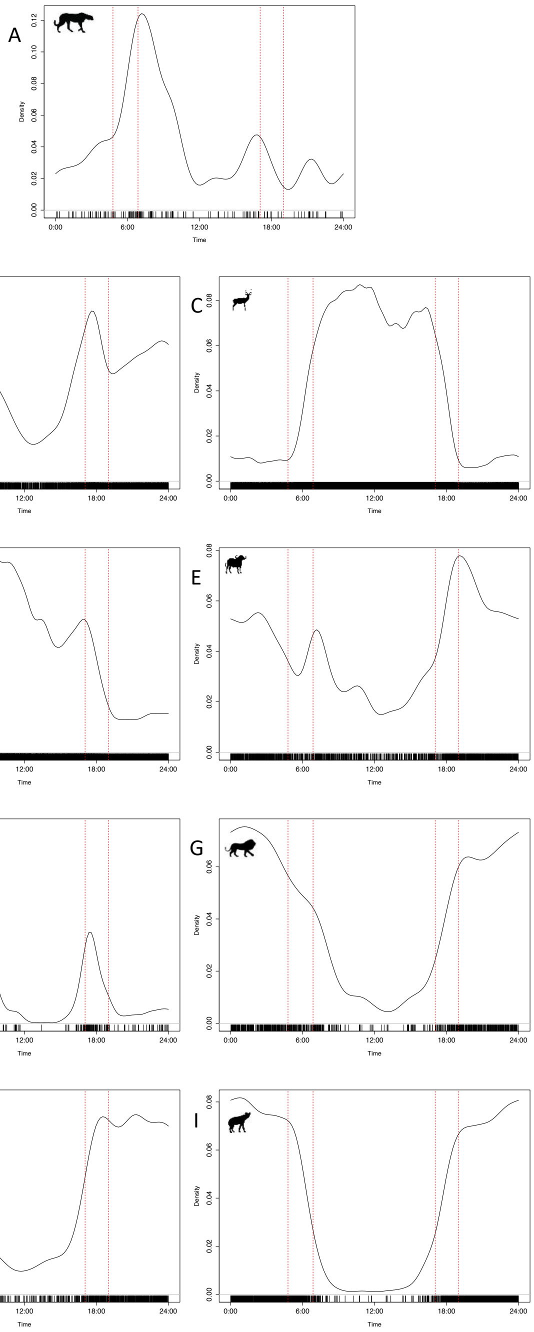

Figure 4.4: Activity patterns for cheetah (A), small-sized prey (B), medium-sized prey (C), large-sized prey (D), extra-large sized prey (E), African wild dogs (F), lions (G), leopards (H) and spotted hyenas (I), showing the density of captures throughout the 24 hour period. Dashed red lines represent sunrise and sunset times throughout the year and the small vertical black lines along the x-axis represent each individual capture.

The activity patterns of cheetahs were significantly different from all other predator and prey species (Appendix: Table A4.5). However, cheetahs had the greatest temporal overlap with small-bodied prey, African wild dogs and large-bodied prey (Figure 4.5A, E, C). Cheetahs had the least temporal overlap with spotted hyenas and lions (Figure 4.5F, H). Leopards, medium-bodied prey and extra-large bodied prey experienced a mid-level amount of temporal overlap with cheetahs (Figure 4.5G, B, D).

DISCUSSION

The results of my study do not support the idea that cheetahs avoid competition with a single large predator species on all resource axes. However, I did find that cheetahs separated themselves from all competitors through at least one resource axis but avoided different competitors on different resources. In addition, I did not find support for my prediction that cheetahs would avoid extra-large bodied prey, as a way to avoid large predators who consume this sized prey (Vanak *et al.*, 2013). In terms of habitat use, I also did not find support for my prediction that cheetahs would select for open habitats. However, although it was been suggested that cheetahs select for open habitat, as it allows for increased visibility (le Roux *et al.*, 2018), other studies have shown that in response to competition, cheetahs select closed habitat (Broekhuis *et al.*, 2013; Rostro-García *et al.*, 2015). I did not find that they selected for closed habitat and I suggest that cheetahs might be making use of both open and closed habitat as open habitat allows them to see predators coming and closed habitat allows them to avoid detection, moreover, the cheetahs use of the different habitats might differ depending on the activity that they are performing.

I found mixed support for my hypothesis that cheetahs should be active at times when other large carnivores are not. My results showed cheetahs to be active throughout the 24 hour cycle. Moreover, the results are aligned with the recently documented nocturnal behaviours of cheetahs (Cozzi *et al.*, 2012; Broekhuis *et al.*, 2014), with my data yielding 28.5% of cheetah camera trap captures occurring at night. Cozzi *et al.* (2012) reported 25.6 ± 3.5% of cheetah activity at night, stating that moonlit

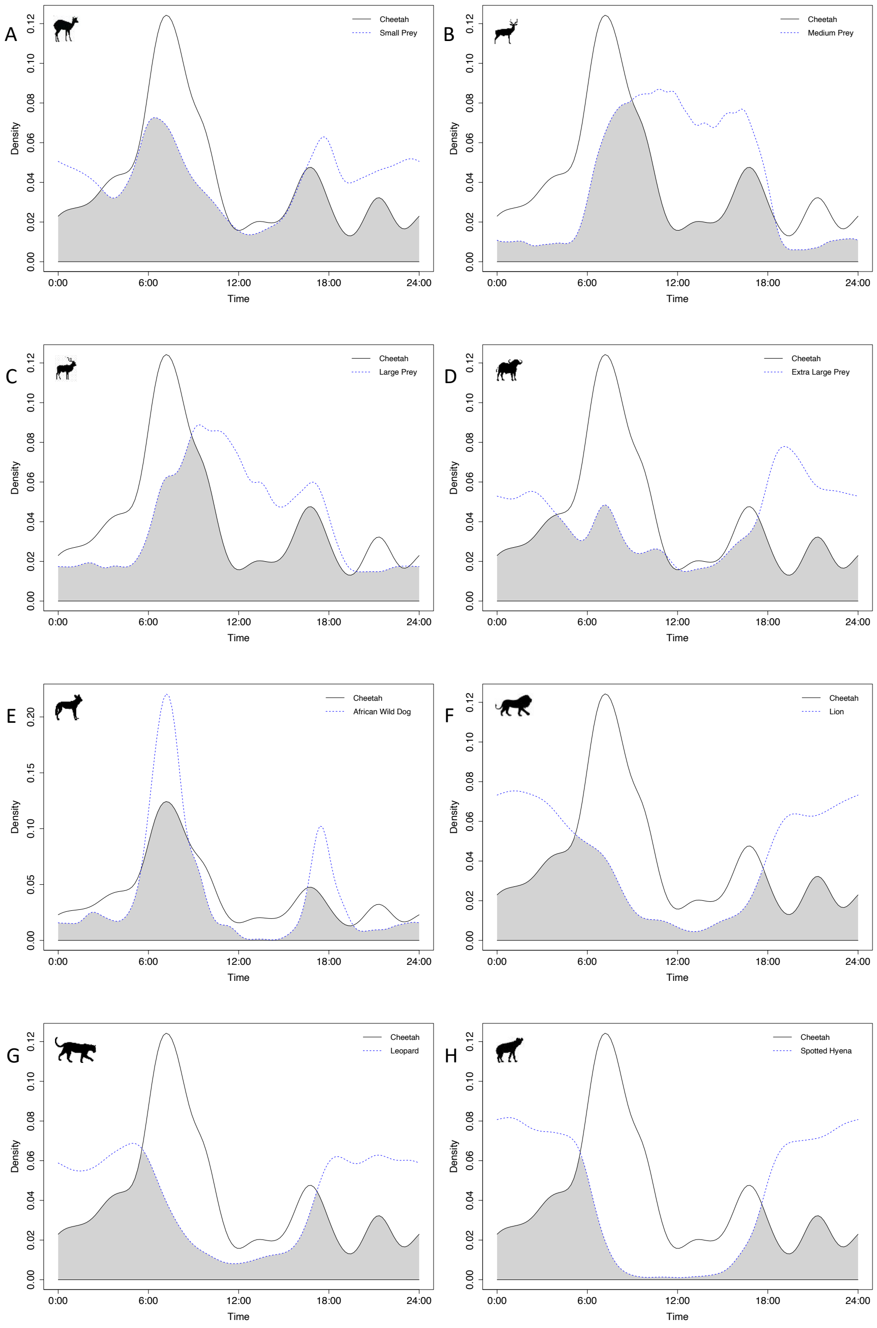

Figure 4.5: Temporal overlap of activity patterns for cheetahs with small-sized prey (A), medium-sized prey (B), large-sized prey (C), extra-large sized prey (D), African wild dogs (E), lions (F), leopards (G) and spotted hyenas (H) from camera trap sites. The solid black line represents cheetah activity patterns, the dotted blue line is the prey or predator species and the grey shaded area indicates the area of overlap.

nights allowed cheetahs to be active. I did not have enough data to test the moonlight hypothesis proposed by Cozzi *et al.* (2012), however, I also suggest it is possible that cheetahs are utilizing the night to avoid tourists. Broekhuis *et al.* (2018) found a negative relationship between cheetah cub recruitment and tourism numbers in the Maasai Mara, with fewer cubs being raised in areas with high vehicle traffic. It is thought that other carnivores learn to watch the vehicles and go to investigate when vehicles begin to cluster at a sighting. In the reserves I studied, almost all vehicle traffic happens during the day, and a shift towards nocturnal activities could be to alleviate the risk of encountering humans. Moreover, 96% of the camera traps sites used in this study were located along roads, further supporting this idea. Cozzi *et al.* (2012) also stated that the increased nocturnal activity of cheetahs would lead to an increase in the overlap of activity patterns with other predators. I noted a greater overlap in activity patterns between cheetahs and other large predators than that documented by Hayward and Slotow (2009), however, they collected their cheetah data from the literature using kill and movement data that could have been biased towards diurnal observation. This emphasizes the importance of using camera-trap data for assessing activity patterns, as opposed to the observer-bias introduced by the methods applied by Hayward and Slotow (2009). However, in order to fully test whether cheetah are becoming more nocturnal, future studies would need to place cameras randomly with respect to human movements, as opposed to mainly along roads, as utilized in this study.

Cheetahs showed the highest overlap in activity patterns with small-bodied prey. This supports my prediction that they are also attempting to align their activity patterns with commonly utilized prey (Clements *et al.*, 2014), not just avoiding competitors. There is thus a trade-off in resource acquisition and risk avoidance. Clearly, if cheetahs focussed exclusively on risk avoidance they would be at risk of starvation if they could not capture prey. This is similar to the response of the Serengeti herbivore community with Sinclair (1985) showing that as grazing became limiting in the dry season, grazers were more willing to accept the risk of predation, than when grazing was abundant. This observed trade-off of risk and resources by cheetah is an important and novel insight, given the prevailing focus on cheetah avoiding dominant predators in the literature. There is also a clear need to explore the drivers of these trade-offs and how this may vary as a function of dominant predator abundance, prey availability and also cheetah social class (solitary vs coalition cheetah).

Spatially, I, again, found mixed support for my hypothesis that cheetahs would select sites with low to no predator use. Cheetah presence at a camera trap site was negatively related to African wild dog presence. This result supports my predictions, as cheetahs had high temporal overlap with African wild dogs, but avoided them across space, selecting for sites that African wild dogs were not using. However, it is also possible that this was not a product of cheetahs avoiding African wild dogs, but African wild dogs avoiding sites where all other large predators were found, a result that is supported by several studies (Vanak *et al.*, 2013; Swanson *et al.*, 2014; Dröge *et al.*, 2017). Cheetah abundance was positively related to large-bodied prey, showing that they selected for sites based on their commonly utilized prey. Similar results were found by Vanak *et al.* (2013) who stated that cheetahs selected for areas with increased prey and open habitat. However, further studies would be needed to determine the mechanism behind the relationship (e.g. field manipulation of prey). Cheetah presence and abundance at a site was not significantly determined by lion, leopard or spotted hyena occurrence, moreover, I found that they selected sites similar to all three of these large competitors. Dröge *et al.* (2017) found no spatial avoidance by cheetahs towards other large carnivores, indicating that cheetahs are most likely to select their area based on the prospects of obtaining prey. This again is contrary to the focus in the literature of cheetah focussing on avoiding competition.

I did not find support for my hypothesis of spatiotemporal avoidance by cheetah. Other studies have reported a reactive response by cheetahs to lions (Broekhuis *et al.*, 2013; Swanson *et al.*, 2016). Specifically, Swanson *et al.* (2016) noted that they did not find cheetahs within 12 hours of lion occurrence at one site. The lack of support for this hypothesis could be due to difference in detectability between sites (e.g. visibility) and species (e.g. number of individuals) resulting in different levels of threat across the data that were all pooled for this study. Future studies with large sample sizes could try to tease apart these differences to see if any spatiotemporal avoidance occurs.

The results of my study show that cheetahs use resource partitioning to avoid the negative effects of competition, but that this also represents a trade-off with the need to acquire prey. Resource partitioning does not need to occur on all axes for all competing large predators, nor was the response by cheetah symmetrical across all competing large predators. As I assessed resource use on multiple axes, I was able to determine that cheetahs avoided different predators on different axes. Cheetahs avoided African wild dogs through space, spotted hyenas and lions through time, and lions and leopards through short term avoidance (spatiotemporal). These results showcase the importance of looking at the intact guild and their use of several resources in order to obtain a full understanding of how competition shapes resource use. Furthermore, my study emphasizes the trade-off between avoiding competition and acquiring resources.

CHAPTER 5

Competition for Prey Between Cheetah and African Wild Dogs

INTRODUCTION

Carnivores compete with one another for shared resources including those that they consume, their prey species (Hayward & Kerley, 2008). Competition for consumable resources can occur directly through aggressive encounters (interference competition) or indirectly by limiting a species' access to the resource (exploitative competition) (Schoener, 1983). Within the guild of African carnivores competition for prey can manifest itself in several forms, especially given the size range of these carnivores and the relationship between predator size and accessible prey (Radloff & Du Toit, 2004; Clements *et al.*, 2014). Thus, subordinate species are limited by their size to which prey are accessible to them (Clements *et al.*, 2014). Furthermore, interference competition can force competitors out of prey rich areas or times, which again limits access to prey (Vanak *et al.*, 2013; Palomares *et al.*, 2016). Moreover, competition from kleptoparasitism can cause predators to select smaller prey or utilize dense areas for kill sites to avoid being detected by dominant carnivores, and thus losing their kills (Hayward *et al.*, 2006b; Rostro-García *et al.*, 2015). In addition, optimal foraging theory says that individuals should maximize their rate of energy intake, and predicts that predators should increase the number of prey species they consume when preferred species become rare (Svanbäck & Bolnick, 2005; Svanback & Bolnick, 2007; Heng *et al.*, 2018).

The large carnivore guild in Africa has been the focus of many studies, with interference competition between the smaller competitors, cheetahs, *Acinonyx jubatus*, and African wild dogs, *Lycaon pictus*, and their larger counterparts, lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta*, being well documented (Durant, 1998, 2000b; Creel, 2001; Caro & Stoner, 2003; Hunter *et al.*, 2007a; Swanson *et al.*, 2014, 2016;

Hilborn *et al.*, 2018). Both cheetahs and African wild dogs are of high conservation value, listed as vulnerable (Durant *et al.*, 2015) and endangered (Woodroffe & Sillero-Zubiri, 2012), respectively. Within South Africa, populations of these two species are mainly relegated to small fenced reserves that may contain high densities of other predators (Lindsey *et al.*, 2011). Both species are described as mainly diurnal/crepuscular (Hayward & Slotow, 2009), are cursorial hunters (Makin *et al.*, 2017) and are the smallest of the large predators, meaning they have access to only the smaller prey species (Clements *et al.*, 2014). One study notes that carnivores, of similar mass will have high dietary overlap (Lanszki *et al.*, 2019), which has been shown for cheetahs and African wild dogs (Radloff & Du Toit, 2004; Hayward & Kerley, 2008; Owen-Smith & Mills, 2008; Clements *et al.*, 2014; Vogel *et al.*, 2019). Even though both cheetahs and African wild dogs experience high overlap in prey preference, with a 99% overlap being cited (Vogel *et al.*, 2019), no studies have looked directly at how competition between these two species could potentially shape cheetah prey use.

In this study, I examine competition over prey resources between cheetahs and African wild dogs in Hluhluwe-iMfolozi Park (HIP), South Africa. I directly compare prey selection by cheetah before and after African wild dog re-introductions in relation to African wild dog prey selection. Based on competition theory (Schoener, 1974), this unplanned experiment should demonstrate (1) high overlap in prey use in the absence of the competitor and (2) shifts in prey use to reduce overlap when the predators co-exist. Thus, I predict that I will find a high overlap in dietary preferences between cheetahs and African wild dogs (Vogel *et al.*, 2019). In addition, I predict that cheetahs and African wild dogs will prefer impala, *Aepyceros melampus* and common duiker, *Sylvicapra grimmia*, as these species are available in the reserve and occupy the preferred size category for both species shown by Clements *et al.* (2014). In terms of competition, my question is, do cheetahs change their prey use given the presence/absence of African wild dogs? If cheetahs and African wild dogs are competing for prey resources, I expect to see a change in cheetah prey selection after African wild dogs were re-introduced away from the prey species most commonly utilized by the re-introduced African wild dogs. This will be done by controlling for prey densities across the time period. Moreover, I should see cheetahs becoming more generalized in their use of prey species with increased competition (Heng *et al.*, 2018). If competition is not occurring, then I should not see a change in cheetah dietary preferences after African wild dog re-introductions.

METHODS

Study Area

This study was conducted in HiP, a state-managed nature reserve in KwaZulu-Natal, South Africa (Figure 1.1). The 900 km^2 park receives most of its rain during the summer months of October to March (Howison *et al.*, 2017). The iMfolozi section, in the south, consists of mainly open savanna woodland and receives less rain than the higher elevated Hluhluwe section in the north (Howison *et al.*, 2017). Cheetah and African wild dog populations went locally extinct in the early 1900s (Somers *et al.*, 2017), however, cheetahs were reintroduced starting in the 1960s with 64 individuals being released over a four year period (Rowe-Rowe, 1992; Somers *et al.*, 2017); African wild dogs were not reintroduced until 1980 (Whateley & Brooks, 1983). By the mid-1990s only 13 cheetahs remained, so a further 22 individuals were translocated from Namibia (Marker-Kraus, 1996). The African wild dog population also hit a low point in the mid-1990s with only one pack of five dogs remaining, and several packs were re-introduced to supplement the population (Somers *et al.*, 2017). By 2016, African wild dog numbers were thriving, with approximately 70 individuals in 5-7 packs, whereas cheetah numbers were down to 5 individuals, further decreasing to 3 during the study period, and with all cheetah located in the southern iMfolozi region (Ezemvelo KwaZulu-Natal Wildlife (EKZNW) unpublished records). Other large carnivores in the park include a lion population estimated at 120 individuals, approximately 108 spotted hyenas and an estimated 46 leopards (*Panthera pardus*) (Somers *et al.*, 2017). The park contains a diverse herbivore community ranging from red duiker, *Cephalophus natalensis*, to elephant, *Loxodonta africana* (le Roux *et al.*, 2017).

Historical Kill Data

These data refer to the period when only cheetahs occurred in HiP, prior to the reintroduction of African wild dogs. Carnivore abundance and kill data were collected opportunistically between 1973 and 1982 by the staff of the then Natal Parks Board, now EKZNW (Whateley & Brooks, 1983). The Natal Parks Board staff assigned a predator to a kill if that predator was observed or heard killing the prey item, seen at a carcass, or its spoor was present at a carcass. I was quite confident that if a cheetah or African wild dog was seen on a carcass, it had made the kill, as cheetahs are not known to scavenge (Caro, 1994), and African wild dogs rarely do (Hayward *et al.*, 2006a).

Although African wild dogs were re-introduced in 1980, we used the historical cheetah data (cheetah without African wild dogs present) until 1982. The pack of African wild dogs were released into the Hluhluwe section of the game reserve, however, cheetah mainly occur in the iMfolozi section both then (Rowe-Rowe, 1992) and now. In addition, the years associated with the kill data were not reported in the Whateley and Brooks (1985) report but rather combined for all years. Given these factors, we felt that it was okay to use the data despite the small overlap.

Scat Samples

I collected scats opportunistically between January 2016 and December 2017 at sightings of African wild dogs or cheetahs, as well as at scent-marking sites commonly used by cheetahs (Cornhill & Kerley, in press). As all cheetahs were located in the iMfolozi region of the park, scats from African wild dogs and cheetahs were only collected from the iMfolozi section. I did not collect scats from the same pack/individual/scent marking site within four days of each collection to ensure independence in the dietary samples (Marker *et al.*, 2003). I identified individuals (cheetahs or African wild dogs) through their unique patterns (Maddock & Mills, 1994; Marnewick, Funston & Karanth, 2008) using ID kits provided by the park scientists. For scats collected from the scent-marking sites, video recording camera traps were placed at these sites for another study and scats were only collected if I could identify the individual on the videos who deposited the scat. I air dried scats in brown paper bags before individually washing each one, separating the hair and bones (Van de Ven, Tambling & Kerley, 2013). I determined which species the hair belonged to using cuticular scale imprints of the hairs (Keogh, 1983; Van de Ven *et al.*, 2013). To get the imprints, I used the method outlined by Keogh (1983). I randomly selected five hairs from each sample. I painted a microscope slide with clear nail polish and pressed the hairs onto the slide. Once the polish had dried, the hairs were removed. I viewed the slides under a Nikon Eclipse 80i compound light microscope at 200x magnification. Each imprint was photographed using a Nikon DS-Fi1-U2 camera. I determined the species consumed by looking at the colour, width, and scale pattern of the hair and comparing it to a reference collection obtained from the Nelson Mandela University (Van de Ven *et al.*, 2013) and Keogh (1979).

Present Day Kill Data

These data refer to the current period when cheetahs and African wild dogs co-occurred in HiP. I used African wild dog and cheetah kill data that was reported by park staff, researchers and tourist sightings between January 2016 and December 2017 to coincide with the scat collection (see above). Again, only cheetah and African wild dog kills that occurred in the iMfolozi section were used.

Prey Data

Herbivore population estimates (prey availability) were taken from previous reports. The present day herbivore population estimated were obtained from an internal EKZNW report (Clinning, 2016). The historical data was published by Whateley and Brooks (1983).

Ethical Note

No animals were harmed during data collection as non-invasive methods were used. Scats were only collected after they had been deposited and individual(s) had moved away from the area. In addition, predator kills were only observed and not interfered with.

Statistical Analysis

I conducted all statistical analysis in R (ver. 3.4.3, R Core Team) unless noted to be done in Primer 7 (Plymouth Routines 2018).

I ran two analysis of sampling variance tests, to determine if there were any significant variation between groups, one for cheetahs and one for African wild dogs to determine if I could pool the present day kill and scat data for each species. Both species showed no differences in diet composition depending on the data collection method (African wild dog: F = 6.8965, df = 8, p = 0.2655, cheetah: F = 0.61691, df = 7, p = 0.5393), therefore, I chose to pool the data. However, as studies have shown that kill datasets underestimate the smaller species (Marucco, Pletscher & Boitani, 2008; Tambling *et al.*, 2012), I excluded small prey species (< 5kg) from my analysis, as the historical data was only collected using kill data. No scats were collected in the four days following a known kill made by the same predator species, which eliminated risks of pseudoreplication between data sets (Marker *et al.*, 2003).

Diet Composition

I tested the predators' dietary species richness estimates through rarefaction analysis and chaos estimates, using the vegan package (Oksanen *et al.*, 2019). I used these tests to determine whether I had sufficient samples to confidently make statements with respect to prey preferences (Gotelli & Colwell, 2010). I also conducted Fisher's exact tests, due to small sample sizes (McDonald, 2014), to compare the proportions in which species occurred in the diet between the present cheetah preferences to African wild dog preferences, and to historical cheetah preferences.

Prey Preferences

I calculated prey preferences for cheetahs both in the historical (African wild dogs absent) and the present (African wild dogs present) data, and for African wild dogs (in the present period). Prey preference was calculated using the Jacobs index (Jacobs, 1974): $I_j = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$ where *r* is the proportion of consumed/killed individuals from species *i* (# of samples from species *i*/# samples) and *p* is the proportion of species *i* available (# of individuals of species *i*/# of all individuals of all prey species). The result, I_j, ranges from -1 to +1 with negative values indicating avoidance of prey species and positive values showing a preference of prey species (Hayward *et al.*, 2006b). I only calculated prey preferences for prey species whose population estimates were available within the EKZNW records.

Dietary Breadth

I measured dietary niche breadth using the Levin's index, as it is a standardized measure that allows for differences in the number of prey species utilized by cheetahs and African wild dogs (Hurlbert, 1978): $B_{sta} = \frac{(\frac{1}{\sum p_i^2} - 1)}{(B_{max} - 1)}$ where *p* is the proportion of each prey species consumed (# of samples with species *i*/# of samples) and B_{max} is the number of species consumed. The result, B_{sta}, ranges from 0 to 1 with 0 meaning the predator is a specialist hunter, and 1 a generalist.

Dietary Overlap

I determined the dietary overlap between present day cheetahs and African wild dogs, and present day cheetahs and historical cheetahs, using Pianka's index (Pianka, 1974): $O_{cw} = \frac{\sum_i^n P_{ic} P_{iw}}{(\sum P_{ic}^2 \sum P_{iw}^2)^{\frac{1}{2}}}$ where P_i is the proportion of species *i* consumed by species *c*, cheetah, or *w*, African wild dog. The result, O_{cw}, will show whether there is overlap in cheetah and African wild dog diet by ranging from 0, no overlap, to 1, complete overlap (Pianka, 1974). I measured overlap in cheetah diets in the present and the historical data sets, and the overlap of present day cheetahs and African wild dogs.

Analysis of Similarity

I did non-metric multidimensional scaling ordinations (nMDS) based on Bray-Curtis similarity matrixes using Primer 7, to visualize the difference in prey use, and I followed this with an analysis of similarity (ANOSIM) and SIMPER analysis to test for differences in prey use (Landman, Schoeman & Kerley, 2013). These tests determined any statistical differences between diets using global R (Clarke, 1993). Global R ranges from -1 to 1 with negative values indicating greater variation within each predator diet (high similarity), positive values showing greater variation between predator diets (low similarity), and zero indicating the diets are distributed randomly (Clarke, 1993).

RESULTS

For the historical period, records of 143 kills by cheetahs were obtained. Seven and 61 kills were recorded for the present day analysis by cheetahs and African wild dogs, respectively. During the present period, a total of 29 and 14 scat samples were collected for cheetahs and African wild dogs, respectively. In three cheetah scat samples, I could not confidently determine which species had been consumed and removed them from the analysis. One African wild dog sample contained hair from more than one prey species.

Diet Composition

African wild dogs were found to consume 6 different species in 75 scat and kill records (Table 5.1). Present day cheetahs consumed 8 species in 33 records, and historically there were 10 species in 143 kills observed (Table 5.1). The rarefaction curve (sampling efficiency) for prey species consumed for both cheetah sampling periods and African wild dogs did not reach a full stable plateau (Figure 5.1). However, all the observed number of species consumed were within the bounds of the estimated number of consumed species. African wild dogs should have consumed an estimated 6.3 ± 0.9 species, and cheetahs were estimated to consume 11.0 ± 4.1 species at present day and 11.0 ± 2.3 historically. Based on this, I assume that I can make reasonable statements about both species' diets in both sampling periods, however, I possibly underestimated the number of species consumed by cheetahs. Given that the focus here is on the major contributions to the diet (and hence the area for potential

Table 5.1: Diet composition for cheetahs and African wild dogs in Hluhluwe-iMfolozi park during the present day (2016-2017) or historically (1973-1982) and whether a prey species' population estimate was available for the present day or (historical). The weight of each prey species was obtained from Clements *et al.* (2014) as ¾ adult female mass.

Prey Species		**Weight (kg)**	**Cheetah**		**African Wild Dog**	**Population Estimates**
Latin Name	**Common Name**		**Present**	**Historical**		
Syncerus caffer	Buffalo	432	0%	1%	0%	Yes (Yes)
Kobus ellipsiprymnus	Waterbuck	188	0%	5%	0%	Yes (Yes)
Connochaetes taurinus	Blue Wildebeest	136	0%	1%	1%	Yes (Yes)
Tragelaphus strepsiceros	Greater Kudu	135	3%	3%	3%	Yes (Yes)
Tragelaphus angasii	Nyala	47	27%	42%	19%	Yes (Yes)
Phacochoerus africanus	Warthog	45	0%	3%	0%	Yes (Yes)
Redunca arundinum	Common Reedbuck	32	0%	7%	0%	No (Yes)
Aepyceros melampus	Impala	30	42%	30%	73%	Yes (Yes)
Tragelaphus scriptus	Bushbuck	23	3%	2%	0%	No (Yes)
Sylvicapra grimmia	Common Duiker	16	12%	6%	1%	Yes (No)
Lepus saxatilis	Scrub Hare	2	3%	0%	3%	No (No)
Galerella sanguinea	Slender Mongoose	1	3%	0%	0%	No (No)
Rodentia spp.	Rodent	-	6%	0%	0%	No (No)

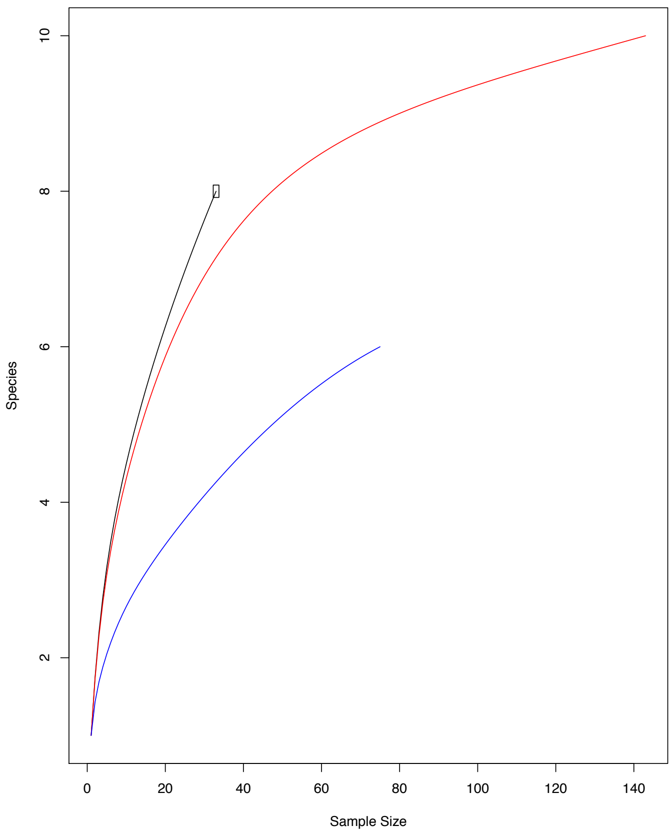

Figure 5.1: Species richness for present day cheetahs (black), historical cheetahs (red) and present day African wild dogs (blue) in Hluhluwe-iMfolozi Park.

competition) and not on the rare species in the diet (which are unlikely to represent significant areas of competition), this assumption is reasonable.

When comparing the proportion that each species contributed to the diets, a difference occurred between cheetahs in the presence of African wild dog, which used common duiker more (12% of the diet) than African wild dogs (1% of the diet) (odds ratio = 10.17, P = 0.028) (Appendix: Table A5.1).

Prey Preferences

Cheetahs, both in the presence and absence of African wild dogs, and African wild dogs avoided buffalo, blue wildebeest and warthog, whereas they consumed greater kudu relative to its availability (Figure 5.2). Waterbuck were preferred by cheetahs in the absence of African wild dogs but avoided by cheetahs in the presence of African wild dogs when they were preferred by African wild dogs. Historically, cheetahs in the absence of African wild dogs preferred common reedbuck and consumed bushbuck relative to its availability, however at present day, both prey species are rare in iMfolozi (Clinning, 2016), thus population estimates do not exist. Impala and nyala were eaten relative to their availability by African wild dogs, as well as by cheetahs in the absence of African wild dogs. However, cheetahs in the presence of African wild dogs avoided impala and preferred nyala. African wild dogs avoided preying upon common duiker but cheetahs preferred common duiker in the presence of African wild dogs. There were no population estimates for common duiker historically, however, Whateley and Brooks (1983) stated that cheetahs preferred this species.

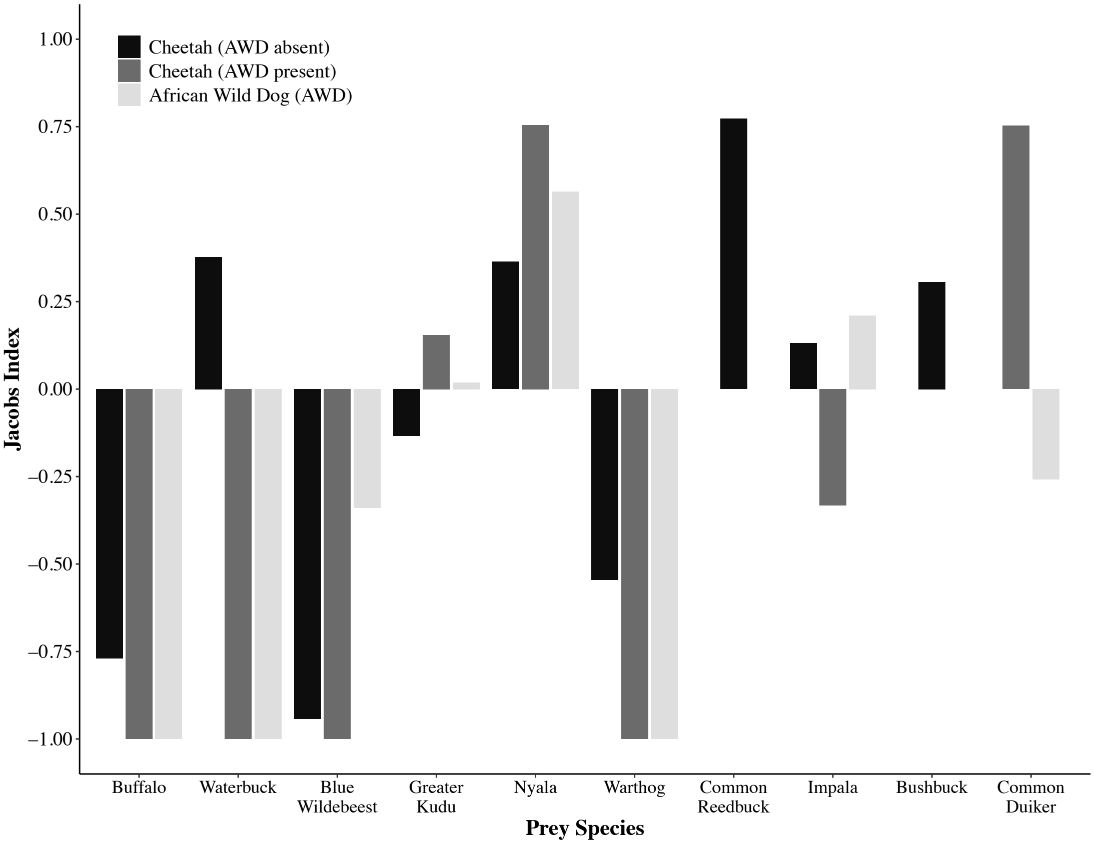

Figure 5.2: Jacobs' index for prey species consumed by cheetahs and African wild dogs in Hluhluwe-iMfolozi Park at present (2016-2017), and for cheetah historically (1973-1982) in the absence of African wild dogs.

Dietary Breadth

Cheetahs in the absence of African wild dogs had a dietary breadth of 0.29. Cheetahs in the presence of African wild dogs became more of a generalist hunter, with a dietary breadth of 0.46. African wild dogs were more specialized in their prey use, with a dietary breadth of 0.16.

Dietary Overlap

Using all data, regardless of collection method and availability of population estimates, I found high overlap in prey use between cheetahs and African wild dogs. Cheetahs with African wild dogs present and African wild dogs experienced a 92.4% overlap in prey species consumed. When comparing cheetahs with and without African wild dogs present, I found a 91.0% overlap in prey species consumed by cheetahs.

Analysis of Similarity

Coexisting cheetahs and African wild dogs showed a difference in their diet (Global R = 0.128, p = 0.005) and their prey consumption had an average dissimilarity of 56% (Figure 5.3). Impala and nyala explained 80% of the difference in diet composition, representing 45% and 35% respectively. Even though the diet of cheetahs with and without African wild dogs presence did not differ (Global R = 0.002, p = 0.47), the SIMPER analysis showed a 69% average dissimilarity between these diets. Impala and nyala made up 70% of the dissimilarity between cheetah diets, representing 36%, and 34% respectively.

DISCUSSION

This study is novel as it compares the diet of cheetahs before and after African wild dogs were reintroduced in a fenced protected area. I determined, through sampling

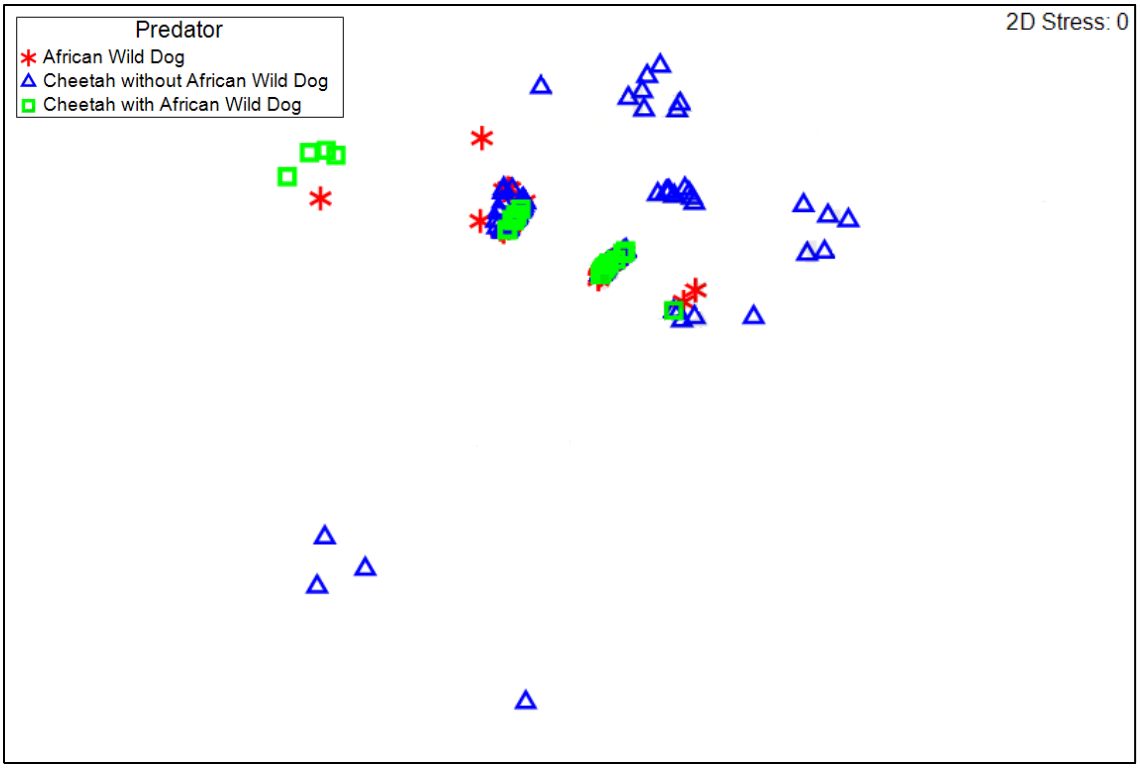

Figure 5.3: Non-metric multidimensional scaling (nMDS) matrix based on Bray-Curtis similarity for cheetahs with African wild dogs present (green ☐), cheetahs without African wild dogs (blue △) and African wild dogs (red ∗). Each point is an individual record/scat.

efficiency analysis, that I may have underestimated the number of species consumed by cheetah both before and after the re-introduction of African wild dogs. However, given that I found cheetahs consumed more species than African wild dogs, this possible underestimate would only strengthen my results. Moreover, I would expect dietary competition to be centred around the dietary items that make of the majority of the diet.

I found support for the hypothesis of high dietary overlap between cheetahs and African wild dogs (Hayward & Kerley, 2008; Clements *et al.*, 2014; Vogel *et al.*, 2019). There were, however, key differences in their prey selection that may reflect a range of factors, including competition, prey population fluctuations, predator population composition and differences in methodology. Common reedbuck and bushbuck, although historically selected for by cheetahs, now occur in low numbers in HiP

(Clinning, 2016), and this is likely why they not regularly consumed by cheetahs or African wild dogs in the present day. Male coalitions of cheetahs are able to hunt (i.e. have accessible prey up to 313 kg) and prefer (i.e. up to 119 kg) larger prey than solitary cheetah (i.e. accessible prey up to 145 kg and prefer less than 31 kg) (Clements *et al*., 2016b; Broekhuis *et al.*, 2018). Thus, the historical use of large antelopes (buffalo, waterbuck, wildebeest and greater kudu) by cheetahs can in part be explained by the coalitions of males that historically occurred within HiP, currently, there are no such coalitions present. Moreover, the use of small prey species (i.e rodents, scrub hare and slender mongoose) by cheetahs during the present day is clearly the result of a change in data collection methods (i.e the inclusion of data from scat analysis) and not an actual reflection in a shift in prey use, and hence although described here were not included in the analyses. Prey consumption based on only observing kills biases the data towards large animals, whereas scat analysis reveals the consumption of smaller prey (Whateley & Brooks, 1983; Kruger, Lawes & Maddock, 1999; Tambling *et al.*, 2012). I, therefore, chose, for further discussions, to focus on the three key species that made up 78-93% of the two predator's diet: impala, nyala and common duiker.

For cheetah diet, I found a shift in their prey use depending on the presence/absence of African wild dogs. When looking at prey preference, common reedbuck was the most preferred species by cheetahs when African wild dogs were absent, whereas nyala and common duiker were the most preferred by cheetahs with African wild dogs present. However, nyala formed the largest percentage of cheetah diet in the absence of African wild dogs, and impala was the most consumed prey species numerically for cheetahs coexisting with African wild dogs. Although nyala made up a smaller percentage of cheetah diet in the presence of African wild dogs, the population had decreased severely, which lead to cheetah preferring this species. On the other hand, impala made up a larger percentage of cheetah diet in the presence of African wild dogs, but the population had increased slightly, yielding a calculated avoidance of this species. The present day data showed cheetahs selected strongly for common duiker, however, there is no population estimate available for common duiker in the past, so I cannot tell if this was a shift in preference by cheetahs.

I was able to show that cheetahs changed their prey preference towards nyala and away from impala in the presence of African wild dogs. However, this was not a shift away from the species preferred by African wild dogs, which also preferred nyala. As cheetahs preferred the same species as African wild dogs, it is unlikely that resource partitioning brought about by competition caused the increased preference for nyala by cheetah. However, it is possible that competition shaped the avoidance of impala by cheetah as African wild dogs selected it relative to its abundance. In addition, I found higher dietary niche breadths for cheetahs and African wild dogs than those reported by Vogel et al. (2018). I documented cheetahs becoming more generalized in the presence of African wild dogs, and, therefore under increased competition, as predicted by optimal foraging theory (Svanbäck & Bolnick, 2005; Svanback & Bolnick, 2007; Heng *et al.*, 2018).

Cheetahs could be selecting for nyala and common duiker, as these prey species occupy denser habitat than impala (Pero, 1994; Kruger *et al.*, 1999; Canter, 2009; Abu Baker & Brown, 2014), and selection of these species could provide relief from kleptoparasitism, through the concealment of prey (Hayward *et al.*, 2006b). However, given that there is no support in the literature of African wild dogs kleptoparasitizing kills from cheetahs, it is unlikely that cheetahs selected prey in dense areas to avoid competition from them. Moreover, there are no documented kills of cheetah by African wild dogs, and I have demonstrated no short term avoidance of African wild dogs by cheetahs (Chapter Two and Four). In addition, I (Chapter Four) and others have documented high temporal overlap between cheetahs and African wild dogs, suggesting that they have access to the same prey species across time (Hayward & Slotow, 2009). Only across space did I (Chapter Four) find differences in cheetahs and African wild dogs space use, however that was most likely shaped by competition with other predators, not each other (Vanak *et al.*, 2013; Swanson *et al.*, 2014; Dröge *et al.*, 2017, Chapter Four). Therefore, the potential for interference competition between cheetahs and African wild dogs over prey species is low, but, exploitative competition could be occurring for impala.

CHAPTER 6

Discussion

Contributions of This Study

In this thesis, I aimed to use cheetahs as a model subordinate predator to determine the responses to possible competition by the other large African carnivores. I was able to explore the behavioural response and changes in resource use by cheetahs due to competition through both direct and indirect methods. Overall, I found that cheetahs conformed to the niche complementarity theory (Vieira & Port, 2007) in terms of its responses, and avoided competition with different carnivores using resource partitioning along different resource axes. In addition, cheetahs responded reactively to dominant members of the guild, using a short term response, which allows species to navigate the trade-off between risk and resource acquisition (Creel, 2018).

Partitioning of the Time Axis

Although cheetahs were traditionally considered to be mainly diurnal/crepuscular (Durant, 1998; Hayward & Slotow, 2009), I found cheetahs to be active throughout the 24 hour period with more than a quarter of the activity being at night (Chapter Two and Chapter Four). The finding of nocturnal activity is in line with recent studies (Cozzi *et al.*, 2012; Broekhuis *et al.*, 2014, 2019). At scent-marking sites (Chapter Two), 48% of the visits occurred at night, similar to that reported by Broekhuis *et al.* (2019) and 28.5% of visits to camera trap sites (Chapter Four) occurred at night, similar to Cozzi *et al.*'s (2012) results. The differences in nocturnal activity (48% versus 28.5%) between the two chapters can be caused by the differences in the activities being performed at the sites. The camera trap data in Chapter Four reflects cheetahs using a range of sites when they were active. In contrast, the scent-marking sites are visited by cheetahs specifically to communicate with other cheetahs. During the day, it has been noted that cheetahs are mainly mobile or hunting/feeding (Broekhuis *et al*., 2014), however in the evenings when it is dark, they are able to spend time communicating.

Cozzi *et al.* (2012) suggested that increased nocturnal activity by cheetahs would cause an increase in the overlap of activity patterns of cheetahs with other predators, something that I documented. When comparing Hayward and Slotow's (2009) results to mine, I found a higher temporal overlap between cheetahs and African wild dogs, lions and leopards, presumably due to those authors using movement and kill data to generate their activity patterns, and these measures have a diurnal bias (Radloff & Du Toit, 2004). It has been suggested that cheetahs use moonlit nights to hunt, as the light allows for this behaviour and that they are "starvation driven" as opposed to "competitive avoidance driven" (Cozzi *et al*., 2012; Broekhuis *et al*., 2014), which I did not test. Yet, I found cheetahs to be active at night at scent-marking sites, where hunting was not the primary focus, indicating a need for cheetah to also communicate at night. However, as the majority of camera trap sites used for activity pattern analyses (Chapter Two and Chapter Four) were located on or very near a tourist road, I also propose that cheetahs could be increasing their nocturnal activity inside fenced reserves as a way to avoid the negative consequences associated with tourist vehicles that are present during the day (Broekhuis, 2018).

Partitioning Through Prey Use

Cheetahs experience high overlap in prey preferences not only with predators of the same body size (Chapter Five; Lanszki *et al*., 2019) but larger predators as well (Broekhuis *et al*., 2018). When assessing competition for prey species by the African apex predators, cheetahs and African wild dogs have been shown to experience the highest overlap (Hayward & Kerley, 2008; Vogel *et al*., 2019), presumably due to their similar small body size and subordinate status within the large predator guild. In Chapter Five, I used optimal foraging theory to show that an increase in cheetah niche breadth, in the presence of African wild dogs, was presumably due to increased competition. This was in contrast to findings reported by Clements *et al.* (2016b), who found an increase in predator density led to cheetahs becoming more specialized in their diet. Those authors suggest that interference competition mediated this diet specialization by cheetahs but did not directly investigate it, as I was able to do (Chapter Five). I also documented a wider niche breadth for cheetahs and African wild dogs than previously noted (Vogel *et al.*, 2019). However, most previous studies that reported cheetah prey preferences rely solely on kill data to investigate diet composition, which can be biased towards species that are easily seen and recorded (e.g. larger species that occupy open areas and take longer to consume). Mills and Mills (2017) are the exception to the rule and use unbiased methods, and they reported cheetahs to utilize larger amounts of small mammals (less than 28 kg) than other biased studies. This use of small mammals was something I also noted when including prey species found in scat. Even though I relied on kill data as well, the inclusion of some scat data (81% for cheetahs and 19% for African wild dogs) can already demonstrate the importance of unbiased methods.

Partitioning of the Space Axis

I did not find support for cheetahs using resource partitioning across space, meaning that they did not use areas devoid of other large predators as a way to reduce competition although previous studies do (Durant, 1998; Broomhall *et al.*, 2003; Rostro-García *et al.*, 2015). In Chapter Three, I found a high overlap between cheetahs space and habitat use with re-introduced lions. Moreover, in Chapter Four, I found that cheetahs selected sites regardless of the fact that they were also used by lions, leopards and spotted hyenas. Dominant predators are thought to distribute themselves in areas where prey species are the most prevalent (Vanak *et al.*, 2013). Therefore, if cheetah were to avoid areas with high predator presence, they would also be avoiding the most prey-rich areas. If cheetahs avoid these areas, they risk starvation, and therefore, must find other ways to avoid competition that are less costly to their survival. A well-known example of this trade-off in food acquisition versus predation, occurred in Serengeti-Mara region, where herbivores accepted increased risks of predation during the dry season when grazing became scarce but not in the wet season when grazing was abundant (Sinclair, 1985). It is therefore likely that competition between cheetahs and other large predators increases when prey is limiting, meaning a higher overlap in resource use, but that they are better able to partition themselves when prey is abundant.

In Chapter Four, I did note cheetah presence at camera trap sites was negatively associated with African wild dog presence. This would support the hypothesis for resource partitioning, as cheetahs and African wild dogs experience high overlap in time of activity (Hayward & Slotow, 2009; Chapter Four) and prey use (Hayward & Kerley, 2008; Vogel *et al.*, 2019; Chapter Five). However, I was unable to determine whether it was cheetahs avoiding sites used by African wild dogs or the reverse. As the sites selected for by cheetahs were also selected for by the other three large carnivore competitors, it seems likely that African wild dogs were selecting for sites that were lacking competitors (Vanak *et al.*, 2013; Swanson *et al.*, 2014; Dröge *et al.*, 2017). This result suggests that cheetahs are able to withstand high spatial overlap with other predators, due to the fact that they experienced a reduced overlap in time (Hayward & Slotow, 2009; Chapter Four) and possibly prey use (Clements *et al.*, 2014) with the other large predators.

Implication of Body Size on Competitive Response

One of the main predictions throughout my thesis was that cheetahs would respond differently to competitors based on their body size, specifically that large predators would elicit a stronger response from cheetahs than smaller competitors (Durant, 2000b). In Chapter Two, I found cheetahs responded more strongly to lions and leopards than spotted hyenas and African wild dogs, in that cheetahs employed spatiotemporal avoidance of lions and leopards, but not spotted hyenas or African wild dogs, demonstrating that body size alone does not determine the response by cheetahs. Although the body size argument holds for why cheetahs did not respond to African wild dogs, it does not hold for spotted hyenas, as they are larger than leopards who did elicit a response. The body size hypothesis was based on a study that only looked at the response of cheetahs to lions and spotted hyenas (Durant, 2000a, 2000b). When Durant (2000a, 2000b) found the response to lions stronger than spotted hyenas, she attributed it to body size. However, given that I found a similarly strong response to leopards and lions, it does not make sense, following the body size argument, as to why I did not get a similarly strong response for spotted hyenas. Instead, I suggest that spotted hyenas are harder to avoid across space, as they form fission-fusion groups, that employ a strict hierarchy over food, so when out hunting spotted hyenas are often alone or in a small group (Holekamp, Sakai & Lundrigan, 2007). This dispersion when hunting causes spotted hyenas to be more widespread across the landscape (space) than lions who form prides that hunt together, grouping them across the landscape (Darnell *et al.*, 2014). Moreover, spotted hyenas are almost entirely active at night (Hayward & Slotow, 2009; Chapter Four) and it could be that cheetahs are able to avoid them through time by being mostly active in the day. I noted the lowest temporal overlap between cheetahs and spotted hyenas (Chapter Four). Given that I looked at competition from all large carnivores, I was able to provide novel insight into the fact that body size alone does not determine the strength of response by competitors.

Reactive Response Utilized by Cheetah

Although cheetahs did employ some resource partitioning to reduce competition with the other large carnivores, they also used a reactive response to avoid the negative effects of direct interactions. In Chapter Two, I found that large carnivores are able to inhibit or delay intraspecific communication between cheetahs through their presence at scent-marking sites. However, as cheetahs did eventually return to the sites, this was a reactive response to avoiding competitors in the short term. A similar response has been noted in zebras, *Equus quagga*, who fled from waterholes when lions were present, but returned the next day (Courbin *et al.*, 2016). This reactive response increases the ability for species to co-exist as they are able to make use of the same resources, separating themselves on the spatiotemporal (short term) axis.

In Chapter Three, I found that cheetahs did not respond to re-introduced lions by shifting their space and habitat use, but rather avoided encounters with lions in the short term by not being in the immediate vicinity of lions. Broekhuis *et al.* (2013), also found that cheetahs positioned themselves further from lions than expected at random.

Finally, in Chapter Four, I found that cheetah experienced a spatiotemporal avoidance of lions and leopards, which is a reactive response as it is the short term avoidance of sites immediately after they had been visited by the competitor. Swanson *et al.* (2016) showed that cheetahs avoided camera trap sites shortly after lions but not spotted hyenas. By choosing to employ a reactive response, cheetahs are balancing the trade-off between resource attainment and risk avoidance. Moreover, when faced with decreasing resources (prey), competition and therefore risk avoidance also decreases.

Implications

Re-introductions of Carnivores

Re-introductions of carnivores into areas that they once occupied is a key tool for conservation today (Armstrong & Seddon, 2007; Hayward *et al.*, 2007b; Lindsey *et al.*, 2011; Boast *et al.*, 2018; Wolf & Ripple, 2018; Bull *et al.*, 2019). My study looked at cheetahs, as a model subordinate species, to determine the response to competition to the other large African carnivores and did so using fenced protected areas. In South Africa, a large portion of the cheetah population is managed using a metapopulation approach inside fenced protected areas (Buk *et al.*, 2018). Globally, this is the only known increasing population of cheetahs occurring today (Weise *et al.*, 2017), therefore, the cheetahs from South Africa’s metapopulation can, and does (Endangered Wildlife Trust, 2017), serve as a source population for other countries. My study provides some insight as to how cheetahs are able to navigate the risks of competition that occur inside these fenced protected areas (Darnell *et al.*, 2014), and can aid managers in their re-introduction attempts. Special concern should be raised to releasing cheetahs into reserves with lions and leopards, as cheetahs avoided direct encounters with these two species (Chapters Two, Chapter Three, Chapter Four). As scent-marking sites are visited by all cheetahs regardless of the demographic status (Cornhill & Kerley, in press), managers can use the sites to monitor when females are coming into estrous, or track dominance tenures, however, large carnivores seemed to inhibit female visits (Chapter Two). Moreover, as prey populations decline, cheetahs switch their prey use to avoid competition (Chapter Five) so adequate prey densities should be stocked within re-introduction areas. Specifically, changes in medium bodied prey populations should be monitored to determine competition levels with other predators.

The result of this study also can be applied to carnivores guilds outside of Africa. In North America, re-introductions are occurring to re-establish intact large carnivore guilds within protected areas, for example in Yellowstone (Boyce, 2018). As Africa contains the last remaining intact large carnivore guild globally, it can serve as a model for how we expect competition to occur elsewhere. By determining that predators can partition their resource use with all competitors on at least one axes, we gain insight into potentially how other subordinate competitors would react to dominant competitors that are re-introduced into an area. For example, models that looked into the effects of wolves, *Canis lupus*, following their re-introduction into Yellowstone National Park overestimated the number of elk, *Cervus elaphus*, that would be present, because the models did not take into account cougars, *Puma concolor*, and bears, *Ursus arctos* and *U. americanus*, predation (Boyce, 2018). In the future, however, similar models should include the estimated effects of competition based on insights from the African system, such as those provided here.

Other Taxa

Flagship animals are normally charismatic species that can be used to attract support, attention and money for conservation efforts (Smith *et al.*, 2012). Cheetahs and most large carnivores can serve as flagship species and research can be biased towards these species as they are able to attract funding. However, competition between species can occur in every guild and the information from this study can be used as a model for how competition affects other species.

Herbivore species respond not only to competition with other herbivores for resources but also to predation from predators (Burkepile *et al.*, 2013). This is similar for cheetahs, only simpler as they compete with the same species who kill them. In addition, herbivores are rarely found in an environment that contains only one predator (Hopcraft, Olff & Sinclair, 2009; Thaker *et al.*, 2011). Below I explore how the response to competition by cheetah is comparable to the response of herbivores to competition. I found cheetahs employ a reactive response to competition (Chapters Two, Three and Four), as they need to balance the trade-off between competition and resource acquisition. Similar responses have been shown in herbivores, with zebras responding reactively to risks of lion predation (Courbin *et al.*, 2016), meaning that sometimes the risk of predation does not outweigh the loss of resource attainment. Herbivores are also thought to respond to predators differently depending on the predators hunting style (Thaker *et al.*, 2011; Wikenros *et al.*, 2015), body size (Hopcraft *et al.*, 2009) as well as varying their response across space and time (Eriksen *et al.*, 2011; Makin *et al.*, 2017). Tambling *et al.* (2015) showed that kudu, *Tragelaphus strepsiceros*, and buffalo, *Syncerus caffer*, adjusted their activity patterns by becoming more diurnal in response to nocturnal predator (lion and spotted hyena) re-introductions, and Creel *et al*. (2005) showed that elk changed their habitat use, selecting for denser habitat to avoid wolves. The basic theories and findings of my study line up with the results previously stated for herbivores and showcase the potential for the information on cheetahs response to competition to be applied to herbivores, mainly that resource partitioning only needs to occur on one axis, or by avoiding predators reactively they can still obtain resources.

Non-mammalian species also compete with one another and similarly experience competition and use resource partitioning to alleviate the effects. Common buzzards, *Buteo buteo*, selected territories away from northern goshawks, *Accipiter gentilis* to avoid nest predation (Björklund *et al.*, 2016) and tree climbing birds (*Sitta pygmaea, S. carolinensis and Certhia americana*) foraged at different parts of trees to avoid competition over food (Lara *et al.*, 2015). Common murres, *Uria aalge*, and thick-billed murres, *U. lomvia*, when occupying the same colony during chick rearing, utilized different prey species, squid and fish respectively (Barger *et al.*, 2016). Three species of sea bream avoid competition through a combination of space and food resources, with white sea bream, *Diplodus sargus*, avoiding sharpsnout sea bream, *D. puntazzo*, through prey use and two-banded sea bream, *D. vulgaris*, through space use (Sala & Ballesteros, 1997). The studies listed above highlight that resource partitioning occurs across species of different guilds. The results of my study, resource partitioning across at least one axis and the use of a reactive response over a proactive response, can be applied to other guilds to determine if those species avoid competition in a similar manner.

Suggestions for Future Research

Many studies on competition look at the inferred response for subordinate species to dominant species (Hutchinson, 1957; Durant, 1998; Broekhuis *et al.*, 2013; Vanak *et al.*, 2013), because having experimental set-ups that allow for the investigation into the direct behaviour response or resource partitioning are rare, as they require the re-introduction or removal of a competitor in order to measure the difference in behaviour or resource use of the other competitor. For my study, I was fortunate to have access to such a natural experiment, as lions and African wild dogs were re-introduced into the reserves several years after cheetah. Future studies should try to make use of similar experiments (planned or unplanned) to determine the direct effects of other large predators on cheetah (or other members of this guild). These unplanned experiments do occur, as reserves re-introduce species (Chapter One) or remove individuals for various reasons (Hunter, 1998; Hayward *et al.*, 2007b) and when this does happen, data can be collected to evaluate competition and the responses of species to competition.

I found cheetahs employed a reactive response to competitors, mainly lions and leopards. An interesting component to a reactive response is a buffer or lag time between the species. Future studies can ask whether there is a minimum distance or time that must occur between competitors? This can be done using simultaneous GPS collar data to determine if there is a minimum distance maintained between competitors. Additionally, predator scats can be used to determine if there is a minimum time that needs to pass before competitors feel comfortable in an area.

During my study I only looked at cheetahs inside fenced protected areas, however, substantial numbers of cheetahs occur in unfenced areas and even outside of protected areas (Durant *et al.*, 2017). Fences likely constrain cheetah movement (Cozzi *et al.*, 2013). In addition, in this study, their home ranges encompassed large portions of the available area within the reserve (Chapter Three) and the home ranges are found to be larger outside of fenced areas (Marker, 2002; Houser, Somers & Boast, 2009). In addition, in the Serengeti (an unfenced protected area), cheetah were found to seek refuge from areas frequented by competitors (Durant, 1998) which is a proactive response to competition. I hypothesize that fences might be limiting cheetahs from employing a proactive response by constraining their movements.

In my study, I was able to provide novel insight that cheetahs respond to competition with leopards that is comparable to their response to lions. However, due to leopards' secretive nature, many studies do not have the data to include them as a factor, as was the case for my chapter involving prey preference. Many studies state that competition from mainly lions influences cheetah behaviour and resource use. Yet, my chapter looking at the effects of predator cues on cheetah behaviour revealed that leopard presence had as strong a response from cheetahs as that elicited by lion presence. In addition, Chapter Four revealed spatiotemporal partitioning by cheetahs towards both lions and leopards. These results showcase the potential for strong competition/avoidance by cheetahs towards leopards and highlights the need for more studies to be conducted with leopards included as a competitor affecting cheetah behaviour.

Through most of my study, I was unable to separate cheetahs based on their social class. However, other studies have shown that different social classes of cheetah (solitary vs coalition vs females with cubs present) use resources differently (Cornhill & Kerley, in press; Broomhall, Mills & du Toit, 2003; Bissett & Bernard, 2007; Clements *et al.*, 2016; Broekhuis *et al.*, 2018). These various social classes are therefore expected to respond to competition differently. I hypothesize that cheetahs with cubs should be more vulnerable than solitary individuals who are in turn more vulnerable than coalitions, at least with respect to interference competition.

Large carnivores were predicted to be the main source of mortality for cheetah cubs (Laurenson, 1994; Laurenson, Wielebnowski & Caro, 1995) until Mills and Mills (2017) demonstrated that in the Kalahari, smaller carnivores, such as jackal or honey badgers, were the likely culprits for the majority of deaths inside the lair. Moreover, smaller carnivores harass or follow cheetah in order to scavenge on the remains of the kills that cheetahs make (Hunter *et al.*, 2007a; Mills & Mills, 2017) and there is potential for dietary overlap with some small carnivores, like black-backed jackals, *Canis mesomelas*, and Cape foxes, *Vulpes chama*, who eat small- to medium-sized mammals (Kamler *et al.*, 2012). Finally, Mills and Mills (2017) documented cheetahs killing bat-eared foxes, *Otocyon* megalotis. Based on these observations, cheetahs and small carnivores likely compete with one another and the interactions between them could further shape niche use. The possibility of resource partitioning between the species could be explored.

Conclusion

In this study, I was able to show that cheetahs navigate the effects of competition with other large carnivores through resource partitioning and a reactive response to the presence of some of the members of this guild. Cheetahs employ strategies predicted by the niche complementarity hypothesis by using different resources to separate themselves from different competitors, mainly lions on the spatiotemporal and temporal axis, spotted hyenas on the temporal axis, leopards on the spatiotemporal axis and African wild dogs on the prey and spatial axis. Moreover, by utilizing a reactive response to competition, cheetahs are able to balance the trade-off between risk and resource attainment. Finally, I provided a new understanding of how the strength of a cheetah's response does not differ solely by the competitors body size.

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Appendix

Table A2.1: Akaike information criteria corrected for small sample sizes (AICc) for all analyses run comparing grouping of predator species versus separating out the five species. Bold entries show the model selected.

Analysis	AICc Value	
	Predators Together	Predators Separated
Duration of Stay	**843.69**	845.61
Visitation Interval	945.19	**942.97**
Scent-Marking Frequency	**479.76**	482.54
Time Allocation	**157.97**	193.73

Table A2.2: Model output for linear mixed-effect model showing visitation intervals to scent-marking sites depending on the previous species that visited. Bold entries indicate significance ($P < 0.05$).

Species	Estimate	SE	DF	t	P
Cheetah * Spotted Hyena	-0.571	0.350	312	-1.630	0.104
Cheetah * Leopard	**-1.813**	**0.731**	**310**	**-2.479**	**0.014**
Cheetah * Lion	**-1.555**	**0.395**	**310**	**-3.935**	**< 0.001**
Cheetah * African Wild Dog	-0.456	0.596	310	-0.766	0.445
Spotted Hyena * Leopard	-1.242	0.806	310	-1.541	0.124
Spotted Hyena * Lion	-0.984	0.521	312	-1.890	0.060
Spotted Hyena * African Wild Dog	0.115	0.684	310	0.168	0.867
Leopard * Lion	0.258	0.826	310	0.313	0.755
Leopard * African Wild Dog	1.357	0.942	311	1.440	0.151
Lion * African Wild Dog	1.099	0.706	308	1.557	0.121

Table A2.3: Pairwise model outputs for the allocation of time to different behaviours at scent-marking sites depending on the previous visitor to the site. Bolded values signify significance (P < 0.05).

Behaviour	Previous Visitor	Estimate	SE	DF	t	P
Scent-Marking * Vigilant	**Cheetah * Cheetah**	**-0.082**	**0.019**	**1486**	**-4.36**	**< 0.001**
Scent-Marking * Sniffing	**Cheetah * Cheetah**	**-0.126**	**0.019**	**1486**	**-6.74**	**< 0.001**
Scent-Marking * Other	**Cheetah * Cheetah**	**-0.215**	**0.019**	**1486**	**-11.47**	**< 0.001**
Vigilant * Sniffing	**Cheetah * Cheetah**	**-0.045**	**0.019**	**1486**	**-2.38**	**0.017**
Vigilant * Other	**Cheetah * Cheetah**	**-0.133**	**0.019**	**1486**	**-7.11**	**< 0.001**
Sniffing * Other	**Cheetah * Cheetah**	**-0.089**	**0.019**	**1486**	**-4.73**	**< 0.001**
Scent-Marking * Vigilant	Other Predator * Other Predator	-0.135	0.081	1486	-1.66	0.097
Scent-Marking * Sniffing	**Other Predator * Other Predator**	**-0.241**	**0.081**	**1486**	**-2.97**	**0.003**
Scent-Marking * Other	Other Predator * Other Predator	-0.114	0.081	1486	-1.41	0.160
Vigilant * Sniffing	Other Predator * Other Predator	-0.106	0.081	1486	-1.30	0.192
Vigilant * Other	Other Predator * Other Predator	0.021	0.081	1486	0.25	0.800
Sniffing * Other	Other Predator * Other Predator	0.126	0.081	1486	1.56	0.119
Sniffing * Sniffing	**Cheetah * Other Predator**	**-0.123**	**0.059**	**1487**	**-2.08**	**0.038**
Scent-Marking * Scent-Marking	Cheetah * Other Predator	-0.009	0.059	1487	-0.14	0.886
Vigilant * Vigilant	Cheetah * Other Predator	-0.062	0.059	1487	-1.04	0.298
Other * Other	Cheetah * Other Predator	0.092	0.059	1487	1.56	0.119

Table A3.4: Model selection for home range (95%) and core area (50%) analysis using utilization distribution (UD) techniques. The fixed effects are: lions (the presence or absence of lions); season (summer or winter); and sex of the cheetah (male or female). Cheetah ID was used as a random effect to control for pseudoreplication. The best model was selected by lowest Akaike information criterion corrected for small sample size (AICc) value and is indicated in bold.

Name	Model	AICc	
		Core Area	Home Range
Full	Lions + Season + Sex + (1 I ID)	402.41	476.74
Without Lions	**Season + Sex + (1 I ID)**	**399.75**	**473.99**
Without Season	Lions + Sex + (1 I ID)	400.59	474.86
Without Sex	Lions + Season + (1 I ID)	402.18	475.06

Table A4.1: Species recorded on camera traps from 2013-2016 in the different reserves surveyed.

Common Name	Species	HiP	Manyoni	Phinda	uMkhuze
Aardvark	*Orycteropus afer*	✓	✓	✓	✓
African Wild Dog	*Lycaon pictus*	✓	✓	✓	✓
African Wildcat	*Felis lybica*				✓
Bat spp.	-	✓	✓	✓	✓
Bird spp.	-	✓	✓	✓	✓
Black Rhinoceros	*Diceros bicornis*	✓	✓	✓	✓
Black-backed Jackal	*Canis mesomelas*	✓	✓		✓
Brown Hyena	*Parahyaena brunnea*		✓		
Buffalo	*Syncerus caffer*	✓	✓	✓	✓
Bushbuck	*Tragelaphus scriptus*	✓	✓	✓	✓
Bushpig	*Potamochoerus porcus*	✓	✓	✓	✓
Cane Rat	*Thryonomys swinderianus*	✓	✓	✓	✓
Cape Clawless Otter	*Aonyx capensis*				✓

Caracal	*Caracal caracal*		✓		✓
Chacma Baboon	*Papio ursinus*	✓	✓	✓	✓
Cheetah	*Acinonyx jubatus*	✓	✓	✓	✓
Common Duiker	*Sylvicapra grimmia*	✓	✓	✓	✓
Common Reedbuck	*Redunca arundinum*	✓	✓	✓	
Domestic Animal	-	✓	✓	✓	✓
Elephant	*Loxodonta africana*	✓	✓	✓	✓
Giraffe	*Giraffa camelopardalis*	✓	✓	✓	✓
Greater Bushbaby	*Otolemur crassicaudatus*	✓	✓	✓	✓
Hippopotamus	*Hippopotamus amphibious*	✓	✓	✓	✓
Honey Badger	*Mellivora capensis*	✓	✓	✓	✓
Impala	*Aepyceros melampus*	✓	✓	✓	✓
Insect spp.	-	✓	✓	✓	✓
Klipspringer	*Oreotragus oreotragus*		✓		
Kudu	*Tragelaphus strepsiceros*	✓	✓	✓	✓
Large-spotted Genet	*Genetta tigrina*	✓	✓	✓	✓
Leopard	*Panthera pardus*	✓	✓	✓	✓
Lesser Bushbaby	*Galago moholi*				✓
Lion	*Panthera leo*	✓	✓	✓	✓
Mongoose spp.	-	✓	✓	✓	✓
Monitor spp.	*Varanus spp.*	✓		✓	✓
Mountain Reedbuck	*Redunca fulvorufola*		✓		
Nyala	*Tragelaphus angasii*	✓	✓	✓	✓
Ostrich	*Struthio camelus*		✓		✓
Porcupine	*Hystrix africaeaustralis*	✓	✓	✓	✓
Red Duiker	*Cephalophus natalensis*	✓	✓	✓	✓
Rodent spp.	-			✓	
Samango Monkey	*Cercopithecus mitis*	✓			
Scrub Hare	*Lepus saxatalis*	✓	✓	✓	✓

Serval	*Felis serval*	✓	✓	✓	
Side-striped Jackal	*Canis adustus*	✓	✓	✓	✓
Spotted Hyena	*Crocuta crocuta*	✓	✓	✓	✓
Steenbok	*Raphicerus campestris*			✓	✓
Striped Polecat	*Ictonyx striatus*	✓		✓	
Suni	*Neotragus moschatus*			✓	✓
Vervet Monkey	*Cercopithecus pygerythus*	✓	✓	✓	✓
Common Warthog	*Phacochoerus africanus*	✓	✓	✓	✓
Waterbuck	*Kobus ellipsiprymnus*	✓	✓	✓	✓
White Rhinoceros	*Ceratotherium simum*	✓	✓	✓	✓
Black Wildebeest	*Connochaetes taurinus*	✓	✓	✓	✓
Plains Zebra	*Equus quagga*	✓	✓	✓	✓

Table A4.2: Model output from the generalized linear models conducted on cheetah spatiotemporal avoidance of other large predators.

Species	Intercept	Estimate	Std Error	t-value	P
Lion	9.025	0.019	0.249	0.074	0.941
Leopard	8.516	0.334	0.262	1.276	0.205
Spotted Hyena	8.834	-0.866	0.237	-0.365	0.716
African Wild Dog	9.339	-0.491	0.724	-0.679	0.51

Table A4.3: Model output from the generalized linear model looking at cheetah presence in response to other factors including intraguild predators, visibility and prey size. Bold entries indicate significance of $P < 0.05$.

	Estimate	Std Error	z	P
Visibility	0.525	0.374	1.405	0.160
Lion	0.354	0.486	0.729	0.466
Spotted Hyena	0.580	0.625	0.927	0.354
Leopard	1.031	0.756	1.364	0.173
African Wild Dog	**-0.891**	**0.412**	**-2.160**	**0.031**
Small Bodied Prey	0.477	1.168	0.409	0.683
Medium Bodied Prey	-16.750	295.604	-0.057	0.955
Large Bodied Prey	14.403	295.605	0.049	0.961
Extra-Large Bodied Prey	-0.535	0.407	-1.313	0.189

Table A4.4: Model output from the generalized linear model for cheetah abundance in response to other factors including intraguild predators, visibility and prey size. Bold entries indicate significance of $P < 0.05$.

	Estimate	Std Error	z	P
Intercept	-0.497	0.683	-0.728	0.466
Visibility	0.053	0.043	1.214	0.225
Lion	0.046	0.027	1.658	0.097
Spotted Hyena	-0.020	0.013	-1.546	0.122
Leopard	0.021	0.017	1.237	0.216
African Wild Dog	-0.003	0.056	-0.057	0.955
Small Bodied Prey	0.000	0.003	0.037	0.971
Medium Bodied Prey	0.000	0.001	-0.529	0.597
Large Bodied Prey	**0.004**	**0.001**	**3.208**	**0.001**
Extra-Large Bodied Prey	0.007	0.010	0.676	0.499

Table A4.5: Coefficient of overlap (Δ_4) between cheetah and other species using a Kolmogorov-Smirnov test (D) and the correlated P values. Bold entries indicate significance of $P < 0.05$.

Overlap with	Δ_4	D	P
Spotted Hyena	**0.47**	**0.33**	**< 0.0001**
Lion	**0.55**	**0.28**	**< 0.0001**
Leopard	**0.61**	**0.28**	**< 0.0001**
Medium Bodied Prey	**0.63**	**0.36**	**< 0.0001**
Extra-Large Bodied Prey	**0.65**	**0.29**	**< 0.0001**
Large Bodied Prey	**0.70**	**0.32**	**< 0.0001**
African Wild Dog	**0.72**	**0.13**	**0.01**
Small Bodied Prey	**0.77**	**0.20**	**< 0.0001**

Table A5.1: Odds ratio and P values obtained from Fisher's exact tests to assess differences in diet composition for cheetah with African wild dog present to cheetah without African wild dog present and cheetah with African wild dogs present to African wild dogs.

Prey Species	Cheetah - Cheetah		Cheetah - African Wild Dog	
	Odds Ratio	P Value	Odds Ratio	P Value
Buffalo	0	1	0	1
Waterbuck	0	1	0	1
Blue Wildebeest	0	1	0	1
Greater Kudu	1	1	1.3	1
Nyala	0.8	0.6	1.7	0.32
Warthog	0	1	0	1
Common Reedbuck	0	1	0	1
Impala	1.5	0.3	0.7	0.28
Bushbuck	0	1	0	1
Common Duiker	2.5	0.2	**10.2**	**0.03**