# Early Post-Release Movements, Prey Preference and Habitat Selection of Reintroduced Cheetah (*Acinonyx jubatus*) in Liwonde National Park, Malawi

by

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# Declaration

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# Abstract

Once widespread throughout Africa and southwestern Asia, the cheetah has disappeared from the majority of its historical range, making it Africa's most endangered large felid. Scenario modelling has demonstrated the survival of the cheetah is highly dependent on protected areas and woodland habitats. Reintroduction into protected areas of recoverable range has the potential to assist in the conservation of the species. However, sizeable knowledge gaps regarding the behavioural ecology of this species within its historical range remain and must be filled to assist in reintroduction success.

In 2017, African Parks in partnership with the Malawi Department of National Parks and Wildlife and the Endangered Wildlife Trust reintroduced seven cheetah into Malawi after a 20-year extirpation. This study aimed to provide an overview of the post-release movements, settlement and behavioural ecology of these reintroduced cheetahs to inform future pre- and post-release management techniques, long-term population management and assist in identifying other reintroduction sites in the country.

Post-release movements were assessed using data collected from five GPS collared founder individuals who were tracked for two years after their release into Liwonde National Park (LNP). Pre-release holding periods greater than 23 days were shown to not affect post-release movements. All cheetah demonstrated release site fidelity; however, males experienced more extensive post-release movements and settled later than females. Reintroduction success was defined for both the individual and the population level. An individual success rate of 57 % was recorded (80 % for GPS collared animals). All females birthed their first litter within four months post-release and, within two years, the population began to conform to demography levels documented in the source population. Therefore, the overall reintroduction was considered successful.

Using scat analysis and carcass observations, 13 prey species were recorded. Cheetah showed the highest preference for greater kudu (*Tragelaphus strepsiceros*) when considering prey populations. Four species comprised the bulk of cheetah diet, namely; kudu, impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*) and bushbuck (*Tragelaphus sylvaticus*), all of which experienced asymmetric predation across their demography. Asymmetric predation, coupled with increasing predator densities in the park, may have long-term implications for the demography of certain prey species. The spatial distribution of GPS collared cheetah appeared restricted, and individuals experienced high levels of both home range (95 % isopleths) and core area (50 % isopleths) overlap. All cheetah lacked exclusivity of both their home range and core areas (>10 % overlap). Intrasexual overlap in females may be indicative of den site selection. The high overlap of females may have long-term implications on both cub and adult male survival. Cheetah used all habitat types in LNP. However, females selected for open woodland habitat with moderate prey frequency of occurrence within their home range. All cheetah demonstrated a preference towards open floodplains with high prey frequency of occurrence for kill sites.

The success of this reintroduction is encouraging for continued range expansion of cheetah in Malawi. However, given the small founder population and low two-year recruitment rate, this population still requires intensive management. Genetic supplementation should be implemented to maintain genetic diversity. It is recommended that a metapopulation node for cheetah in Malawi is developed to assist in the long-term management of this population. It is further recommended that additional research into the effects of intraguild competition with cheetah in LNP is conducted once the full carnivore guild is restored.

# Opsomming

Die jagluiperd was voorheen wydverspreid oor Afrika en Suidwes-Asië, maar het grootliks verdwyn vanuit hul historiese verspreidingsgebied. Die gevolge is dat die jagluiperd vandag die mees bedreigde groot katsoort op die Afrika-kontinent is. Scenario-modellering het getoon dat die oorlewing van die jagluiperd hoogs afhanklik is van beskermde areas en bosveldhabitat. Hervestiging in beskermde areas van herkrygbare verspreidingsgebiede het groot potensiaal om die bewaring van dié spesie te ondersteun. Dit is egter nodig om kennisgapings aangaande die jagluiperd se gedragsekologie in die historiese verspreidingsgebied aan te vul om suksesvolle hervestiging in die hand te werk.

In 2017 het African Parks, in samewerking met die Malawi Departement van Nasionale Parke en Natuurlewe en die Trust vir Bedreigde Natuurlewe (EWT), sewe jagluiperds ná ’n 20-jaar lange afwesigheid in Malawi hervestig. Hierdie studie was gemik daarop om ’n oorsig te bied rakende jagluiperds se aktiwiteitspatrone, vestiging en gedragsekologie na vrylating, om toekomstige voor- en na-vrylatingsbestuurstegnieke en langtermyn populasiebestuur toe te lig, en om ander hervestigingsgebiede in die land te identifiseer.

Na-vrylatingsaktiwiteitspatrone was geassesseer deur verspreidingsdata vir vyf individue met GPS-halsbande oor ‘n periode van twee jaar na vrylating in die Liwonde Nasionale Park (LNP) in te samel. Voor-vrylatingswagperiodes langer as 23 dae het nie na-vrylatingsaktiwiteitspatrone beïnvloed nie. Al die jagluiperds het in die omgewing van die vrylatingsgebied gebly. Mannetjies het egter uitgebreide na-vrylatingsaktiwiteitspatrone getoon, en hulself later as die wyfies in ’n tuisgebied gevestig. Hervestigingssukses was omskryf op die individuele- sowel as die populasievlak. ’n Individuele suksessyfer van 57 % was aangeteken (80 % vir jagluiperds met halsbande). Binne vier maande na vrylating het alle wyfies hul eerste werpsel gehad, en binne twee jaar was die populasie-demografievlakke soortgelyk aan dié wat in die bronpopulasie aangeteken is. Gevolgtelik word die hervestiging in sy geheel as ’n sukses beskou.

Dertien prooispesies is met behulp van misanalise en karkasobservasie geïdentifiseer. Jagluiperddieet het hoofsaaklik uit vier prooispesies bestaan: koedoe (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), waterbok (*Kobus ellipsiprymnus*) en bosbok (*Tragelaphus sylvaticus*), met asimmetriese predasie oor elke prooispesie se demografie en ’n sterk dieetvoorkeur vir koedoe. Asimmetriese predasie tesame met toenemende roofdierdigtheid in die park kan langtermyn nagevolge inhou vir die demografie van sekere prooispesies. Die ruimtelike verspreiding van jagluiperds met GPS-halsbande blyk om beperk te wees, en individue het hoë vlakke van tuisgebied- (95% isoplete) en kernarea-oorvleueling (50% isoplete) ervaar. Alle jagluiperds het ’n gebrek aan eksklusiwiteit in die tuisgebied en kernareas ervaar (>10 % oorvleueling). Hoë ruimetlike oorvleueling by wyfies kan aanduidend wees van lêplekseleksie en kan langtermyn nagevolge vir die oorlewing van welpies en volwasse mannetjies inhou. Die jagluiperds het alle habitatsoorte in LNP gebruik, maar wyfies het egter oop bosveld met matige prooifrekwensie in hul tuisgebied verkies. Alle jagluiperds het ’n voorkeur getoon vir oop vloedvlaktes met hoë prooifrekwensie.

Hoë hervestigingssukses is aanmoedigend vir die voortdurende tuisgebiedsuitbreiding van jagluiperds in Malawi. Gegewe die klein stigterspopulasie en lae twee-jaar aanwinskoers, benodig hierdie populasie egter steeds intensiewe bestuur. Genetiese aanvulling moet geïmplementeer word om genetiese diversiteit te onderhou. Dit word aanbeveel om ’n metapopulasienodus vir jagluiperds in Malawi te ontwikkel om langtermynbestuur van dié populasie aan te vul. Dit word voorts aanbeveel dat addisionele navorsing rakende die effekte van interspesie-kompetisie met jagluiperds in LNP gedoen moet word soos wat algehele roofdiergetalle toeneem.

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# Preface

This thesis is presented as a compilation of six chapters. Chapter 1 and 2 provide an overall literature review and background on the study site. Chapters 3, 4 and 5 are introduced separately and are written as stand-alone manuscripts to assist in the future publication in peer-reviewed journals. Therefore, there is some repetition between these chapters and the introductory chapters. Chapter 6 is prepared for African Parks Liwonde (Pty) Ltd. to summarize major findings and provide recommendations towards the future management of the cheetah population in Liwonde National Park.

**Chapter 1.** **General introduction of the role of reintroductions and outline of project aims**

Introduction

**Chapter 2.** **Literature review of the study species.**

Focal Species: The Cheetah

**Chapter 3.** **Research Chapter**

Post-Release Movements and Early Establishment of a Reintroduced Cheetah Population

**Chapter 4.** **Research Chapter**

Prey Preference of Cheetah in Liwonde National Park, Malawi and a Comparison of Diet Composition Methodologies.

**Chapter 5.** **Research Chapter**

Spatial Distribution and Habitat Selection of Reintroduced Cheetahs in Liwonde National Park, Malawi

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Research Findings and Management Implications

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# Chapter One

## Introduction

### 1.1. General introduction

The global expansion of human populations has resulted in increased anthropogenic factors that have affected the natural world and consequently, caused a rapid decline in biodiversity (Brown *et al*., 2013; Kerr & Currie, 1995; McKee, Chambers & Guseman, 2013). The current human population growth rate is projected at 83 million people per year (United Nations, 2017). Over half of this growth is expected to occur within Africa; with 26 African nations predicted to double their population size by 2050 (United Nations, 2018). This continued growth in human populations across Africa is expected to increase anthropogenic pressures on biodiversity and protected areas (Cardillo *et al*., 2004; Crist, Mora & Engelman, 2017).

Across sub-Saharan Africa, areas of high biodiversity are consistent with high human densities (Blamford *et al*., 2001). These areas have therefore been marked by severe habitat conversion to peri-urban, rural and agricultural areas (Blamford *et al*., 2001). This leads to reductions in biodiversity and the potential for increased conflict between humans and animals. This is especially true for large carnivores, who's large home range requirements and dietary needs often place them in direct conflict with humans. Therefore, large carnivores are particularly sensitive to anthropogenic growth (Darimont *et al*., 2015; Woodroffe, 2000). Consequently, as the human population increases, anthropogenic pressures intensify, creating both biotic and abiotic challenges that negatively impact carnivores and biodiversity (Šálek, Drahníková & Tkadlec, 2014).

Large carnivores are important ecosystem drivers as they promote healthy biodiversity by exerting top-down regulatory pressures on herbivores and meso-predators (Atkins *et al*., 2019; du Preez *et al.*, 2017; Owen-Smith & Mills, 2008). However, despite their ecological, economic and social value, large carnivore populations are in decline globally, with an average of 53 % of their historical range now lost (Ripple *et al.*, 2014). Subsequently, 59 % of large carnivore species are now threatened with extinction (Ripple *et al.*, 2014). Currently, all three of Africa's large felid species are globally assessed as "Vulnerable" (Bauer *et al*., 2016; Durant *et al*., 2015; Stein *et al*., 2016). However, recent data suggests the uplisting of the cheetah (*Acinonyx jubatus*) to "Endangered" due to their susceptibility to rapid population decline and their recent range contraction (Durant *et al.*, 2017). While decline of all three of Africa's large felids can be attributed to numerous factors, a large proportion of threats are due to anthropogenic disturbances, including; habitat destruction, habitat fragmentation, poaching and both direct and indirect persecution (Durant *et al.*, 2017; Winterbach *et al*., 2013; Woodroffe, 2000; Woodroffe & Ginsberg 1998).

One method of combatting biodiversity losses is through the development of protected areas (PAs), which are expected to be crucial to the future of biodiversity conservation within Africa (Wegmann *et al.*, 2014). Large PAs can maintain genetically viable, self-sustaining, populations, while smaller PAs are dependent on their connectivity to maintain populations in the long term (Cantú-Salazar & Gaston, 2010; Minin *et al*., 2013). The perceived size, large or small, and subsequent value of each PA is based on range size of each species; therefore, connectivity between any sized PA is fundamental for large scale biodiversity conservation. The connectivity between PAs forms the basis for metapopulation dynamics, as it allows individuals to move through a matrix, the portion of the landscape in which suitable patches or corridors are embedded (Akcakaya, Mills & Doncaster, 2015; Minin *et al*., 2013). Preserving PA connectivity is fundamental to metapopulation dynamics, as it helps facilitate immigration from a source population to "rescue" a declining or sink population, thus maintaining overall population persistence (Wegmann *et al*., 2014). Therefore, well-connected smaller PAs can provide long-term conservation benefits comparable to large PAs (Akcakaya *et al*., 2015).

Conserving connectivity between PAs is especially important for Africa's large carnivores; lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah, spotted hyena (*Crocuta crocuta*) and African wild dog (*Lycaon pictus*). These species have large home ranges that exceed the size of many PAs and are highly persecuted within the human-dominated landscape that commonly constitutes the matrix between PAs (Marker & Dickman, 2004; Minin *et al*., 2013; Swanepoel *et al*., 2012; Thorn *et al.*, 2015). While the matrix is often a viable habitat, anthropogenic threats are increased in these areas, thereby negatively affecting dispersal and population growth which, can essentially isolate populations (Barton *et al*., 2019; Ricketts, 2001; Williams *et al.*, 2017). It has therefore been suggested that many of the remaining carnivore populations in Africa are dependent on the protection of dispersal routes; leopard in South Africa (Swanepoel *et al*., 2012) and Cameroon (Toni & Lode, 2013), African wild dog in South Africa (Minin *et al*., 2013) and lion in Tanzania and Kenya (Dolrenry *et al*., 2014). In each study, adaptive management strategies targeting increased human tolerance of carnivores were recommended for the protection of dispersal routes, as many are already located within human-dominated landscapes. However, as human population expansion continues, intensified habitat augmentation and fragmentation within the matrix is anticipated, thereby further decreasing dispersal success. Human-mediated dispersal through translocations is developing into a recommended tool for the conservation of large carnivores within PAs (Briers-Louw, Verschueren & Leslie, 2019; Buk *et al*., 2018; Minin *et al*., 2013).

Translocations have already taken place for many of Africa's large carnivores and have become a common management practice in South Africa (Buk *et al.*, 2018; Davies-Mostert, Mills & Macdonald, 2015; Hayward *et al.*, 2007a; Hayward *et al*., 2007b; Hunter, 1998; Minin *et al*., 2013). Human-managed metapopulations have also been developed as a longer-term conservation initiative on smaller fenced PAs where natural movements are restricted. African wild dog and cheetah metapopulations developed across South Africa have grown to consist of 250 individuals in 28 packs (Endangered Wildlife Trust, 2018), and 325 individuals on 54 reserves (Boast *et al.*, 2018) respectively. These numbers are substantial considering that African wild dog are classified globally as "Endangered" and cheetah as "Vulnerable", with wild populations of both species estimated below 8,000 individuals worldwide (Durant *et al*., 2015; Woodroffe & Sillero-Zubiri, 2012). As metapopulations increase, additional translocations in the form of reintroductions can take place, allowing for range expansion. For example, reintroductions have recently been conducted with the African wild dog in

Gorongosa National Park, Mozambique (Endangered Wildlife Trust, 2018) and cheetah in Liwonde National Park, Malawi (Sievert, Reid & Botha, 2018).

## 1.2. An overview of reintroductions

Translocations are the deliberate movement of individuals from one location to another for release (IUCN/SSC, 2013). Not all translocations are conducted solely for conservation purposes, with many taking place to help mitigate human-wildlife conflict or to increase photographic tourism (Buk *et al.*, 2018; Sillero-Zubiri & Switzer, 2004; Weise *et al.*, 2015a; Weise *et al.*, 2015b). Conservation translocations are therefore separately described as a translocation that yields a measurable conservation benefit for a population, species or ecosystem (IUCN/SSC, 2013). Conservation translocations can take place in two forms, reinforcement and reintroduction. Reinforcements act to enhance the viability of an existing population whereas, reintroductions aims to re-establish an organism within its indigenous range (IUCN/SSC, 2013).

Reintroductions have taken place across most taxa, including *Reptilia* (Sites, 2013), *Amphibia* (Harding, Griffiths & Pavajeau, 2015) and *Aves* (Jamieson, 2011). However, large predators are amongst the most frequently reintroduced organisms (Seddon, Soorae & Launay, 2005). The frequency at which large carnivore reintroductions take place is attributed to their ability to restore ecosystem function (Sinclair, Mduma & Brashares, 2003), their financial benefits to ecotourism (Hayward *et al.*, 2007b) and, their susceptibility to local extinction from naturally low densities and anthropogenic impacts (Dickman *et al.*, 2015; Woodroffe & Ginsberg 1998). Despite the frequency of large carnivore reintroductions, their space and prey requirements pose an increased difficulty in the reintroduction process when compared to smaller species (Stoskopf, 2012).

Prior to the reintroduction of any species, numerous ecological and socio-economic considerations need to be addressed, most important being the initial cause of extirpation (Stoskopf, 2012). By addressing past and recent changes in the targeted ecosystem and surrounding area, researchers and managers can increase the likelihood of a successful reintroduction (Stoskopf, 2012). Regardless, evaluating the success of reintroduction projects has proven difficult, and definitions of success are often considered arbitrary when applied to large carnivore reintroductions. For example, reintroduction success has often been defined as when a self-sustaining population reaches over 500 individuals (Griffith *et al.*, 1989), yet few protected areas are large enough to accommodate carnivore populations of that size. Therefore, the reintroduction success of large species in small areas has been re-defined as the first wild-born generation or a three-year breeding population with a positive natural recruitment rate (Hayward *et al.*, 2007a). Nonetheless, these alternative definitions neglect long-term management considerations that are incorporated into reintroductions on small reserves, such as, subsequent introductions to maintain genetic stability for long-term sustainability of the population (Buk *et al*., 2018).

Regardless, successful reintroductions of large carnivores have taken place, and the most well-known include the gray wolf (*Canis lupus*) in Yellowstone National Park, USA (Ripple & Beschta, 2012), Eurasian lynx (*Lynx lynx*) across Europe (Breitenmoser, Breitenmoser-Wursten & Capt, 1998; Kramer-Schadt, Revilla & Wiegand, 2005) and African wild dog in South Africa (Davies-Mostert *et al.*, 2015). These reintroductions have resulted in the increase of ecological drivers and thus have facilitated self-perpetuating biologically diverse ecosystems. While these case studies are encouraging, long-term monitoring and adaptive management are recommended for all reintroductions to aid in project success (Buk *et al*., 2018; IUCN/SSC, 2013; Hayward & Somers, 2009).

### 1.2.1. Reintroductions as a tool for cheetah conservation

The first cheetah translocations took place during the 1960s and 1970s in protected areas in Namibia and South Africa, to reintroduce and reinforce existing populations (Buk *et al.*, 2018). The vast majority of these translocations consisted of releasing cheetah into closed-fenced systems in South Africa (Buk *et al.*, 2018). In the 1990s, the frequency of cheetah translocations increased in response to a change in South African legislation permitting a user right of wildlife to landowners, meaning landowners possessed the right to sell animals inhabiting their land (Taylor, Lindsey & Davies-Mostert, 2015). Granting landowners the ability to sell and buy wildlife coupled with an upsurge in ecotourism resulted in an increase in the number of private wildlife reserves in South Africa, which lead to an increase in cheetah translocations for tourism purposes (Buk *et al.*, 2018).

Approximately 186 Namibian and 157 South African cheetah, deemed problem animals, were caught from free-roaming populations and placed into small fenced reserves in South Africa between 1965-2009 (Buk *et al.*, 2018). Unfortunately, these 343 cheetah decreased to a population of 281 in fenced reserves by 2009. This population decrease was attributed to multiple factors, including; inadequate fences, inadequate management resulting in inbreeding and prey collapse and, lion unsavvy cheetah and high lion densities in certain areas (Buk *et al.*, 2018). The practice of using free-roaming cheetah to supplement populations in fenced reserves began to raise concerns that continuous translocations would transform Namibia, South Africa and subsequently, Botswana and Zimbabwe’s free-roaming cheetah populations into sink populations (Lindsey *et al.*, 2009). While increased regulations halted the capture and translocation of free-roaming cheetah from Namibia in 1998, it took until 2009 for similar regulations to be put in place in South Africa (Buk *et al.*, 2018).

Although a cheetah metapopulation strategy was proposed in 1994, the termination of translocations and supplementations from free-roaming populations renewed its necessity. In 2011, the Cheetah Metapopulation Project (CMP) was formally implemented by the Endangered Wildlife Trust (EWT) to ensure the development of a genetic and demographically viable cheetah population on South Africa’s small fenced reserves with minimal outside supplementations (Buk *et al.*, 2018). While the success of cheetah reintroductions on each individual fenced reserve has not been established, the CMP has increased from 241 cheetah on 41 reserves in 2011, to 325 individuals on 54 reserves in 2017, with minimal outside supplementation (Boast *et al.*, 2018). This success, along with increased protected area security through the work of African Parks (AP) and the Malawi Department of National Parks and Wildlife (DNPW), has allowed for the expansion of the metapopulation outside of South Africa. The first reintroductions took place in Liwonde National Park, Malawi between 2017 and 2018 and in Majete Wildlife Reserve in 2019 (African Parks, 2019; Sievert *et al.*, 2018).

Historically widespread throughout Africa and southwestern Asia, the cheetah has disappeared from vast tracks of its historical range (Durant *et al.*, 2017). Thirty-three remnant cheetah populations are now scattered across 32 of their 53 original range states, comprising 9 percent of their historical distribution (Durant *et al.*, 2015; Durant *et al*., 2017). In 1975 Malawi's cheetah population was estimated at 50 individuals spread across two national parks, however by 1989 this population was confined to Kasungu National Park and believed to be mainly transient with Zambia's Luangwa Valley (Gros, 1996; Myers, 1975). Continued reduction of habitat and prey base coupled with the depletion of the Luangwa Valley's cheetah population prevented any re-colonization events in Malawi, resulting in the full extirpation of the cheetah by the early 1990s (Gros, 1996; Purchase & Purchase, 2007). The partnership between AP and DNPW has resulted in an increase in financial contributions to AP managed protected areas in Malawi. The increased funding has facilitated law enforcement reforms and the construction of perimeter fences. AP Malawi's protected area network allowed for the re-establishment of cheetah in Malawi. Due to an ample prey base, Liwonde National Park was the first protected area to undertake this endeavor.

Cheetah display suitable characteristics for successful translocation, including their capacity to tolerate a wide range of environments and consume a broad range of small to medium-sized prey species (Boast *et al.*, 2018). Therefore, cheetah reintroductions have the potential to increase their current distribution into recoverable historical range, as well as the ability to improve connectivity to isolated populations and boost genetic diversity (Boast *et al.*, 2018). The CMP success is strongly attributed to effective translocation planning, implementation and long-term monitoring of translocated individuals. However, it is imperative that long-term monitoring and research on cheetah reintroductions continues to better adapt management strategies and refine future pre- and post-release techniques which will increase the success of future reintroductions. Furthermore, information collecting during monitoring may assist in the continued range expansion of cheetah by identifying suitable habitat and potential threats to reintroduced populations.

## 1.3. Study area

### 1.3.1. Location and history

Liwonde National Park (LNP) covers an area of 548 km$^2$ and is located in the Upper Shire Valley in the Southern Region of Malawi (Figure 1.1). Located 53 km northeast from the colonial capital of Zomba, LNP was a sport hunting ground for European planters and administrators from 1920-1969 (Morris, 2006; Taylor, 2002). Historical sport hunting and the rapid increase in the human population are thought to have resulted in the decline of large mammals. In response to the decline of wildlife, LNP was declared a controlled shooting area in 1962, updated to a game reserve in 1969, and by 1973 gazetted into a National Park (Morris, 2006). In 1977 it was then extended to include a corridor that linked LNP and Mangochi Forest Reserve, this allowed for an increased flow of wildlife in the area, especially elephants (*Loxodonta africana*). Finally, in 1978 LNP was formally opened to the public for game-viewing (Morris, 2006).

The increase in LNP's protection status over the 1970s, however, did not stem the loss of wildlife. By 1987 over 1,000 people were residing inside the LNP boundary, and the extirpation of buffalo (*Syncerus caffer*), plains zebra (*Equus burchelli*), eland (*Tragelaphus oryx*), black rhino (*Diceros bicornis*), hartebeest (*Alcelaphus lichtensteini*) and African wild dog had taken place (Morris, 2006; Taylor, 2002). As the human population surrounding the park continued to expand, encroachment and human-wildlife conflict increased (Munthali & Mkanda, 2002). In an attempt to halt human-wildlife conflict, the government of South Africa donated funds for a solar-powered fence (Morris, 2006). However, the fence was quickly vandalized to create wire-snares for poaching, and as a result, human-wildlife conflict remained high with seven elephants, 215 hippopotami (*Hippopotamus amphibius*) and 31 people killed in recorded conflict events between 1989 and 1992 (Morris, 2006; Taylor, 2002).

Loss of human life and crops along with the decrease in mammal numbers in the park led to appeals by local communities for the degazetting of LNP (Munthali & Mkanda, 2002). In the 1990s the Frankfurt Zoological Society granted assistance to the park and funded the Liwonde Law Enforcement Project. This project increased security and allowed for the reintroduction of two black rhinos from Kruger National Park, South Africa (Knight & Kerley, 2009), followed by the reintroduction of buffalo, roan (*Hippotragus equinus*), hartebeest, plains zebra, and eland from Kasungu National Park, Malawi (Munthali & Mkanda, 2002; Taylor, 2002). Regardless, increased human pressure surrounding LNP resulted in years of extensive poaching, illegal fishing, and human-wildlife conflict (Morris, 2006). By the early 2000s, LNP's lion, leopard, and vulture populations had been extirpated (P. Taylor pers. comm.; Sievert *et al.*, 2018).

In 2015, the AP assumed management of LNP in partnership with DNPW. The partnership saw an increase in financial contributions which allowed for the overhauling of law enforcement and the construction of a new perimeter fence along the boundary (Sievert *et al.*, 2018). Increased management further led to the removal of 36,000 snares, the reduction in elephant and rhino poaching, the translocation of 1,329 animals for restocking other Malawian reserves, the return of five vulture species, the supplementation of the remnant black rhino population and the reintroduction of lion and cheetah (African Parks, 2018; Sievert & Reid, 2018; Sievert *et al.*, 2018).

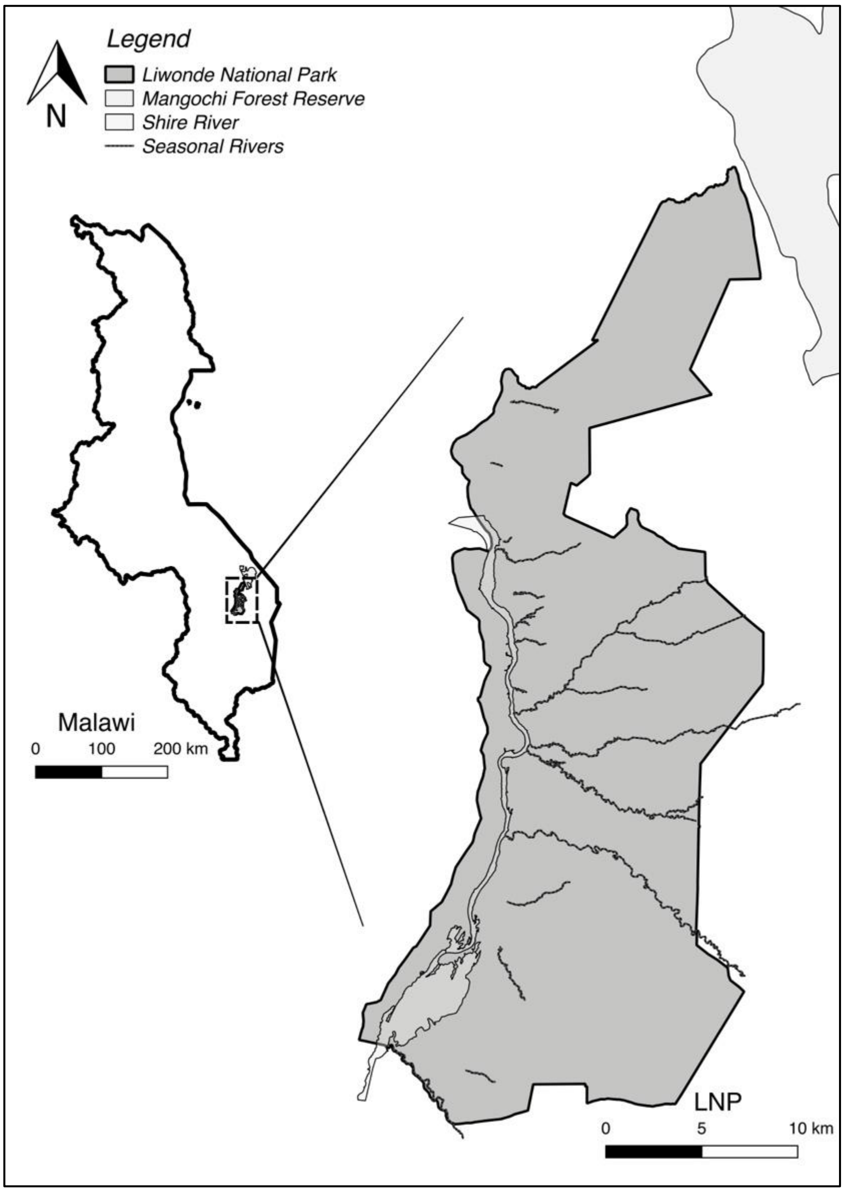

**Figure 1.1.** Map of Liwonde National Park depicting the Shire River as well as the park's location in Malawi and in reference to Mangochi Forest Reserve.

### 1.3.2. Watercourses

The northwestern park boundary consists of Lake Malombe, which flows into the Shire River at its southern point. The Shire River is the sole perennial river and the dominant feature of LNP. The Shire River splits the western side of LNP from the eastern side. The eastern side of LNP contains the bulk of the park's area, whereas, the western bank comprises a 2 km wide buffer zone created to enhance the protection of the Shire River (Morris, 2006).

In the wet season, the Shire River creates extensive lagoons and marshland along the floodplains which border the river on both the eastern and western sides of LNP (Bhima & Dudley, 1997). Additionally, the park has a multitude of seasonal rivers and streams that flow from the east into the Shire River; most notable is the Likwenu River which demarcates the southernmost boundary of the park. Other major seasonal rivers are the Kombe, Mwalasi, Namadanje, Nongondo, Namatunu, Ntangi, Masanje and Mpwapwata all of which maintain small pockets of water into the mid-dry season (pers. obs.). By September only small pockets of water remain scattered around the park, of these, four are borehole pumped artificial waterholes, two located in the southernmost section of the park and two in the centre of the park (Sievert & Reid, 2018).

### 1.3.3. Climate

LNP has distinct wet and dry seasons, with an annual rainfall of 700-1400 mm (Bhima & Dudley, 1996). The average precipitation is 944 mm per year, with the majority of rainfall occurring between December and March. Additional rainfall often occurs in late November and early April, with June to October being dry months. Mean high temperatures range from $28^{o}$ in July to $40^{o}$ C in November (Bhima & Dudley, 1996).

### 1.3.4. Topography and altitude

LNP is generally described as relatively flat with a slight slope rising from the Shire River to the eastern boundary (Mzumara, Perrin & Downs, 2018). There are seven distinctive hills found in the park; the two Chioli Hills in the north, the two Naifulu Hills located near the eastern boundary, Katuengusi and Nainyani Hills located in the south, and Chinguni Hill located in the southernmost section of the park. Altitude ranges from 474 m to 921 m above sea-level, with a mean altitude of 500 m (Mzumara *et al.*, 2018). LNP's northern boundary consists of an escarpment, which makes up the 6 km unfenced corridor to Mangochi Forest Reserve. AP recently assumed management of Mangochi Forest Reserve and has begun fencing the area in conjunction with the LNP fenceline. The expansion of the park fence to include Mangochi Forest Reserve will expand the LNP protected system by 375 $km^2$ to a total of 923 $km^2$ (C. Reid, pers. comm.).

### 1.3.5. Vegetation and soil

LNP is part of the southern Rift Valley ecosystem and consists mainly of dry deciduous woodland (Dudley, 2004). The dominant tree in the park is *Colophospermum mopane*, with the mopane woodland complex occupying roughly 74 % of the park (Dudley, 2004; Mzumara, Perrin & Downs, 2015). Grasslands, floodplains, forest thickets, and mixed woodlands are interspersed throughout the park occurring mostly in north-south bands that run parallel to the Shire River (Dudley, 2004).

Floodplain grasslands make up 3 % of the park, the majority of which lies in the southern section of LNP. Scattered along the floodplain grasslands are *Hyphaene* palm savannahs that developed due to the fossil alluvial sand deposits (Dudley, 2004). On the isolated hillsides, the dominant vegetation belongs to the *Combretum* genera (Dudley, 2004).

Overall, 1006 vascular plant species have been identified with an estimated 1200 species present (Dudley, 2004). The soil is graded at medium to high nutrient status which has resulted in maximum tree height being 30 % higher than that of the same species in Ruaha National Park and Selous National Park, Tanzania (Dudley, 2004).

### 1.3.6. Fauna

The 2018 aerial survey observed 16646 animals across 25 species, including 17 ungulate species (Sievert & Reid, 2018; Appendix 1.A). The dominant herbivore species in the park are waterbuck (*Kobus ellipsiprymnus*) and impala (*Aepyceros melampus*). Herbivore distribution in LNP is highly dependent on water availability; therefore, dry season distribution is highest on the Shire River floodplain with densities reaching 103 animals/km$^2$ (Sievert & Reid, 2018). The highest diversity of herbivores can be found on the eastern side of the Shire River. In 2017, small populations of buffalo, sable (*Hippotragus niger*), hartebeest and plains zebra were relocated to the western side of the Shire River as part of a restoration effort for this isolated habitat (Sievert & Reid, 2018). Three species of large carnivore are now present in the park; spotted hyena, which has been present consistently since LNP was gazetted, as well as cheetah and lion which were recently reintroduced after extirpation (Sievert & Reid, 2018; Appendix 1.B).

LNP is classified as an Important Bird Area; over 380 species of birds have been recorded in the park (BirdLife International, 2011). It is especially important for wetland and migratory birds. In 2016, 1345 wetland birds consisting of 42 different species were counted along the LNP section of the Shire River (CAWS, 2016). Furthermore, the sections of the Shire River and Lake Malombe that are protected by the park are considered important breeding grounds for over 40 different species of fish, including IUCN Red Listed species (Kapute, 2018).

## 1.4. Study animals

A founder population of seven cheetah was reintroduced into LNP between June 2017 and February 2018 (Table 1.1). Of these seven, five were fitted with Pinnacle LITE global positioning system (GPS) satellite collars (Sirtrack, Hawkes Bay, New Zealand) and one with a very high frequency (VHF) tracking collar (African Wildlife Tracking, Pretoria, South Africa). GPS collars were programmed to collect daily GPS locations based on monitoring needs, with each collar collecting a minimum of three points a day (Table 1.2). The social structure of LNP's cheetah has fluctuated over the study period based on births and deaths. A total of 23 cheetah were identified from June 2017 until July 2019, with four birthing events and six mortalities recorded.

**Table 1.1.** The biological and translocation details of reintroduced cheetah in Liwonde National Park, Malawi.

| ID Code | Sex | Estimated Age at Translocation (months) | Period in Boma (days) | Release Date [event] | Known Birthing Events [# of cubs] | Translocation Distance (km) | Origin |
|---|---|---|---|---|---|---|---|
| **CM1**[a] | M | 23 | 31 | 12-06-17 [2] | N/A | 1450 | Phinda Private Game Reserve, SA |
| **CM2** | M | 77 | 23 | 05-06-17 [1] | N/A | 1277 | Welgevonden Game Reserve, SA |
| **CM3**[b,c] | M | 22 | 58 | 07-02-18 [4] | N/A | 1105 | SanWild Wildlife Sanctuary, SA |
| **CM4**[b,c] | M | 22 | 58 | 07-02-18 [4] | N/A | 1105 | SanWild Wildlife Sanctuary, SA |
| **CF1**[a] | F | 22 | 31 | 12-06-17 [2] | 1 [3] | 2140 | Mountain Zebra National Park, SA |
| **CF2** | F | 25 | 32 | 13-06-17 [3] | 2 [4, 6] | 2252 | Amakhala Game Reserve, SA |
| **CF3**[c] | F | 22 | 58 | 07-02-18 [4] | 1 [3] | 1105 | SanWild Wildlife Sanctuary, SA |

[a] Paired as sub-adults in the boma and released together. [b] Male coalition (full siblings). [c] Released as a sibling coalition.

## 1.5. An overview of post-release monitoring methodology

Since the release in LNP, the cheetah have been monitored closely following guidelines set by the IUCN for reintroductions and translocations (IUCN/SSC, 2013). Park management implemented an active adaptive monitoring approach (*see* IUCN/SSC, 2013) for this reintroduction; therefore, monitoring strategies were adapted over the course of the study. GPS collars were scheduled to collect a minimum of three GPS points per day, and this scheduling was increased during birthing events or for injured animals. GPS points were also investigated for evidence of kills, and this was conducted *ad libitum* with an emphasis on females with dependent cubs, to assist in evaluating their cub rearing success. Regardless, efforts were made to investigate points evenly across each individual.

Radio-tracking took place a minimum of twice a week, with attempts of one observation per cheetah per week. An R-1000 telemetry receiver (Communication Specialists Inc, California, USA) attached to a flexible H-Type antenna (RA-23K VHF antenna; Telonics, Arizona, USA) was used to locate each animal during radio-tracking. The signal strength ranged from about 500 m to 1.5 km depending on vegetation structure and season. The success of each radio-tracking event was therefore dependent on vegetation as well as each individual's degree of habituation. Opportunistic sightings outside of scheduled radio-tracking events were also recorded. All successful sightings were recorded with the GPS location and the general behaviour (*e.g.*, resting, vigilant, travelling, feeding) of the animal upon initial sighting. All GPS collars were replaced prior to battery depletion, and animals were re-fitted with VHF collars (Sirtrack, Hawkes Bay, New Zealand) modified with a Long Range (LoRa) Geolocation transmitter (Smart Parks, Rotterdam, Netherlands). Re-fitted collars weighed 359 g and allowed for continued weekly observation attempts. Over the course of this study, 16 cubs were born, of which six reached independence during the study. Three of the six cubs to reach independence were fitted with Sirtrack VHF collars modified with LoRa Geolocation transmitters to allow for monitoring during dispersal and home range establishment (Table 1.2).

Den sites were checked within the first two weeks of denning to assess litter size and cub survival. Dens were checked by one person while the female was hunting, and no handling of cubs took place to minimize disturbance to the denning process (Laurenson & Caro, 1994)

**Table 1.2.** Data collection specifications (June 2016-July 2019) for cheetah reintroduced into Liwonde National Park, Malawi. Only one male from each coalition was fitted with a VHF collar.

| ID code | Social Grouping | Collar Type | Transmission Success Rate (%) | No. Transmission Days | No. Locations | No. Sightings | No. Kills Identified |
|---|---|---|---|---|---|---|---|
| **CM1** | Single Male | GPS/VHF | 54.9 | 297 | 594 | 26 | 12 |
| **CM2** | Single Male | GPS/VHF | 66.3 | 520 | 2157 | 113 | 49 |
| **CM3** | Two Male Coalition | VHF | N/A | N/A | N/A | 19 | 2 |
| **CF1** | Breeding Female | GPS | 97.2 | 759 | 3747 | 45 | 52 |
| **CF2** | Breeding Female | GPS/VHF | Unknown | 508 | 1633 | 79 | 87 |
| **CF3** | Breeding Female | GPS | 95.0 | 307 | 1032 | 16 | 21 |
| **Ch1*** | Two Male Coalition | VHF | N/A | N/A | N/A | 27 | 2 |
| **Ch3*** | Non-breeding Female | VHF | N/A | N/A | N/A | 24 | 1 |
| **Ch6*** | Two Male Coalition | VHF | N/A | N/A | N/A | 5 | 1 |

* Individuals born in LNP that reached independence and were subsequently collared.

## 1.6. Aims and objectives

The overall aim of this research was to provide an accurate overview of the behavioural ecology of reintroduced cheetah in LNP and increase our understanding of cheetah spatial and foraging ecology in woodland habitats. Therefore, the primary objectives of this study were:

1. Assess early post-release movements of cheetah in LNP.
    a. *By determining distances travelled by each cheetah during post-release exploration.*
    b. *By investigating what factors affect post-release exploration.*
    c. *By defining if and when home range development occurred.*
2. Examine the prey preference of the reintroduced cheetah population and compare methodologies for this process.
    a. *By determining which prey species are avoided and which are selected for in LNP.*
    b. *By determining the best data collection methodology for investigating diet composition of large carnivores in LNP based on methods employed.*
3. Determine the spatial distribution and habitat selection of the reintroduced cheetah population in LNP.
    a. *By comparing home range size and percent overlap to that of other study areas.*
    b. *By determining habitat selection within the home range.*
    c. *By determining kill site habitat selection.*

The results of this research will be used to adapt management strategies and refine future pre-release management to increase the success of future reintroductions. By identifying suitable habitat and potential threats to reintroduced populations, this study will inform the continuing re-establishment of cheetah in Malawi. Furthermore, providing scientific data to park management will allow for the development of informed carnivore management strategies. This research will, therefore, fill a gap in the knowledge of behavioural ecology of cheetah in Malawi, a historical range encompassed by woodland habitat, where no previous research was conducted prior to extirpation.

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## 1.8. Appendices

**Appendix 1.A.** Game census numbers from the 2018 Liwonde National Park Aerial Survey. Obtained from Sievert and Reid (2018).

| **Common name** | **Scientific name** | **Total Count** |
|---|---|---:|
| Buffalo | *Syncerus caffer* | 940 |
| Bushbuck | *Tragelaphus scriptus* | 289 |
| Bushpig | *Potamochoerus larvatus* | 5 |
| Crocodile | *Crocodylus niloticus* | 377 |
| Common Duiker | *Sylvicapra grimmia* | 61 |
| Eland | *Tragelaphus oryx* | 109 |
| Elephant | *Loxodonta africana* | 597 |
| Sharpe's Grysbok | *Raphicerus sharpei* | 1 |
| Hippopotamus | *Hippopotamus amphibius* | 1978 |
| Impala | *Aepyceros melampus* | 3089 |
| Klipspringer | *Oreotragus oreotragus* | 3 |
| Kudu | *Tragelaphus strepsiceros* | 315 |
| Lichtenstien's Hartebeest | *Alcelaphus lichtensteinii* | 43 |
| Oribi | *Ourebi ourebi* | 13 |
| Porcupine | *Hystrix cristata* | 1 |
| Southern Reedbuck | *Redunca arundinum* | 176 |
| Roan | *Hippotragus equinus* | 8 |
| Sable | *Hippotragus niger* | 754 |
| Warthog | *Phacocherus africanus* | 1066 |
| Waterbuck | *Kobus ellipsiprymnus* | 6673 |
| Plains Zebra | *Equus quagga* | 58 |

**Appendix 1.B.** Yearly large carnivore population estimates for LNP, Malawi.

| **Year** | **Species** | | | |
|---|---|---|---|---|
| | **Spotted Hyena** | **Cheetah** | **Lion** | **Leopard** |
| **2017** | 12 | 10 | 0 | 0 |
| **2018** | 17 | 10 | 9 | 0 |
| **2019** | 13 | 17 | 9 | 0 |
| **Notes** | Population estimates determined through targeted camera trapping throughout the year. | Population known not estimated. | Population known not estimated. | Population estimated from camera trapping and reports. |

# Chapter Two

## Focal Species: The Cheetah (*Acinonyx jubatus*)

### 2.1. Distribution

Historically widespread throughout Africa and southwestern Asia, cheetah (*Acinonyx jubatus*) have disappeared from the majority of their historical range (Durant *et al.,* 2017). Thirty-three remnant cheetah populations are now scattered across 32 of their 53 range states, comprising 9 % of their historical distribution (Durant *et al.,* 2015, Durant *et al*., 2017). In Asia, cheetah distribution is now limited to the deserts of Iran with an estimated population size of 40, while African population strongholds remain in eastern and southern Africa with an estimated 2290 and 4297 individuals, respectively (Durant *et al*., 2017).

In southern Africa cheetah populations occur across Namibia, Botswana, South Africa and Zimbabwe with remnant populations in Mozambique, Zambia and Angola (Durant *et al.,* 2017; Purchase *et al.,* 2007). During the 2007 and 2017 population assessments, Malawi was the only southern African range state where cheetah were extirpated (Durant *et al*., 2017; Purchase *et al.*, 2007). Cheetah were present in Malawi in 1975, with an estimated population of 50 individuals spread across two national parks (Gros, 1996). However, by 1989 this population was confined to Kasungu National Park and believed to be mainly transient with neighbouring Zambia (Gros, 1996; Myers, 1975). Recommendations were made to maintain a protected corridor between Zambia's Luangwa Valley and Malawi to allow for the re-colonization of cheetah in Malawi's northwestern parks (Gros, 1996). Unfortunately, increased human population growth resulted in the decrease of habitat and prey base within Malawi's protected areas (PAs) and the unprotected corridor with Zambia (Purchase & Purchase, 2007). The reduction of habitat and prey base, along with the depletion of the Luangwa Valley cheetah population is believed to have prevented any population rescue events in Malawi, resulting in the full extirpation of cheetah from Malawi by the early 1990s (Gros, 1996; Purchase & Purchase, 2007).

### 2.2. Morphology

The cheetah is one of Africa's iconic carnivores due to its extreme speed, reaching up to 110 km/h within a few seconds (Marker & Dickman, 2003). This impressive morphological ability is a trade-off for overall bulk, made clear in its anatomy when compared to other large carnivores. The cheetah has an aerodynamically efficient frame with long foot and leg bones that allow for increased speed, and their eyes are positioned for maximum binocular vision and nostrils are enlarged to increase oxygen flow (Ewer, 1973). There are currently five debated sub-species of cheetah (Durant *et al.,* 2017). However, few thorough genetic or morphological comparisons have been conducted. Genetic analysis that has occurred on subspecies has shown a recent divergence (4400-6100 years ago) between the African and Asian subspecies (O'Brien *et* al., 2017). Morphological measurements appear to vary regionally, which has been attributed to resource availability (Boast *et al*., 2013; Marker & Dickman, 2003), and while sexual dimorphism is present in the cheetah, it also remains understudied. Therefore, body mass ranges from 35-65 kg and height ranges from 70-90 cm (Estes, 2012).

## 2.3. Reproduction and cub survival

Female cheetah become reproductively active around 26-36 months of age (Bissett & Bernard, 2011; Kelly *et al*., 1998; Laurenson, Caro & Borner, 1992; Marker *et al.*, 2003) and have a litter of one to eight cubs after a 90 – 95 day gestation period (Bissett & Bernard, 2011; Estes, 2012). Cubs are altricial and are born in a den where they remain for 51-65 days (Laurenson, 1993). Upon emergence from the den, cubs remain dependent on their mothers until 14-20 months of age, at which point they separate and form an adolescent group (Bissett & Bernard, 2011; Laurenson, 1993; Marker *et al.*, 2003).

An early study examining genetic viability in the cheetah hypothesized that genetic monomorphism resulted in breeding difficulties and high juvenile mortality (O'Brien *et al.*, 1985). Laurenson, Wielebnowski and Caro (1995) later disputed these assertions citing data from three captive breeding institutions in which 78.8 % of cub mortality was attributed to extrinsic factors and 3.8 % to congenital defects. While the paucity of overall genome variability poses conservation challenges for the cheetah, it is unlikely rate-limiting; otherwise the species would not have expanded in range and population size following their genetic bottleneck, which occurred 10-thousand years ago (Menotti-Raymond & O'Brien, 1993; O'Brien *et al.*, 2017). Many cases of breeding depressions in captive cheetah have since been attributed to the species susceptibility to asymmetric reproductive ageing, which, moderates reproductive performance and further reduces genetic variability in captive populations (Ludwig *et al.*, 2019; Wachter *et al.*, 2011).

Cub survival in wild cheetah populations appears to be mostly moderated by predation. High occurrences of predation on cheetah cubs were first documented by Laurenson *et al.* (1992) in the Serengeti National Park, where only 27.7 % of litters emerged from dens. Predation by large predators, mainly lion (*Panthera leo*) was attributed to 73.2 % of cub mortalities (Laurenson, 1994). Predation continues to be deemed an important cause of cub mortality; however, the rate of occurrences appears to vary across the species range. In the Kgalagadi Transfrontier Park, predation was an important factor of cub survival but not rate limiting, with 35.7 % of cubs reaching adolescence (Mills & Mills, 2014) as opposed to 4.8 % in the Serengeti (Laurenson, 1994). In South African small fenced reserves with varying densities of large carnivores, cub survival post-emergence was 60.0 % (Bissett & Bernard, 2011), and on Phinda Resource Reserve, South Africa, where the lion population was low, cub survival post den emergence was 75.0 % (Hunter, 1998). In Namibia, in areas absent of spotted hyena (*Crocuta crocuta*) and lion, studies found that between 50.0-78.5 % of cubs monitored from emergence to independence survived (Marker *et al.*, 2003; Wachter *et al.*, 2011). In comparison, leopard (*Panthera pardus*) cub survival rate in an open system such as the Sabi Sand Game Reserve, South Africa, was 37.0 % (Balme *et al.*, 2012) and lion cub survival was 86.9 % on South African small fenced reserves where infanticide is uncommon (Miller & Funston, 2014).

The similarities between cheetah cub survival rates outside of the Serengeti National Park and those of other large African felids demonstrates that the 4.8 % survival rate recorded in the Serengeti National Park may be an outlier due to extrinsic factors. It has been suggested that vegetative cover is important for concealment and thus can influence cheetah cub survival (Durant, 1998; Mills & Mills, 2014). This hypothesis was tested in the Masai Mara, Kenya, by Broekhuis (2018) who determined that habitat density and tourism abundance affected cub survival regardless of lion and hyena abundance. Therefore, habitat homogeneity and elevated levels of tourism in the Serengeti National Park study site may contribute to low cub survival. This highlights the importance of habitat heterogeneity and tourism quotas, before large predator control, when considering habitat protection and reintroduction programs for cheetah conservation (Broekhuis, 2018).

## 2.4. Sociality and territorially

A facultatively social carnivore, the cheetah can form three different social groupings, namely; mother and cubs, adolescent cubs, and male coalitions (Bissett & Bernard, 2007; Durant, Kelly & Caro, 2002; Eaton, 1968). Although adult female cheetah have been found on multiple occasions resting and travelling together, these groupings are poorly understood and believed to be temporary (Dalton *et al*., 2013). Male coalitions are the most complex social grouping for cheetah, as they have been shown to consist of both related and non-related males (Caro & Collins, 1987). Male coalitions are the only long-term social grouping and are attributed to greater territory control, which increases both survival and female encounter rates when compared to nomadic males (Bradshaw, 2014; Caro & Collins, 1987; Caro, Fitzgibbon & Holts, 1989).

Home range size varies based on a multitude of factors, including prey distribution, human conflict, patch suitability, distribution of females and presence of other large carnivores (Bissett & Bernard, 2007; Broomhall, Mills & du Toit, 2003; Houser, Somers & Boast, 2009; Hunter, 1998; Purchase & du Toit, 2000; Marker *et al.*, 2007; Rostro-Garcia, Kamler & Hunter, 2015). Cheetah home ranges have been found to span from 32 km$^2$ on small fenced reserves in South Africa to 1651 km$^2$ on Namibian farmland (Bissett & Bernard, 2007; Marker *et al.*, 2007). Changes or disturbances in social grouping also influence home range sizes and can induce shifts. For example, home ranges have been found to increase when a male coalition is reduced to a single male (Marker *et al.*, 2007), whereas female home range greatly reduces during denning (Houser *et al.*, 2009). Despite variation in home range size, the area of core utilization (50 % home range) appears to remain relatively consistent between 10.0 - 13.9 % of the overall home range size (Broomhall *et al.*, 2003; Houser *et al.*, 2009; Marker *et al.*, 2007; Marnewick & Somers, 2015). While home range overlap between male-female ranges is attributed to breeding, male-male overlap and female-female overlap has been shown to also occur at higher than expected frequencies (Broomhall *et al.*, 2003; Marker *et al.*, 2007; Welch *et al.*, 2015). The small area of core utilization may, therefore, account for the high frequency of overlapping home ranges.

## 2.5. Habitat selection

Due to its complexity, habitat selection should be viewed as a scale sensitive process and analysed as such (Mitchell & Hebblewhite, 2012). Most commonly examined as a nested hierarchy, habitat selection has been described in four orders; geographic range (1st order), location of home ranges (2nd order), use of habitat within the home range (3rd order) and selection of foraging sites (4th order; Johnston, 1980). Habitat selection should further be considered as a time-sensitive process as seasonality can affect selection in most species (Mitchell & Hebblewhite, 2012). Factors found to affect habitat selection in cheetah include kleptoparasitism, anthropogenic pressures, presence of conspecifics, and prey abundance (Durant, 1998; Klaassen & Broekhuis, 2018; Rostro-Garcia *et al.,* 2015; Welch *et al.,* 2015). These elements are dynamic and can affect habitat selection at different intensities for each selection order.

The historical distribution of the cheetah spans most of Africa and into Asia, thereby encompassing multiple biomes. However, early studies of the behavioural ecology of the cheetah centred on the plains of the Serengeti National Park and erroneously deemed the cheetah a grassland specialist (*see*, Caro & Collins, 1987; Durant, 1998; Durant *et al*., 1988; Fitzgibbon, 1990; Kelly *et al*., 1998; Schaller, 1968). Improvement in and the decreasing cost of tracking technology however, increased research capabilities and demonstrated that the cheetah can successfully exploit a wide range of woodland, thicket and arid habitats (Bissett & Bernard, 2007; Broomhall *et al.*, 2003; Cristescu, Bernard & Krause, 2013; Klaassen & Broekhuis, 2018; Marker *et al*., 2007; Mills, Broomhall & du Toit, 2004; Nghikembua *et al*., 2016; Rostro-Garcia *et al.,* 2015; Welch *et al.,* 2015). The behavioural flexibility of the cheetah is now evident at the home range scale (2nd order) when comparing selection drivers across study sites. For example, anthropogenic activity and abundance of competing large carnivores appears to have the greatest effect on the location of home ranges for cheetah in open systems (Durant, 1998; Klaassen & Broekhuis, 2018; Van der Weyde *et al*., 2017) whereas, prey abundance is a driver in home range selection for cheetah fenced systems where they are unable to escape competition (Broomhall *et al.,* 2003; Rostro-Garcia *et al.,* 2015; Welch *et al.,* 2015).

Factors affecting 3rd order selection, selection of habitat within the home range, also varies at a study site level. For example, cheetah in Matusadona National Park, Zimbabwe selected open grasslands for hunting and wooded areas for resting and travelling (Purchase & du Toit, 2000). Whereas in South African reserves such as Kwandwe Game Reserve (Bissett & Bernard, 2007), Phinda Private Resource Reserve (Rostro-Garcia *et al.,* 2015), Mountain Zebra National Park (Welch *et al.,* 2015), and Kruger National Park (Broomhall *et al.,* 2003) habitat selection varied based on sex, with females selecting for thicket vegetation significantly more than males. The 4th order of habitat selection for cheetah has not been as thoroughly investigated as that of 3rd order selection. However, semi-closed habitats appear to be selected as kill sites when available, irrespective of prey density, and this is likely a response to kleptoparasitism (Rostro-Garcia *et al.,* 2015). This is further supported by the fact that kleptoparasitism decreases across study sites as cover increases (Mills *et al*., 2004). Therefore, environmental features related to cover are important in habitat selection of the cheetah on a smaller scale as it is used for the spatial avoidance of intraguild competitors. Anthropogenic factors and prey abundance, however, are thought to affect habitat selection at a larger scale.

## 2.6. Prey preference

Cheetah require less food per day than other large African carnivores (Lindsey *et al.*, 2011). Captive cheetah are fed an average of 1.3 kg/day to maintain a healthy condition (Dierenfeld, 1993). However, calorie needs for captive animals are often lower than those in the wild due to a more sedentary lifestyle. Regardless, wild cheetah consumption rates have been found to range from 0.4 kg/day (Mills *et al.*, 2004) to 4.0 kg/day (Schaller, 1968). Discrepancies in consumption rates are affected by levels of kleptoparasitism, the consumable biomass of captured prey and competition between conspecifics such as cubs or coalition members at a kill (Mills *et al.*, 2004; Schaller, 1968).

Due to the morphological limitations of the cheetah, the size range of catchable prey is reduced compared to that of other large carnivores (Hayward *et al*., 2006). The upper limits of prey that a lone cheetah can successfully capture while minimizing the risk of injury is estimated at 56 kg, while the optimal prey mass has been defined as approximately 27 kg (Hayward *et al*., 2006). Studies on the prey preferences of cheetah reflect these size limitations as well as demonstrate effects of local prey abundances on preference, with the most abundant medium-sized prey being preferred; impala (*Aepyceros melampus*) in Matusadona National Park (Purchase & du Toit, 2000), Kruger National Park (Mills *et al*., 2004) and the Northern Tuli Game Reserve (Craig, Brassine & Parker, 2017), and Thomson's gazelles (*Eudorcas thomsonii*) in the Serengeti (Schaller, 1968). However, on Kwandwe Game Reserve in South Africa, greater kudu (*Tragelaphus strepsiceros*) were the preferred prey species regardless of their large size (>120 kg) (Bissett & Bernard, 2007). The preference towards kudu on Kwandwe Game Reserve is thought to reflect how prey preferences can be altered based on small-scale preferences when the studied population does not mimic natural composition. Small-scale influences on prey preference are therefore important to consider when analysing prey requirements for the desired cheetah population during reintroductions (Lindsey *et al*., 2011).

Male cheetah have been found to hunt larger prey than females in certain populations (Bissett & Bernard, 2007; Mills *et al*., 2004; Tambling *et al.*, 2014). However, in conflicting studies, no significant differences between male and female prey preferences were found (Clements, Tambling & Kerley, 2016). Contradictory reports in sex disparity for prey preference are attributed to the social dynamics at the study site level, whereas studies in which prey preferences varied greatly between male and female cheetah, often consisted of multiple male coalitions rather than lone males. This indicates that group structure rather than sexual dimorphism is modifying perceived prey preference (Clements *et al*., 2016). The higher nutritional demands of cheetah social groups are thought to rationalize the preference of larger prey items. While male coalitions have been documented hunting cooperatively (Bissett & Bernard, 2007), females with dependent cubs have been seen to increase their kill rate to account for the additional nutritional demands (Schaller, 1968) further emphasizing the cheetah's predatory limitations.

The presence of intraguild competition and the composition of prey populations have also been shown to affect prey preference. While it has been predicted that areas with low levels of kleptoparasitism would result in cheetah consuming larger prey (Bissett & Bernard, 2007; Hayward *et al.*, 2006), varying densities of competing predators have not been found to influence the size of prey chosen (Clements *et al*., 2016). Rather, high levels of kleptoparasitism could reflect denser habitat type selected for hunting, and prey preference a factor of predator avoidance behaviours reducing or altering prey options (Clements *et al*., 2016; Hayward *et al*., 2006). Finally, cheetah have been shown to display a preference for male antelopes (Fitzgibbon, 1990). This preference is attributed to the reduced vigilance and solitary behaviour of male antelopes as well as the frequency in which they are found on the periphery of groups (Fitzgibbon, 1990; Mills *et al*., 2004).

## 2.7. Intraguild competition

Cheetah are described as a subordinate carnivore as they are reported to suffer from intraguild competition with spotted hyena, lion, and leopard (Hunter, Durant & Caro, 2007; Rostro-Garcia *et al.*, 2015). In the Serengeti National Park, intraguild predation accounts for 73.4 % of cheetah cub mortalities (Laurenson, 1994; Laurenson *et al.,* 1992). While in Matusadona National Park, intraguild predation along with kleptoparasitism is believed to have caused the cheetah population to remain well below the estimated carrying capacity (40 cheetah), with only a maximum of 17 cheetah recorded in the population (Purchase & du Toit, 2000). This demonstrates the significance of interspecific interactions on population dynamics within the large African carnivore community.

Cheetah show predator avoidance behaviour by seeking spatial and/or temporal refuges from dominant carnivores (Durant, 1998; Rostro-Garcia *et al.,* 2015). Factors affecting which predator avoidance strategies are exhibited have been correlated to the size of suitable habitat, densities of dominant carnivores and prey availability (Bissett & Bernard, 2007; Durant, 1998; Rostro-Garcia *et al.*, 2015). In Namibia and Botswana, cheetah show large-scale spatial avoidance of predators by inhabiting farmlands where lion and leopard populations are low, as opposed to PAs where dominate carnivore populations are large (Klein, 2006; Marker & Dickman, 2004). However, cheetah on fenced reserves must adopt different predator avoidance strategies. In small fenced PAs cheetah commonly demonstrate temporal avoidance behaviours as there is little room for spatial avoidance, this has been documented by Bissett & Bernard (2007) on Kwandwe Game Reserve (160 km$^2$) and by Cristescu *et al*. (2013) on Shamwari Game Reserve (250 km$^2$). In both studies cheetah home ranges overlapped with that of the lion. Avoidance was therefore demonstrated in the form of activity pattern variation as well as habitat preference where cheetah selected for denser habitats, which were commonly avoided by lion.

In larger PAs habitat selection appears to be the common mechanism used for minimizing intraguild interactions (Mills *et al.*, 2004; Purchase & du Toit, 2000; Rostro-Garcia *et al.*, 2015). Habitat selection in the form of predator avoidance is a trade-off between resource acquisition and intraguild competition (Rostro-Garcia *et al*., 2015). Sex disparities are revealed in this trade-off as cubs are at the greatest risk of predation;

therefore females have been shown to utilize thicker habitats at a greater frequency than males (Bissett & Bernard, 2007; Mills *et al.*, 2004; Rostro-Garcia *et al.*, 2015). In the Serengeti, selection of dense habitats is not as feasible, here cheetah demonstrate avoidance and decreased hunting attempts when lion or hyena vocalizations are heard (Durant, 2000a), as well as exhibit multiple prey handling strategies to reduce kleptoparasitism and intraguild predation (Hilborn *et al.*, 2018).

This demonstrates that predator avoidance is a flexible behaviour strategy that is adapted based on an individual's sex, habitat availability as well as prey and predator densities. Furthermore, predator avoidance behaviour in cheetah has been identified as a learned behaviour that is reinforced by breeding success (Durant, 2000b) and predator naïve cheetah are thought to have lower reintroduction success (V. Van der Merwe, pers. comm.).

## 2.8 Conservation status

Currently listed as Vulnerable by the IUCN Red-List, it is the large-ranging nature of the cheetah that has been recognized as the main cause for its global population decline (Durant *et al.*, 2017). Once present throughout Africa and into Asia, the cheetah population is now fragmented into 33 populations across 32 range states, totalling an estimated 6700 to 7100 individuals (Durant *et al.*, 2017; Durant *et al.*, 2015). The current range for cheetah consists of only 9 % of their historical range which is primarily found outside of protected areas (Durant *et al.*, 2017). Scenario modelling has demonstrated that cheetah are dependent on PAs as populations outside of these areas are suppressed (Durant *et al.*, 2017). Therefore, population growth inside PAs must remain high to compensate for declines outside of these areas (Durant *et al.*, 2017). Consequently, cheetah are extremely susceptible to a loss of habitat and prey base, as habitat conversion continues in-line with human population growth throughout their remaining range (Durant *et al.*, 2017; Houser *et al.*, 2009; Klein, 2006; Purchase *et al.*, 2007).

Currently, over half of the world's cheetah population presides in six counties within southern Africa; Angola, Botswana, Mozambique, Namibia, South Africa and Zambia (Durant *et al.*, 2017). Cheetah conservation initiatives are broad and differ regionally based on socio-economic and locality factors. In South Africa, a managed metapopulation was developed from cheetah relocated from farmland as part of a conflict resolution initiative (Buk *et al.*, 2018; Lindsey *et al.*, 2011). The metapopulation assists in maintaining a genetically viable population on fenced reserves and PAs in South Africa (Buk *et al.*, 2018). Cheetah often seek spatial refuge from competing carnivores, the practice of fencing of South African reserves and PAs, therefore, prevents cheetah from moving onto farmlands and requires the individual to seek refuge on a small scale (Cristescu *et al.*, 2013). Fenced reserves have therefore been found to maintain carnivore populations closer to their estimated carrying capacities than unfenced areas (Lindsey *et al.*, 2011; Minin *et al.*, 2013; Packer *et al.*, 2013). Cheetah are commonly subjected to kleptoparasitism and at times predation by lion, leopard, and spotted hyena (Durant, 2000b; Durant, 1998). Consequently, cheetah populations outside of fenced PAs are at risk of collapse as they fall into ecological traps while seeking refuge from intraguild competition (Marker &

Dickman, 2004). This phenomenon has been recorded in free-ranging populations in Namibia and South Africa, which reside outside of PAs and are highly subjected to retaliatory killings (Marker & Dickman, 2004; Marnewick & Somers, 2015; Muntifering *et al*., 2006). Conservation of these populations requires intense human-wildlife conflict mitigation in order to increase human tolerance of cheetah (Marker & Dickman, 2004; Purchase *et al*., 2007).

The trade in cheetah poses another sizeable risk to remaining wild populations. Cheetah are included in CITES Appendix I with export quotas for live specimens and hunting trophies from Botswana, Namibia and Zimbabwe (Nowell, CAT & IUCN, 2014). The trade in live specimens poses a unique threat to cheetah compared to other large carnivores. Cheetah can habituate relatively easily especially if obtained while young, and this has primarily fuelled the demand for cheetah as pets (Nowell *et al.*, 2014). Whilst east Africa exhibits the highest records of illegal trade; South Africa has the highest number of breeding facilities and legal live specimen exports (Nowell *et al*., 2014). Only two of South Africa's breeding facilities, however, are CITES accredited and many boast an unusually high breeding success rate when compared to North American captive facilities (Nowell *et al.*, 2014). This success has resulted in concerns that live-trapped wild animals are illegally entering the legal captive export trade (Buk & Marnewick, 2010; Nowell *et al.*, 2014). South Africa’s legal trade in captive cheetah and the illegal trade in east Africa have therefore been flagged as threats to wild populations in southern and eastern Africa by CITES (Nowell *et al.*, 2014). However, South Africa has recently implemented genetic passports for captive cheetah in order to prove parentage. Genetic passports are now a requirement for the export of cheetah from South Africa, thus have closed a legislative gap that allowed for the illicit laundering of wild cheetah under the guise of the captive trade (Selier & Marnewick, 2019). Whilst the increase in trade regulations are promising, the varying threats, conservation requirements, and sizeable knowledge gap for populations outside of intensely studied PAs has resulted in a formal recommendation for the up-listing of cheetah under IUCN Red List criterion A3b to Endangered (Durant *et al*., 2017).

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# Chapter Three

## Post-Release Movements and Early Establishment of a Reintroduced Cheetah Population

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### 3.1. Abstract

Large carnivores have experienced dramatic geographical range contractions and population reductions in the past two centuries. Their ability to restore ecosystem functioning coupled with the financial benefits they provide through ecotourism and the need for geographical range recovery has resulted in many protected areas undertaking large carnivore reintroductions. Similar to natural dispersal, reintroduced animals often undertake long-distance movements before settlement, which can consequently impact reintroduction success. However, the mechanisms behind this are rarely investigated. The post-release movements of five cheetah (*Acinonyx jubatus*) reintroduced into Liwonde National Park, Malawi between 2017 and 2018 were analysed. Cheetah were released an average straight line distance of 1644 km away from their capture site and held in temporary enclosures at the release site for an average of 41 days. All cheetah showed release site fidelity and all females birthed their first litter within the first four months post-release, an average of 2 km from the release site. Within the first two-years post-reintroduction the established population began to conform to the demography recorded in the source population, indicating overall successful population establishment. An acclimatisation (temporary holding) period greater than 23 days had no significant impact on the post-release exploration. Sex did significantly affect post-release exploration, with males traveling further and settling later than females. These findings have strong implications on the planning of post-release monitoring of reintroduced and translocated cheetah. Additionally, it is proposed that differences in post-release movements could be explained by one of two factors; the presence of suitable denning and hunting habitat near the release site, or sex-specific disparities in the effects of soft-releases. It is suggested these factors be closely investigated in subsequent reintroduction events.

### 3.2. Introduction

Human population expansion has resulted in a global increase of anthropogenic disturbances, which have caused increased fragmentation and augmentation of natural habitats resulting in biodiversity declines (Brown *et al.*, 2013; Kerr & Currie, 1995; McKee, Chambers & Guseman, 2013). To offset biodiversity losses, reintroductions, described as the deliberate movement of individuals to an area in which the species was extirpated with the end goal of population re-establishment, are increasingly used (IUCN/SSC, 2013; Seddon

2015). Reintroductions have taken place across most taxa with large carnivores amongst the most reintroduced organisms (Seddon, Soorae & Launay, 2005).

Large carnivores are susceptible to habitat fragmentation and augmentation, and their dietary requirements and wide-ranging behaviour often brings them into competition or conflict with humans (Durant *et al.*, 2017; Winterbach *et al.*, 2013; Woodroffe, 2000; Woodroffe & Ginsberg 1998). Consequently, large carnivores are often the first species to become locally extinct (Cardillo *et al.*, 2004; Winterbach *et al.*, 2013; Woodroffe, 2000). Large carnivores, therefore, have experienced dramatic geographical range contractions and subsequent population reductions in the past two centuries (Ripple *et al*., 2014). However, the financial benefits of large carnivores for ecotourism (Di Minin *et al.*, 2013), coupled with their ability to restore ecosystem functions (Atkins *et al.*, 2019; Sinclair, Mduma & Brashares, 2003) and the need for geographical range recovery, has resulted in many protected areas undertaking large carnivore reintroductions. Despite the increasing popularity of large carnivore reintroductions, the large space and prey requirements essential to each species makes any reintroduction effort challenging (Stoskopf, 2012). Furthermore, post-release monitoring of reintroduced carnivores rarely occurs, and where it has, results vary and causes of failures are under-reported and poorly understood (Buk *et al.*, 2018; Boast *et al.*, 2018; Hayward *et al.*, 2007a).

During reintroductions, animals are often placed in novel landscapes, large distances from where they originated. Reintroduced and translocated animals must, therefore, make behavioural adaptations to novel resource distributions and environmental conditions, similar to those undergoing natural dispersal (Berger-Tal & Saltz, 2014). Two forms of natural dispersal have been defined; i) natal dispersal, the movement from a birth site to a site of potential reproduction and, ii) breeding dispersal, movement between sites of reproduction (Clobert, Massot & Le Galliard, 2012). Both forms of dispersal are crucial for the persistence of a species by ensuring gene flow and/or population rescue (Clobert *et al.*, 2012). A dispersing animal is defined to have settled (reached settlement; established a home range) when daily displacement begins to stabilize, and movements become geographically confined (Bastille-Rousseau *et al.*, 2016). Dispersal and settlement can occur numerous times over an animal's lifespan, and animals may develop temporary home ranges or undergo home range shifts. Animals undergoing dispersal have been shown to face increased survival difficulties compared to non-dispersers as they move between novel landscapes often taking them across fragmented habitat or into conflict with competitors (Bartón *et al*., 2019; Fattebert *et al.*, 2013).

Reintroductions can be viewed as a 'forced-dispersal' as the process resembles natural dispersal in which the animals must balance a trade-off between exploration and exploitation of their new habitat (Berger-tal & Saltz, 2014; Stamps & Swaisgood, 2007). Many species, however, exhibit male biased dispersal (*e.g.*, American black bear, *Ursus americanus* and leopard, *Panthera pardus;* Costello, 2010; Fattebert *et al*., 2015) or short dispersal distances (*e.g.*, Eurasian otter, *Lutra lutra*; Quaglietta *et al.*, 2013) and therefore may lack the behavioural plasticity required during reintroductions. This often results in a rejection of the release site habitat and subsequently rapid long-distance movements (Berger-Tal & Saltz, 2014; Stamps & Swaisgood, 2007).

However, settlement is a critical step in population establishment, as successful population establishment requires the settlement of a enough dispersers to develop a viable population based on species' specific life histories (Hovestadt & Poethke, 2005). Therefore, reintroduced populations may fail to establish because of large post-release movements, lack of individuals developing home ranges or low survival and reproductive rates (Armstrong & Seddon, 2007; Linnell *et al.*, 1997; Stamps & Swaisgood, 2007). These factors are strongly related, as increased post-release exploration can result in high mortality rates and a greater spatial spread between reintroduced individuals, thereby effecting reproduction potential (Armstrong & Seddon, 2007).

In South Africa, ecotourism demands coupled with the historic loss of wildlife have led to an influx in the reintroductions of charismatic carnivores into fenced protected areas. This has resulted in population increases in lion (*Panthera leo*; Ferreira & Hofmeyer, 2014; Miller & Funston, 2014), cheetah (*Acinonyx jubatus*; Buk *et al*., 2018) leopard and African wild dog (*Lycaon pictus*; Davies-Mostert, Mills & McDonald, 2015). However, dispersal is restricted in these populations as the reserves in which they are found are fenced. These populations therefore often require individuals to be captured and translocated as a form of 'human mediated dispersal'. Regardless, the increase in these populations and the need for human-mediated dispersal has renewed opportunities for range expansion projects in the region, most recently in Mozambique (Endangered Wildlife Trust, 2018; National Geographic, 2019) and Malawi (Briers-Louw, Verschueren & Leslie, 2019; Sievert, Reid & Botha, 2018). While the understanding of pre-release procedures for these species has improved over time (*e.g.*, soft-releases; Hayward *et al.*, 2007b) few studies have evaluated early post-release movements, settlement and their effects on population establishment (Briers-Louw *et al.*, 2019; Hunter, 1998a; Weise *et al*., 2015a; Weise *et al*., 2015b; Yiu *et al*., 2015).

Understanding early post-release movements allows us to investigate the trade-offs animals face during settlement after a reintroduction event. This is important as reintroduced populations may fail to survive the establishment phase in conditions that have been deemed viable for long-term population persistence (Berger-tal & Saltz, 2014; Armstrong & Seddon, 2007). Increasing our understanding of early post-release movements and population establishment is therefore crucial in determining variations in strategies used to adapt to novel environments, and the affects these strategies have on reintroduction success. Improving our understanding of these processes will, therefore, assist in ensuring early-stage reintroduction and translocation success by allowing for the adaptation of pre- and post-release methodologies.

This study investigates early post-release movements, settlement, and establishment of reintroduced cheetah. The reintroduction was part of a range expansion project; therefore, the cheetah underwent a forced-dispersal for conservation purposes to Malawi from South Africa. Early post-release exploration and home range establishment were investigated by comparing movement direction and distances with similar studies for cheetah (Hunter, 1998a; Weise *et al*., 2015b). It was expected that daily displacement would be highest immediately after release, decrease over time and eventually stabilize, thus representing a change from exploratory to knowledge-based movements. Stabilization of movement distances should, therefore, be indicative of home range establishment. It was anticipated that this process would be more rapid for females than males based on maternal care requirements. Finally, the demography of the reintroduced population was compared to similar source populations (Bissett & Benard, 2011; Hunter, 1998b; Power *et al.*, 2019) as an indication of population establishment and early stage reintroduction success.

## 3.3. Methods

### 3.3.1. Context of reintroduction

Historically widespread throughout Africa and southwestern Asia, the cheetah has disappeared from vast tracks of its historical range (Durant *et al.*, 2017). Thirty-three remnant cheetah populations are now scattered across 32 of their 53 range states, comprising 9 % of their historical distribution (Durant *et al.*, 2015; Durant *et al*., 2017). In 1975, Malawi's cheetah population was estimated at 50 individuals spread across two national parks, however by 1989 this population was confined to Kasungu National Park and believed to be mainly transient with Zambia's Luangwa Valley (Gros, 1996; Myers, 1975). Continued reduction of habitat and prey base coupled with the depletion of the Luangwa Valley's cheetah population prevented any re-colonization events in Malawi, resulting in the full extirpation of the cheetah by the early 1990s (Gros, 1996; Purchase & Purchase, 2007).

In 2015, a public-private partnership was signed between African Parks Network (AP) and the Malawi Department of National Parks and Wildlife to manage two of Malawi's protected areas, Liwonde National Park (LNP) and Nkhotakota Wildlife Reserve. This partnership saw an increase in financial contributions to these protected areas and resulted in the reform of law enforcement and construction of perimeter fences. It also increased the size of protected areas under AP Malawi management from 700 km$^2$ to 3048 km$^2$ (C. Reid, pers. comm.). The increase in AP Malawi's protected area network provided an opportunity to re-establish a cheetah population in the country. Due to an ample prey base, LNP was the first protected area to undertake this endeavour. Between June 2017 and February 2018, in partnership with the Endangered Wildlife Trust's (EWT) Cheetah Metapopulation Project (CMP), AP reintroduced seven cheetah (four males and three females) into LNP (Sievert *et al.*, 2018).

### 3.3.2. Study site

Spanning 548 km$^2$, LNP is in the Upper Shire Valley in the Southern Region of Malawi (Figure 3.1). LNP has distinct wet and dry seasons, the average precipitation is 944 mm per year, with the majority of rainfall occurring between December and March, with June to October classified as dry months (Bhima & Dudley, 1996). Mean high temperatures range from 28$^o$ in July to 40$^o$ C in November (Bhima & Dudley, 1996). The Shire River is the sole perennial river and the dominant feature of the park as it runs the length of the boundary splitting the park into an eastern and western side. In the wet season, the Shire River creates extensive lagoons and marshlands along the floodplains which border both sides of the river. While LNP contains a multitude of seasonal rivers and streams, only a few pockets of water remain scattered around the park by September, making the Shire River the main water source.

As part of the southern Rift Valley ecosystem, LNP is relatively flat and consists mainly of dry deciduous woodland (Dudley, 2004). The dominant tree in the park is *Colophospermum mopane*, with mopane woodland complex occupying approximately 74 % of the park (Dudley, 2004). Grasslands and floodplains (*Setaria* spp. *Digitaria* spp. *Sporobolus* spp.) along with forest thickets and mixed woodlands (*Combretum* spp., *Terminalia* spp. *Borassus* spp. *Vachellia* spp. *Cordyla* spp. *Trichilia* spp.) are interspersed throughout the park, mostly occurring in north-south bands that run parallel to the Shire River (Dudley, 2004). There are seven distinctive hills found throughout the park with a maximum altitude of 921 m (Mzumara, Perrin & Downs, 2018). The northern boundary consists of a 6 km unfenced corridor to Mangochi Forest Reserve. The recent inclusion of Mangochi Forest Reserve under LNP management expanded the protected system by 375 km$^2$ (3368 km$^2$ total for AP Malawi Management; C. Reid, pers. comm.).

### 3.3.3. Pre-release management

Seven cheetah (four males, and three females) were reintroduced into LNP over four different release events between June 2017 and February 2018 (Table 3.1). To ensure maximum genetic diversity based on animals available, cheetah were sourced through the EWT CMP. Reintroduced individuals originated from five separate reserves in South Africa with a mean translocation distance of 1644 km (range 1105-2252 km). This study defines translocation distance as the straight linear distance between the reserve in which the animals originated before capture and the release site in LNP. Prior to arrival in LNP, three females and two males were fitted with Pinnacle LITE global positioning system (GPS) satellite collars (Sirtrack, Hawkes Bay, New Zealand) and one male was fitted with a very high frequency (VHF) tracking collar (African Wildlife Tracking, Pretoria, South Africa). Collars weighed approximately 465 g (GPS) and 253 g (VHF), 0.4-1.3 % of body weight. All individuals were kept in temporary holding enclosures (bomas; 50x50 m) prior to release. Holding periods ranged between 23 and 58 days. LNP’s carnivore boma is located in the southern section of the park due to its year-round accessibility, abundant prey, and water availability (Figure 3.1). Individuals were held in the boma within their respective social groups (Table 3.1). An artificial sibling group was formed between CF1 and CM1, due to the age at which CF1 was captured for relocation. This bonding was an attempt to assist them in acclimatizing and hunting upon release (V. van der Merwe, pers. comm.). Once individuals were sufficiently settled, they were released directly from the boma through coaxing with a final feed; the gate was then closed behind them to ensure they did not return to the boma. No animals were fed post-release, regardless, this methodology is defined as a soft-release.

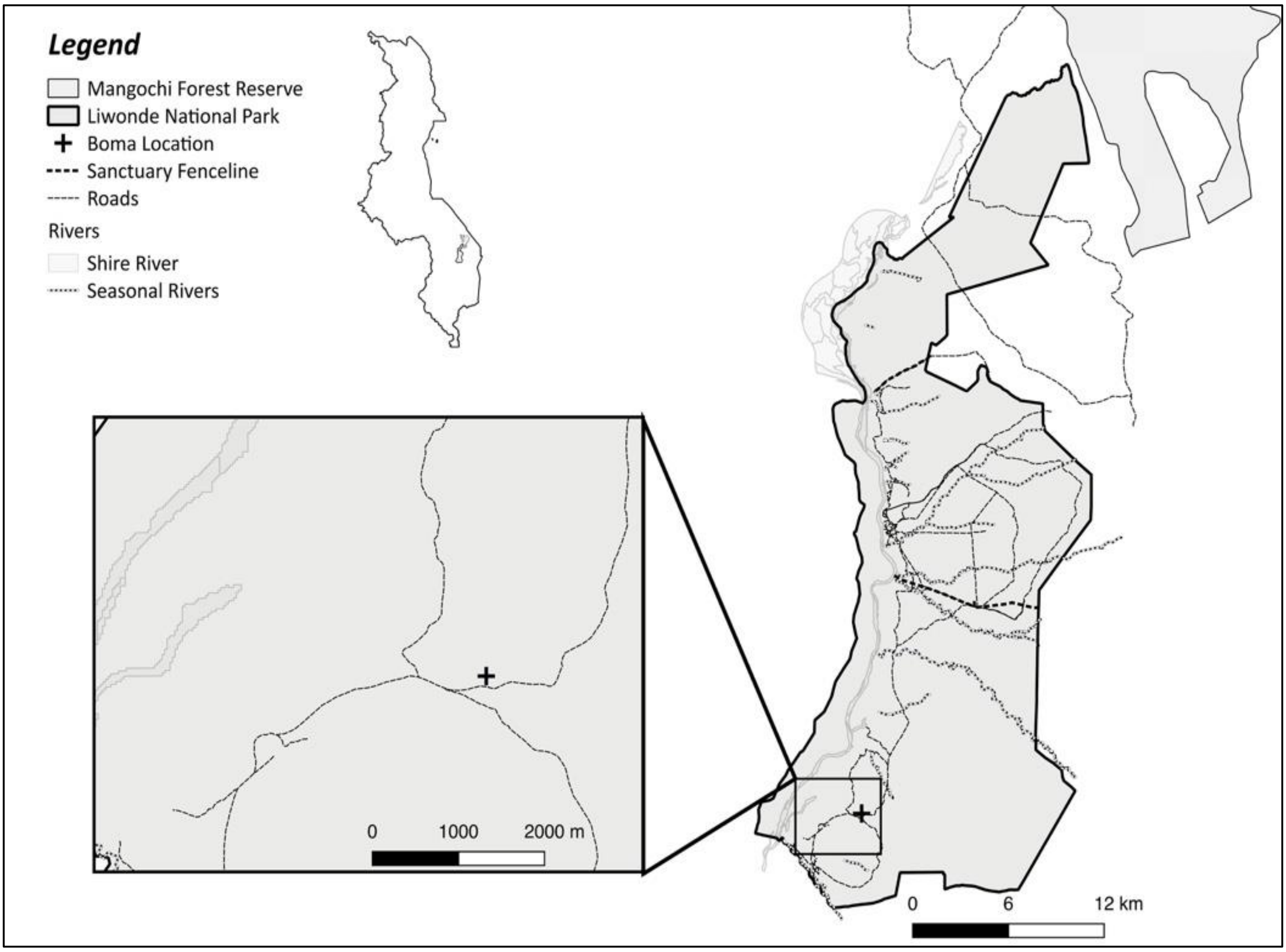

**Figure 3.1.** Map of LNP indicating the location of the carnivore boma, the park's location in Malawi and in reference to Mangochi Forest Reserve.

**Table 3.1.** Biological and translocation details of seven cheetah reintroduced into LNP during four reintroduction events between June 2017 and February 2018. (GR = Game reserve; WS = Wildlife Sanctuary; NP = National Park).

| ID Code | Sex | Estimated Age at Release (months) | Period in Boma (days) | Release Date [event] | Translocation Distance (km) | Origin | Social Grouping |
|---|---|---|---|---|---|---|---|
| **CM1** | M | 24 | 31 | 12-06-17 [2] | 1450 | Phinda Private GR | Artificially bonded with CF1. |
| **CM2** | M | 78 | 23 | 05-06-17 [1] | 1277 | Welgevonden GR | Single male |
| **CM3** | M | 22 | 58 | 07-02-18 [4] | 1105 | SanWild WS | Sibling group CM4, CF3 |
| **CM4** | M | 22 | 58 | 07-02-18 [4] | 1105 | SanWild WS | Sibling group CM3 CF3 |
| **CF1** | F | 23 | 31 | 12-06-17 [2] | 2140 | Mountain Zebra NP | Artificially bonded with CM1. |
| **CF2** | F | 26 | 32 | 13-06-17 [3] | 2252 | Amakhala GR | Single female |
| **CF3** | F | 22 | 58 | 07-02-18 [4] | 1105 | SanWild WS | Sibling group CM3 CM4 |

### 3.3.4. Post-release monitoring

Since the release in LNP, cheetah have been monitored following the guidelines set by the IUCN/SSC (2013) for reintroductions and translocations. Park management implemented an active adaptive monitoring approach (*see,* IUCN/SSC, 2013) for this reintroduction, as monitoring strategies were adapted over the course of the study. GPS collars were scheduled to collect a minimum of three GPS points per day (default schedule, 06:00 08:00 & 12:00, GMT+2). This scheduling was increased based on birthing events or for injured animals to intensify monitoring capabilities (Table 3.2). Radio-tracking took place a minimum of twice a week, with attempts of one observation per cheetah per week. An R-1000 telemetry receiver (Communication Specialists Inc, California, USA) attached to a flexible H-Type antenna (RA-23K VHF antenna; Telonics, Arizona, USA) was used to locate each animal during radio-tracking events. The signal strength ranged from 500 m to 1.5 km depending on vegetation structure and season. The success of each radio-tracking event was, therefore, dependent on vegetation as well as the level of habituation for each individual. Opportunistic sightings outside of scheduled radio-tracking events were also recorded. All sightings were recorded with the GPS location and the behaviour (*e.g.,* resting, vigilant, travelling, feeding) of the animal upon initial sighting.

Den sites were checked within the first two weeks of denning to assess litter size and cub survival. To minimize disturbance, dens were checked by one person while the female was hunting, and no handling of cubs took place (Laurenson & Caro, 1994). All GPS collars were replaced before battery depletion, and animals were re-fitted with VHF collars (Sirtrack, Hawkes Bay, New Zealand) modified with a Long Range (LoRa) Geolocation transmitter (Smart Parks, Rotterdam, Netherlands). Re-fitted collars weighed 359 g and allowed for continued weekly observation attempts.

**Table 3.2.** Details of the post-release monitoring of seven cheetah reintroduced into LNP, Malawi.

| **ID code** | **Collar type** | **Collar Success Rate** | **No. Fixes** | **No. Transmission Days** | **No. Sightings** | **Status** [a] |
|---|---|---|---|---|---|---|
| **CM1**[b] | GPS | 54.9% | 594 | 297 | 26 | Alive |
| **CM2** | GPS | 66.3% | 2157 | 520 | 113 | Deceased |
| **CM3**[c] | VHF | N/A | N/A | N/A | 19 | Unknown |
| **CM4**[c] | None | N/A | N/A | N/A | 16 | Unknown |
| **CF1**[b] | GPS | 97.2% | 3747 | 759 | 45 | Alive |
| **CF2** | GPS | Unknown | 1633 | 508 | 79 | Alive |
| **CF3**[c] | GPS | 95.0% | 1032 | 307 | 16 | Deceased |

[a] Status as of 30 June 2019. [b] Artificially bonded as sub-adults and released together. [c] Members of a sibling coalition released together

### 3.3.5. Data analysis

This study took place over two years (June 2017-July 2019). The first year of post-release movements was analysed for each GPS collared animal, except for CM1 whose collar was damaged and malfunctioned (297 days post-release analysed) and CF3 who died during the study (307 days post-release analysed). Post-release movements of CM3 and CM4 were not investigated as data was insufficient for these animals. Data was standardized across all individuals by selecting one location (closest to 12:00 GMT+2) in every 24-hour cycle (Weise *et al*., 2015a; Briers-Louw *et al.*, 2019). Although two mixed-sex groupings of cheetah were released from the boma, CF1 and CF3 separated from their groupings between 2-19 days post-release; therefore each GPS collared animal analysed was considered as a singleton adult or female with dependent cubs. All analysis was conducted using R v. 3.5.1. (R Core Team 2018) unless otherwise stated.

### 3.3.5.1. Post-release exploration

To investigate initial post-release exploration, daily displacement was calculated for each individual as the Euclidean distance between two successive locations in a 24-hour cycle (Bartón *et al*., 2019) using the adehabitatLT package (Calenge, 2006). A linear mixed model was developed using lme4 (Bates *et al*., 2015) to assess which factors contributed to post-release exploration. Factors included in the model were: the age at translocation, time spent in the boma, sex, time since release and season (cold dry, hot dry and wet). Different individuals were considered as a random factor, nested in sex.

### 3.3.5.2. Settlement and home ranges

Progressive 100 % minimum convex polygons (MCPs) were calculated for each of the five cheetah to determine the duration of exploratory behaviour and settlement. Progressive MCPs were developed by creating an 11-day window which began at first point collected after release. The window was shifted continuously one day for the first year of movement data until only 11 days remained. This method is similar to that outlined by Weise *et al.* (2015a & 2015b) and creates a progressive estimate of range for the first-year post-release. Ten-day estimates conducted by Weise *et al.* (2015b) were not possible in this study as at least five data points were required for each 10-day segment. Due to collar functionality, 11-day segments were the nearest in which this methodology was possible for this study. 100 % MCP were used as they uniformly increase, whereas 95 % MCPs are a statistical estimate used to remove potential exploratory outliers making interpretation of settlement more difficult (Flanagan *et al*., 2016).

The net squared displacement (NSD) for each cheetah was also calculated to determine release site fidelity and settlement (home range establishment; Börger & Fryxell, 2012). NSD is obtained by calculating the square of the Euclidean distance between each location and the known origin location (Bastille-Rousseau *et al*., 2016). The origin location in this study was set to the first location collected post-release for each cheetah, which was within 1 km of the boma. NSD is a common tool used to visually represent and analyse different movement strategies, such as; migration, nomadism, and dispersal (*e.g.*, Bastille-Rousseau *et al*., 2016; Bunnefeld *et al*., 2011; Fattebert *et al*., 2015). Progressive MCPs and NSD curves were visually inspected to identify the point in time after release when individuals settled, and their space use patterns stabilized (Weise *et al*., 2015a; Weise *et al*., 2015b). Home ranges estimates were then calculated using the Time Local Convex Hull method (T-

LoCoH) in the T-LoCoH package (Lyons, Turner & Getz, 2013). Data points from settlement until one-year post-settlement were included in home range estimates in order sample evenly across seasons (wet and dry), with the exception of CF3 in which there was only data for 278 days due to her death.

Local convex hulls are the most effective method in demarcating hard boundaries and internal structures in which animals are excluded, such as fences, thereby reducing Type II errors found in home range estimates (Getz *et al*., 2007). The T-LoCoH method further modifies the local convex hulls algorithm by incorporating a time scale that acts to separate points that are far apart in time regardless of their proximity in the two-dimensional space (Lyons *et al*., 2013). The algorithm requires the input of two parameters: the number of nearest neighbours (a) and the time-scaled distance (s). The T-LoCoH algorithm was run with different values for these two parameters based on steps outlined by Lyons (2014). The values which created the best-fit home range were selected. While it is acknowledged that the data collected is not independent, removal of data points in an attempt to account for autocorrelation has not always proven successful and can act to reduce biologically relevant data (Börger *et al*., 2006; Crushman, Chase & Griffi, 2005; De Solla, Bonduriansky & Brooks, 1999). Furthermore, by incorporating the time stamp of each location, the T-LoCoH algorithm considers time data within the home range calculation (Lyons *et al*., 2013). To ensure sufficient data for home range calculations, home range size using a 100 % MCP was plotted against GPS locations using the adehabitatHR package (Calenge, 2006), to visually determine if home ranges reached asymptotes. For cheetah in which home range data reached an asymptote, home range calculations were conducted for 95 % and 50 % isopleths. The 95 % isopleths were selected as they are generally considered the closest approximation of total range size, whereas, 50 % isopleths are the most robust estimators of an animal’s centre of activity (Burt 1943; Jaremovic & Croft, 1987; Harris *et al*., 1990).

### 3.3.5.3. Survival, breeding, and demography

Survival, breeding and demography of the population were reported to evaluate the early reintroduction success. Individual reintroductions were considered successful if the individual showed: 1) release site fidelity [therefore no homing] 2) successful reproduction 3) settlement and 4) survival of at least one year. The short-term survival of a reintroduced population has been described as successful when recruitment exceeds adult death rate in a breeding population during the first three years (Hayward *et al.*, 2007b). The current study, however, only spanned the first two-years post-release. The reintroduction of the population was therefore measured as successful if the population reached establishment, in this case, defined as the settlement rate of 80 % of the adult groupings within the first-year post-release, as that would ensure multiple breeding individuals remaining in the population, and the population conformed to demographic levels documented within the source population of the CMP (Bissett & Benard, 2011; Hunter, 1998b; Power *et al.*, 2019).

## 3.4. Results

### 3.4.1. Post-release exploration

Sex had a significant effect on daily displacement ($F_{1,2}$ = 252.16, $p$ = 0.01), with males traveling larger distances than females (Figure 3.2). Mean daily displacement was 3.55 ± 3.33 SD km for males, and 1.19 ± 1.22 SD km for females (1.22 ± 1.23 SD km when denning period excluded). Daily displacement for each cheetah was significantly affected by days after release ($F_{1,1647}$ = 39.06, $p < 0.01$) and this relationship was negative, indicating a decrease in the daily displacement over time. Age at the time of translocation had no significant effect on daily displacement ($F_{1,1}$ = 7.73, $p > 0.05$). Additionally, time spent in the boma also had no significant effect on the daily displacement ($F_{1,1}$ = 2.54, $p > 0.05$).

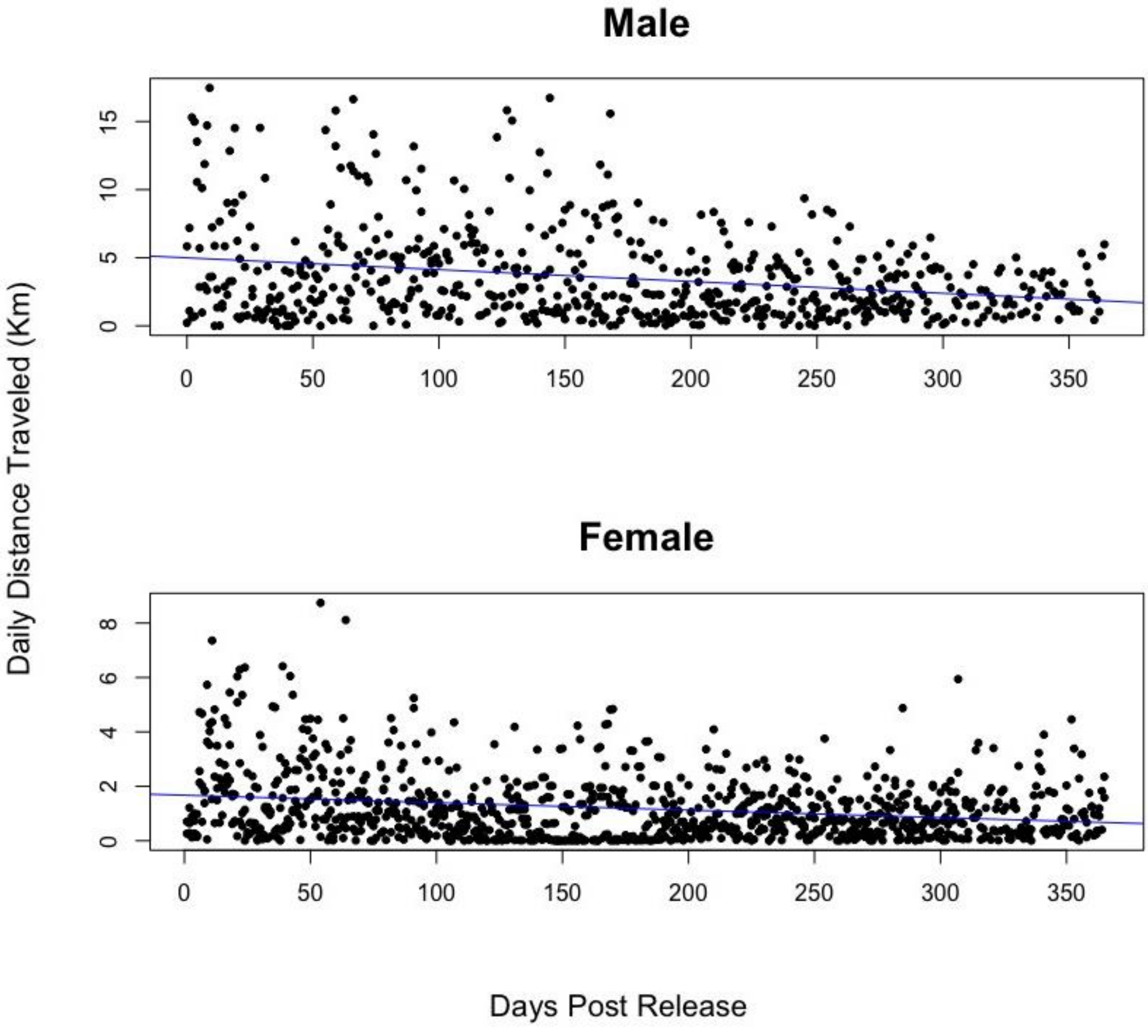

**Figure 3.2.** Daily displacement (km) of reintroduced male ($n$ = 2) and female ($n$ = 3) cheetah for the first-year post-release in LNP. Regression line indicated in blue.

### 3.4.2. Settlement and home ranges

All reintroduced cheetah, for which data could be analysed (five adults) successfully established home ranges. Progressive MCPs indicated all females established a home range within their first three months post-release (Figure 3.3). CF3 had the earliest home range establishment which occurred not long after the separation from her brothers (CM3 and CM4) at roughly 29 days post-release. CF1 separated from CM1 (unrelated) two days after release, however, she did not establish a home range until roughly 73 days post-release. CF2 established her home range 63 days post-release. All female home ranges were established an average of 76 days before the estimated start of the denning period (CF1, 65 days; CF2, 60 days; CF3, 104 days). All females exhibited release site fidelity, especially during denning (Figure 3.4). CF2 had the largest 100 % MCP during the denning period, however, this is an indicator of diurnal hunting behaviour during denning (pers. obs.). Both CF1 and CF2 demonstrated a period of early settlement prior to the final settlement phase between 23-44 and 34-55 days post-release, respectively. Settlement of males took longer than that of females (CM2, 159 days post-release; CM1, 206 days post-release). Although CM1 briefly settled in an area between 148-188 days post-release, his 100 % MCP area increased drastically after this time, indicative of a range shift. Both males showed high levels of release site fidelity after initial exploratory movements (Figure 3.4).

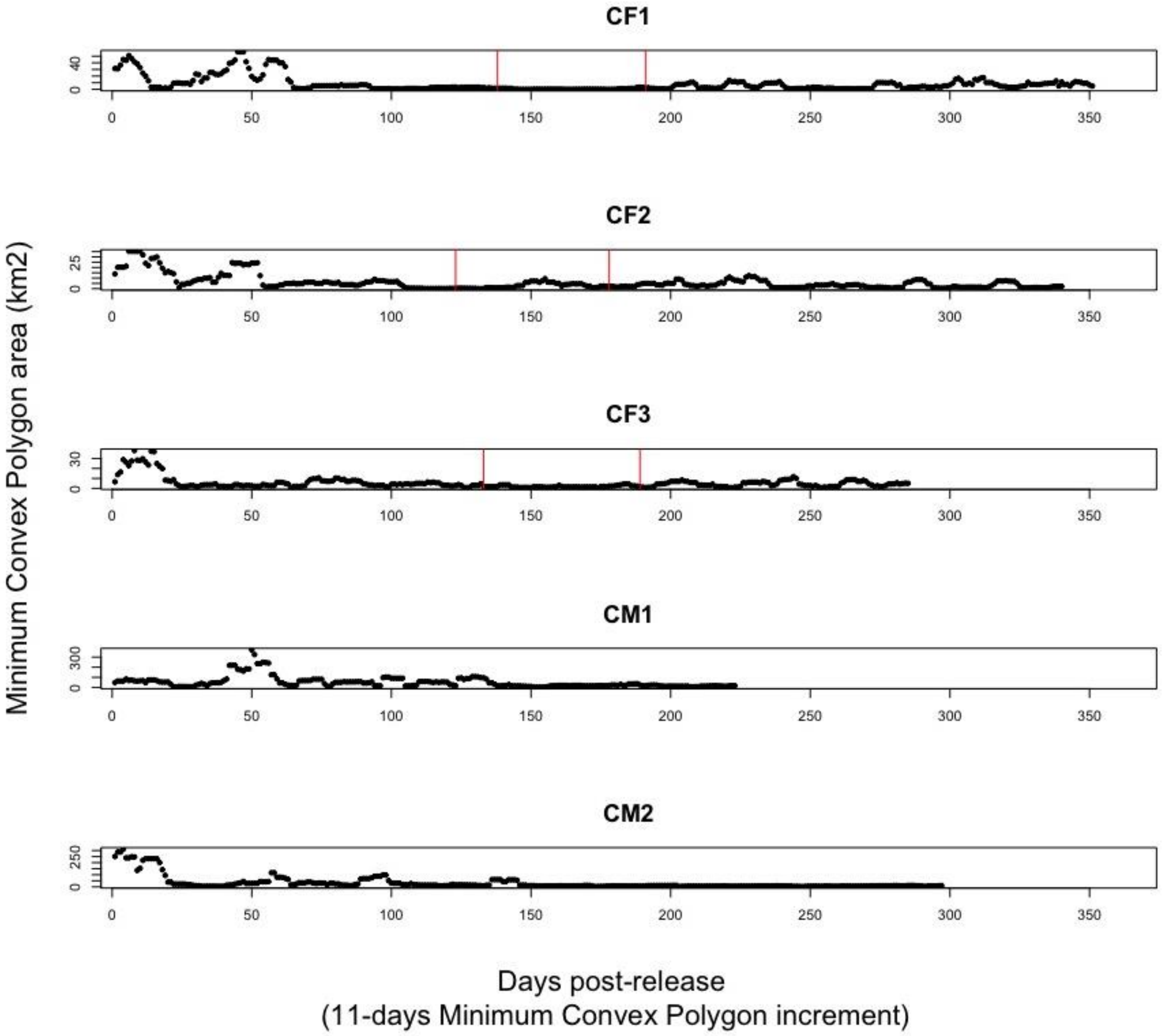

**Figure 3.3.** Progressive 11-day 100 % minimum convex polygons (MCP) assessment for five reintroduced cheetah over their first-year post-release. Red bars indicate the known beginning and end of denning periods. **Note: y-axis scales differ between individual case studies** and x-axis is indicative of the first 11-day MCP, not day-0 post-release.

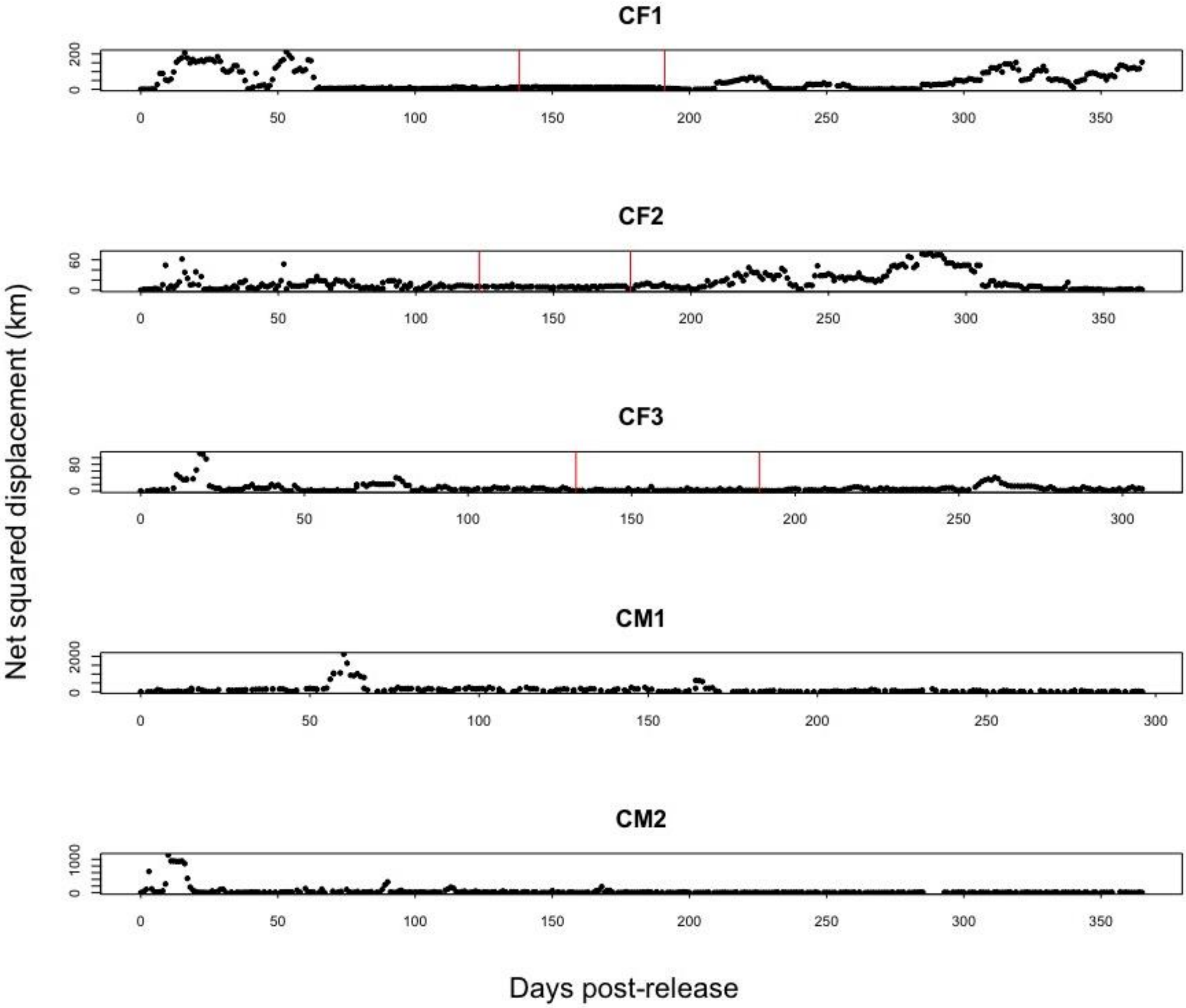

**Figure 3.4.** Net squared displacement (NSD) patterns for five reintroduced cheetah over their first year for post-release. Red bars indicate the known beginning and end of denning periods. **Note: y-axis scales differ between individual case studies** and is representative of the square of the Euclidean distance between each location and the known original location.

Home range estimates were calculated for four of the five cheetah that reached settlement (Table 3.3). CM1's collar collected 176 fixes after settlement, however, this amount of data did not reach an asymptote thereby indicating insufficient data for home range calculations. Home ranges (95 % isopleths) varied between 41-97 km$^2$, with the core area of use (50 % isopleths) ranging from 13-28 km$^2$.

**Table 3.3.** Details of home range analysis for reintroduced, GPS collared, cheetah after settlement. Table includes parameters used for T-LoCoH analysis when assessing 95 % and 50 % isopleths.

| ID Code | Monitoring Days Used | No. Fixes | Asymptote Reached (Y/N) | T-LoCoH ($km^2$) 95% [50%] | T-LoCoH Parameters Selected |
|---|---|---|---|---|---|
| **CM1**[a] | 91 | 176 | N | N/A | N/A |
| **CM2** | 365 | 1592 | Y | 41 [23] | a = 90,000<br>s = 0.03 |
| **CF1** | 365 | 1757 | Y | 97 [28] | a = 70,000<br>s = 0.03 |
| **CF2** | 365 | 1217 | Y | 63 [28] | a = 90,000<br>s = 0.07 |
| **CF3** | 278 | 952 | Y | 41 [13] | a = 40,000<br>s = 0.03 |

[a] Insufficient data to create home range estimate.

### 3.4.3. Survival, breeding, and demography

All reintroduced females reproduced during the study. Each female gave birth to their first litter after home range establishment (131.1 ± 7.6 SD days post-release; *n* = 3; range = 123-138). However, considering a gestation period of up to 95 days (Estes, 2012), females must have conceived within two months post-release. CM2 and CM1 were observed during courtship behaviour with CF2, 39 days and 567 days post-release, respectively. Successful denning lasted between 53-56 days (55.0 ± 1.4 SD days; *n* = 4 litters) and litter size ranged from three to six cubs (4 ± 1.4 SD cubs; *n* = 4 litters). Cub mortality was highest between birth and six months. Of the four cubs lost, the cause of death was not formally identified as no remains were found. Regardless, all recorded litters survived denning. Of the four recorded litters, two reached independence, one was lost, and at the time of writing one was still dependent (< 6 months; Table 3.4).

Sixteen births and six confirmed mortalities were recorded within the total population over the course of the two-year study. Of the reintroduced individuals; CF3 was killed in a snare 307 days after release, and CM2 was killed by a crocodile (*Crocodylus niloticus*) 612 days after release, CM4 and CM3 were labelled as missing (CM4 85 days post-release; CM3 152 days post-release) as no mortality was confirmed. CF1, CF2, and CM1 survived the first two years post-release.

**Table 3.4.** Details of the reproduction success of female cheetah reintroduced into LNP.

| Female | Age at First Reproduction (months)[a] | Interbirth Interval (months)[b] | Litter | DOB | Litter Size (in den) | Litter Size (6 months) | Independence Reached | Age at Independence (month) |
|---|---|---|---|---|---|---|---|---|
| **CF2** | 30 | 17.7 | CF2a<br>CF2b | Oct-17<br>Apr-19 | 4<br>6 | 3<br>N/A[c] | 3<br>N/A[c] | 15.9<br>N/A[c] |
| **CF1** | 27 | N/A | CF1a | Oct-17 | 3 | 3 | 3 | 15.4 |
| **CF3** | 26 | N/A | CF3a | Jun-18 | 3 | 0 | 0 | N/A |

[a] The age of the female when she gave birth to her first litter. [b] Time between known birthing events. [c] Litter < 6 months of age at end of study.

## 3.5. Discussion

This study found that post-release movements of reintroduced cheetah were sex-specific, with males displaying larger exploratory movements than females. Of the cheetah for which post-release movements were analysed, settlement took place an average of 106 days post-release (range 29-206 days post-release). This is comparable to findings of translocated cheetah in Namibia, which settled between 13 and 190 days (Weise *et al*., 2015b). Considering the differences between these two case studies; translocation of ‘problem’ cheetah to unfenced reserves with variable holding periods, including hard-releases, versus the reintroduction of select individuals from a founder population into a fenced reserve using a soft-release acclimatization technique, settlement time was likely not a factor of reserve type (closed or open) or individuals selected for relocation. As predicted settlement occurred sooner for females than males with all females establishing home ranges before the denning period.

When considering a gestation period of 90-95 days (Bissett & Bernard, 2011; Estes, 2012), all females released into LNP conceived within their first two-months post-release. This time frame is similar to that of a female reintroduced into Pilanesberg National Park, South Africa (Power *et al.*, 2019) and sooner than those translocated into Namibian PAs (>3 months; Weise *et al*., 2015b). Increased habitat heterogeneity has been attributed to reduced kleptoparasitism, flexibility in hunting strategies and higher survival rates for cheetah (Bissett & Bernard, 2007; Broomhall *et al.*, 2003; Rostro-Garcia, Kamler & Hunter, 2015; Durant, 1998a; Durant, 1998b). Vegetation cover is also particularity important for cub survival (Durant, 1998a). Weise *et al.* (2015b) suggested that translocated cheetah, which originated from woodland vegetation and were released in sparsely vegetated deserts, exhibited increased post-release movements in search of familiar or more suitable habitat conditions. It is therefore suggested that LNP’s mixed habitat structure, low density of competitors, and high prey populations provided suitable habitat, and likely reduced post-release displacement and influenced breeding and settlement for females. While CF1 and CF2 settled after conceiving, CF3 established a home range prior to conceiving, indicating pregnancy may not have influenced settlement behaviour. All females released into LNP denned within 1.6-2.4 km of the holding boma, further indicating that the presence of suitable habitat near the release site may have influenced post-release exploration and time to reproduction for females.

Male home ranges took longer to establish than females. CM2’s home range overlapped with all females (*see* Chapter 5) and he is believed to have sired the first three litters in the park (pers. obs.; DNA test pending). As CM2 aged and CM1 reached maturity, CM1 began to encroach on CM2s territory, and eventually commandeered the territory upon CM2s death (pers. obs.). This behaviour indicates male territoriality in LNP is strongly influenced by female home ranges. Based on high levels of female home range overlap, females are possibly a limited resource.

Cheetah have the necessary characteristics for translocation and reintroduction; they can tolerate a variety of habitats, undertake long-distance movements and consume a variety of prey species (Caro, 1994). However, cheetah experience lower survival rates during the first-year post-release when compared to other large African carnivores (Fontúrbel & Simonetti, 2011; Hayward *et al*., 2007b). Regardless, LNP's one-year post-release survival rate (57 %, assuming the loss of CM3 and CM4 from the monitored population) was greater than the average found for felids in a review of translocations (39 ± 6 SE %; Fontúrbel & Simonetti, 2011). When compared to individual case studies, LNP's survival rate was higher than that of cheetah in Matsuadona National Park (36 %; Purchase & Vhurumuku, 2005) but considerably lower than those released into South African fenced reserves (84 %; Marnewick *et al.*, 2009). While soft-releases are thought to decrease post-release movements and thereby increase survival (Adania *et al.*, 2016; Devineau *et al.*, 2011; Fritts *et al*., 2001; Hayward *et al.*, 2007a; Hunter, 1998b), cheetah naturally exhibit wide-roaming movements. The current study found no significant relationship between additional time (>23 days) in a holding boma and post-release movements. Furthermore, the one-year post-release survival rates were lower than those of cheetah hard-released into unfenced PAs in Namibia (67 %; Weise *et al.*, 2015b). Therefore, the current study suggests that holding periods greater than 23 days do not influence post-release movements in cheetah, which is supported by Weise *et al*. (2015b). Similar studies with leopard (Weise *et al*., 2015a) and tiger (*Panthera tigris*; Sarkar *et al*., 2016) have also demonstrated that hard-releases can yield comparable successes to soft-releases. Results reported in this study, therefore support the notion that external factors, rather than pre-release management, largely impact post-release movements and ultimately reintroduction success of the population.

A magnitude of external factors can affect post-release success in reintroduced carnivores. In this case study, it was presumed that LNP's large prey base, suitable denning habitat, and low levels of intraguild competition influenced post-release movements and settlement of reintroduced female cheetah. This is further supported by the rapid post-release breeding (*see*, Weise *et al.*, 2015b). However, it must also be considered that the holding period may have affected females differently than males, with females retaining release site fidelity at a different intensity. Prolonged confinement of African wild dogs has been found to negatively impact reproduction and overall success of the released pack, such that ultimate holding periods have been defined based on artificial pack size (Marneweck *et al*., 2019). It is, therefore, possible that there is an optimal holding period for females versus male cheetah or, holding time and age at which females were released may influence breeding success and thus promote rapid settlement, as seen with the females in this study.

While at least one male cheetah bred soon after release, it is unclear what factors influenced their extensive post-release movements, as intra- and interspecific conflict within the recipient park was low at the time of release. Although two of the four males returned to the area of the release site, they encountered the perimeter fence on numerous occasions during post-release exploration. It is therefore unclear what their fate would have been if the protected area was not semi-closed. In open systems it has been suggested that to prevent extensive male exploration, male cheetah should be released first, while females remain in a holding boma as an "anchor" (Boast *et al*., 2018). CM2 was released one week prior to CF1 and CF2, during this time he undertook the majority of his post-release exploration and did not revisit the boma location. This study, therefore, suggests that the post-release movements and reintroduction success of male cheetah was strongly influenced by natural and physical barriers of the recipient park. While this extensive exploration is comparable to natural dispersal for male cheetah, factors influencing this behaviour, post-translocation or reintroduction, are not immediately clear and warrant further investigation.

Long-distance translocations have shown to prevent homing in most large carnivores (Briers-Louw *et al.*, 2019). In a study of translocated cheetah, animals released >137 km from their capture site showed no evidence of directional homing movements (Weise *et al*., 2015b). This reintroduction relocated cheetah an average of 1644 km (straight line distance) from their capture reserves. Therefore, this study did not investigate homing behaviour. Released cheetah did exhibit high levels of release site fidelity, indicative of release site acceptance and minimal homing. While this may be a factor of the soft-release procedure, a study of translocated cheetah in Namibia found that the amount of acclimatization time and additional translocation distance did not significantly influence site fidelity on recipient reserves (Weise *et al*., 2015b). The current study therefore proposes that site fidelity in this case study may be attributed to ecological factors near the release site that created suitable home range patches.

Reintroductions are a costly conservation practice. As an example, in Namibia and South Africa, the cost of a single cheetah translocation was estimated at 2730 USD (Marnewick *et al*., 2009; Weise *et al*., 2015b). These figures rarely include fixed costs such as holding enclosures and general resource availability. Financial, human and biological resources such as food, which in this case was limited, are especially important when implementing pre-release management techniques such as soft-releases (Marneweck *et al*., 2019). The current study highlights that the effects of pre-release techniques and external factors on post-release movements and subsequent release success requires further investigation. A holding period is important in the prevention of disease spread, forming social groups, and where applicable, exposing individuals to electrified fences (Hunter, 1998a). However, in this study, holding periods greater than 23 days had no significant effect on post-release movements. It is therefore suggested to investigate optimal acclimatization times as well as site-factors that may contribute to reducing post-release exploration, such as predator-proof fencing, natural barriers, heterogeneous habitats, low densities of competing carnivores and sufficient prey base. Improving our understanding of how pre-release management and external factors interact to affect post-release movements and settlement will encourage well-informed cheetah reintroduction and translocation projects and ultimately reduce unnecessary costs and increase overall project success.

Lion are a major cause of mortality in cheetah populations (Buk *et al*., 2018; Durant, Kelly & Caro, 2004; Laurenson, 1994) and can, therefore, pose a threat to reintroduced individuals and population establishment. It is recommended that cheetah undergoing translocation or reintroduction to areas with resident lion populations have prior lion knowledge (Hayward *et al*., 2007a). Lion were reintroduced to LNP between 107 and 354 days post cheetah release. Fifty-one percent (4/7) of LNP's reintroduced cheetah were sourced from reserves with lion populations. Cheetah tend to have higher survival rates when reintroduced prior to lion reintroductions (V. van der Merwe, pers. comm.). No lion caused mortalities were recorded during this study, contrasting other fenced reserves where lion caused mortalities accounted for most post-release mortalities (Buk *et al*., 2018; Hayward *et al*., 2007b; Marnewick *et al.*, 2009). Although CM3 and CM4 had unknown fates, it is unlikely either were killed by lion, due to lion movement at the time. LNP is protected by predator-proof fencing, with a 6 km open corridor to Mangochi Forest Reserve (unfenced during this study). Regardless, fences have been shown to be permeable to cheetah (Cozzi *et al.*, 2003), it is therefore possible that these animals exited the protected area or moved into Mangochi Forest Reserve during their post-release exploration.

Intraspecific competition is generally believed to be more detrimental to released animals than residents (Massei *et al*., 2010), and male cheetah have been shown to demonstrate high levels of intrasexual aggression (Caro & Collins, 1987; Eaton, 1968). Currently, LNP has areas that are devoid of cheetah activity which appear to be suitable habitat due to low levels of intraguild competitors and high prey populations. However, encounters with females will not occur in these areas, which may result in these habitats ceasing to be attractive. It is, therefore, possible that the presence of CM1 and CM2 within the habitat patch that allowed for access to females, resulted in the competitive exclusion of CM3 and CM4 and in turn influenced their post-release exploration. Non-territorial male behaviour (male floaters; Caro, 1994) is common for cheetah and has shown to increase mortality rates. A similar phenomenon was recorded by Hunter (1998a) during the reintroduction of cheetah in Phinda Private Resource Reserve and by Fattebert *et al*. (2013) with a male leopard during dispersal. The loss of CM3 and CM4 mimics natural dispersal and loss of males within the population under these circumstances. In the Serengeti, male survival was found to be lower than female survival, and although males are thought to gain higher survival from group living, male coalitions only benefited during periods when coalitions were numerous (Durant *et al.*, 2004), which was not the case upon the release of CM3 and CM4. Prioritizing the early post-release monitoring of male cheetah is therefore recommended as their large-scale movements will increase their potential of encountering threats. However, these long-distance movements pose an increased difficulty for VHF based monitoring. Therefore, it is recommended that LNP prioritize funds towards GPS collars for male cheetah and allocate VHF collars to females who travel minimal distances post-release.

One founder individual (CF3) died in an old wire-snare set for ungulates. No other snaring events were recorded in the population during this study. LNP's law enforcement removed >27000 snares in the two-years prior to this reintroduction. Nevertheless, it is impossible to account for all snares within the PA. Due to the proximity of impoverished communities, poaching remains inevitable and extensive patrols and snare sweeps are needed to ensure minimal anthropogenic impact on LNP's cheetah population.

Home ranges for cheetah in woodland environments have been found to vary greatly from 24 km$^2$ in Matusadona National Park, Zimbabwe (Purchase & Vhurumuku, 2005) to 195 km$^2$ in Kruger National Park, South Africa (Broomhall *et al.*, 2003). Variations can be attributed to biological and ecological factors, as well as the analysis methods employed. While home range size for cheetah in LNP fell into this range, no previous studies have used T-LoCoh methods to estimate cheetah home ranges in woodland environments. Regardless, the core area of use (50 % home range isopleths) for cheetah have often been found to average an area of 10-14 % of the 95 % home range size (Broomhall *et al.*, 2003; Houser, Somers & Boast, 2009; Marker *et al.*, 2007; Marnewick & Somers, 2015). The reasoning for this phenomenon is unknown; however it was not found within LNP's population where core areas comprised 28-56 % of home range size. Influences on home range size and overlap should be investigated further.

Overall, this reintroduction had a 57 % (80 % for GPS collared animals) success rate based on the earlier definition of individual reintroduction success: an individual demonstrating release site fidelity, successful reproduction, settlement, and survival of at least one year. Furthermore, 83 % (5/6) of LNP's cheetah social groupings established home ranges within the first-year post-release, indicating a successful population establishment based on the earlier definition. LNP's reintroduced population also appears to have conformed to demography seen in the source population of CMP reserves. Although the average age at which cubs reached independence, 15.6 months, was slightly lower (16-17 months; Bissett & Bernard, 2011; Power *et al.*, 2019), cub survival to independence (60 %) was similar (50-60 %; Bissett & Bernard, 2011; Hunter, 1998b; Power *et al.*, 2019). LNP's cheetah population has grown since reintroduction and consisted of 14 individuals two-years after initial reintroduction (three breeding adults, six sub-adults and five dependent cubs). Therefore, based on all three outlined definitions, the reintroduction of cheetah to LNP was deemed successful.

Reintroduction biology traditionally focuses on factors that determine the success of a reintroduction event (Armstrong & Seddon, 2007). Reintroduction success can be viewed on three scales: an individual's settlement, the establishment of a population and the overall population persistence (Armstrong & Seddon, 2007). If post-release movements and mortality are low, individuals will reach settlement sooner thereby allowing the population to reach establishment with only a small founder population (*eg.*, Briers-Louw *et al.*, 2019; Hayward *et al.*, 2007b; Towns & Ferreira, 2001; Taylor, Jamieson & Armstrong, 2006). The population reintroduced to LNP succeeded in reaching establishment with a founder population of seven individuals (five individuals reaching settlement and four surviving the first-year post-release). Successful establishment, however, is not indicative of population persistence. In CMP reserves that did not experience population persistence, extirpation of the population occurred an average of 8.4 ± 4.9 SD years after initial reintroduction (Buk *et al.*, 2018). LNP park management must, therefore, consider long-term population persistence and address factors that may cause extirpation as carnivore numbers in the park increase, such as increased intra- and interspecific competition, inbreeding depression, reduced prey populations and stochastic events.

Small populations are extremely susceptible to stochastic events, such as disease outbreaks, this, therefore, poses a high risk to LNP's cheetah population in its current state (14 individuals) and could result in extirpation. In the long term, inbreeding depression due to the small population of breeding animals is the greatest threat to the persistence of LNP's cheetah population. Due to its semi-closed state and the lack of free-roaming populations in neighbouring areas, LNP’s cheetah population is at high risk of inbreeding. Similar issues have been addressed in reintroduced lion populations, where inbreeding and rapid population growth resulted in intensive management and the debated value of the population to the conservation of the species on a larger scale (Hunter *et al*., 2007). While the long-term conservation value of LNP’s cheetah population is unclear, effective population management can increase its potential to assist in the development of a source population. The importance of long-term genetic sampling is therefore emphasised to ensure paternity and inform management decisions. Should CM2 have sired all six cubs that reached independence, then their removal from LNP is imperative as the increased number of male coalitions risks the tenure of CM1 and may result in males’ mating with their mothers and sisters. The supplementation of an unrelated male coalition to LNP's current population is therefore recommended, as they could naturally take tenure from CM1 and prevent inbreeding. LNP's connection within the EWT's CMP enables a human-mediated metapopulation approach to this population which is strongly encouraged. The removal and supplementation of individuals will assist in mimicking natural dispersal (Ferreira & Hofmeyr, 2014) and ensuring the long-term genetic integrity of the population. Furthermore, the recent reintroduction of cheetah unrelated to LNP’s cheetah to Majete Wildlife Reserve, Malawi, allows for the development of a metapopulation node within Malawi. Continued monitoring of these two populations is highly recommended to allow for the adaptive and predictive management which will allow for strategic and pre-emptive planning surrounding Malawi’s cheetah population, which will assist in the long-term persistence of the species in Malawi. The importance of investigating subsequent reinforcement events to further examine the effects intraspecific competition has on post-release movements, and how to reduce the potential for competitive exclusion to ensure individual reintroduction success must also not be neglected.

The conservation value of PAs in Malawi have declined over the last few decades due to a lack of funding, high levels of poaching, and encroachment. Certain PAs are now shifting towards a fenced-system approach to stem natural resource off-take and edge effect pressures caused by surrounding communities. With the projected doubling of populations within 26 African nations by 2050 (United Nations, 2018), Malawi is a microcosm of the issues that will encompass PAs across Africa within the next few decades. The initial success of this reintroduction is therefore not only encouraging for the continued re-establishment of cheetah populations across fenced-systems in Malawi, but for the future of range expansion projects within the continent.

## 3.6. Conclusion

The reintroduction of cheetah in LNP was the first reintroduction or translocation of cheetah to occur in Malawi. This reintroduction experienced varying levels of individual success. However, it was considered overall successful based on individual survival and reproduction rates. Although most of the reintroduced cheetah demonstrated release site fidelity and established home ranges, future reinforcements of the population and reintroductions within other protected areas should undergo rigorous recipient area and release site selection to improve individual and population level success. The success of this reintroduction is encouraging for continued range expansion of cheetah populations in Malawi.

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Relevant permits for the work were obtained by African Parks during the routine monitoring. (CITES permit numbers: 175828; 0000062; 0000079). Ethical clearance for the use of collar data as a third-party user was obtained through Stellenbosch University (ethics reference number: ACU-2018-8311).

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## 3.10. Appendices

**Appendix 3.A.** Yearly large carnivore population estimates for LNP, Malawi.

| **Year** | **Species** | | | |
|---|---|---|---|---|
| | **Spotted Hyena** | **Cheetah** | **Lion** | **Leopard** |
| **2017** | 12 | 10 | 0 | 0 |
| **2018** | 17 | 10 | 9 | 0 |
| **2019** | 13 | 17 | 9 | 0 |
| **Notes** | Population estimates determined through targeted camera trapping throughout the year. | Population known not estimated. | Population known not estimated. | Population estimated from camera trapping and reports. |

# Chapter Four

## Prey Preference of Cheetah in Liwonde National Park, Malawi, and a Comparison of Diet Composition Methodologies

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### 4.1. Abstract

Understanding carnivore diet is essential for evaluating a species impact on its environment, local prey populations and other carnivores. A comprehensive understanding of the dietary requirements for carnivores is therefore critical to their conservation management. The cheetah is Africa's most endangered felid, with an estimated 6700-7100 individuals remaining in the wild. Whilst numerous studies have investigated cheetah diet; local assessments are still required to develop our understanding of regional variations in prey selection in order to inform conservation management strategies of individual populations. In 2017, seven cheetah were reintroduced into Liwonde National Park (LNP), Malawi, as part of a range expansion project after a 20-year absence from the country. This study aimed to develop the first comprehensive diet assessment of cheetah in Malawi, as no previous research had been conducted on this species in the country prior to its extirpation. Additionally, this study compared diet assessment methodologies for large carnivores within the protected area in order to inform future large carnivore research. Diet was determined through direct carcass observations and cross-section analysis of hair from scats. In total, thirteen prey species were identified. Cheetah were found to predominantly feed on greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), and bushbuck (*Tragelaphus sylvaticus*), and demonstrated the highest preference for kudu. All four of these important prey species experienced asymmetrical predation across their demographics. Asymmetric predation has strong implications on population demographics of prey species and may increase the likelihood of population collapse in certain species. It is therefore recommended that additional diet studies are conducted across the large carnivore guild in LNP to assess the level of multi-species predation which will better inform predator-prey management. Due to the minimal road network, moderate tourism levels, and mixed woodland habitat of LNP, combining scat analysis and GPS site investigation provided the most complete estimate of diet. Due to the similarities in protected areas across Malawi these findings have countrywide applicability. Therefore, it is recommended that future large carnivore diet studies in Malawi employ both GPS site investigation and scat analysis in order to form the most robust carnivore dietary assessment.

## 4.2. Introduction

Carnivores are important ecosystem drivers as they exert top-down regulatory pressure on herbivores, mesopredators and competitors (Atkins *et al*., 2019; du Preez *et al.*, 2017; Owen-Smith & Mills, 2008). A thorough understanding of carnivore diet is therefore essential in evaluating a species' impact on its environment, local prey populations and other carnivores. Numerous methodologies have been adapted to assess carnivore diet, namely; stomach content analysis, direct feeding observations, carcass observations through GPS cluster investigation, scat analysis and isotope analysis (*see*, Balestrieri, Remonti & Claudio, 2011; Bissett & Bernard, 2007; Boast *et al*., 2016; Davies-Mostert *et al.*, 2010; du Preez *et al.*, 2017; Perilli *et al.*, 2016; Pitman *et al.*, 2014; Tambling *et al.*, 2014; Tambling *et al.*, 2012; Voigt *et al.*, 2014). While these techniques are effective in determining diet composition, they are not exempt from bias. Scat analysis, for instance, can incur varying biases based on hair identification, analysis and scat collection techniques (Marucco, Pletscher & Boitani, 2008; Steenweg *et al*., 2015). For example, double sampling can occur when collecting scats blindly from group living carnivores (Davies-Mostert *et al.*, 2010), and an overestimation of small prey species consumed can occur when employing certain analysis methods (Klare, Kamler & MacDonald, 2011). GPS cluster investigation and direct observations, on the other hand, can result in data favouring prey captured on accessible terrain and larger prey items, which tend to leave more remains (Davies-Mostert *et al.*, 2010; Perilli *et al.*, 2016). Irrespective, diet composition studies are crucial to informing carnivore management and conservation.

The cheetah (*Acinonyx jubatus*) is Africa's most endangered large felid with an estimated 6700 to 7100 wild individuals remaining (Durant *et al*., 2017). Most remaining cheetah populations are in southern Africa as cheetah have been extirpated from over 90 % of their historic range (Durant *et al.*, 2017). Extensive information regarding cheetah prey requirements and feeding ecology has therefore been reported to assist in their conservation. Collated diet studies have determined that cheetah are opportunistic predators that predominantly kill the most abundant medium-sized (10-35 kg) antelope such as Thomson's gazelle (*Eudorcas thomsonii*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*) and young kudu (*Tragelaphus strepsiceros*) (Bissett & Bernard, 2007; Boast *et al.*, 2016; Craig, Brassine & Parker, 2017; Hayward *et al*., 2006; Klein, 2006; Mills, Broomhall & du Toit 2004; Schaller 1968). However, prey demographics, kleptoparasitism and habitat preference modify prey selection on a local scale (Bissett & Bernard, 2007; Clements, Tambling & Kerley, 2016; Fitzgibbon, 1990; Hayward *et al.*, 2006). Therefore, local diet composition studies will contribute to an increased understanding of regional variations in cheetah diet and subsequently, the conservation management of both predator and prey populations (Davidson *et al.*, 2019; Hayward *et al*., 2006; Makin & Kerley, 2016; O'Brien *et al.*, 2018; Power, 2002).

Despite Myers' (1975) description of Malawi as unsuitable cheetah habitat due to low prey densities within its miombo woodlands, sightings of cheetah were reported across three of the country's protected areas into the 1980s (Gros, 1996; Purchase & Purchase, 2007). However, by 1989 Malawi's cheetah population was confined to Kasungu National Park and believed to be mainly transient with Zambia's Luangwa Valley (Gros, 1996). By the 1990s, the continued reduction of Malawi's habitat and prey base, coupled with the depletion of Zambia's Luangwa Valley cheetah population resulted in the extirpation of cheetah from Malawi (Purchase & Purchase, 2007). In 2017, African Parks (AP) in partnership with the Endangered Wildlife Trust (EWT) began cheetah reintroduction efforts in Malawi. Seven founder cheetah (four males and three females) were released in Liwonde National Park (LNP) between 2017 and 2018 as part of a range expansion project initiated by the two organizations. Intensive post-release monitoring was conducted, which included the collection of diet data through two methodologies, scat collection and direct carcass observations.

This study sought to determine diet composition and prey preference of reintroduced cheetah in LNP and outline the most comprehensive diet estimation methodology for large carnivores within the protected area. As the first study to assess the diet of cheetah in Malawi, the findings are expected to greatly contribute to the conservation of the newly established populations within the country and assist in evaluating other recoverable range in Malawi. Furthermore, this is the first carnivore diet study to be conducted in LNP, and one of the few conducted in-country to date. It will, therefore, act to inform the development of future carnivore research and monitoring initiatives in Malawi's protected areas. It was hypothesized that reintroduced cheetah would select the most abundant medium-sized prey, impala, and favour males due to the lack of previous predation within the population (Fitzgibbon, 1990). Direct observation of kills was projected to be difficult due to the park's limited road network. It was therefore hypothesized that scat analysis would provide the most detailed depiction of cheetah diet for LNP.

## 4.3. Methods

### 4.3.1. Study site

Spanning 548 km$^2$, LNP is located in the Upper Shire Valley in the southern region of Malawi (Figure 4.1). LNP has distinct wet and dry seasons, the average precipitation is 944 mm per year, with the majority of rainfall occurring between December and March, with June to October classified as dry months (Bhima & Dudley, 1996). Mean high temperatures range from 28$^{o}$ in July to 40$^{o}$ C in November (Bhima & Dudley, 1996). The Shire River is the sole perennial river and the dominant feature of the park as it runs the length of the boundary splitting the park into an eastern and western side. In the wet season, the Shire River creates extensive lagoons and marshlands along the floodplains which border both sides of the river. While LNP contains a multitude of seasonal rivers and streams, only a few pockets of water remain scattered around the park by September, making the Shire River the main water source.

As part of the southern Rift Valley ecosystem, LNP is relatively flat and consists mainly of dry deciduous woodland (Dudley, 2004). The principal tree in the park is *Colophospermum mopane*, with mopane woodland complex occupying approximately 74 % of the park (Dudley, 2004). Grasslands and floodplains (*Setaria* spp. *Digitaria* spp. *Sporobolus* spp.) along with forest thickets and mixed woodlands (*Combretum* spp., *Terminalia* spp. *Borassus* spp. *Vachellia* spp. *Cordyla* spp. *Trichilia* spp.) are interspersed throughout the park, mostly occurring in north-south bands that run parallel to the Shire River (Dudley, 2004). There are seven distinctive hills found throughout the park with a maximum altitude of 921 m (Mzumara, Perrin & Downs, 2018). The northern boundary consists of a 6 km unfenced corridor to Mangochi Forest Reserve (MFR), the recent inclusion of MFR into the management of LNP expands the protected system by 375 km$^2$ (923 km$^2$ total; C. Reid, pers. comm.).

The 2018 aerial survey observed 16646 animals across 25 species including, 17 ungulate species, within LNP (Sievert & Reid 2018; Appendix 4.A). The dominant herbivore species' in the park are waterbuck (*Kobus ellipsiprymnus*) and impala. Herbivore distribution in LNP is highly dependent on water availability, therefore, dry season distribution is highest on the Shire River floodplain with densities reaching 103 animals/km$^2$ (Sievert & Reid, 2018). The highest diversity of herbivores can be found on the eastern side of the Shire River where three species of large carnivore are now present, spotted hyena (*Crocuta crocuta*), as well as cheetah and lion (*Panthera leo*) which were recently reintroduced after extirpation (Sievert & Reid, 2018).

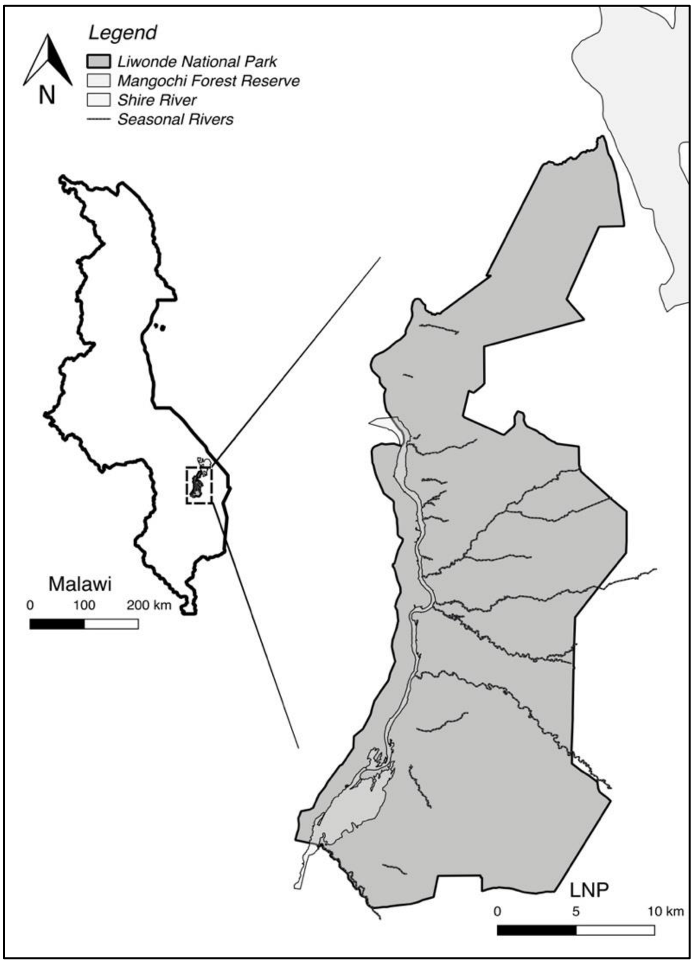

**Figure 4.1.** Map of LNP depicting the Shire River as well as the park's location in Malawi and in reference to MFR.

### 4.3.2. Pre- and post-release management

Seven cheetah (four males and three females) were reintroduced into LNP over four different release events between June 2017 and February 2018 (Table 4.1). To ensure maximum possible genetic diversity, animals were sourced through the EWT's Cheetah Metapopulation Project (CMP). Reintroduced individuals originated from five separate reserves in South Africa. Before arrival in LNP, three females and two males were fitted with Pinnacle LITE global positioning system (GPS) satellite collars (Sirtrack, Hawkes Bay, New Zealand) and one male was fitted with a very high frequency (VHF) tracking collar (African Wildlife Tracking, Pretoria, South Africa). Collars weighed approximately 465 g (GPS) and 253 g (VHF), 0.4-1.3 % of body mass respectively. All individuals were kept in temporary holding enclosures (bomas; 50x50 m) before release. Holding periods ranged between 23 and 58 days. Once individuals were sufficiently settled they were released directly from the boma through coaxing with a final feed, the gate was then closed behind them to ensure they did not return to the boma. No animals were fed post-release.

Since the release in LNP, cheetah have been monitored closely following guidelines set by the IUCN for reintroductions and translocations (IUCN/SSC, 2013). Park management implemented an adaptive monitoring approach (*see*, IUCN/SSC, 2013) for this reintroduction, therefore monitoring strategies were adapted over the course of the study. GPS collars were scheduled to collect a minimum of three GPS points per day, and this scheduling was increased based on birthing events or for injured animals to intensify monitoring capabilities. GPS points were also investigated for evidence of kills *ad libitum* with an emphasis on females with dependent cubs, to assist in evaluating their cub rearing success. However, efforts were made to investigate GPS points evenly across animals. VHF Radio-tracking (herein VHF tracking) took place a minimum of twice a week, with attempts of one observation per cheetah per week. An R-1000 telemetry receiver (Communication Specialists Inc, California, USA) attached to a flexible H-Type antenna (RA-23K VHF antenna; Telonics, Arizona, USA) was used to locate each animal during VHF tracking events. Signal strength ranged from 500 m to 1.5 km depending on vegetation structure and season. The success of each VHF tracking event was therefore dependent on vegetation as well as each individuals level of habituation. Opportunistic sightings outside of scheduled VHF tracking events were also recorded. All sightings were recorded with a GPS location and the behaviour (*eg*, resting, vigilant, traveling, feeding) of the animal upon initial sighting was also noted.

Where applicable GPS collars were replaced prior to battery depletion and animals were re-fitted with Sirtrack VHF collars (Sirtrack, Hawkes Bay, New Zealand; Table 4.1) modified with a Long Range (LoRa) Geolocation transmitter (Smart Parks, Rotterdam, Netherlands). Re-fitted collars weighed 359 g and allowed for continued weekly observation attempts. Over the course of this study 16 cubs were born, of which six reached independence during the study. Of the six cubs to reach independence, three were fitted with the LoRa modified Sirtrack VHF collars to allow for monitoring during dispersal and settlement.

**Table 4.1.** Specification for collars, VHF tracking (June 2017 – July 2019) and GPS investigation (July 2017 – November 2018) of cheetah reintroduced into LNP, Malawi. Only one male from each coalition was fitted with a VHF collar.

| ID Code | Release Date [event] | Social Grouping | Collar Type | Transmission Success Rate (%) | No. Transmission Days | No. Locations Transmitted | No. Sightings | No. kills (*VHF Tracking)* | No. kills *(GPS Investigation)* |
|---|---|---|---|---|---|---|---|---|---|
| **CM1** | 12-06-17 [2] | Single Male | GPS/VHF | 54.9 | 297 | 594 | 26 | 3 | 6 |
| **CM2** | 05-06-17 [1] | Single Male | GPS/VHF | 66.3 | 520 | 2157 | 113 | 9 | 31 |
| **CM3** | 07-02-18 [4] | Two Male Coalition | VHF* | N/A | N/A | N/A | 19 | 0 | N/A |
| **CF1** | 12-06-17 [2] | Breeding Female | GPS | 97.2 | 759 | 3747 | 45 | 8 | 44 |
| **CF2** | 13-06-17 [3] | Breeding Female | GPS/VHF | Unknown | 508 | 1633 | 79 | 14 | 67 |
| **CF3** | 07-02-18 [4] | Breeding Female | GPS | 95.0 | 307 | 1032 | 16 | 2 | 19 |
| **Ch1** | ** | Two Male Coalition | VHF | N/A | N/A | N/A | 27 | 2 | N/A |
| **Ch3** | ** | Single Female | VHF | N/A | N/A | N/A | 24 | 1 | N/A |
| **Ch6** | ** | Two Male Coalition | VHF | N/A | N/A | N/A | 5 | 1 | N/A |

* VHF collar not modified with LoRa device. ** Individuals born in LNP that reached independence and were subsequently collared.

### 4.3.3. Data collection

#### 4.3.3.1. Carcass observations

Direct carcass observations took place during GPS site investigation (herein GPS investigation) between July 2017 and November 2018 (514 days). Unlike other large carnivores, cheetah do not remain in close proximity to their kill until it is mostly consumed, instead, they reduce prey handling time to minimize the potential for kleptoparasitism (Hilborn *et al.*, 2018). Therefore, GPS investigation was not determined based on time spent in an area, as with other apex carnivores (*e.g.*, Blecha & Alldredge, 2015; Cassaigne *et al*., 2016; Martins *et al*., 2011; Pitman *et al*., 2014), but rather conducted *ad libitum* based on monitoring requirements outlined by park management. While emphasis was placed on females with dependent cubs to assist in evaluating cub rearing success, efforts were made to investigate GPS points evenly across individuals. A Garmin eTrex® 10 (Garmin International, Olathe, KS, USA) was used to navigate to GPS sites no older than two weeks. A search for prey remains was conducted at each site within a 30 m radius. Once found, prey remains were photographed and where possible, identified to species level, sexed and aged. Age classifications were: infant (<1 year), juvenile (not fully developed) or adult (fully developed). When a prey item was unidentifiable, hair samples were collected and analysed to the species level through cross-section analysis, described by Douglas (1989).

During data collection, it was assumed that the cheetah associated with the carcass made the kill, as cheetah rarely scavenge (Caro, 1982; Pienaar, 1969). Additionally, carcasses were assessed for signs that they had been killed and consumed by a cheetah. Teeth marks and/or saliva on the neck, minimal bone-crushing and visible skinning from consumption were representative of a cheetah kill of a medium-sized antelope (Bothma, 2016; Schaller, 1968). The area surrounding the carcass was also assessed for signs of cheetah activity such as tracks and scats, all signs were recorded.

Carcass data was further supplemented by feeding events recorded during weekly VHF tracking sessions or opportunistically between June 2017 and July 2019 (756 days). Kill data was labelled as opportunistic if it was collected outside of distinct VHF tracking events, or from reports provided by members of park management or tourism guides. All kill data collected from VHF tracking or opportunistically was visually confirmed and data collected by the cheetah monitor in the same manner as that collected during GPS investigation. All carcass observation sites can be seen in Figure 4.2.

#### 4.3.3.1. Scat analysis

Cheetah scats were collected between July 2018 and July 2019 (365 days) at kill sites, scent-marking sites and opportunistically (Figure 4.2). Roughly half of each scat was collected as male cheetah use scats as a means of territorial marking (Marnewick, Bothma & Verdoorn, 2006). To avoid double sampling, GPS locations were taken of each scat, and scent marking sites were sampled once in the wet season and once in the dry season, with only fresh scats, scats still dark in colour, being collected. Cheetah scats were distinguished based on appearance, the presence of tracks, kills or cheetah hair due to grooming (*see*, Stuart & Stuart, 2013).

Scats were stored in brown envelopes and labelled with the GPS coordinates, time, date, and where applicable, cheetah identification code. Scats were then dried in the sun for two days. After drying, scats were soaked in warm water for 24-48 hours, then washed in a 1.5 mm sieve until the water ran clear. After washing the remaining hair and contents were left to dry. Approximately 20 hairs from each scat sample were selected at random for analysis, and additional efforts were made to ensure all hair types based on general appearance were included.

Cross-sections of hairs were prepared using the techniques described by Douglas (1989). Hairs were positioned longitudinally in a 3 mm plastic Pasteur pipette which was then filled with molten wax (Paraplast Plus®, Leica Biosystems). The sample was then immediately cooled on ice. Once solidified, thin cross-sections were cut using a minora razor blade. Two pipettes were prepared per sample, each containing roughly ten hairs. Six sections of each pipette were mounted on a labelled glass slide. A Leica™ DM 2000 light microscope was used to examine each slide at 10x magnification. Photographs and measurements of cross-sections were taken using an Axiocam 208 Color camera with ZEN Imaging Software (Zeiss, Germany). Prey species were identified based on the cortex, medulla colouration, shape and thickness of the hair (Keogh, 1983). Hairs were identified to the species level using Rhodes University's and Cheetah Conservation Botswana's hair reference collection.

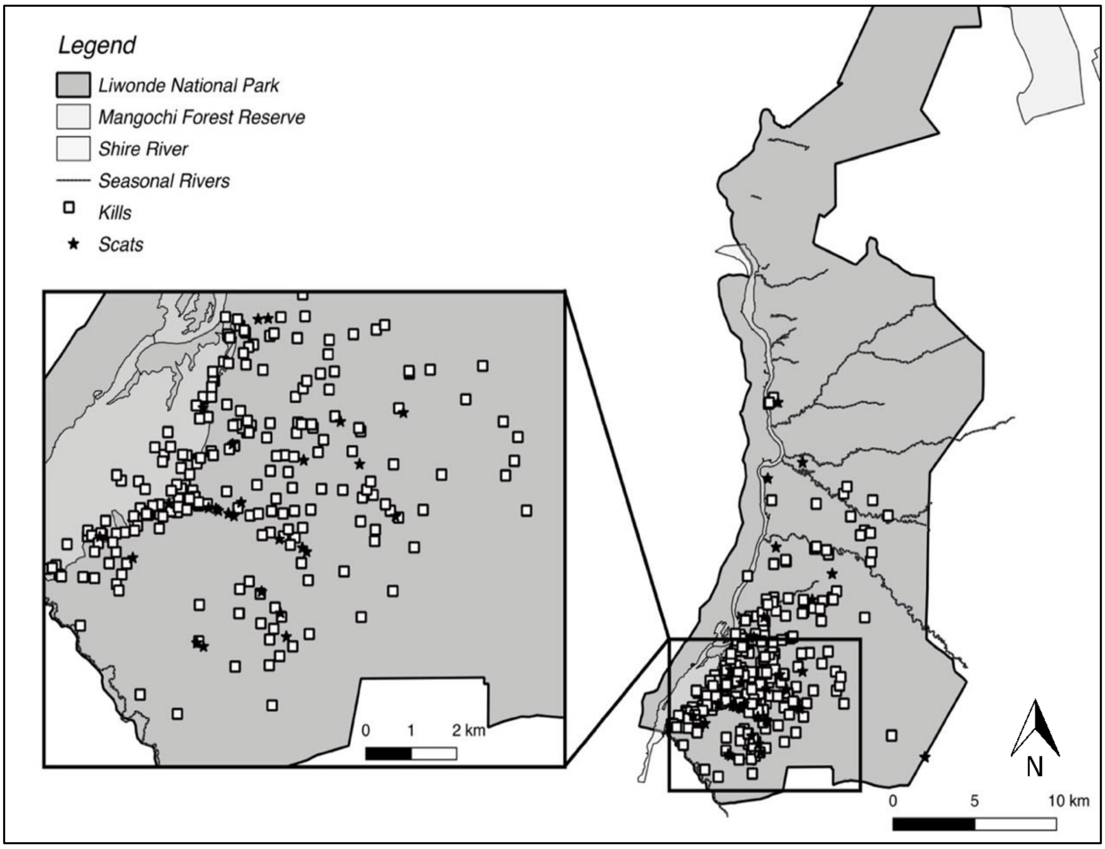

**Figure 4.2.** Map of LNP indicating the location of all carcass observations (*n* = 265) and scats collected (*n* = 43) during data collection for the assessment of cheetah diet

### 4.3.4. Data analysis

#### 4.3.4.1. Prey threat levels

To reduce the risk of injury and potential kleptoparasitism, cheetah predate asymmetrically across the demographic classes of most species, often preferring smaller individuals such as calves, juveniles and females. Not all individuals within the larger antelope species are, therefore a catchable size for cheetah (Boast *et al.*, 2016; Hayward *et al*., 2006). Threat levels from Hayward *et al.* (2006) were used to determine which species may experience high levels of asymmetric predation. Threat levels represent a species likelihood to exhibit elevated aggression or protection to its young during a predation event, thereby increasing their cost of capture to the point that outweighs the benefits of consumption (Hayward *et al.*, 2006). It was assumed that a species with a threat level of one or greater (*e.g.*, waterbuck) were generally inaccessible to cheetah and thus, only juveniles and calves of these species were potentially exposed to predation risks.

#### 4.3.4.2. Diet composition

Diet composition from carcass observations was analysed by calculating the relative frequency of each prey species identified, which was then converted into biomass consumed (Appendix 4.B). Diet composition from scat analysis was determined using three methodologies; frequency of occurrence per food item (FO), corrected frequency of occurrence per food item (CFO) and relative biomass. FO determines the frequency of predation on each species by developing a percentage by dividing the number of times a prey item was identified by the total number of prey items (Klare *et al*., 2011). CFO determines the occurrence of each prey species per scat by assigning a weighting of one to each scat, this weighting is then split between each prey item identified in that scat. Occurrence of a prey species is then developed into a percentage by dividing the occurrence per scat by the number of scats analyzed (Karanth & Sunquist, 2000). The biomass of each species consumed was then calculated using a relative biomass correction factor developed for cheetah by Marker *et al*. (2003). This calculation accounts for the different rates of digestibility of each prey species.

$$y = 0.0098x + 0.3425$$

The relative biomass correction factor calculates for the mass of prey consumed per scat ($y$) based on the average mass of an individual of a given species ($x$; Boast *et al*., 2016; Marker *et al*., 2003). The average mass of an individual prey species was collected from Boast *et al*. (2016) and Bothma (2016). All species categorized with a threat level greater than one were calculated with only the newborn body mass (Appendix 4.C). For small- to medium-sized prey, body masses were calculated as 75 % of adult female body mass, which accounted for the predation of all age classes (Boast *et al.*, 2016; Hayward *et al*., 2006). Additionally, although classified as a threat level of 0.5 (Hayward *et al*., 2006), cheetah have not been recorded preying upon adult male kudu in LNP, to account for this, the body mass for kudu was calculated at 50 % of female body mass.

### 4.3.4.3. Prey preference

All data analysis was conducted using prey population estimates collected during the 2018 dry season aerial survey (Sievert & Reid, 2018). Based on threat levels per species "catchable populations" were developed. Species classified with a threat level of one or greater were thought to only experience predation on juveniles and calves in the population. Due to a lack of predators in LNP before the reintroduction of cheetah, the demographics of a predation free kudu population were used to calculate an estimated "catchable population" (16.8 % of the total population; Makin & Kerley, 2016). Additionally, although classified as a threat level of 0.5, cheetah have not been recorded preying upon adult male kudu in LNP, therefore, the estimated male kudu population (18.6 %; Makin & Kerley, 2016) was removed from the total population to develop a catchable population estimate for the species.

The Jacobs' Index (Jacobs, 1974) was employed to calculate prey preference as it reduces the bias seen in other preference indices, such as an over-representation of rare food items (Jacobs, 1974).

$$D = \frac{r - p}{r + p - 2rp}$$

The Jacobs' Index standardizes the relationship between the relative abundance of the prey species ($p$) and the relative proportion of the species killed ($r$). If a species is killed more frequently than its relative abundance within the population it is considered preferred (+1 indicating maximum preference), whereas if it is killed less frequently than its relative abundance it is avoided (-1 indicating maximum avoidance). This is, however, a simplification, as the Jacobs' Index does not always reflect a predator's prey preference and consideration must still be given to a species vulnerability to predation, habitat in which it is found and ease at which it is captured (Hayward *et al.*, 2006).

Prey preference was calculated for species that were countered during the 2018 game count, therefore, rare or small prey species were not included in the calculations as no population data was available (Appendix 4.D). Calculations of prey preference were conducted independently for both scat analysis and carcass observations. Prey preference calculations were then conducted twice for each data collection method, once using total prey populations and once using "catchable" prey populations, thus providing a robust assessment of preference. It is important to note that while certain species (*eg.*, bushbuck) may experience predation across their demography, the relative abundance within the population of prey species changes when calculating catchable populations. It is therefore expected that Jacob's Index values will change for all species when calculating preference of the catchable population.

#### 4.3.4.4. Methodology comparison

Cumulative species detection curves were developed to compare data collection methodologies (Davies-Mostert *et al*., 2010). Species detection curves were generated by plotting the proportion of species observed each month over time, per scat or carcass observation. Two separate comparisons were made due to the data collection time frame, which allowed for GPS investigation to be compared against opportunistic carcass observations and VHF tracking (July 2017 – July 2018), and for scat analysis to be compared to opportunistic carcass observations and VHF tracking (July 2018 – July 2019). The proportion of the species observed was based on the total number of prey species documented across all methodologies (*n* = 13; July 2017 – July 2019).

## 4.4. Results

### 4.4.1. Diet composition

A total of 265 carcasses comprising nine species were recorded over the course of this study. Furthermore, scat analysis revealed one Order and three additional species (Table 4.2). Impala comprised the bulk of carcasses observed (45.3 %), but the species was identified in only 12 of the 43 scats and therefore only represented a small proportion of biomass consumed in scat calculations (15.3 %). Kudu was the third most numerous species documented during carcass observations (14 % of carcasses) and accounted for the majority of biomass consumed for both carcass observations (37.9 %) and scat analysis (50.5 %).

LNP's cheetah appear to exhibit asymmetric predation across the sex classes of three species (impala, bushbuck, *Tragelaphus sylvaticus*, and southern reedbuck, *Redunca arundinum*) and age classes of four species (bushbuck, impala, kudu, and waterbuck; Table 4.3). Bushbuck experienced the highest level of asymmetric predation across sex classes with female animals comprising 73.1 % (19/26) of carcasses observed. Kudu and waterbuck experienced the highest level of age-specific predation with 97.3 % (36/37) and 100.0 % of carcasses, respectively, recorded as either juveniles or infants. Whilst, suni (*Neotragus moschatus*), sable (*Hippotragus niger)*, and eland (*Taurotragus oryx*) also experienced asymmetric predation, their sample sizes ($n < 3$) were too limited to draw any conclusions.

**Table 4.2.** Diet composition of cheetah in LNP from carcass observations (July 2017 – July 2019) and scat analysis (July 2018 – July 2019). The frequency of occurrence (FO) is reported as the percentage of each prey item relative to the total number of prey items identified during scat analysis (*n* = 67). Corrected frequency of occurrence (CFO) is reported as the percentage of occurrences (per scat) relative to the total number of scats.

| **Prey Species** | **Carcass Observations *n = 265*** | | | **Scats *n = 43*** | | | |
|---|---|---|---|---|---|---|---|
| | **No. of Kills** | **% of Kills** | **Biomass Consumed (%)** | **No. of Scats with Prey Remains** | **FO (%)** | **CFO (%)** | **Biomass Consumed (%)** |
| Bushbuck, *Tragelaphus sylvaticus* | 26 | 9.8 | 7.1 | 9 | 13.4 | 15.1 | 10.3 |
| Bushpig, *Potamochoerus larvatus* | 0 | N/A | N/A | 2 | 3.0 | 2.3 | 1.3 |
| Common Duiker, *Sylvicapra grimmia* | 9 | 3.4 | 1.4 | 2 | 3.0 | 2.3 | 1.9 |
| Eland, *Taurotragus oryx* | 1 | 0.4 | 0.4 | 0 | N/A | N/A | N/A |
| Impala, *Aepyceros melampus* | 120 | 45.3 | 41.0 | 12 | 17.9 | 17.4 | 15.3 |
| Kudu, *Taurotragus strepsiceros* | 37 | 14.0 | 37.9 | 20 | 29.8 | 32.5 | 50.5 |
| *Squamata* Order | 0 | N/A | N/A | 1 | 1.5 | 1.2 | N/A |
| Sable, *Hippotragus niger* | 2 | 0.7 | 0.3 | 0 | N/A | N/A | N/A |
| Scrub Hare, *Lepus saxatilis* | 0 | N/A | N/A | 1 | 1.5 | 1.2 | 1.5 |
| Sharpe’s Grysbok, *Raphicerus sharpei* | 0 | N/A | N/A | 2 | 3.0 | 2.3 | 0.7 |
| Southern Reedbuck, *Redunca arundinum* | 14 | 5.3 | 4.5 | 7 | 10.4 | 9.3 | 8.7 |
| Suni, *Neotragus moschatus* | 1 | 0.4 | 0.0 | 0 | N/A | N/A | N/A |
| Waterbuck, *Kobus ellipsiprymnus* | 55 | 20.7 | 7.3 | 11 | 16.4 | 16.3 | 9.8 |
| ***Total*** | ***265*** | ***100*** | ***100*** | ***67**** | ***100*** | ***100*** | ***100*** |

*Does not represent the number of scats analysed, rather the number of prey unique predation events per total scat sample size (*n* = 43).

**Table 4.3.** Proportions (%) of sex and age classes of carcasses found during cheetah kill site investigations (carcass observations) in LNP, Malawi (July 2017 – July 2019).

| **Prey Species** | **Sex** | | | **Age** | | | |
|---|---|---|---|---|---|---|---|
| | **Male** | **Female** | **Unknown** | **Adult** | **Juvenile** | **Infant** | **Unknown** |
| Bushbuck | 19.2 | 73.1 | 7.7 | 73.1 | 19.2 | 0.0 | 7.7 |
| Common Duiker | 22.2 | 33.3 | 44.4 | 55.5 | 22.2 | 0.0 | 22.2 |
| Eland | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 100.0 | 0.0 |
| Impala | 54.2 | 30.0 | 15.8 | 72.5 | 21.7 | 3.3 | 2.5 |
| Kudu | 5.4 | 27.0 | 67.6 | 2.7 | 70.3 | 27.0 | 0.0 |
| Sable | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 100.0 | 0.0 |
| Southern Reedbuck | 14.3 | 64.3 | 21.4 | 78.6 | 14.3 | 7.1 | 0.0 |
| Suni | 100.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 |
| Waterbuck | 14.5 | 7.3 | 78.2 | 0.0 | 32.7 | 67.3 | 0.0 |

### 4.4.2. Prey preference

The Jacobs' Index (Figure 4.3) revealed a strong preference for bushbuck, common duiker (*Sylvicapra grimmia*), kudu, and southern reedbuck, regardless of the population estimate or diet composition methodology used (Figure 4.3). D-values for impala varied between preferred (D = 0.38; kills) and avoided (D = -0.35; scats) when total population counts were used. However, the Jacobs' Index indicated avoidance of impala (D = -0.29, -0.79) when considering "catchable" population estimates. Sable were strongly avoided regardless of prey populations used (D = -0.79, -0.52), however, their sample size was small (*n* = 2) which would naturally allow for this conclusion. Regardless of population estimates, the Jacobs' Index revealed an avoidance of waterbuck, the intensity of which varied based on methodology. Scats, with total population counts indicating the highest level of waterbuck avoidance (D = -0.85) and carcass observations (kills) with "catchable" population estimates indicating a slight avoidance where consumption was almost proportionate to their relative abundance (D = -0.03).

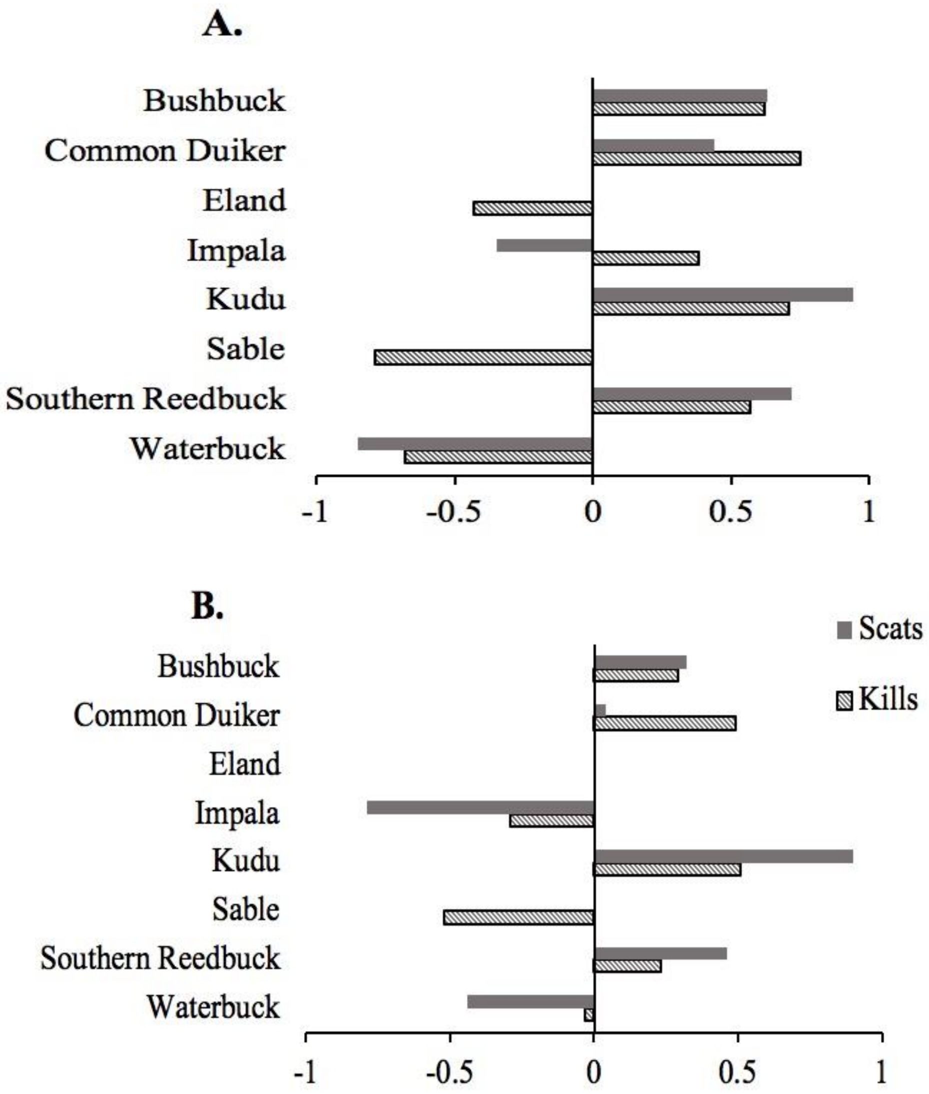

**Figure 4.3.** Dietary preference of cheetah in LNP, Malawi, using the Jacobs' Index. Values indicate how often a species is preyed upon in accordance to their relative abundance within the prey populations. Positive values indicate more frequent predation than abundance and therefore preference, and negative values indicate an avoidance. Predation was determined by scat analysis (July 2018 – July 2019) and carcass observations (kills; July 2017 – July 2019) and prey abundances were either taken from the total game count (**A**) or calculated based on an estimate of "catchable" prey (**B**).

### 4.4.3. Methodology comparison

As predicted scat analysis was able to detect a larger number of prey species (*n* = 10) than any carcass observation methodology over a one-year period (Table 4.4). Cumulative species curves indicated that over 50.0 % of recorded prey species were detected after two months of data collection with scat analysis, whereas both carcass observation methodologies combined (VHF tracking and opportunistic) were only able to detect 30.0 % of prey species (Figure 4.4).

**Table 4.4.** Data collected, and species recorded across four different methodologies used to determine the cheetah diet composition in LNP, Malawi.

| | **Methodology Employed** | | | | |
|---|---|---|---|---|---|
| | **VHF Tracking** | **Opportunistic** | **GPS Investigation** | **Scat Collection** | **Total** |
| **Sample Size** | 41 | 55 | 169 | 43 | **265 / 43** |
| **Species Recorded** | 5 | 6 | 8 | 10 | **13** |
| **Data Collection Period (days)** | 756 | 756 | 514 | 365 | **756** |

When comparing solely carcass observation methodologies, GPS investigation was able to detect a higher proportion of the prey species (53.8 %) than the other two methodologies combined (38.5 %; Figure 4.5). Furthermore, GPS investigation was able to collect double the sample size compared to VHF tracking and opportunistic sightings combined, and surpassed both methodologies in the proportion of species detected after only two months (or 24 carcasses). It is important to note that cumulative species curves were analysed for two separate years, however, over both years the combination of VHF tracking and opportunistic sightings were only able to detect 38.5 % of prey species.

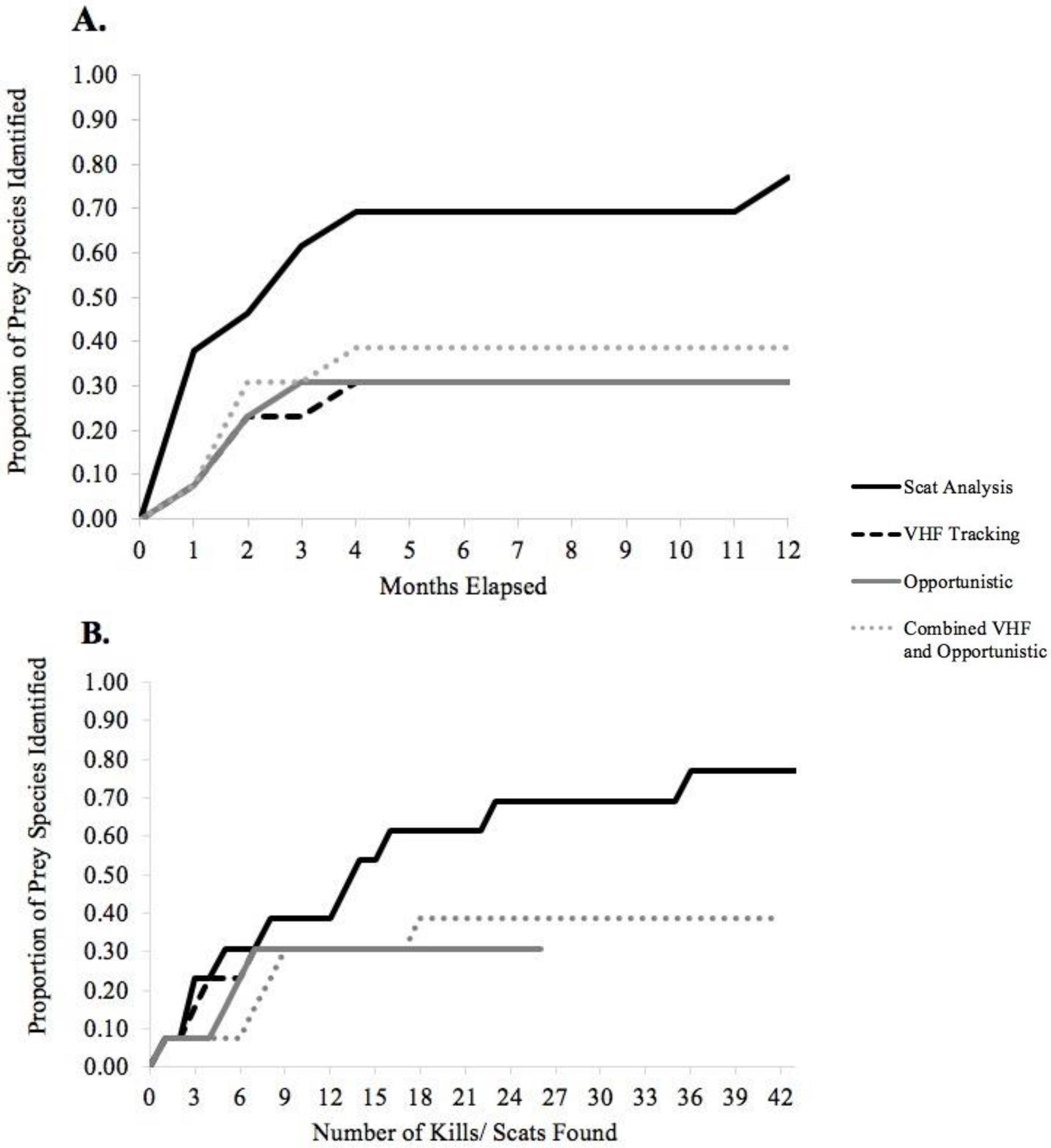

**Figure 4.4.** Cumulative curves of the proportion of species identified by three different methodologies used to determine carnivore diet over (**A**) elapsed time of the study period and (**B**) sample size (scats or kills), in the diet of cheetah in LNP, Malawi (July 2018 – July 2019).

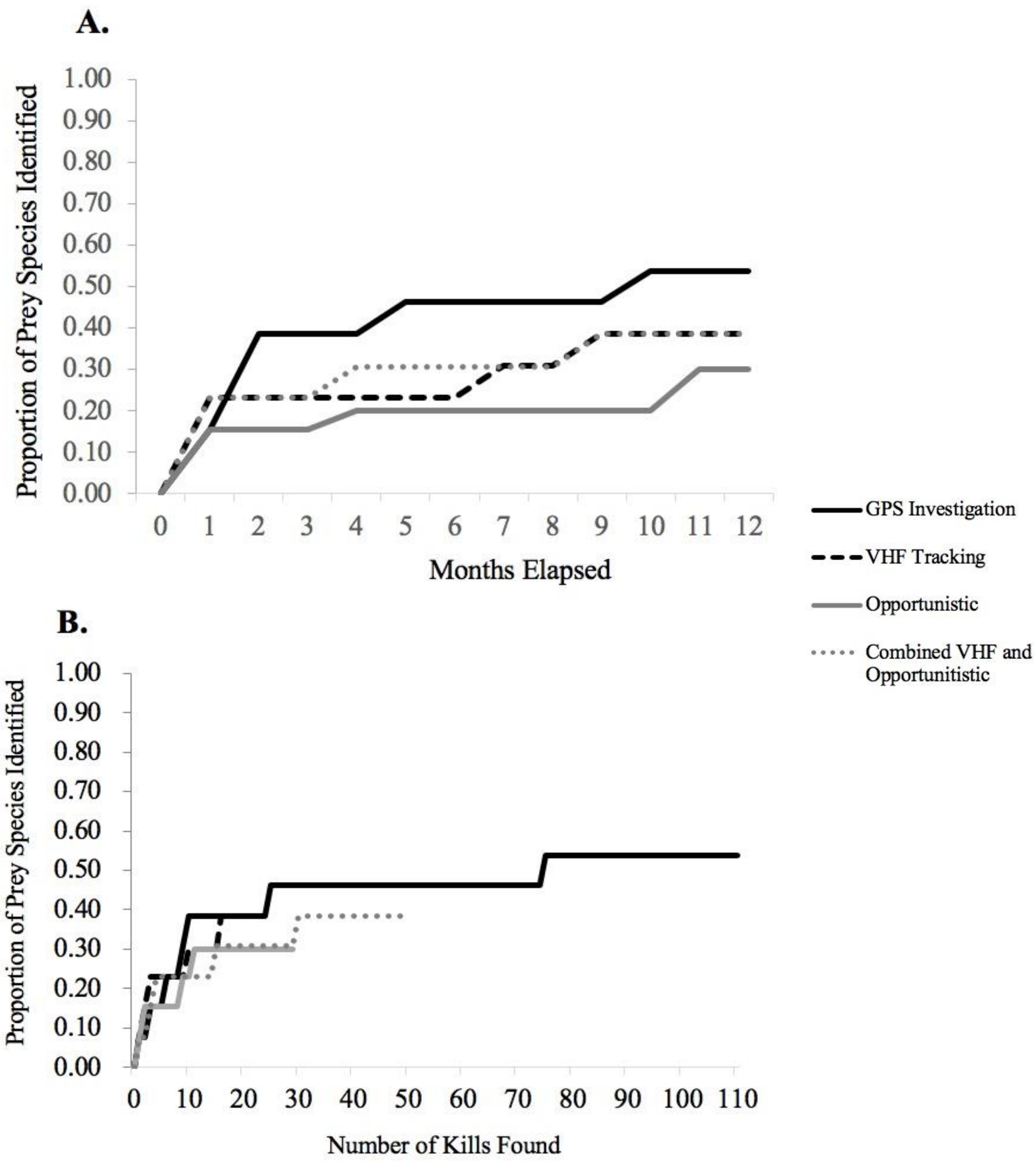

**Figure 4.5.** Cumulative curves of the proportion of species identified by three carcass observation methodologies in relation to (**A**) elapsed time and (**B**) sample size (carcasses) in the diet of cheetah in LNP, Malawi (July 2018 – July 2019).

## 4.5. Discussion

The cheetah in LNP preyed on 13 different species. However, cheetah diet consisted primarily of four prey items; kudu, impala, waterbuck and bushbuck. It is important to note that while both FO and CFO are widely used methodologies, they have inherent biases and often overestimate the frequency of small prey species. Therefore, the results can be misleading and, as such, they were used solely as comparatives to other studies (Klare *et al.*, 2011; van Dijk *et al.*, 2007). Relative biomass calculations are thought to derive the most accurate approximation of diet and are therefore more biologically meaningful, especially if the model was developed for a similar species (Klare *et al.*, 2011; van Dijk *et al*., 2007). The relative biomass calculations used in this study were developed for cheetah and are therefore highly relevant.

While kudu, impala, waterbuck and bushbuck were the prominent prey species for both carcass and biomass calculations, their abundance in the diet varied greatly, and prey preference did not always represent the prey species' relative importance (*eg.*, waterbuck were avoided in Jacobs' Index calculations). Although the common duiker was highly preferred across most methodologies, the species accounted for < 5 % of the total carcasses found and species identified in scats. Small antelope species, such as common duiker, are notoriously difficult to count during aerial surveys and they are therefore often under counted. The population estimate for common duiker in LNP is therefore likely an under-estimate which would effect prey preference calculations for this species. Therefore, the common duiker was not considered an important species in this study (Klare *et al.*, 2011). The consumption of a wide variety of prey species, with a high importance of only a few species, has been recorded for cheetah across study sites (*eg.*, Boast *et al*., 2016; Craig *et al.*, 2017; Hayward *et al.*, 2006; Marker *et al.*, 2003; Mills *et al*., 2004; Tambling *et al*., 2014). It is noted that bushpig (*Potamochoerus larvatus*) and *Squamata* are unusual prey items for cheetah (Hayward *et al*., 2006). The *Squamata* skin was found in the scat of a dispersing adolescent male and may be a result of hunting immaturity and food desperation. However, the bushpig hair was found in the scat of an adult female. Predation on bushpig by cheetah is uncommon, and additionally no warthogs (*Phacocohoerus africanus*) were recorded as prey during this two-year study. However, one unsuccessful hunt on a young warthog was noted during the study period (pers. obs.) which demonstrates the opportunistic hunting behaviour of the cheetah. It is therefore likely that young bushpig or warthog comprise a very small portion of cheetah diet seasonally.

Kudu was the only species found to be highly important in cheetah diet regardless of methodology. While young kudu fall within the preferred weight range for cheetah (23-56 kg), they are not commonly reported as a preferred species (Craig *et al*., 2017; Hayward *et al*., 2006). Dissimilar to other studies in which the most abundant small- to medium-size antelope is most preferred (Hayward *et al*., 2006), kudu is not the most abundant antelope in LNP. A preference towards kudu may, therefore, be a factor of hunting behaviour or habitat preference. Bissett and Bernard (2007) explained a high selection of kudu as a means for male coalitions to meet nutritional demands. However, similar cooperative hunting events were not observed in LNP. It is suggested that a preference for kudu may be a result of habitat choice, as kudu in LNP is most often found in edge habitats, which have been described as optimal cheetah habitats (Mills *et al*., 2004). Kudu are also found in smaller herds than the two most abundant species, waterbuck and impala, smaller herds are less vigilant (Fitzgibbon, 1990) which may also be a factor in their perceived preference, however, this should be investigated further.

Waterbuck are the most populous antelope species in LNP with an estimated population of 6673 individuals (Sievert & Reid, 2018). While previous studies have found cheetah to prey upon waterbuck in accordance to their relative abundance (Hayward *et al*., 2006), Jacobs' Index calculations using scat data revealed a high level of avoidance by cheetah in LNP even when considering "catchable" population estimates (*D* = -0.85, -0.44). Although a common species observed during carcass observations in LNP (*n* = 55) when comparing these numbers to the relative abundance of waterbuck a high level of avoidance (*D* = -0.68) was also found. Hayward & Kerley (2005) suggested a lion avoidance of waterbuck due to scent glands causing taste aversions. However, as mentioned waterbuck accounted for a large number of the cheetah kills recorded in LNP (*n* = 55; 21 %). In LNP the majority of the waterbuck population forms large herds on the floodplain (Sievert & Reid, 2018). Increased group size results in enhanced vigilance, this coupled with the open habitat may act to decrease the catchability of this species in LNP, resulting in a perceived avoidance.

Cumulative species curves illustrated that scat analysis can quickly identify the most important species in the cheetah diet, as well as detect the highest diversity while maintaining a low sample size. However, the accuracy of scat analysis is strongly dependent on a researcher's ability to manually identify prey hairs and the robustness of the hair reference database. Scat analysis is, therefore, strongly subjected to observer biases and may result in the over-representation of certain species (Davies-Mostert *et al.*, 2010). Furthermore, the use of the linear regression correction factors has the potential for biases, especially when considering sex-specific differences in predation and prey mass estimations (Wachter *et al.*, 2012).

The majority of this study's scat samples were collected from cheetah scent-marking sites. Although females have been recorded to visit scent marking sites, they are predominantly used by males (Eaton, 1970; Marnewick *et al.*, 2006). The greater body size and ability to form coalitions increases the likelihood that male cheetah will kill larger prey (Bissett & Bernard, 2007). Therefore, a bias towards the collection of male scats may have resulted in an underestimation of prey mass in the calculations conducted for the current study (Boast *et al.*, 2016; Craig *et al.*, 2017). Furthermore, this study collected 43 scats over a one-year period, which is less than the recommended 59 scats necessary for identifying the principal prey species (Trites & Joy, 2005). However, this is a common difficulty when researching cryptic species that occur in low densities (Leigh & Dominic, 2015; Sollmann *et al.*, 2013). The combination of scat analysis and carcass observations was therefore important in developing a reliable understanding of cheetah diet in LNP.

Incorporating carcass observations was especially critical in determining the potential for asymmetric predation. The high selection of females for uncommon species such as bushbuck and southern reedbuck, as well as the intensive preference towards kudu young, will have long-term implications for the demography of these species in LNP as the cheetah population increases (Fitzgibbon, 1990; Makin & Kerley, 2016). The preference for female reedbuck and bushbuck indicates that the males of these species may pose an increased capture difficulty. Conversely, the majority of impala carcasses in which the sex was identifiable were males (64.3 %), which was similar to findings in the Serengeti National Park where cheetah select for male Thomson's gazelles (Fitzgibbon, 1990) and confirms the earlier prediction for the current study. Understanding prey preference and selection within the demographics of a population is crucial to management's understanding of predator-prey dynamics. For example, management decisions in the Kruger National Park resulted in an increased habitat congruence for roan antelope (*Hippotragus equinus*), and lion's preferred prey species, which resulted in an increase of predation caused mortalities for roan, abetting their subsequent collapse (Harrington *et al.*, 1999). Additionally, selective predation pressure of juvenile and subadult male kudu on Samara Private Game Reserve resulted in significantly lower proportions of these two sex and age classes in the demographics of the species when compared to predator absent areas (Makin & Kerley, 2016). While the effects of asymmetric predation within terrestrial systems are not widely known, experimental data has suggested a potential reduction in female fecundity when populations experience a high off-take of adult males (Ginsberg & Milner-Gulland, 1994). Therefore, populations experiencing long-term asymmetrical predation of other forms are also likely to face demography and life-history changes.

The cheetah suffers from high levels of intraguild competition (Durant, 1998; Hunter, Durant & Caro, 2007; Rostro-Garcia, Kamler & Hunter, 2015). Cheetah demonstrate predator avoidance behaviour by seeking spatial and/or temporal refuges from dominant carnivores (Durant, 1998; Rostro-Garcia *et al.*, 2015). It is anticipated that the cheetah in LNP will change their behaviour as large carnivores (*e.g.*, lion, hyena, and leopard; *Panthera pardus*) populations increase. A change in either temporal or spatial activity may result in dietary shifts as different species become accessible and are selected for. It is noted that the cheetah activity in LNP is highly localized to the Spine Road in the southern section of the park (*see*, Chapter 5, Figure 5.1), and diet composition is likely to change as the population grows and activity is less localized. It is therefore important to re-evaluate cheetah diet in LNP once carnivore populations are nearing management estimated carrying capacities.

If determining dietary diversity is an important objective of future diet studies, then it is recommended that scat analysis is conducted. It is further recommended that LNP considers the development of a hair reference database which would allow for localized variations to be accounted for with the inclusion of rarer species such as oribi (*Ourebia ourebi*) and small mammals. To better account for observer bias, it is also recommended that blind tests are conducted to identify the level of research error (Davies-Mostert *et al.*, 2010). Nevertheless, scat analysis is limited in its ability to inform population management on a finer scale and should, therefore, be supplemented with carcass observations to allow for assessment of demographics targeted within medium- to large-sized antelope. Drawing diet composition conclusions solely from VHF tracking or opportunistic carcass sightings is not recommended, as these methodologies were limited in their ability to detect species diversity and both maintained small sample sizes over the two-year study period (VHF tracking $n$ = 41; opportunistic $n$ = 55). The small sample size from VHF tracking represents 11.6 % (41/354) success rate of obtaining carcass observations during tracking sessions. Limitations of these methodologies are mainly attributed to the minimal road network in LNP and relatively low tourism levels. These methods are also subjected to species biases based on habitats where roads are located and are therefore likely to overestimate prey species that are predominantly caught in open habitats.

GPS investigation has been widely used across the large carnivore guild as a method of determining diet composition (Bacon *et al*., 2011; Davidson *et al.*, 2013; Fröhlich *et al.*, 2012; Martins *et al.*, 2011; Perilli *et al.*, 2016; Allen *et al.*, 2015; Pitman *et al.*, 2014; Tambling *et al*., 2012). However, to the authors' knowledge, this is the first study to implement this methodology for cheetah diet. Most studies that employ GPS investigation assess time spent at a given location to inform the priority of site investigations, as longer periods often denote the probability of a kill taking place (Bacon *et al.*, 2011; Davidson *et al.*, 2013; Blecha & Alldredge, 2015; Cassaigne *et al*., 2016; Martins *et al*., 2011; Pitman *et al*., 2014). As a subordinate carnivore, the cheetah is subjected to high levels of kleptoparasitism and therefore does not spend prolonged periods at a kill (Hilborn *et al*., 2018), thereby reducing the effectiveness of this method. Furthermore, GPS investigation in this study was limited by monitoring requirements outlined by park management and therefore conducted *ad libitum*. Regardless, *ad libitum* GPS investigation was the most effective carcass observation method in LNP, as a larger sample size (*n* = 110) was collected and the method detected a higher proportion of prey species (58.3 %) over one year when compared to other carcass observation methods. GPS investigation encounters similar biases as VHF tracking, as both are susceptible to the effects of prey handling time and terrain accessibility (Davies-Mostert *et al.*, 2010; Perilli *et al.*, 2016). GPS investigation is however not restricted by the same ethical considerations of VHF tracking (*e.g.*, daily disturbance) nor daylight hours. It, therefore, has the potential to incorporate a wider timeframe to account for rapidly consumable or nocturnal prey species. This is especially important in woodland environments, such as in LNP, where 24-hour VHF follows are not possible, or in environments where night time VHF tracking does not occur and therefore nocturnal hunting behaviour is not accounted for (Bissett & Bernard, 2007; Broekhuis *et al.*, 2014).

While carcass observations are recognized as biased towards larger prey items, the bias against smaller items is inherent across studies and generally considered to be alleviated by the undercounting of small prey species during aerial counts (Hayward & Kerley, 2005; Clements *et al*., 2014). However, prey weighing 14 kg or less is described as below the prey-mass threshold for which the energetic cost of capture outweighs the benefit of consumption and therefore is generally avoided by cheetah (Clements *et al.*, 2014). The adult weights of both scrub hare (*Lepus saxatilis*) and suni are below the 14 kg threshold, and the presence of these species in LNP cheetah diets may only represent opportunistic predation and not the overall importance of these species in the diet. These findings are paralleled to other studies in which GPS investigation under-represented prey diversity but gave an accurate representation of relevant prey items (Bacon *et al.*, 2011; Tambling *et al.*, 2012), and when coupled with scat analysis gave the most detailed dietary estimates (Bacon *et al*., 2011; Pitman *et al.*, 2014; Martins *et al.*, 2011; Tambling *et al.*, 2012).

Although many limitations in this study are highlighted, given the lack of information on cheetah diet in Malawi and the incorporation of multiple methodologies, this data provides the best possible depiction of diet composition of cheetah in LNP. Therefore, results can contribute practically and meaningfully to understanding the diet requirements of cheetah in other protected areas in Malawi. As reintroductions of large carnivores continue in LNP and populations slowly increase, it is recommended that subsequent diet composition studies occur across the carnivore guild. This will allow for the incorporation of this study's recommendations, as well as develop an understanding of carnivore dietary overlap within LNP, which is important for species of conservation concern. For example, in Kenya, multi-species predation has been listed as a credible threat to the survival of Grevy's zebra (*Equus grevyi*; Davidson *et al*., 2019). Understanding the impact of multi-species predation on prey populations is therefore crucial in developing dynamic multi-species conservation strategies.

Wildlife populations and tourism have drastically declined across Malawi's protected areas over the last decade, and while conservation action in recent years has resulted in decelerating wildlife losses, targeted research is needed to inform management activities going forward. Few carnivore diet studies have taken place in Malawi to date. While different methods for determining diet composition can yield varying results, managers must consider benefits, challenges, biases and overall goals before implementing diet studies. Due to the similarities in protected areas across Malawi: woodland habitat, minimal road networks and low to moderate tourism levels, these finding have countrywide applicability. It is recommended that a mixture of GPS investigation and scat analysis are employed when assessing diet of carnivores in Malawi. The amalgamation of these methodologies will create the most robust diet estimation for carnivore species across Malawi's protected areas. If GPS investigation does not meet with management budgets, then scat analysis should be the main method employed.

## 4.6. Conclusion

In LNP four species comprised the bulk of cheetah diet, namely impala, kudu, bushbuck and waterbuck. These species did not experience even levels of predation across their demography which may result in conservation implications as LNP's cheetah population increases in size. Trade-offs between logistical, financial and practical considerations must be considered before implementing diet studies, as different methods can yield varying results that will influence management decisions. While managers must choose the method that will best fit their objectives, budget and time constraints, a scat analysis should be conducted in conjunction with GPS investigation to best inform management of large carnivore diet in LNP and Malawi's other protected areas.

## 4.7. Acknowledgements

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## 4.8. Ethical clearance

Relevant permits for the work were obtained by African Parks during the routine monitoring. (CITES permit numbers: 175828; 0000062; 0000079). Ethical clearance for the use of collar data as a third-party user was obtained through Stellenbosch University (ethics reference number: ACU-2018-8311).

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## 4.10. Appendices

**Appendix 4.A.** Game census numbers from the 2018 Liwonde National Park Aerial Survey. Obtained from Sievert and Reid (2018).

| Common name | Scientific name | Total Count |
|---|---|---|
| Buffalo | *Syncerus caffer* | 940 |
| Bushbuck | *Tragelaphus scriptus* | 289 |
| Bushpig | *Potamochoerus larvatus* | 5 |
| Crocodile | *Crocodylus niloticus* | 377 |
| Common Duiker | *Sylvicapra grimmia* | 61 |
| Eland | *Tragelaphus oryx* | 109 |
| Elephant | *Loxodonta africana* | 597 |
| Sharpe’s Grysbok | *Raphicerus sharpei* | 1 |
| Hippopotamus | *Hippopotamus amphibius* | 1978 |
| Impala | *Aepyceros melampus* | 3089 |
| Klipspringer | *Oreotragus oreotragus* | 3 |
| Kudu | *Tragelaphus strepsiceros* | 315 |
| Lichtenstien’s Hartebeest | *Alcelaphus lichtensteinii* | 43 |
| Oribi | *Ourebi ourebi* | 13 |
| Porcupine | *Hystrix cristata* | 1 |
| Southern Reedbuck | *Redunca arundinum* | 176 |
| Roan | *Hippotragus equinus* | 8 |
| Sable | *Hippotragus niger* | 754 |
| Warthog | *Phacocherus africanus* | 1066 |
| Waterbuck | *Kobus ellipsiprymnus* | 6673 |
| Plains Zebra | *Equus quagga* | 58 |

**Appendix 4.B.** Converting the number of kills per species into the percentage of biomass consumed for cheetah kills (carcass observations) recorded in LNP, Malawi.

| Prey Species | # Kills | Assumed Prey Mass (kg)* | Biomass Consumed (kg) | Biomass Consumed (%) |
|---|---|---|---|---|
| Bushbuck, *Tragelaphus sylvaticus* | 26 | 27.0 | 702.0 | 7.1 |
| Common Duiker, *Sylvicapra grimmia* | 9 | 15.7 | 141.3 | 1.4 |
| Eland, *Taurotragus oryx* | 1 | 36.0 | 36.0 | 0.4 |
| Impala, *Aepyceros melampus* | 120 | 33.7 | 4044 | 41.0 |
| Kudu, *Taurotragus strepsiceros* | 37 | 101.0 | 3737.0 | 37.9 |
| Sable, *Hippotragus niger* | 2 | 16.5 | 33.0 | 0.3 |
| Southern Reedbuck, *Redunca arundinum* | 14 | 32.0 | 448.0 | 4.5 |
| Suni, *Neotragus moschatus* | 1 | 4.1 | 4.1 | 0.0 |
| Waterbuck, *Kobus ellipsiprymnus* | 55 | 13.0 | 715.0 | 7.3 |
| ***Total*** | ***265*** | **-** | ***9860.4*** | ***100*** |

* Prey mass calculated based on the catchable individuals for the species.

**Appendix 4.C.** Calculations for frequency of occurrence, corrected frequency of occurrence, correction factor and overall biomass consumed per prey species found during scat analysis while assessing cheetah diet in LNP, Malawi.

| Prey Species | Assumed Prey Mass (kg) | # Scats with Prey Remains | FO (%) | Occurrence per Scat | CFO (%) | Correction Factor | Biomass Consumed (kg) |
|---|---|---|---|---|---|---|---|
| Bushbuck, *Tragelaphus sylvaticus* | 27.0 | 9 | 13.4 | 6.5 | 15.1 | 0.607 | 5.46 |
| Bushpig, *Potamochoerus larvatus* | 1.0 | 2 | 3.0 | 1.0 | 2.3 | 0.352 | 0.704 |
| Common Duiker, *Sylvicapra grimmia* | 15.7 | 2 | 3.0 | 1.0 | 2.3 | 0.496 | 0.992 |
| Impala, *Aepyceros melampus* | 33.7 | 12 | 17.9 | 7.5 | 17.4 | 0.673 | 8.076 |
| Kudu, *Taurotragus strepsiceros* | 101.0 | 20 | 1.5 | 14.0 | 32.5 | 1.332 | 26.640 |
| *Squamata* Order | - | 1 | 1.5 | 0.5 | 1.2 | N/A | N/A |
| Sharpe's Grysbok, *Raphicerus sharpei* | 5.8 | 2 | 29.8 | 1.0 | 2.3 | 0.399 | 0.798 |
| Scrub Hare, *Lepus saxatilis* | 1.9 | 1 | 3.0 | 0.5 | 1.2 | 0.361 | 0.361 |
| Southern Reedbuck, *Redunca arundinum* | 32.0 | 7 | 10.4 | 4.0 | 9.3 | 0.656 | 4.592 |
| Waterbuck, *Kobus ellipsiprymnus* | 13.0 | 11 | 16.4 | 7.0 | 16.3 | 0.469 | 5.159 |
| ***Total*** | **-** | ***67*** | ***100*** | ***43*** | ***100*** | - | ***52.782*** |

**Appendix 4.D.** Calculations of the prey preference for cheetah in Liwonde National Park, Malawi, using the Jacob's Index.

| Species | % Kills | % Biomass from Scats | Total Population | Catchable Population | Jacobs Index Values (kills)* | | Jacobs Index Values (scats - biomass) | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Total Population | Catchable Population | Total Population | Catchable Population |
| Bushbuck | 9.8 | 0.103 | 289 | 289 | 0.62 | 0.29 | 0.63 | 0.32 |
| Common Duiker | 3.4 | 0.013 | 61 | 61 | 0.75 | 0.49 | 0.44 | 0.04 |
| Eland | 0.4 | N/A | 109 | 18 | -0.43 | 0 | N/A | N/A |
| Impala | 45.5 | 0.15 | 3089 | 3089 | 0.38 | -0.29 | -0.35 | -0.79 |
| Kudu | 14.0 | 0.5 | 315 | 257 | 0.71 | 0.51 | 0.94 | 0.9 |
| Sable | 0.8 | N/A | 754 | 126 | -0.79 | -0.52 | N/A | N/A |
| Southern Reedbuck | 5.3 | 0.087 | 176 | 176 | 0.57 | 0.23 | 0.72 | 0.46 |
| Waterbuck | 20.8 | 0.098 | 6673 | 1121 | -0.68 | -0.03 | -0.85 | -0.44 |
| **Total** | **100** | **100** | **11466** | **5137** | **N/A** | **N/A** | **N/A** | **N/A** |

*Based on the number of individuals caught in reference to their relative abundance within the population of prey species.

# Chapter Five

## Spatial Distribution and Habitat Selection of Reintroduced Cheetah in Liwonde National Park, Malawi.

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### 5.1. Abstract

Understanding the spatial distribution and habitat use of carnivores is critical to their conservation and management. The cheetah (*Acinonyx jubatus*) is Africa's most endangered felid with 6700-7100 wild individuals remaining. Scenario modelling has demonstrated the survival of the cheetah is highly dependent on protected areas and the woodland habitats which encompass large proportions of their remaining range. Despite this, few studies have investigated the habitat selection of cheetah in a woodland habitat. This study sought to address this knowledge gap by assessing the spatial distribution and habitat selection of cheetah reintroduced into the mixed woodland habitat of Liwonde National Park (LNP), Malawi. To the author's knowledge, this study was the first to assess the spatial distribution and habitat selection of cheetah in a woodland habitat with low competition levels. The aim of this study was to inform the adaptive long-term management of this newly reintroduced population and assist in assessing other reintroduction sites in Malawi. Home ranges estimates were developed for four reintroduced cheetah one-year post home range establishment. Cheetah demonstrated high levels of intra- and intersexual spatial overlap (40-71 % home range; 22-62 % core area). The high degree of female spatial overlap was attributed to den site selection, which may indicate that suitable den sites are a limited resource. This degree of spatial overlap is expected to have a negative impact on both cub and male survival and should be addressed in future release events. Cheetah demonstrated a high flexibility in habitat use by occupying all six habitat types at varying levels. Cheetah used open woodland, with moderate levels of prey frequency of occurrence, more than expected based on availability. Additionally, there was a significant difference in the proportion of kills on the floodplain compared to the proportion in which the floodplain was selected for. Comparatively, significantly less kills occurred in open woodland habitats than expected based on its use. The ongoing large carnivore reintroductions (lion, *Panthera leo*, and leopard, *Panthera pardus*) in the park are expected to increase competition and create a knock-on effect for cheetah habitat selection. It is anticipated that LNP's cheetah will demonstrate spatial avoidance of competition by inhabiting areas with more cover. The habitat flexibility demonstrated by cheetah in this study is, therefore, encouraging for the populations continued growth under increased intraguild competition but may have implications for certain prey populations should this competition create a spatial shift to habitats with higher cover.

## 5.2. Introduction

As human populations increase, anthropogenic pressures result in wildlife becoming either confined to a mosaic of protected areas (PAs) or adapted to human-altered landscapes (Dellinger *et al.*, 2013). Large carnivores are particularly sensitive to human population growth due to their dietary needs and large home range requirements which often place them in direct conflict with humans (Darimont *et al.*, 2015; Woodroffe, 2000). Anthropogenic pressures have, therefore, had a substantial impact on large carnivores, with 59 % of large carnivore species now threatened with extinction (Ripple *et al*., 2014). Therefore, understanding how carnivores use remaining available habitats is crucial to conservation efforts.

Home ranges, defined as the area an animal traverses during daily activities such as foraging, reproduction and shelter-seeking (Burt, 1943), are most commonly studied to investigate animals' spatial distributions within their environment. However, presence of an animal within an environment does not deem a habitat as suitable, as it does not consider the requirements for survival or reproduction (Hirzel & Le Lay, 2008; Mitchell & Hebblewhite, 2012). Therefore, home range studies must be coupled with the study of habitat selection in order to develop a robust understanding of habitat suitability which will effectively inform population management (Mitchell & Hebblewhite, 2012). For obligate carnivores, understanding habitat selection and suitability requires further knowledge of prey distributions and the environmental influences that facilitate prey capture (Hopcraft, Sinclair & Parker, 2005; Mitchell & Hebblewhite, 2012; Miquelle *et al.*, 1999).

The impact of prey distribution and catchability on habitat selection for large carnivores has given rise to two main hypotheses; the prey abundance hypothesis (Davidson *et al.*, 2012), and the ambush-habitat hypothesis (Hopcraft *et al*., 2005). The prey abundance hypothesis states that habitats are selected to include the highest prey abundance, thus home range size is inversely correlated to prey density (Davidson *et al*., 2012). Under the ambush-habitat hypothesis, carnivores are expected to select habitats based on environmental attributes which increase hunting success (Hopcraft *et al*., 2005). Both hypotheses have been supported by numerous studies (*prey abundance hypothesis;* Murray, Boutin & O'Donoghue, 1994; Palomares *et al*., 2001; Spong, 2002; *ambush-habitat hypothesis;* Balme, Hunter & Slotow, 2007; Davidson *et al.*, 2012; Hebblewhite, Merrill & McDonald, 2005; Hopcraft *et al*., 2005). However, this is a simplification of selection drivers as spatial scale also largely influences the proximal factors that shape selection (Davidson *et al.*, 2012; Hopcraft *et al.*, 2005; Johnston, 1980; Mitchell & Hebblewhite, 2012; Rostro-Garcia, Kamler & Hunter, 2015). Habitat selection must therefore be viewed as a scale sensitive process and analysed as such.

Most commonly described as a nested hierarchy, habitat selection has been portrayed in four orders; geographic range (1st order), location of home range (2nd order), use of habitat within the home range (3rd order) and selection of foraging sites (4th order) (Johnston, 1980). Determinants of habitat selection per spatial scale differ, for example, home range locations are mainly driven by competition, especially in large territorial carnivores, meaning 2nd order selection is often density dependent (Sommer & Worm, 2002; Mitchell & Hebblewhite, 2012). However, habitat selection within the home range is often influenced by factors that impact fitness such as prey distribution, prey catchability, protection of young and interspecific competition (Balme *et al.,* 2007; Hopcraft *et al.*, 2005; Mitchell & Hebblewhite, 2012).

Historically distributed across Africa and parts of Asia, remnant populations of cheetah (*Acinonyx jubatus*) are now scattered across 32 of their 53 range states, making the cheetah Africa's most endangered large felid (Durant *et al.,* 2015; Durant *et al*., 2017). Early studies of the behavioural ecology of the cheetah centred on the plains of the Serengeti National Park and erroneously deemed the cheetah a grassland specialist (*see*, Caro & Collins, 1987; Durant, 1998a; Durant *et al*., 1988; Fitzgibbon, 1990; Kelly *et al*., 1998; Schaller, 1968). However, the improvement and decreasing cost of tracking technology has increased research capabilities and demonstrated that the cheetah can successfully exploit a wide range of woodland, thicket and arid habitats (Bissett & Bernard, 2007; Broomhall, Mills & du Toit, 2003; Cristescu, Bernard & Krause, 2013; Klaassen & Broekhuis, 2018; Marker *et al*., 2007; Mills, Broomhall & du Toit, 2004; Nghikembua *et al*., 2016; Rostro-Garcia *et al.,* 2015; Welch, *et al*., 2015). The behavioural flexibility of the cheetah is now evident at the home range scale (2nd order) when comparing selection drivers across study sites. For example, anthropogenic activity and abundance of competing large carnivores appear to have the greatest effect on the location of home ranges for cheetah in unfenced systems (Durant, 1998a; Klaassen & Broekhuis, 2018; Van der Weyde *et al*., 2017). However, prey abundance is a driver in home range selection for cheetah in fenced systems where they are unable to escape competition on a large spatial scale (Broomhall *et al.,* 2003; Rostro-Garcia *et al.,* 2015; Welch *et al.,* 2015).

Whilst the past two decades have resulted in an increase of ecological and behavioural studies of the cheetah in varying habitats, the logistical constraints associated with woodland habitats still limits our knowledge. Few studies have examined habitat selection at the home range and foraging site scale (3rd and 4th order selection) and, those that have varied in results. For example, in the Kruger National Park (KNP; Broomhall *et al.,* 2003; Mills *et al.,* 2004) and Matusadona National Park (MNP; Purchase & du Toit, 2000) cheetah have been shown to use the most open habitat for hunting. However, cheetah in Phinda Private Resource Reserve (PPRR) preferred closed habitats with low prey densities for hunting (Rostro-Garcia *et al.,* 2015). Differences in findings have been attributed to varying levels of kleptoparasitism, interspecific competition and overall prey distribution (Broomhall *et al.,* 2003; Purchase & du Toit, 2000; Mill *et al*., 2004; Rostro-Garcia *et al.*, 2015).

Scenario modelling has demonstrated that the survival of the cheetah is highly dependent on protected areas for sustained population growth, and woodland habitats, which encompass large proportions of their remaining range. (Durant, 1998b; Durant *et al.,* 2017). However, spatial distribution and habitat selection research has focused primarily on protected areas that are dominated by savannah grassland habitats and free-ranging populations in farmland environments (Caro, 1994; Houser, Somers & Boast, 2009; Klaassen & Broekhuis, 2018; Marker *et al.,* 2007; Marnewick & Cilliers, 2006; Marnewick & Somers, 2015; Nghikembua *et al.,* 2016). Few studies of cheetah habitat selection in woodland habitat outside of South Africa have occurred (Purchase & du Toit, 2000). The knowledge gap surrounding the spatial distribution and habitat selection in woodlands limits the ability to employ informed conservation management of populations in these habitats.

Further research is therefore required in order to adequately conserve remaining populations and inform continued range expansion projects in this habitat. Therefore, the aim of this study was to increase our understanding of the behavioural adaptability and habitat requirements of the cheetah in woodland habitats by examining the spatial distribution and habitat use of cheetah reintroduced into a protected area dominated by a mixed mopane (*Colophospermum mopane*) landscape (Liwonde National Park, Malawi; LNP). Due to the low density of competing large carnivores (spotted hyena, *Crocuta crocuta,* population estimate, 25; lion *Panthera leo,* population, 9; pers. obs.) and high densities of prey (23.3 animals/km$^2$; Sievert & Reid, 2018) it is anticipated that this study will describe the 'ideal' habitat for cheetah in a mixed woodland at the 3rd and 4th selection order. This study will, therefore, assist in determining the effects of intraguild competition on habitat selection by developing a baseline of cheetah habitat preference under low competition levels. Furthermore, no research was conducted on cheetah in Malawi prior to their extirpation, it is therefore anticipated that this study will provide vital information for the management of the newly reintroduced populations and assist in identifying additional reintroduction sites in the region.

## 5.3. Methods

### 5.3.1. Study site

Spanning 548 km$^2$, LNP is in the Upper Shire Valley in the Southern Region of Malawi (Figure 5.1). LNP has distinct wet and dry seasons, the average precipitation is 944 mm per year, with the majority of rainfall occurring between December and March, with June to October classified as dry months (Bhima & Dudley, 1996). Mean high temperatures range from 28° in July to 40° C in November (Bhima & Dudley, 1996). The Shire River is the sole perennial river and the dominant feature of the park as it runs the length of the boundary splitting the park into an eastern and western side. In the wet season, the Shire River creates extensive lagoons and marshlands along the floodplains which border both sides of the river. While LNP contains a multitude of seasonal rivers and streams, only a few pockets of water remain scattered around the park by September, making the Shire River the main water source.

As part of the southern Rift Valley ecosystem, LNP is relatively flat and consists mainly of dry deciduous woodland (Dudley, 2004). The dominant tree in the park is *Colophospermum mopane*, with mopane woodland complex occupying approximately 74 % of the park (Dudley, 2004). Grasslands and floodplains (*Setaria* spp. *Digitaria* spp. *Sporobolus* spp.) along with forest thickets and mixed woodlands (*Combretum* spp., *Terminalia* spp. *Borassus* spp. *Vachellia* spp. *Cordyla* spp. *Trichilia* spp.) are interspersed throughout the park, mostly occurring in north-south bands that run parallel to the Shire River (Dudley, 2004). There are seven distinctive hills found throughout the park with a maximum altitude of 921 m (Mzumara, Perrin & Downs, 2018). The northern boundary consists of a 6 km unfenced corridor to Mangochi Forest Reserve, the recent inclusion of Mangochi Forest Reserve expands the protected system by 375 km$^2$ (923 km$^2$ total size; C. Reid, pers. comm.).

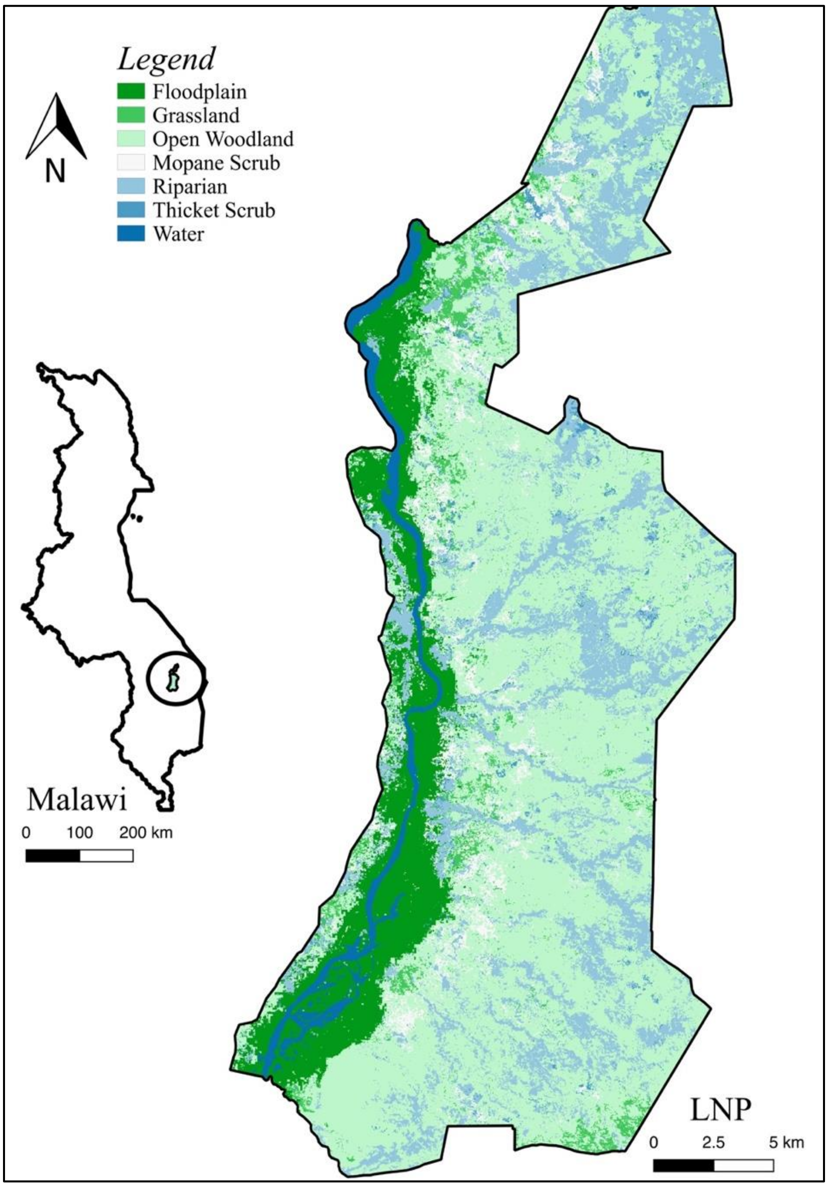

**Figure 5.1.** Map of LNP depicting six habitat classifications and the location of the park within Malawi.

### 5.3.2. Pre- and post-release management

Seven cheetah (four males and three females) were reintroduced into LNP over four different release events between June 2017 and February 2018 (Table 5.1). To ensure maximum possible genetic diversity, animals were sourced through the Endangered Wildlife Trust's (EWT) Cheetah Metapopulation Project (CMP). Reintroduced individuals originated from five separate reserves in South Africa. Prior to arrival in LNP three females and two males were fitted with Pinnacle LITE global positioning system (GPS) satellite collars (Sirtrack, Hawkes Bay, New Zealand) and one male was fitted with a very high frequency (VHF) tracking collar (African Wildlife Tracking, Pretoria, South Africa). Collars weighed approximately 465 g (GPS) and 253 g (VHF), 0.4-1.3 % of body mass respectively. All individuals were kept in temporary holding enclosures (bomas, 50x50 m) prior to release. Once individuals were sufficiently settled they were released directly from the boma through coaxing with a final feed, the gate was then closed behind them to ensure they did not return to the boma. No animals were fed post-release. After release cheetah were monitored closely in accordance with the guidelines set by the IUCN for reintroductions and translocations (IUCN/SSC 2013). Park management implemented an active adaptive monitoring approach (*see*, IUCN/SSC, 2013) for this reintroduction, therefore, monitoring strategies were adapted over the course of the study.

**Table 5.1.** Details of the post-release monitoring of seven cheetah reintroduced into LNP, Malawi.

| ID Code | Collar Type | Collar Success Rate | No. Fixes | No. Transmission Days | No. Sightings | Status [a] |
|---|---|---|---|---|---|---|
| **CM1** | GPS | 54.9% | 594 | 297 | 26 | Alive |
| **CM2** | GPS | 66.3% | 2157 | 520 | 113 | Deceased |
| **CM3[b]** | VHF | N/A | N/A | N/A | 19 | Unknown |
| **CM4[b]** | None | N/A | N/A | N/A | 16 | Unknown |
| **CF1** | GPS | 97.2% | 3747 | 759 | 45 | Alive |
| **CF2** | GPS | Unknown | 1633 | 508 | 79 | Alive |
| **CF3[b]** | GPS | 95.0% | 1032 | 307 | 16 | Deceased |

[a] Status as of 30 June 2019. [b] Members of a sibling coalition released together

### 5.3.3. Data collection

#### 5.3.3.1. Collar and radio-tracking data

GPS collars were scheduled to collect a minimum of three GPS points per day (default setting; 05:00, 06:00 & 12:00 GMT+2). This scheduling was increased based on birthing events or for injured animals to increase monitoring capabilities (Table 5.1). GPS points were therefore collected during varying times of the day including at night depending on scheduling. Radio-tracking took place a minimum of twice a week, with attempts of one observation per cheetah per week. A R-1000 telemetry receiver (Communication Specialists Inc, California, USA) attached to a flexible H-Type antenna (RA-23K VHF antenna; Telonics, Arizona, USA) was used to locate each animal during radio-tracking. Signal strength ranged from 500 m to 1.5 km depending on vegetation structure and season. The success of each radio-tracking event was therefore dependent on vegetation as well as the level of habituation for each individual. Opportunistic sightings outside of scheduled tracking events were also recorded. All successful sightings were recorded with a GPS location and the behaviour (*e.g.*, resting, travelling, feeding) of the animal upon initial sighting was noted.

#### 5.3.3.2. Kill sites

Kill sites were recorded by investigating points collected by GPS collars, during radio-tracking events and opportunistically from reports made by guides and members of park management. GPS points were investigated between July 2017 and November 2018 (514 days). Unlike other large carnivores, cheetah do not remain in close proximity to their kill until it is entirely consumed, instead they employ reduced prey handling time in order to minimize potential kleptoparasitism (Hilborn *et al.*, 2018). Therefore, GPS site investigation was not determined based on time spent in an area, as with other apex carnivores (*e.g.*, Blecha & Alldredge, 2015; Cassaigne *et al*., 2016; Martins *et al*., 2011; Pitman *et al*., 2014), but rather conducted *ad libitum* based on monitoring requirements outlined by park management. While emphasis was placed on females with dependent cubs to assist in evaluating their cub rearing success, efforts were made to investigate evenly across all GPS collared individuals. A Garmin eTrex® 10 (Garmin International, Olathe, KS, USA) was used to navigate to GPS sites no older than two weeks. A search for prey remains was conducted at each site within a 30 m radius, and GPS locations were collected if prey remains were found. This data was further supplemented by carcasses observed during radio-tracking sessions or opportunistically between June 2016 and July 2019 (756 days). All kill data collected from radio-tracking or opportunistically were visually confirmed and data collected by the cheetah monitor in the same manner as that collected during GPS site investigation.

During data collection, it was assumed that the cheetah associated with the carcass made the kill, as cheetah rarely scavenge (Caro, 1982; Pienaar, 1969). Additionally, carcasses were assessed for signs that they had been killed and consumed by a cheetah. Teeth marks or saliva on the neck, minimal bone crushing and visible skinning from consumption were mostly representative of a cheetah kill of a medium sized antelope (Bothma, 2016; Schaller, 1968). The area surrounding the carcass was also assessed for signs of cheetah activity such as tracks and scats, and all signs were recorded.

### 5.4.4. Data analysis

#### 5.4.4.1. Home ranges

To ensure collars collected sufficient data across one year for accurate home range calculations, home range size using a 100 % MCP was plotted against GPS locations using the adehabitatHR package (Calenge, 2006), in order to visually determine if home ranges reached asymptotes. Home ranges estimates were then calculated for all cheetah in which asymptotes were reached using the Time Local Convex Hull methods (T-LoCoH) in the T-LoCoH package (Lyons, Turner & Getz, 2013). Local convex hulls have been shown to be the most effective method in demarcating hard boundaries and internal structures from which animals are excluded, such as fences, thereby reducing Type II errors found in home range estimates (Getz *et al*., 2007). The T-LoCoH method further modifies the local convex hulls algorithm by incorporating a time scale which acts to separate points that are far apart in time regardless of their proximity in the two-dimensional space (Lyons *et al.*, 2013). The algorithm requires the input of two parameters: the number of nearest neighbours (a) and the time scaled distance (s). The T-LoCoH algorithm was run with different values for these two parameters based on steps outlined by Lyons (2014), and the values which created the best fitted home range were selected. All data points from settlement until one-year post-settlement were included in home range estimates, in order to sample across seasons evenly, with the exception of CF3 in which there was only data for 278 days because of her death. Whilst it is acknowledged that the data collected is not independent, removal of data points in an attempt to account for autocorrelation has not always proven successful and can act to reduce biologically relevant data (Börger *et al*., 2006; Crushman, Chase & Griffin, 2005; De Solla, Bonduriansky & Brooks, 1999). Furthermore, by incorporating the time stamp of each location, the T-LoCoH algorithm considers time data within the home range calculation (Lyons *et al.*, 2013).

Home range calculations were conducted for 100 %, 95 % and 50 % isopleths. The 95 % home range isopleths were selected as they are generally considered the closest approximation of total range size, whereas, 50 %

isopleths are the most robust estimators of an animal's core area of activity (Burt, 1943; Jaremovic & Croft, 1987; Harris et al., 1990). Additionally, 100 % isopleth home ranges were constructed in order to determine the full amount of habitat available to each individual within the area it traverses (Hunter, 1998).

Home range overlap between each individual was calculated for both the 95 % home range and the core area of use (50 % isopleths). Area of overlap was calculated using the QGIS geoprocessing tool Intersection (QGIS 2.18.9; QGIS Development Team, 2018). The percentage of overlap was then calculated as the percentage of overlap between individual A and individual B using the following equation (Cristescu *et al*., 2013).

$$overlap\ (\%) = 100\ x\ [\frac{2\ x\ area\ of\ overlap}{Area\ A + Area\ B}]$$

### 5.4.4.2. Habitat mapping

LNP's habitat was classified into six categories based on vegetation structure (Table 5.2). The LNP habitat map (Figure 5.1) was created using the Random Forest algorithm pixel-based method. Layers included for classification were: all brands of Landsat Imagery (at 30 m resolution), NDVI as calculated from Landsat, Global ALOS Landforms (Theobald *et al.*, 2015), Global ALOS CHILI (Theobald *et al.*, 2015), Global Forest Canopy Height (2005; Simard *et al.*, 2011) and SRTM Digital Elevation Data (Version 4; Jarvis *et al.*, 2008). Map accuracy on training data was classified at 97.4 % and 256 GPS locations, along with associated habitat information collected around the park to inform the classification of each habitat point. The area (km$^2$) for each habitat type was then calculated using the package 'raster' (Hijmans, 2018) in R v. 3.5.1. (R Core Team, 2018) for each home range (95 % isopleths) and the whole of LNP.

### 5.4.4.3. Prey frequency of occurrence

In order to separate the effects of prey distribution and habitat characteristics, the frequency of occurrence for important prey species was calculated for each habitat type. The bulk of cheetah diet in LNP consisted of four main species, kudu (*Taurotragus strepsiceros*), bushbuck (*Tragelaphus sylvaticus*), impala (*Aepyceros melampus)* and waterbuck (*Kobus ellipsiprymnus; see*, Chapter 4). Using QGIS (QGIS 2.18.9; QGIS Development Team, 2018) the locational data from the 2018 aerial census (Sievert & Reid, 2018) for each of the four species was overlaid with the LNP habitat raster layer in order to extract habitat data per sighting. The frequency of occurrence per species in each habitat type was then calculated by dividing the number of individuals within a habitat by the total number of individuals counted (Table 5.2).

### 5.4.4.4. Habitat selection

Third order habitat selection, selection within the home range, was analysed using the used-versus-available approach to determine which habitat cheetah selected for (Davidson *et al.*, 2012; Johnson, 1980). To achieve this, a 1:1 ratio was employed for used and available points, meaning the same number of random points were generated as GPS points collected from collars from the one-year in which the home range was calculated (Davidson *et al.*, 2012; Klaassen & Broekhuis, 2018; Recio *et al*., 2014; Yiu *et al.*, 2018). As LNP's cheetah are not distributed across the whole park, random points were generated within the boundary of each 100 % home range using the Random Points in Layer Bounds research tool in QGIS (QGIS 2.18.9; QGIS Development Team, 2018). Only cheetah (CM2, CF1, CF2 and CF3) in which sufficient data was available for home range calculations had home ranges and therefore habitat selection analysed.

Fourth order habitat selection, selection of kill sites, was analysed using a used-versus-used approached where the proportion of habitat used for kill sites was compared to the proportion of habitat used within the home range (Rostro-Garcia *et al.*, 2015). Only kills that were attributed to a cheetah in which habitat selection was analysed were used to ensure consistency. It is important to note that not all GPS points collected from the collars were investigated. Therefore, non-kills sites were not compared to kill-sites, however, the bulk of GPS collar data should represent non-kill sites, thus allowing for this comparison.

The proportion in which each habitat was expected to be used and the proportion of habitat selected by the cheetah was plotted into a categorized histogram to allow for descriptive comparisons. Both chi-square goodness-of-fit and Fisher Exact tests were used to determine if the proportions of habitats used differed significantly from those selected at random (Hunter, 1998). A chi-square with Bonferroni corrections was then conducted to determine which of the habitats differed significantly in their proportions recorded. All individual data for both used and available locations were combined to allow for comparisons across the population (Dellinger *et al.*, 2013). A second analysis was done in which the male animal (CM2) was excluded, allowing for the analysis of only female habitat selection. All statistical analyses were performed using statistical software R v. 3.5.1. (R Core Team, 2018). Proportions were considered significantly different when $p < 0.05$ except for each Bonferroni corrected chi-square test in which $p < 0.01$ demonstrated significance. Selection or avoidance of a habitat was assumed if there was a significant difference in the expected versus used habitat, regardless of the proportion in which the habitat was used.

**Table 5.2.** Summary of the six habitat types classified for LNP, Malawi, along with the frequency of occurrence of the four most important prey species in the park's cheetah diet. Descriptive classifications were made using a vegetation report created for LNP (Dudley, 2004).

| Vegetation Structure | Habitat Type (area) | Prey Frequency of Occurrence | | Description |
|---|---|---|---|---|
| **Open** | Floodplain (65.6 km$^2$) | Kudu | 18.1 | Open grassland bordering the Shire River dominated by *Setaria* spp., *Digitaria* spp., *Sporobolous* spp., *Echinochloa* spp. and, *Panicum* spp. Flooding of these areas varies seasonally and are also affected by changing water levels in Lake Malawi and the barrage just south of the park. This area is also marked by scatterings of trees including *Hyphaena* spp. |
| | | Impala | 70.5 | |
| | | Bushbuck | 51.2 | |
| | | Waterbuck | 95.6 | |
| | Grassland (18.3 km$^2$) | Kudu | 4.8 | Similar species composition as the floodplain, however, flooding only occurs mid- to late-wet season. Grasslands are generally interspersed amongst the open woodland on the eastern side of the park. |
| | | Impala | 0.4 | |
| | | Bushbuck | 1.0 | |
| | | Waterbuck | 0.4 | |
| **Semi-open** | Open Woodland (288.6 km$^2$) | Kudu | 53.7 | Three woodland types were categorized as open woodland due to their sparse undergrowth. 1) Cathedral mopane, a *C. mopane* dominated woodland which contains wide even spacings of trees that vary from 31 to 12 m in height with short grass cover. 2) Clumped woodland, widely spaced clumps of woodland interspersed with grassland, predominantly made up of tall *C. mopane* (<27 m). 3) Mixed open woodlands dominated by *Combretum* spp., *Terminalia* spp. and, *Diplorhynchus spp.*, varying from 10 to 12 m in height, grass varies in height depending on seasonal brush fires. |
| | | Impala | 17.1 | |
| | | Bushbuck | 17.9 | |
| | | Waterbuck | 2.2 | |
| **Closed** | Mopane Scrub (25.2 km$^2$) | Kudu | 1.9 | A very dense vegetation area of predominately immature *C. mopane* 4 to 6 m in height. Low bush such as *Adenium spp.*, is interspersed between the mopanes. Scatterings of mature species such as *C. mopane*, *Adansonia* spp. and *Euphorbia ingens* can also be found here. |
| | | Impala | 3.6 | |
| | | Bushbuck | 3.8 | |
| | | Waterbuck | 0.4 | |
| | Thicket (7.6 km$^2$) | Kudu | 0.0 | An area that contains the highest diversity in vegetation with a broken canopy around 8 and 15 m. Low vegetation is dense and predominantly *Vachellia* spp. There is almost no grass cover in this area. |
| | | Impala | 0.6 | |
| | | Bushbuck | 1.4 | |
| | | Waterbuck | 0.0 | |
| | Riparian (107.5 km$^2$) | Kudu | 2.1 | A narrow band of well-developed forest which falls along all perennial rivers. Species vary from *Borassus* spp., *to Vachellia* spp. The sub-canopy is dense and grass cover is minimal in due to the significant canopy covering. |
| | | Impala | 7.9 | |
| | | Bushbuck | 24.6 | |
| | | Waterbuck | 1.4 | |

## 5.4. Results

### 5.4.1. Home ranges

Home range estimates (Figure 5.2) were calculated for four of the five cheetah that were found to have reached settlement (*see*, Chapter 3). CM1's collar collected 176 fixes after settlement which was insufficient for home range calculations (Table 5.3). Home ranges (95 % isopleths) varied between 41-97 km$^2$, with the core area of use (50 % isopleths) ranging from 13-28 km$^2$.

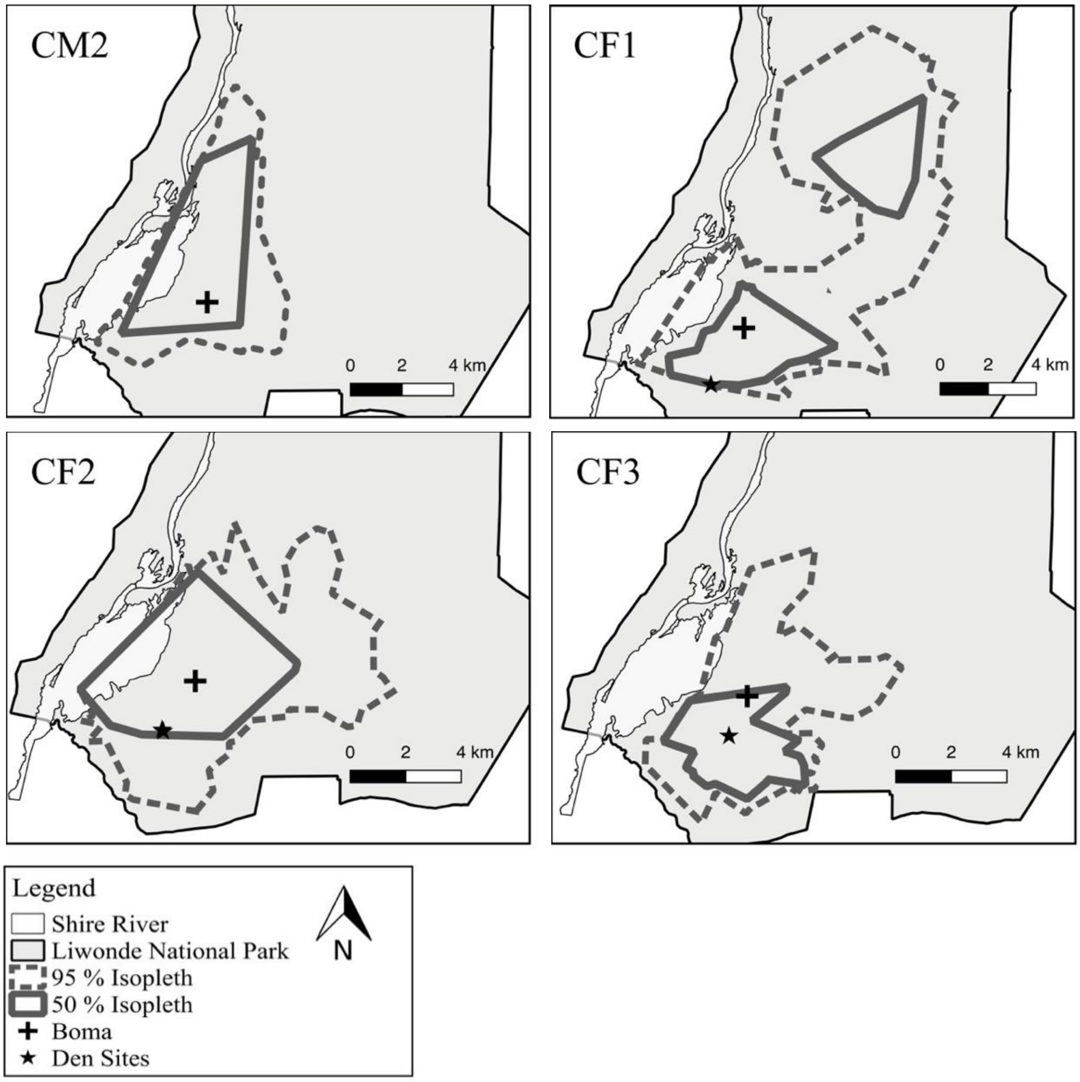

**Figure 5.2.** Home ranges (95 % and 50 % isopleths) for cheetah reintroduced into LNP as estimated by the T-LoCoh technique, with reference to the release site (boma) and each females' denning location.

All home ranges and core areas of use experienced overlap (Table 5.4). CF3 and CF2 were found to have the highest percentage of home range overlap (71.1 %), whereas CF2 and CF1 had the highest area of overlap (43 km$^2$). CM2's home range overlapped with each female's home range by 40.1-60.9 %. Core home ranges experienced similar levels of overlap with CM2 and CF2 having the greatest amount of overlap, 62.7 % (16 km$^2$).

**Table 5.3.** Details of home range analysis for reintroduced, GPS collared, cheetah after settlement. Table includes parameters used for T-LoCoH analysis when assessing 95 % and 50 % isopleths.

| ID Code | Monitoring Days Used | No. Fixes | No. Kills within Monitoring Days | No. Sightings within Monitoring Days | Asymptote Reached (Y/N) | T-LoCoH ($km^2$) 95% [50%] | T-LoCoH Parameters Selected |
|---|---|---|---|---|---|---|---|
| **CM1**[a] | 91 | 176 | 5 | 0 | N | N/A | N/A |
| **CM2** | 356 | 1592 | 35 | 53 | Y | 41 [23] | a = 90,000<br>s = 0.03 |
| **CF1** | 365 | 1757 | 35 | 13 | Y | 97 [28] | a = 70,000<br>s = 0.03 |
| **CF2** | 365 | 1217 | 61 | 28 | Y | 63 [28] | a = 90,000<br>s = 0.07 |
| **CF3** | 278 | 952 | 21 | 7 | Y | 41 [13] | a = 40,000<br>s = 0.03 |

[a] Insufficient data to create home range estimate.

**Table 5.4.** Area of home range overlap ($km^2$) of cheetah in LNP, Malawi. Values above the diagonal represent home range (95 % isopleth) overlap, values highlighted in grey represent core area (50 % isopleth) overlap. Parentheses represent percentage of home range overlap.

| ID Code | CM2 | CF1 | CF2 | CF3 |
|---|---|---|---|---|
| **CM2** | ■ | 28<br>(40.6) | 31<br>(59.6) | 25<br>(60.9) |
| **CF1** | 6<br>(23.5) | ■ | 43<br>(53.8) | 28<br>(40.6) |
| **CF2** | 16<br>(62.7) | 13<br>(46.4) | ■ | 37<br>(71.1) |
| **CF3** | 4<br>(22.2) | 8<br>(39.0) | 7<br>(34.1) | ■ |

### 5.4.2. Habitat selection

Pooled data across all cheetah and seasons incorporated 5518 locations, with an average of 1379 locations per cheetah (range 952-1757; $n = 4$). Home ranges encompassed most habitat types, with open woodland dominating female home ranges and floodplain the dominant habitat in CM2's home range (Appendix 5A). CF1 was the only cheetah to incorporate a large proportion of riparian habitat within her home range. For the 3rd order of selection, selection within the home range, there was a significant difference in the proportions of habitats used compared to expected ($p < 0.0005$). Cheetah used more open woodland (10 % more; $p < 0.01$) and less riparian (7 % less; $p < 0.01$) and grassland (2 % less; $p < 0.01$) than expected based on its availability (Table 5.5).

**Table 5.5.** Results of Bonferroni corrected Chi-square test on proportions of habitats used compared to expected for both the 3rd and 4th selection order. Differences in habitat use for the 3rd order was also investigated and is reported as seasonal variation. P-values reported in italics represent significant differences.

| **Habitat** | **All Cheetah** *n* **= 4** | | | **Female Cheetah** *n* **= 3** | | |
|---|---|---|---|---|---|---|
| | **3rd Order Selection** | **4th Order Selection** | **Seasonal Variation** | **3rd Order Selection** | **4th Order Selection** | **Seasonal Variation** |
| **Floodplain** | 0.48 | *<0.01* | 0.08 | *<0.01* | *<0.01* | *<0.01* |
| **Grassland** | *<0.01* | 0.18 | 1 | *<0.01* | 0.04 | 1 |
| **Open Woodland** | *<0.01* | *<0.01* | 1 | *<0.01* | *<0.01* | 1 |
| **Mopane Scrub** | 1 | 1 | 0.26 | 0.12 | 1 | 0.41 |
| **Riparian** | *<0.01* | 0.04 | 0.49 | *<0.01* | 0.04 | 0.87 |
| **Ticket** | 0.05 | 1 | 0.33 | 0.84 | 1 | 1 |

Floodplain, mopane scrub and thicket habitats were all used equivalent to its availability (Figure 5.3). The 152 known cheetah kills recorded in this study occurred in habitats disproportionally to how often each habitat was used ($p < 0.01$; Table 5.5). There was a significant difference in the proportion of kills on the floodplain compared to the proportion in which the floodplain was selected for (15% more; $p < 0.01$), comparatively, significantly less kills occurred in open woodland habitats than expected based on its use (23 % less; $p < 0.01$). There was no significant difference ($p > 0.01$) in the use of grassland, mopane scrub, riparian and thicket habitats for both the 3rd and 4th selection orders (Figure 5.3).

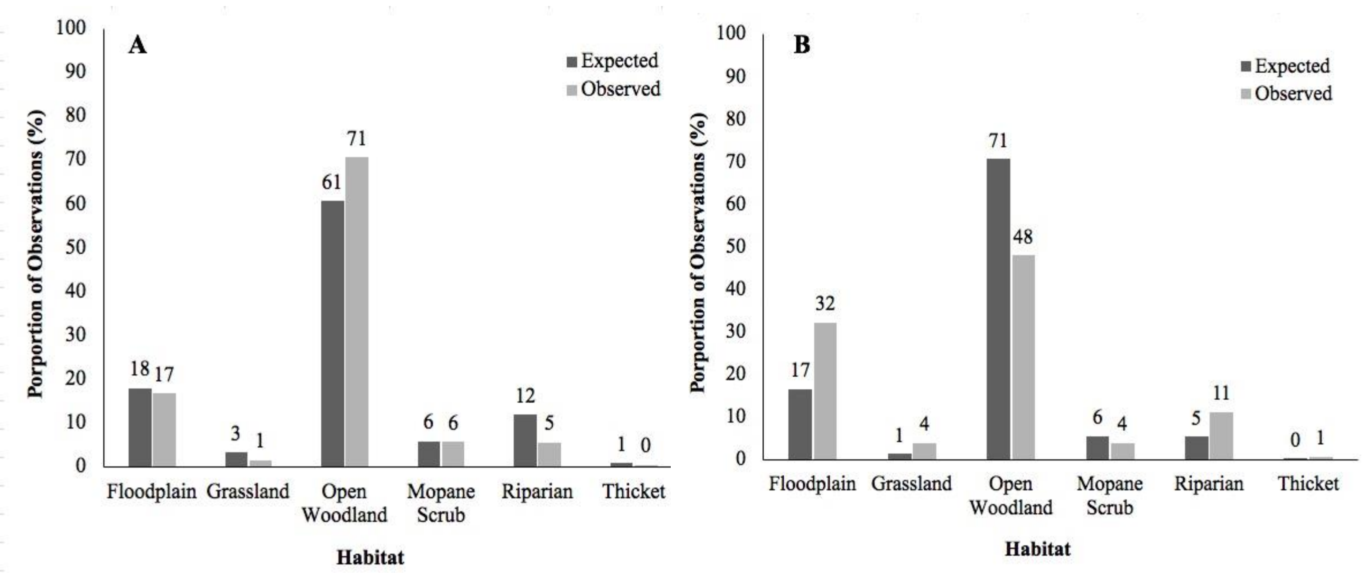

**Figure 5.3.** Proportions of habitats used (observed) compared to the expected proportions of habitats used for both 3rd order (**A**) and 4th order (**B**) habitat selection of cheetah ($n = 4$) in LNP, Malawi.

Pooled data for females incorporated all seasons and the denning period for each female (total 3926 locations; average 1308 locations per cheetah; range 952-1757; $n = 3$). There was a significant difference in the proportion of habitats used compared to expected ($p < 0.001$), similar to that of the pooled data (Figure 5.4). However, females used floodplain, grassland and riparian habitats less than expected ($p < 0.01$ for all) and, open woodland significantly more than expected (16 % more; $p < 0.01$). There was no significant difference in the proportion of mopane scrub and thickets used when compared to the expected. Female cheetah made kills significantly less in open woodland compared to the proportion in which it was used (26 % less; $p < 0.01$), instead killing prey significantly more in floodplain habitats (13 % more; $p < 0.01$). Although kills occurred in grassland, mopane scrub, riparian and thicket habitats, there was no significant difference in the proportion as kill sites compared to the proportion in which these habitats were used.

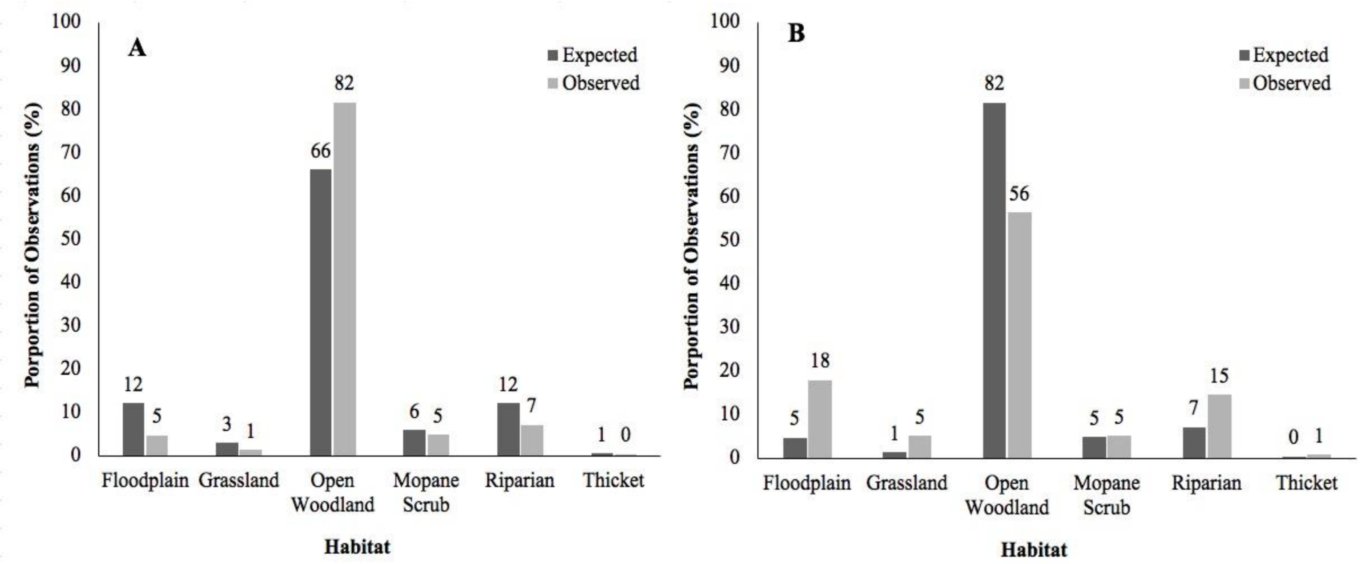

**Figure 5.4.** Proportions of habitats used (observed) compared to the expected proportions of habitats used for both 3rd order (**A**) and 4th order (**B**) habitat selection of female cheetah (*n* = 3) in Liwonde National Park, Malawi.

When comparing the proportions of each habitat type used in the wet versus in the dry season, a significant difference was found for both pooled data ($p = 0.0066$) and female cheetah ($p = 0.0021$). Female cheetah used a significantly ($p < 0.01$) smaller proportion of floodplain (4 % less) in the wet season (Figure 5.5).

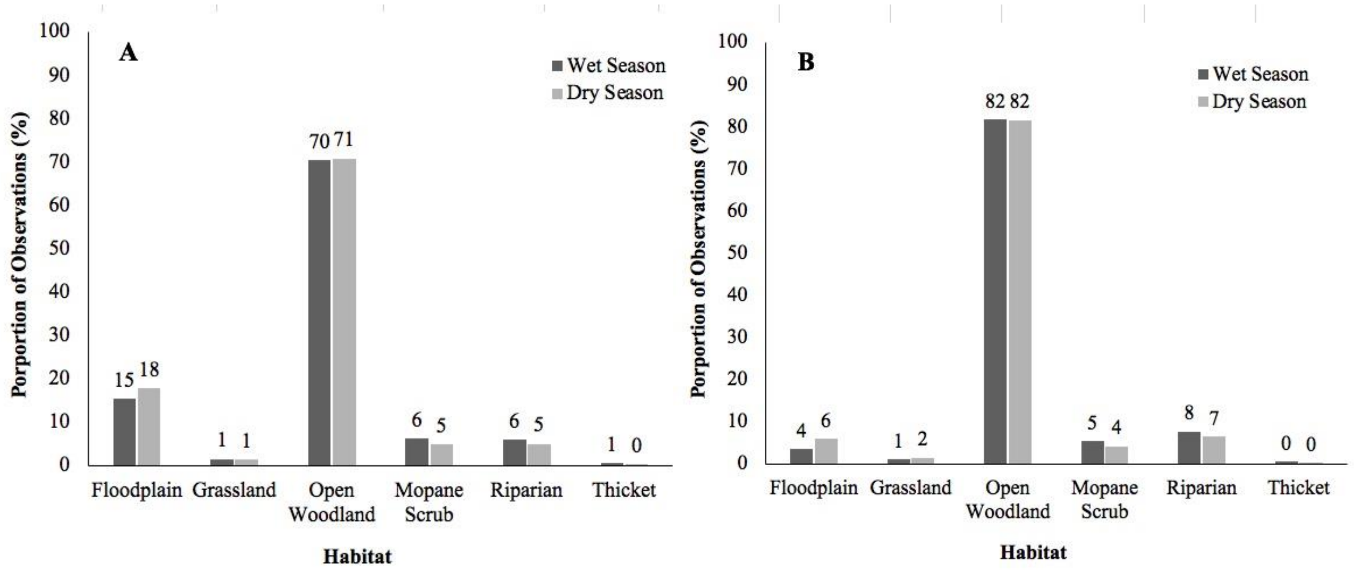

**Figure 5.5.** Proportions of habitats used in wet season compared to dry season for 3rd order habitat selection across all cheetah (**A**; *n* = 4) and across all female cheetah (**B**; *n* = 3) in LNP, Malawi.

## 5.5. Discussion

Reintroduced cheetah in LNP developed relatively small home ranges compared to the available area in the park. Based on the prey abundance hypothesis, the relatively small home ranges in LNP are indicative of high prey abundances (Davidson *et al*., 2012). Home ranges averaged 60.5 ± 26.5 SD km$^2$. Home range estimates for LNP's cheetah fell within the range estimated in previous studies which have reported great variation, from 11 km$^2$ in MNP (Purchase & Vhurumuku, 2005) to over 1651 km$^2$ on Namibian farmlands (Marker *et al*., 2007). However, studies in fenced-systems with woodland habitat have documented less variation, 22 km$^2$ (Rostro-Garcia *et al*., 2015) to 195 km$^2$ (Broomhall *et al*., 2003). When compared to home ranges, a lesser size disparity was found in core areas (50 %; range 13-23 km$^2$). Core areas have been reported as averaging 10-14 % of home range size (Broomhall *et al*., 2003; Houser *et al*., 2009; Marker *et al*., 2007; Marnewick & Somers, 2015), however, the reasoning for this phenomenon is unknown. In LNP, this was not documented, instead core areas comprised 28-56 % of overall home range size.

Disparities in reported home range size can be attributed to biological and ecological factors, as well as analytic methods employed. In woodland environments home range size has been attributed to habitat structure and variation of prey densities across landscapes, which create suitable foraging patches and alter home range size based on patch spacing (Broomhall *et al*., 2003; Hunter, 1998; Purchase & du Toit, 2000). Average home range size in LNP was smaller than that in PPRR (Hunter, 1998) and KNP (Broomhall *et al*., 2003) which may indicate a higher density of suitable habitat patches at LNP. However, it is important to note that no previous studies have used T-LoCoh methods to estimate cheetah home ranges in woodland environments, which may alter these comparisons. In carnivores, it is unusual for males to have smaller home ranges than females (Sandell, 1989). However, two of LNP's female cheetah had home ranges larger than that of the male, and the average female home range size was larger than that of the male (Female, $\bar{x}$ = 67 ± 28.2 SD km$^2$; Male, 41 km$^2$). For cheetah, when female home range size increases it becomes indefensible by males, thereby reducing male home range size (Caro, 1994). Similar to the findings in the current study, male home range size has been documented as smaller than female home range size in other cheetah populations (Broomhall *et al.*, 2003; Purchase & du Toit, 2000; Rostro-Garcia *et al.*, 2015; Welch *et al.*, 2015).

This study found that home ranges and core areas for all four-cheetah overlapped considerably (40-71 % overlap). Intersexual home range overlap is extensively documented as it increases mating opportunities (Caro & Collins, 1987; Sandell, 1989), and intrasexual home range overlap has been well documented in cheetah (Broomhall *et al.*, 2003; Houser *et al.*, 2009; Marker *et al*., 2007; Marnewick & Cilliers, 2006). Interestingly, intrasexual core area overlap, which was found in LNP (22-62 % overlap) is not as commonly documented. Core area exclusivity is typical of asocial felids (Mizutani & Jewel, 1998), and although cheetah are a facultatively social carnivore, females are often solitary or with dependent cubs (Durant, Kelly & Caro, 2002). However, in this study intrasexual overlap in female core area was well above the 10 % threshold (34-46 %) which is thought to demonstrate exclusivity (Sandell, 1989). This low level of core area exclusivity is partly indicative of restricted movements during the denning period. All females in LNP denned within close proximity (≤ 1.3 km). However, removing this time period from the analysis removes biologically relevant data and may skew both home range and core area estimations. Instead, similar to the concept of suitable patch spacing affecting home range size, suitable denning locations may have affected core area size and location. This is further supported by CF1's two areas of core use, one of which overlapped with her den site, which otherwise was located on the edge of her home range. Therefore, including this data allows one to conclude that suitable den sites may be limited within LNP. Consequently, denning periods may cause home range shifts and increased overlap for females, which may have a knock-on effect for both cub survival and male territorial behaviour.

Concealment at a suitable den site is important for early cub survival (Laurenson, 1995a; Laurenson, 1993; Laurenson, Caro & Borner, 1992). The litter survival rate recorded during the two years of post-release monitoring in LNP (100%; *see*, Chapter 3) is indicative of suitable den site selection. Although Laruenson (1993) found that litter survival in the den was predominantly based on avoiding predator attacks, protection against the elements also proved important. Additionally, the proximity to water was assessed as an important factor of den site selection, as females increase time spent drinking during lactation (Laurenson, 1995a). Interestingly, female CF3 birthed her litter in the wet season when water was wide-spread throughout the park. Regardless, CF3 selected a den site <650 m from CF2 and <1.2 km from CF1's dry season dens, indicating that water availability may not be a factor in den site selection for cheetah in LNP. All four den sites examined in this study had difficult access routes, no game trails, moderate to high vegetation cover and a steep slope (pers. obs.). Considering the relative flatness and high prey densities of LNP, areas with these specifications are not commonly found. Furthermore, these den sites are expected to provide a high amount of drainage, an important factor in LNP which floods seasonally.

CF2 and CF1 birthed their first litters <650 m and two weeks apart. Based on GPS collar data, these females showed no interaction during this time and both litters reached the emergence and independence stage. However, an increase in cheetah activity in this area due to multiple females denning at one time may act to reduce prey catchability (*e.g.,* ecology of fear; Brown, Laundré & Gurung, 1999). A reduction in prey catchability will prolong hunting periods which will incur an overall risk to cub survival through larger periods of minimal protection, abandonment or reduction in milk production (Laurenson *et al.*, 1992; Laurenson, 1995b). Furthermore, the high degree of denning overlap and the specifications of selected den sites is indicative of low den-site suitability in the southern section of the park. Den sites selected away from this area may, therefore, experience lower levels of success. It is recommended that factors affecting den site selection and litter survival continue to be investigated over the long-term for this population in order to better understand selection factors and predict female spatial distribution.

Male cheetah display high levels of intrasexual aggression (Caro & Collins, 1987; Eaton, 1968). The high amount of spatial overlap in LNP results in large areas that are relatively devoid of cheetah activity. These areas may appear as suitable habitat due to low numbers of conspecifics and high prey populations. However, if encounters with females do not occur in these areas it will result in these habitats ceasing to be attractive. This is commonly recorded in large carnivores, especially during the dispersal stage, where males remain as "floaters" and travel through suitable habitat while searching for females (Hunter, 1998; Fattebert *et al.,* 2013). Non-territorial behaviour is common for cheetah and has shown to increase mortality rates (Caro, 1994). A high degree of spatial overlap in the female population will, therefore, limit suitable territories for males. This, in turn, will increase male-male aggression as well as result in a higher proportion of the male population demonstrating "floating" behaviour, thus increasing male mortality rates. High male mortality rates could have catastrophic consequences on the long-term viability of this small population. Therefore, priority should be placed on creating a greater spread in the distribution of females in LNP. This can be accomplished during future supplementation events by employing a hard-release methodology (*eg.,* no acclimation time in the southern section of LNP) into northern sections of the park (*see,* Chapter 3). This is especially important, as females born into the system are also now demonstrating high overlap with the females in this study (pers. obs.). It is important to note that LNP floods extensively during the wet season, therefore creating multiple bomas in the park to spread out soft-release sites may not be feasible as they will be inaccessible to management during the wet season.

Cheetah home ranges incorporated all six habitat types. When examining habitat selection within the home range (3rd order selection), cheetah (pooled and females) selected for semi-open areas with high occurrences of their preferred prey, namely kudu, but low occurrences of other species. These findings contrast that of studies in other wooded habitats which found that cheetah select for open areas with high prey densities (Broomhall *et al.,* 2003; Rostro-Garcia *et al.,* 2015). Similar studies found that female cheetah select for more closed habitats than males at the 3rd order (Bissett & Bernard 2007; Broomhall *et al.,* 2003; Rostro-Garcia *et al.,* 2015). In LNP, females selected against both open and closed habitats (floodplain, grassland and riparian) and only selected for open woodland. Whilst female preference for thicker habitat has been correlated with prey availability (Broomhall *et al.*, 2003), this preference is more widely interpreted as a predator avoidance strategy (Bissett & Bernard 2007; Cristescu *et al.*, 2013; Durant, 2000; Rostro-Garcia *et al.*, 2015). Interestingly, all three females in this study demonstrated this behaviour to an extent, by avoiding open habitats at the 3rd order. During this study, the population of competing carnivores in LNP is relatively low and, prior to a reintroduction of three lion (between 79 and 284 days into this study), only a small population of hyena (~ 25 individuals) were present in the system. Interestingly, predator avoidance behaviour by female cheetah has been described as a learned behaviour that is reinforced by breeding success (Durant, 2000). During this study, all three females had their first litter of cubs. Considering the low density of competing carnivores, it is possible that the selection of semi-closed habitats by females with dependent cubs is a more innate behaviour than originally thought. However, it is noted that the sample size of females is limited, and this should be further investigated. Males have been described as selecting for more open habitats than females (Bissett & Bernard, 2007; Broomhall *et al.*, 2003; Rostro-Garcia *et al.*, 2015). This selection has been interpreted as a strategy for detecting intruding males (Broomhall *et al*., 2003). The current study supports these findings as CM2's home range encompassed a greater proportion of open floodplain habitat than that of female home ranges.

On a finer scale (4th order selection), LNP's cheetah selected for floodplain habitat which had a high prey frequency of occurrence and selected against open woodland environments which had lower prey frequency of occurrence. Previous studies on 4th order habitat selection for cheetah have found varying results. For example, in Kwandwe Private Game Reserve (Bissett & Bernard, 2007), KNP (Mills *et al.*, 2004) and MNP (Purchase & du Toit, 2000) cheetah were found to hunt in the most open habitats, however in PPRR (Rostro-Garcia *et al.*, 2015) cheetah selected for kill sites in closed habitats. One would expect that the vast open areas and large herd sizes would decrease the catchability of prey in LNP's floodplain habitat (Mills *et al.*, 2004; Fitzgibbon, 1990). However, in MNP (Purchase & du Toit, 2000) and PPRR (Hunter, 1998) it was determined that while cheetah selected open habitats for hunting, they made use of wooded edge habitats for ambushing of prey. The adjacent woodland and scatterings of palm thickets in LNP's floodplain habitat may, therefore, assist cheetah in prey capture. Consequently, while it appears LNP's cheetah are selecting for areas with high prey encounter rates rather than high catchability, it is possible that both are true of this habitat. Using open areas for hunting is likely further reinforced by the low levels of kleptoparasitism currently in the system.

While this study attempted to assess the effects of both habitat structure and prey occurrence on habitat selection, a major limitation of this study must be noted. Prey frequency of occurrence was only accessed in the peak dry season, when ungulates were congregated near water sources. The Shire River is the most prominent water source during the dry season resulting in a higher abundance of ungulates inhabiting the floodplain and adjacent woodland habitats. However, seasonality appeared to have little effect on 3rd order habitat selection, therefore vegetation structure rather than prey distribution may have a greater effect on larger scale habitat selection for cheetah in LNP. Regardless, the effects of seasonality need to be investigated further.

As the full carnivore guild is restored in LNP, cheetah are likely to undergo a niche shift (Bissett *et al.* 2015). Cheetah demonstrate predator avoidance behaviour by seeking spatial and/or temporal refuges (Bissett *et al.*, 2015; Bissett & Bernard, 2007; Durant, 1998a; Rostro-Garcia *et al.*, 2015). Heterogenous environments, such as LNP, allow for competitive refuges which are crucial in promoting the persistence of species with low competitive abilities (Durant, 1998a). In systems with high levels of intraguild competition, an increased selection of closed habitats for hunting by cheetah has been recorded and shown to decrease intraguild predation and kleptoparasitism (Mills *et al.*, 2004). Cheetah in LNP have demonstrated a high versatility in habitat use and therefore should remain successful should a niche shift occur. However, a niche shift to denser habitats may adversely affect certain prey species. Cheetah in LNP hunt kudu disproportionally to their abundance (*see,* Chapter 4). However, kudu occur in lower numbers than impala and waterbuck in the cheetah's preferred hunting habitat and only represented 2 % of the kills recorded there (Appendix 5.B). In denser habitats such as open woodland, riparian and mopane scrub, kudu accounted for 14-33 % of recorded kills. A shift to hunting in denser habitats as a response to increased kleptoparasitism may result in an increase in kudu predation. This could increase selective predation pressures on this population (Makin & Kerley, 2016) and negatively impact the demographics and consequently the population of kudu in LNP. It is therefore recommended that the habitat selection of cheetah in LNP is re-assessed as intraguild competition increases.

This study found no habitats which cheetah completely avoided. Although no prolonged behavioural observations occurred during this study, initial sightings behaviour demonstrated a multi-use approach to the habitat available (Appendix 5.C). For example, although cheetah selected floodplain habitats for hunting, cheetah were recorded resting during the majority of the sightings in this environment (Appendix 5.B). Furthermore, cheetah displayed a high flexibility in hunting, with kills recorded in all six habitats and females selecting for hunting sites in habitats with varying levels of cover (floodplain, riparian and grassland). Additionally, there were limited changes in habitat selection seasonally. The results, therefore, support the notion that the cheetah is more adaptable to a wide range of habitats than previously described (Bissett & Bernard 2007; Mills *et al*., 2004; Welch *et al*., 2015). It is proposed that habitat selection described in this study is the ideal habitat for cheetah in a mixed woodland environment with low levels of intraguild competition. Given the spatial distribution, habitat use and high levels of home range overlap, LNP could sustain a high population of cheetah if prey densities are maintained.

## 5.6. Conclusion

To the authors' knowledge, this study was the first to assess the spatial distribution and habitat selection of cheetah in woodland habitat with low levels of intraguild competition. Cheetah preferred open and semi-open habitats with medium prey frequency of occurrence. However, when selecting kill sites cheetah preferred open areas of relatively high prey frequency of occurrence. Irrespective of the low levels of intraguild competition, female cheetah appeared to favour one area for denning, which resulted in a high level of home range and core area overlap. This intensive den site selection may affect cub survival, the spatial distribution of females and male survival as the population grows. The importance of attempting to produce a greater spread in female distribution with subsequent translocation events is emphasised. Regardless, the cheetah in LNP demonstrated a high versatility in their habitat use, and the habitat use flexibility demonstrated by reintroduced individuals is encouraging for additional reintroductions into Malawi's woodland dominated protected areas.

## 5.7. Acknowledgements

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## 5.8. Ethical clearance

Relevant permits for the work were obtained by African Parks during the routine monitoring. (CITES permit numbers: 175828; 0000062; 0000079). Ethical clearance for use of collar data as a third-party user was obtained through Stellenbosch University (ethics reference number: ACU-2018-8311).

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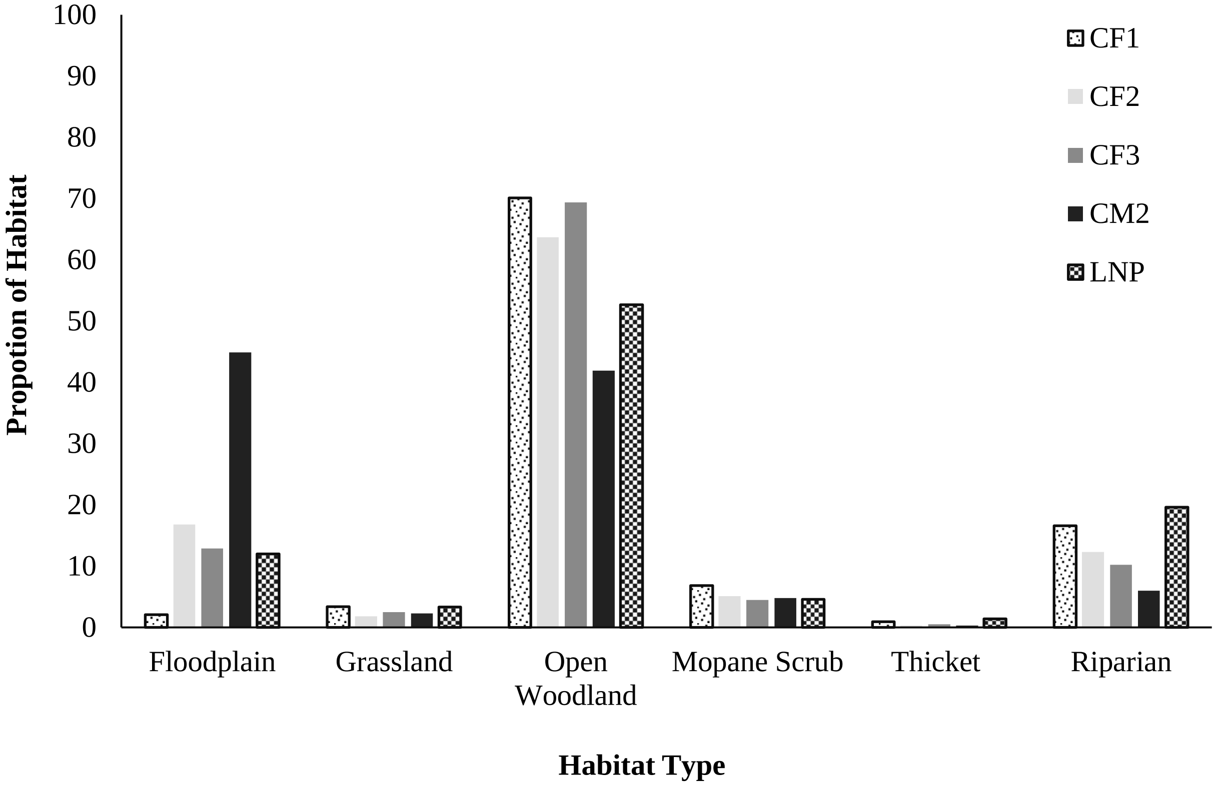
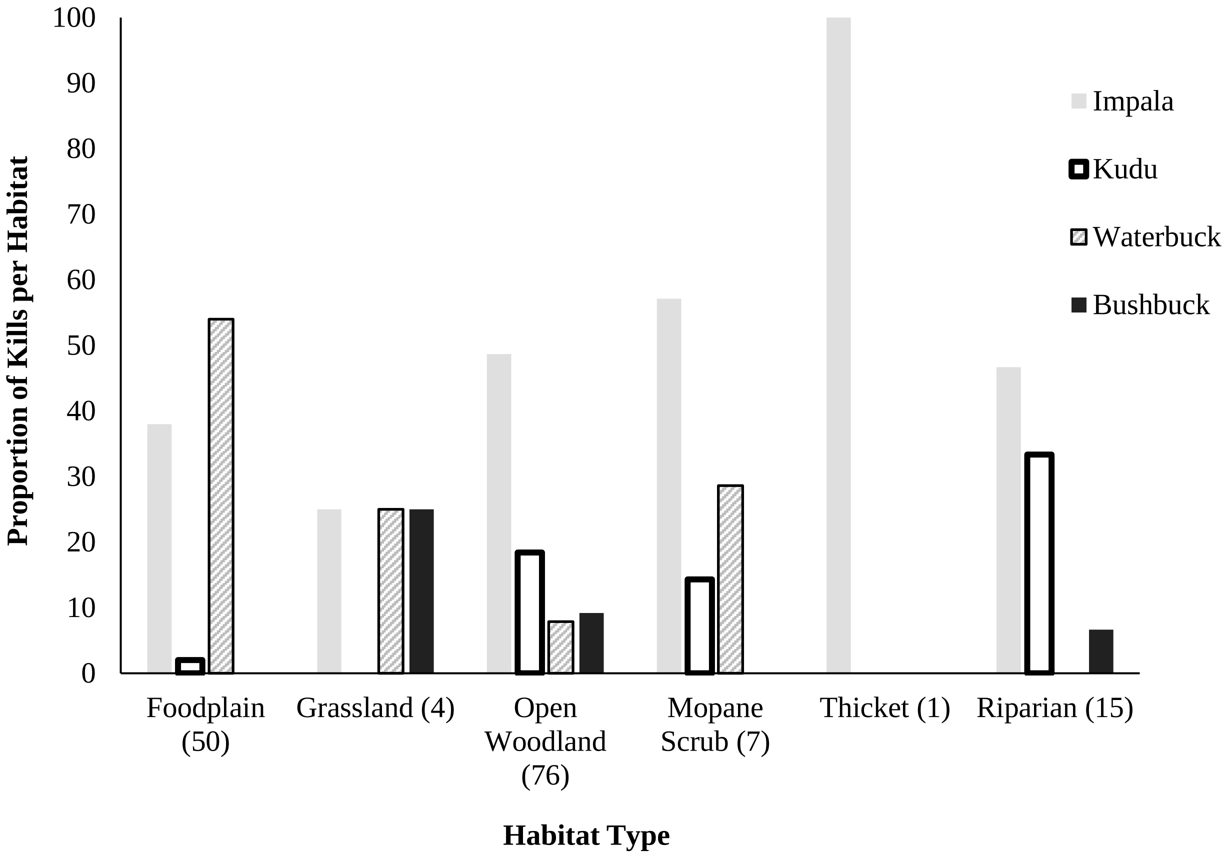
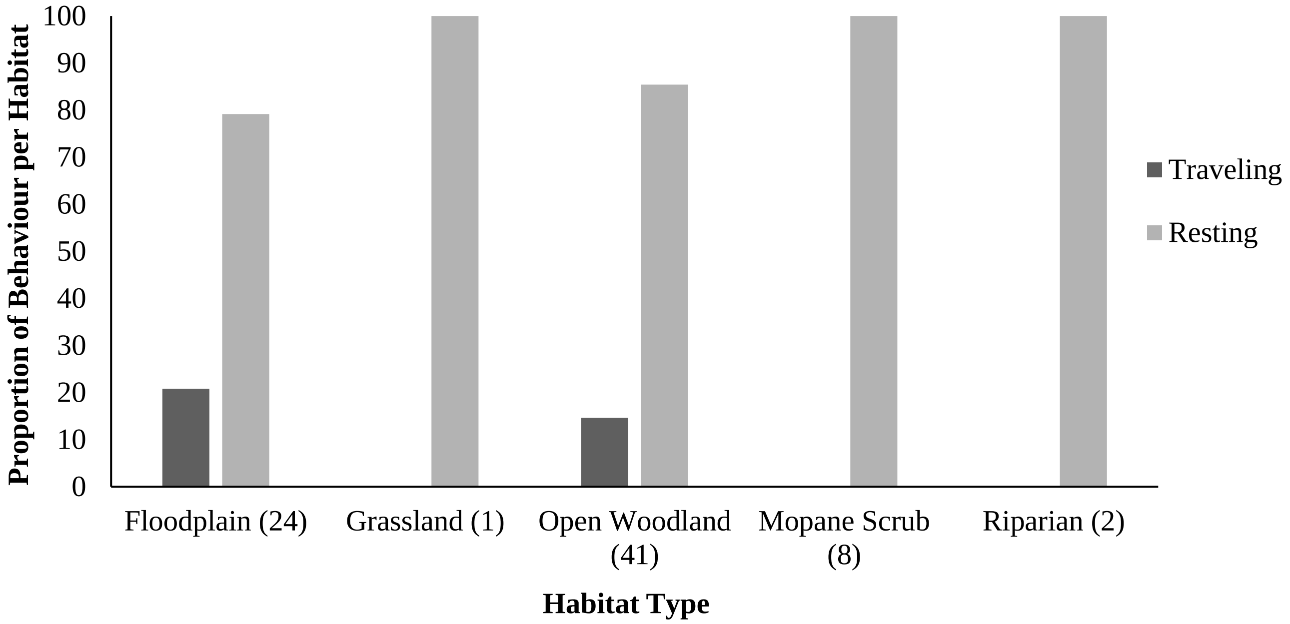
## 5.10. Appendices



**Appendix 5.A.** The proportion of habitat type in the home ranges (95 % isopleths) of each cheetah and for LNP. Water not included in habitat type but considered when calculating LNP proportions.



**Appendix 5.B.** The proportion of kills per habitat type in LNP. Only kills that were confirmed to one of the four cheetah and occurred within the one-year analysis period were included. The graph includes only the four most important prey species for LNP's cheetah. However, other species were killed and included in the total kills per habitat type when calculating proportions. Total kills recorded per habitat type are in parentheses.



**Appendix 5.C.** The proportion of behaviours observed per habitat type in LNP. Only sightings that occurred within the one-year analysis period were included. Total sightings per habitat type are in parentheses. It is noted that time of day will greatly affectaffect behaviours observed.

# Chapter Six

## Research Findings and Management Implications

### 6.1. Overview

The cheetah (*Acinonyx jubatus*), Africa's most endangered felid, has experienced rapid range and population contractions in the last decade (Durant *et al*., 2017). A remaining population of an estimated 6700-7100 individuals is now scattered across 32 of the species' 53 historical range states, comprising roughly 9 % of the historical distribution (Durant *et al.,* 2015; Durant *et al.,* 2017). The nearest resident cheetah population to Malawi is over 250 km away, in Tanzania (Durant *et* al., 2017). Whilst the sighting of a single cheetah in Lower Zambezi National Park, Zambia, in 2017 (>380 km from Malawi; Luxury Safari, 2017) suggests dispersal to historical range in the region is possible, the high human density surrounding Malawi's protected areas renders it unlikely that a viable population will establish in the country through natural dispersal. Furthermore, the realised conservation value of Protected Areas (PAs) in Malawi have declined over the last few decades due to a lack of funding, high levels of poaching and human encroachment (Morris, 2006). As such, certain PAs are now shifting towards a fenced-system approach to stem natural resource off-take and edge effect pressures caused by surrounding communities. Consequently, reintroductions are currently the most viable tool to ensure the restoration of cheetah to Malawi.

In 2017, African Parks (AP) Liwonde in partnership with the Endangered Wildlife Trust (EWT) conducted the first human-mediated cheetah range expansion efforts in the region by reintroducing a founder population of seven individuals to Liwonde National Park (LNP), Malawi. Although the population has grown to 14 individuals, its small size renders it extremely susceptible to extirpation due to stochastic events. Additionally, given the two-year population recruitment and the small founder population, this population is at high risk of inbreeding. LNP's cheetah population, therefore, still requires intensive management to ensure its long-term viability and conservation value. Genetic supplementation in the form of additional translocations should be implemented to maintain genetic diversity and ensure population growth. Moreover, animals that are at high risk of inbreeding should be identified for translocation. It is highly recommended that AP Malawi establishes a comprehensive agreement between their management areas to ensure the development of a metapopulation node complimentary to the EWT's Cheetah Metapopulation Project (CMP). A well informed metapopulation node will allow for human-mediated dispersal and the implementation of a conceptual population management approach which will ensure the long-term genetic integrity and viability of the population. This chapter summarises the findings of this thesis, provides scientifically informed recommendations for the management of LNP's cheetah population and outlines future research which will aid in the ongoing management of LNP's carnivore populations.

## 6.2. Research findings

### 6.2.1 Post-release movements and establishment

Studies on the effectiveness of the soft-release procedures in large carnivore reintroductions and translocations have had varying results, from highly effective (Adania *et al.*, 2016; Devineau *et al.*, 2011; Fritts *et al*., 2001; Hunter, 1998), to not effect (Weise *et al.*, 2015a; Weise *et al*., 2015b; Sarkar *et al.*, 2016) and even detrimental (Marneweck *et al*., 2019). Cheetah released into LNP were held for an average of 41 days (range 23-58 days), at which point they were released and monitored weekly for two-years to evaluate reintroduction success. Using similar studies (Briers-Louw, Verschueren & Leslie 2019; Griffith *et al*., 1989; Weise *et al.*, 2015a; Weise *et al*., 2015b; Yiu *et al.*, 2015) reintroduction success was defined for both the individual and the population level. Individual reintroductions were considered successful if an individual showed release site fidelity, successfully settled (established a home range), reproduced and survived for one-year post-release. The reintroduction of the population was considered successful (established) if 80 % of adult groupings settled within the first year and if the population conformed to demography levels documented within the source population after two years (*e.g.*, Bissett & Benard, 2011; Hunter, 1998; Power *et al.*, 2019).

Cheetah were released an average of 1644 km away from there capture site, therefore, homing behaviour was not investigated (*see,* Weise *et al.*, 2015a). Seventy-one percent (5/7) of reintroduced cheetah demonstrated release site fidelity and formed home ranges in the first-year post-release. Additional time in the boma (>23 days) had no effect on post-release movements. However, sex had a significant effect on post-release movements, with males travelling larger distances and for a longer period of time than females. Females quickly conceived their first litter after release (estimated range, 30-46 days), and the population appears to have conformed to demography levels similar to the source population. Reintroductions on the individual level experienced a 57 % success rate (80 % for GPS collared animals) and the reintroduction of the population was deemed successful based on the definitions outlined for measuring reintroduction success. The variation in the post-release movements could be attributed to one of two factors; sex-specific disparities in the effects of the soft-release procedure on post-release exploration, or the high density of suitable patches (*e.g.*, high prey density, low intraguild competition and suitable denning habitat) near the release site resulting in females breeding soon after release. This was one of the first studies to closely investigate post-release behaviour of cheetah (Boast, Good & Klein, 2016; Hunter, 1998; Weise *et al.,* 2015a), and it suggests that further research is required to optimize both pre-release management and release site choice in order to improve reintroduction success.

### 6.2.2. Prey preference and comparison of diet composition methodologies

The cheetah is an opportunistic predator that predominately preys upon the most abundant medium-sized antelope (Hayward *et al.*, 2006). The feeding ecology and prey requirements of the cheetah have been extensively studied; however, prey selection varies on a local scale and therefore local diet composition studies are critical in the understanding of predator-prey dynamics and ecological system management. This study, therefore, developed a robust diet assessment for cheetah in LNP through the application of multiple diet assessment methodologies (carcass observations and scat analysis). While this was the first study to assess cheetah diet in Malawi it was also one of the first to assess carnivore diet in the country. Given the similarities between protected areas in Malawi: limited road network, mixed woodland habitat and low to moderate tourism levels, this study further acted to inform future carnivore diet research in Malawi.

Thirteen prey species were identified, of which four comprised the bulk of diet composition, namely: kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*) and bushbuck (*Tragelaphus scriptus*). However, diet composition was not representative of cheetah prey preference. Species were classified as preferred when the proportion of individuals caught was greater than their relative abundance within the prey population. Prey preference calculations found that kudu, bushbuck and southern reedbuck (*Redunca arundinum*) were preferred by cheetah regardless of data collection methodology (*e.g.,* scat analysis or carcass observations). Because not all demographics within a prey species are a catchable size for cheetah (*e.g.,* adult waterbuck) ‘catchable’ prey populations were developed to derive a more accurate picture of prey preference based on individuals susceptible to cheetah predation within a population. Considering ‘catchable’ populations when calculating prey preference proved important as it altered prey preference results. For example, impala was an avoided species for both scats and carcass observations when calculating preference based on ‘catchable’ population estimates.

When comparing data collection methodologies, scat analysis was able to identify the highest prey diversity while maintaining a small sample size. However, GPS site investigation was able to detect a high sample size and was important for informing asymmetric predation. It is therefore concluded that a combination of GPS site investigation and scat analysis is required to provide the most robust diet estimation. This is especially important for smaller carnivores that are likely to asymmetrically predate. In LNP, the high selection of females for bushbuck and southern reedbuck populations, as well as the preference towards young kudu could have implications on the demography of these populations.

### 6.2.3. Spatial distribution and habitat selection

Woodland habitats have been suggested as the key to the cheetah’s survival (Durant, 1998a), however, few studies have assessed the cheetah’s spatial distribution and habitat requirements in such environments (*see,* Bissett & Bernard, 2007; Broomhall, Mills & du Toit, 2003; Mills, Broomhall & du Toit, 2004; Purchase & du Toit, 2000; Rostro-Garcia, Kamler & Hunter, 2015). In order to contribute to the understanding of cheetah in woodland habitats GPS collar data was used to estimate one-year home ranges (95 % home range and 50 % core area) for the four cheetah that reached settlement after reintroduction (CM2, CF1, CF2 and CF3). This allowed us to assess the spatial distribution and habitat selection in a mixed woodland habitat with low competition levels.

All cheetah demonstrated high levels of spatial overlap (40-71 % home range; 22-62 % core area) well over the 10 % threshold thought to demonstrate home range exclusivity (Sandell, 1989). Although the high degree of spatial overlap may be attributed to high prey abundance, females also denned in close proximity (≤ 1.3 km) which explains the high level of intrasexual overlap. The proximity of dens may be indicative of limited suitable den sites which may result in female home range shifts during denning. High overlap of den sites may result in lower pre-emergence cub survival as the cheetah population increases. Furthermore, a high spatial overlap of females may result in a decrease of preferred male territory resulting in elevated levels of male-male interactions, male-floating behaviour and ultimately decrease male survival. Regardless, this spatial distribution in LNP indicates a substantial prey base which could sustain a high cheetah population if maintained and if the female population begins to disperse further across the park.

Cheetah home ranges incorporated all six habitat types. The only male included in the analysis, CM2, had a home range which comprised of more floodplain habitat than that of the females. The amount of floodplain incorporated in CM2's home range was disproportionate to the amount of floodplain habitat available in the park. However, female home ranges comprised open woodland habitat disproportionally to its availability within the park. This sex disparity in habitat selection at the home range level has been documented in other cheetah populations (Bissett & Bernard, 2007; Broomhall *et al.*, 2003; Rostro-Garcia *et al.*, 2015). When hunting, cheetah demonstrated high habitat flexibility, with kills recorded in all habitat types. A selection for open areas with high prey frequency of occurrence was found for kill sites across the population, however, females also selected for riparian and grassland habitats as kill sites. These results support the notion that the cheetah is more adaptable to a wide range of habitats than originally described. Furthermore, the flexibility in habitat documented is encouraging for the survival of LNP's cheetah population, as intraguild competition increases in the park cheetah should be able to seek spatial refuge by occupying habitats avoided by competing carnivores.

## 6.3. Management implications

### 6.3.1. Potential implications for prey populations

Impala and waterbuck are the predominant ungulate species in LNP (3089 and 6673 individuals, respectively; Sievert & Reid 2018). Based on trends recorded in other fenced reserves, these two species should comprise the bulk of prey consumed and be the preferred prey for cheetah (Hayward *et al*., 2006). Impala and waterbuck were two of the most important prey species recorded for cheetah in LNP and comprised the majority of carcass observations recorded over the two-year study (45% impala; 21% waterbuck). However, neither species were classified as preferred when considering their predation rate relative to their abundance. Rather, kudu, southern reedbuck and bushbuck were preferred species, meaning they experienced predation levels greater than their relative abundance. These three species also experienced asymmetric predation across their demography. The effects of asymmetric predation within terrestrial systems has been poorly investigated, however it is likely to result in demography and life-history changes within the population if experienced over the long-term (Ginsberg & Milner-Gulland, 1994; Makin & Kerley, 2016).

Cheetah suffer from high levels of intraguild competition and therefore demonstrates predator avoidance behaviour by seeking spatial and/or temporal refuges from dominant carnivores such as lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*; Bissett *et al.*, 2015; Hunter, Durant & Caro, 2007). An increase in habitat cover has been related to a decrease in kleptoparasitism (Mills *et al.*, 2004). Consequently, a preference towards habitats with increased cover is one predator avoidance strategy that has been recorded in numerous cheetah populations (Bissett *et al.*, 2015; Broomhall *et al.*, 2003; Rostro-Garcia *et al.*, 2015). A change in cheetah habitat selection and activity patterns may result in changes of prey availability thereby causing a dietary shift in the cheetah population. Currently, cheetah in LNP select predominantly for open floodplain when hunting. Interestingly, preferred species such as kudu and bushbuck only represented a small proportion of the kills recorded in this habitat over a one-year period (2 % kudu; 2 % bushbuck). However, in habitats with greater cover kudu and bushbuck comprised a greater proportion of the kills (*eg.*, 33 % kudu and 7 % bushbuck in riparian; 18 % kudu and 9 % bushbuck in open woodland; 14 % kudu in mopane scrub). Therefore, should an increase in intraguild competition result in a shift of cheetah habitat selection towards higher cover, greater predation pressure is expected on these species.

In LNP, southern reedbuck, hartebeest (*Alcelaphys lichtensteinii*), klipspringer (*Oreotragus oreotragus*), oribi (*Ourebia ourebi*), roan (*Hippotragus equinus*) and plains zebra (*Equus quagga*) have been reported in low densities (Sievert & Reid, 2018). Fortunately, for these species, predation events by cheetah have only been recorded on southern reedbuck. Nevertheless, a move in cheetah habitat selection may increase the spatial congruence with these species, resulting in an increase in predation related mortalities. This phenomenon was recorded with lion in the Kruger National Park and abetted in the collapse of the roan population (Harrington *et al.*, 1999). Furthermore, as reintroductions of large carnivores continue in LNP and populations across the carnivore guild grow, the potential for dietary overlap increases. Multi-species predation has been demonstrated as a credible threat for species of conservation concern in other protected areas and must, therefore, be considered in LNP (Davidson *et al.*, 2019).

Currently, LNP's growing cheetah population has the potential to assist both impala and waterbuck populations reach ecologically sustainable levels. In the short-term, asymmetric predation of preferred species, especially kudu and bushbuck, may have detrimental effects on their population demographics. In the long-term, consideration must be given to the effects of cheetah spatial shifts and multi-species predation on prey populations. Large carnivore diet and hunting frequency should, therefore, continue to be investigated and paired with bi-annual game surveys to ensure adaptive management of LNP's predator-prey dynamics.

### 6.3.2. Intraspecific competition potential for cheetah in LNP

The cheetah is a facultatively social carnivore with males forming complex social groups that can consist of both related and non-related males (Caro & Collins, 1987). Regardless, male cheetah are territorial and have been shown to demonstrate high levels of intrasexual aggression (Caro & Collins, 1987; Eaton, 1968). However, intersexual aggression and infanticide is rarely recorded (Hunter & Skinner, 2003).

In LNP, cheetah currently experience high levels of intra- and intersexual home range and core area overlap. Although inter- and intrasexual home range overlap has been recorded in cheetah (Caro & Collins, 1987; Broomhall *et al.*, 2003; Houser, Somers & Boast, 2009; Marker *et al.*, 2007; Marnewick & Cilliers, 2006), core area overlap is less documented. Intersexual home range overlap is associated with an increase in mating opportunities (Caro & Collins, 1987). Conversely, female intrasexual overlap in LNP may be a factor of restricted movements during the denning period and the close proximity of selected den sites (≤ 1.3 km). Female cheetah have been recorded resting and travelling together in temporary groupings (Dalton *et al.*, 2013; pers. obs.), however, these groupings are poorly understood. Therefore, the high core area overlap during the denning period is unlikely to result in direct intrasexual competition with females although, it may have secondary long-term population consequences.

Current high overlap of selected den sites indicates potentially low levels of suitable denning areas. If true, high levels of female home range overlap is expected to continue and the spatial spread of female cheetah in LNP will be limited. Although two females denned <650 m apart over the same time period, no interactions were recorded and, both litters reached emergence. However, an increase in cheetah activity in one area due to multiple females denning at once may act to reduced prey catchability (*eg.*, ecology of fear; Brown, Laundré & Gurung, 1999). A reduction in prey catchability will prolong hunting periods which will incur an overall risk to cub survival by, increasing time periods with minimal protection and causing a reduction in milk production (Laurenson, Caro & Borner, 1992; Laurenson, 1995). Currently, LNP has areas devoid of cheetah activity which appear suitable due to the high prey densities and low levels of competition. However, if suitable habitat has minimal possibilities for female encounters, it results in areas ceasing to be attractive to males. Such events have been recorded by Hunter (1998) with reintroduced cheetah in Phinda Private Resource Reserve and Fattebert *et al.* (2013) with a dispersing male leopard. Restricted spatial spread of females and the presence of a territorial male in the overlapping home ranges is expected to result in competitive exclusion of additional males. This is especially a concern for newly released animals as intraspecific competition is more detrimental to released individuals than residents (Massei *et al.,* 2010).

Consideration must, therefore, be given to the spatial distribution of both males and females in LNP prior to supplementation events, and the removal of territorial males may be required to ensure the end of territory tenure. Priority should to be placed on creating a greater spread in the distribution of females in LNP as well as a closer investigation into factors affecting den site selection and litter survival.

### 6.3.3. Intraguild competition potential for cheetah in LNP

The spotted hyena is the only large predator that escaped complete extirpation in LNP. Spotted hyena are well known to compete with cheetah and account for a large portion of cheetah mortalities on fenced reserves in South Africa (V. van der Merwe, pers. comm.) and cub mortalities in the Serengeti National Park, Tanzania (Laurenson, 1994). However, due to the small population of spotted hyena in LNP, their effect on the reintroduced cheetah population was negligible, with no hyena caused mortality or kleptoparasitism events were observed during the two-years of post-release monitoring. The current low density of spotted hyena in

LNP is a direct result of historical persecution (C. Reid, pers. comm.). Therefore, it is expected that the spotted hyena population will grow with the increased protection of both LNP and Mangochi Forest Reserve. Future consideration should be given to their potential impact on the established cheetah population.

Lion were reintroduced to LNP over three release events between May 2018 and February 2019. Lion are the number one cause of cheetah mortalities in fenced reserves in South Africa (Buk *et al*., 2018). As a result, cheetah have been shown to demonstrate spatial and/or temporal avoidance of lion (Bissett *et al.*, 2015; Bissett & Bernard, 2007; Cristescu, Bernard & Krause, 2013; Rostro-Garcia *et al*., 2015). The current lion population in LNP consists of two prides totalling ten individuals. One pride experiences range overlap with multiple cheetah (pers. obs.). Range overlap between competing carnivores is indicative of small scale spatial and temporal avoidance (Bissett & Bernard, 2007; Cristescu *et al*., 2013). Regardless of this overlap, no lion caused mortalities have been recorded in LNP's cheetah population.

When re-establishing a large carnivore guild, it has been recommended that smaller carnivores, such as cheetah, undergo reintroduction first, prior to their competitors (Ferreira & Hofmeyr, 2014; Hayward *et al.*, 2007). This allows subordinate carnivores to develop home ranges and locate refugia prior to the reintroduction of dominate competitors. This has likely resulted in the cheetah's ability to overlap home ranges with lion in LNP. Additionally, competitor-naïve cheetah should not be reintroduced into a system with a full carnivore guild, as they have been found to experience higher mortality rates (Hayward *et al.*, 2007). As the management of the established cheetah population in LNP continues, genetic supplementation will be required. This will result in new individuals being released into LNP. Although initial survival rates post-reintroduction were moderate (57 %; known survival rate), and the current population is persisting post-lion reintroduction, the release of new individuals into a system in which the multiple competing carnivores are present may result in an increased post-release mortality rate.

Although cheetah in LNP currently appear successful in their avoidance of lion and spotted hyena, lion have been documented as the cause of the local extirpation of cheetah in three small-fenced reserves in South Africa (Buk *et al.*, 2018). While no correlation has been found between cheetah population retention on reserves with or without lion, it is important to note that many of South Africa's small fenced reserves supplement prey populations in order to maintain predator numbers and reduce potential competition (Buk *et al*., 2018). Regardless, cheetah coexist with competitors on many of the small fenced reserves in South Africa (84 % with lion; 67 % with leopard; 42 % with spotted hyena; Buk *et al*., 2018). Heterogenous environments, such as LNP, increase competitive refuges which are critical in promoting the persistence of a species with low competitive abilities (Durant, 1998b). Cheetah in LNP demonstrated a high versatility in habitat use and therefore are likely to remain successful as competition increases. Regardless, a high density of competing carnivores will reduce the overall success of LNP's cheetah population. This was demonstrated in Matusadona National Park, Zimbabwe, were intraguild predation and kleptoparasitism were attributed to maintaining the cheetah population well below the estimated cheetah carrying capacity (Purchase & du Toit, 2000). Prior to their extirpation, lion were reported as abundant in LNP with the largest pride consisting of 16 individuals (P.

Taylor, pers. comms.). Lion have a high reproductive potential and therefore are able to recover quickly after disturbance often resulting in rapid overpopulation in small protected areas (Ferreira & Hofmeyr, 2014; Miller & Funston, 2013). The large prey base and low level of human disturbance in LNP is therefore expected to result in a rapidly increasing lion population. Close monitoring and management of LNP's lion population will be required in order to maintain a healthy diversity of the large carnivore guild.

Nevertheless, cheetah born in LNP will learn intraguild competition avoidance strategies and will also have an advantage in avoiding intraguild competition over those translocated into the system, as they will have an innate understanding of competition in the park. This should be considered when planning translocations, and individuals born into LNP should only be identified for translocation from the park should they risk inbreeding or overpopulation.

## 6.4. Recommendations to management

### 6.4.1. Pre-release recommendations

A holding (boma) period for animals being translocated into the park is important in the prevention of disease spread, reduction of homing behaviour, the formation of social groups, habituation and, exposing animals to electric fencing (Hunter, 1998). However, holding periods require financial, biological and human resources and can be detrimental on both an individual and population level (Marneweck *et al.*, 2019; Marnewick *et al*., 2009). Cheetah that underwent reintroduction into LNP were held in a boma for 23-58 days upon arrival. This study found that a holding period greater than 23 days did not affect post-release movements, and males explored further and settled later than females. Based on these findings and a literature review (*see*, Chapter 3) the following management recommendations were developed.

#### 6.4.1.1. Holding periods

It is recommended that the holding period for all animals remain as short as possible. The current study found that holding periods >23 days were not successful in decreasing post-release movements. Furthermore, Weise *et al*., (2015a) found no difference between post-release movements of cheetah that underwent soft-release or hard-release. This indicates that hard-release is also an option in LNP. Regardless, the holding period is an ideal time to conduct any essential procedures that will aid in management's monitoring abilities. Therefore, park management should consider the following tasks during this time:

- Collar fitting
- Vaccinations
- Photo-identification
- Habituation
- Collection of DNA samples
- Microchipping

While most small fenced reserves habituate large predators to game drive vehicles during the boma period to increase chances of game viewing, habituation should only take place when necessary. Habituation of cheetah is highly recommended as it increases management's monitoring and capture capabilities. Holding periods may need to be extended to ensure sufficient habitation. It is important to note that in this study an extended boma period of 58 days was not found to negatively affect body condition nor did it affect hunting ability of individuals upon release (pers. obs.).

#### 6.4.1.2. Homing considerations

Cheetah released in LNP were translocated an average of 1644 km from their capture sites. Long-distance translocations have shown to prevent homing in most large carnivores (Briers-Louw *et al.*, 2019; Weise *et al.*, 2015a; Weise *et al.*, 2015b). Therefore, homing behaviour was not assessed in this study. However, homing behaviour in cheetah appears to vary. For example, in a study of translocated cheetah in Namibia, animals released >137 km from their capture site showed no evidence of homing (Weise *et al.*, 2015a). Whereas another translocation of cheetah in Namibia documented an individual homing over 170 km to its capture site (Boast *et al.*, 2016). Majete Wildlife Reserve (MWR) recently reintroduced cheetah from South Africa (African Parks, 2019), rendering it the nearest resident cheetah population to LNP. MWR is a minimum straight-line distance of 110 $km^2$ from LNP. If translocations between these two populations occur consideration must be given to the possibility that animals may attempt to home to their capture site. A prolonged boma period may assist in reducing homing behaviour. Intensive post-release monitoring and investigation of post-release movements and homing should be conducted for individuals that undergo translocation between these protected areas. This will assist in informing pre- and post-release management of future translocations between these populations.

### 6.4.2. Release recommendations

Due to the current high level of cheetah spatial overlap near the predator boma, the ideal procedure would be to conduct pre-release holding periods in a new location. Unfortunately, the cost associated with constructing multiple bomas and wet season accessibility renders this option unfeasible. Cheetah released into LNP demonstrated high levels of release site fidelity, indicative of release site acceptance and minimal homing. While this may be a factor of the soft-release procedure, this study suggests that site fidelity may be attributed to ecological factors that created suitable home range patches near the release site. Therefore, it is recommended that once animals have spent sufficient time in the boma (if required), they are sedated and transferred to a suitable area for release. The predator proof park perimeter fencing and the minimal effect of holding periods on post-release movements makes the option of a semi-hard or hard release viable. The transfer and release of individuals away from the carnivore boma is expected to assist in reducing the potential for competition during the first few days post-release. Employing this release method will allow for further investigation into the effects of pre-release and release management on post-release exploration and settlement. Management should consider the following when evaluating potential release sites:

- Where are there established cheetah home ranges

- Where are areas that have high density of competing carnivores
- Where are areas with moderate to high prey densities and, heterogeneous habitat structure
- Where are there habitats similar to that found at recorded den sites

When considering release sites for female cheetah, areas that contain established female cheetah home ranges and/or high density of competitors should be avoided, as it may result in increased post-release movements or encourage high female spatial overlap. Areas with moderate prey densities, heterogeneous habitat structure and near suitable denning habitats (*eg.*, isolated hills) may increase female site fidelity to the area. For males, consideration should be given to both the level of intra- and intersexual overlap near the release site, as habitats in which encounters with females is possible may act to decrease post-release exploration.

The semi-hard release method should result in a wider spatial distribution of cheetah in LNP. This is especially important for females, who have the greatest level of spatial overlap. Additionally, consideration should be given to the release of females prior to males. Although this is contrary to previous recommendations, which suggested females in a boma act as an “anchor” for males (Boast *et al.*, 2018), cheetah release into LNP did not demonstrate reduced post-release movements while females were in the boma. Developing desirable open male territories by ensuring the potential of high intersexual and low intrasexual overlap, prior to the release of a male cheetah may assist in reducing post-release movements. Desirable territories for male cheetah would allow for overlap with females and therefore require a larger spread in the spatial distribution of females in LNP. Finally, releasing female cheetah near breeding age may assist in reducing their post-release movements. As found in LNP, female cheetah released at sexual maturity reproduced quickly and established home ranges soon after conceiving, which, may have resulted in decreased post-release movements.

### 6.4.3. Post-release recommendations

Ideally all animals (*exception*, one per natural male coalition) should be fitted with GPS collars prior to release. Collar scheduling would begin at one GPS location per hour on a 24-hour schedule. This scheduling could then be reduced after settlement in order to maintain collar battery-life. Furthermore, collars should be scheduled to transmit data points once a day. This would act to minimize data back-logging should a transmission not be successful and assist in obtaining the minimum data required to meet daily monitoring objectives. However, these recommendations may not be financially feasible. Post-release monitoring is a trade-off between financial and human resources, and information acquired. The significant effect sex had on post-release movements in LNP has strong implications on the post-release monitoring. Therefore, given the movements demonstrated by cheetah post release in LNP, it is recommended that under financial constraints, female cheetah be fitted with VHF collars and newly released males with GPS collars. This should allow for proper monitoring during the exploration stage, especially for males who have a greater likelihood of leaving the park boundary.

### 6.4.3. Population management going forward

Social factors have been shown to regulate large carnivore abundances by limiting home range size and reducing both survival and fecundity (Ferreira & Hofmeyr, 2014). A major limitation of fenced systems is the decrease in social mechanisms that contribute to natural population regulation. Reduced social mechanisms may manifest themselves through an increase in social tolerance of conspecifics, thereby reducing conflict events, such as those seen between territorial males (Ferreira & Hofmeyr, 2014). Therefore, it is suggested that park management employs a conceptual approach to cheetah population management by mimicking the behaviour and social dynamics of unrestricted cheetah populations (Ferreira & Hofmeyr, 2014). This approach requires a large portion of the cheetah population to be collared and sufficiently monitored due to their wide ranging and solitary nature. Proper monitoring will allow for well-informed management decisions that will maintain a genetically viable population. The following three feasible management options outlined by Ferreira and Hofmeyr (2014) are recommended. These management options focus on mimicking natural social dynamics seen in cheetah populations:

- Mimic male dispersal through removal and introductions of subadult males.
- Mimic territory tenure by removing a territorial male, and potentially introducing an adult male or male coalition.
- Mimic high death rates of old males by removing the oldest males.

Further consideration must be given to the individuals being removed from and introduced to the population, especially when attempting to force or mimic territory tenure take-over. For example, male survival and territory control is often thought to be greatest for those in coalitions, therefore, the introduction of a male coalition may be best to remove a singleton territorial male. However, in the Serengeti, group living was found to only be beneficial to males during periods when coalitions were numerous (Durant, Kelly & Caro, 2004). Therefore, in systems with multiple coalitions, the removal of coalitions may act to change the dynamics of the population more than the addition of new individuals. Furthermore, only individuals with no genetic relation to those already within the population should be introduced.

Contraception should only be conducted with caution and as a last resort for population control. Captive cheetah have been shown to be prone to asymmetric reproductive aging when natural breeding processes are restricted, meaning female reproductive organs age at a faster rate under these constraints (Ludwig *et al.*, 2019). Contraception of females may, therefore, trigger reproductive ageing, thereby lowering fecundity and increasing interbirth intervals in the population in the long-term. Contraception of males in the population should also be approached with caution as it has the potential to reduce population control mechanisms seen in unrestricted populations (*eg.*, territorial aggression; Ferreira & Hofmeyr, 2014). However, contraception of males increases management's ability to prevent potential inbreeding events when translocations are not possible. The fecundity of females and population recruitment rate should be continuously monitored in order to ensure the LNP population maintains reproductive levels the park can support. Dedicated monitoring is required to inform management of the cheetah population. Therefore, the following is recommended:

- The development of ID kits for each individual
- The collaring of as many individuals as feasible, especially females
- Genetic sampling and microchipping during each capture event
- The creation of a studbook which records all births, deaths and relevant life history information

The importance of genetic sampling must not be underestimated, as a litter can be formed from multiple mating events and may not reflect mating events recorded (*see*, Gottelli *et al.*, 2007). Collaring of females will allow for fecundity to be recorded as well as dispersing cubs to be removed when required. Finally, a studbook will assist in informing management decisions during translocation events and act as a long-term demography record for the population.

Although LNP's reintroduced population reached establishment, it is important to note that it is not indicative of population persistence. In CMP reserves that did not experience population persistence, extirpation of the population occurred an average of 8.4 ± 4.9 SD years after initial reintroduction (Buk *et al.*, 2018). LNP management must, therefore, consider long-term population persistence and address factors that may cause extirpation as carnivore numbers in the park increase, such as increased intra- and interspecific competition, inbreeding depression and reduced prey populations.

At its current state (14 individuals) a stochastic event, such as disease outbreaks poses the high risk to LNP's cheetah population and could result in rapid extirpation. Whilst pathogens are key in ecological functioning, human-induced disturbances can affect disease-host dynamics and small populations have the potential to become severely or completely depleted from an outbreak. Many diseases are multi-host (*e.g.*, rabies, canine distemper virus, etc.) and can enter the population through neighbouring communities. Considering the lack of a buffer zone between LNP and surrounding communities, management should consider disease mitigation measures for this small cheetah population. Panleukopaenia, feline herpes, canine distemper virus and rabies are easily spread by domestic dogs and cats entering from the boundary (A. Salb. pers. comm.). These are therefore key diseases to control. LNP's ability to immobilize cheetah for vaccinations is limited, however recombinant monovalent vaccines can be given during re-collaring events to act as a booster for the canine distemper virus vaccine, this along with a rabies vaccine should be considered during immobilizations events (A. Salb. pers. comm.). In the long term, inbreeding depression due to the small population of breeding animals is the greatest threat to LNP's cheetah population persistence.

Currently, only one male in the LNP population is unrelated to the breeding females (CM1). Although this singleton male holds territory tenure in the overlapping area of these females, the increase in male coalitions (currently two) may result in territory take-over. A territory take-over by either coalition in LNP risk inbreeding as both were born in the park and therefore maintain a high level of relatedness to a minimum of two females each (maximum three females each). To better understand the relatedness, genetic sampling is required (and pending). It is recommended that the removal of one or both coalitions as well as the supplementation of unrelated males occurs in the immediate future. When supplementing this population, it is important to also consider relatedness within other Malawian cheetah populations (*see*, 6.4.4).

### 6.4.4. Metapopulation approach for cheetah in Malawi

Although it is preferable to allow excess large carnivores to disperse naturally if occupying their natal range, the nature of many parks does not often allow for this due to the potential for conflict scenarios beyond the resident park's boundary. LNP is not large enough to support genetically viable populations of cheetah without supplementation, and the isolated nature of the park prevents natural gene flow. Therefore, human mediated gene flow is recommended as a form of mimicked dispersal, to aid in genetic supplementation.

Due to the large population size required to prevent inbreeding, small isolated populations have minimal conservation value on a regional scale (Frankham, Bradshaw & Brook 2014; Miller & Funston, 2013). Moving cheetah between protected areas in Malawi will increase genetic heterozygosity and assist in the viability and conservation value of each population. Therefore, the establishment of a cheetah metapopulation in Malawi is recommended with the aim of creating a regional node in which frequent translocations will assist in implementing the conceptual approach to population management (*see*, section 6.4.3; Ferreira & Hofmeyr, 2014). This metapopulation development will require the inclusion and collaboration of multiple in country stake-holders such as, AP and the Malawi Department of Parks and Wildlife (DNPW). Currently, only two protected areas within Malawi contain resident unrelated cheetah populations, LNP and Majete Wildlife Reserve (MWR), with LNP's cheetah population being the largest and most established. Movements of large carnivores (namely lion) between these AP managed areas has already taken place (C. Reid, pers. comm.) thus, this is a viable option for human-mediated cheetah dispersal. The goal of a Malawi cheetah metapopulation node should be to allow for the management of Malawi's cheetah independently but in collaboration with South Africa's metapopulation. Therefore, the EWT's CMP should be approached to assist in identifying suitable candidates for supplementation to, or translocation from Malawi should an outside source be required.

The development of a cheetah metapopulation in Malawi was previously recommended during the development of the National Conservation Action Plan for Cheetah and African Wild Dog in Malawi (Department of National Parks and Wildlife, 2011). In this plan, six protected areas were identified as the potentially recoverable range (~6,399 km$^2$ of recoverable range), LNP was not included in these six, due to its isolated nature requiring a managed metapopulation approach. Unfortunately, to date, none of the six parks identified except for MWR, have yet to report a cheetah sighting since the Plan's development. AP Malawi now manages 3,368 km$^2$ of protected area in Malawi and has created the capacity for a human-mediated metapopulation approach to carnivore conservation management in Malawi. If the growth of the cheetah in the recommended metapopulation continues, it increases the possibility of reintroduction to other recoverable sites identified in the country.

Recordkeeping and capacity building is crucial in the metapopulation approach. The importance of proper genetic sampling and individual identification is particularly critical for informing translocation management.

With the growth of the metapopulation, an accountable metapopulation manager may need to be appointed to ensure proper management and monitoring of individual populations. A metapopulation manager can provide long-term oversight of the metapopulation and is especially important should the metapopulation expand past AP reserves, as the manager can assist in cross organization cooperation and ensure consistent genetic sampling, record keeping and proper monitoring of individual populations. It is recommended that a genetic database and studbook for cheetah is compiled and shared between all populations in the country. This genetic database can be developed from samples collected during captures and translocation events. Considerations for genetic samples should be made prior to any translocations as sampling kits, refrigeration and permits are necessary. A metapopulation approach to cheetah in Malawi requires cross park cooperation and communication but is critical to the long-term conservation value of these reintroduction projects.

Continued monitoring of these two populations is recommended to allow for adaptive management and strategic planning for Malawi's cheetah population, which will assist in the long-term persistence of the species within Malawi.

## 6.4. Future research recommendations

Targeted research projects should be viewed as a separate entity from monitoring activities in the LNP. Targeted research can be adapted from data collected during monitoring activities and should assist in answering questions developed by park management with the goal of supporting the management of the cheetah population. Research projects are further distinctive from monitoring as they should have a detailed outlined approach, a stringent timeline and a clear exit strategy. This study has outlined several unanswered questions which should be investigated further to contribute to the development of well-informed population management plans. These includes the following:

- An assessment of dietary overlap of all large carnivores once the full carnivore guild is restored.
- An assessment of niche partitioning as well as impacts of intraguild competition on cheetah once the full carnivore guild is restored.
- Further assessment of post-release movements based on pre-release techniques, including the effects of semi-hard releases on settlement and spatial distribution.
- Investigating den site selection, cub survival and population recruitment.

## 6.5. Conclusion

The early success of the reintroduction of cheetah to LNP is encouraging for the ongoing range expansion of cheetah to Malawi. The recent reintroduction of unrelated cheetah to MWR further increases the conservation value of this range expansion project by creating the opportunity to develop a genetically diverse cheetah metapopulation node within Malawi. A conceptual approach which mimics natural behaviour and social dynamics is recommended for the long-term management of these populations. This approach requires monitoring as well as commitments and agreements between protected areas and government entities. This is possible given that AP Malawi manages both cheetah populations in the country. The growth of Malawi's cheetah population may create an opportunity for continued range expansion to other parks in the country.

## 6.6. References

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