The status and behavioural ecology of large carnivores in a human-impacted miombo woodland

Robert Davis

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A thesis submitted in partial fulfilment of the requirements of Nottingham Trent University for the degree of Doctor of Philosophy

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Chapter Six: Dietary composition and niche overlap between competing large carnivores in Kasungu National Park, Malawi

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All aspects of research were granted ethical approval by Nottingham Trent University ethics committee. Research conducted in Kasungu National Park, Malawi, was conducted under the Memorandum of Understanding (MoU) between the Department of National Parks and Wildlife Malawi and Carnivore Research Malawi (2015).

Cover page photo credits

Chapter Two

Cover image: A spotted hyaena responding to a call-in in Kasungu National Park, Malawi. **Photo credit:** Owen Slater.

Chapter Three

Cover image: A sub-adult male lion in Kasungu National Park, Malawi. May 2017.

Photo credit: Katie Baillie-David.

Abstract

Decline in global carnivore populations has led to an increased demand for the assessment of carnivore densities in understudied habitats and the use of robust survey techniques to obtain these estimates. Furthermore, growing levels of anthropogenic disturbance can alter community structure and disrupt carnivore guild dynamics, thereby risking further population decline. This thesis examines the population status and intraguild dynamics of large carnivores in Kasungu National Park (KNP), Malawi. KNP is an example of a protected area that has experienced large-scale reductions in both carnivore and prey populations, whilst the miombo woodland of KNP has been identified as a habitat lacking baseline data on large carnivore density and behavioural ecology. Consequently, KNP is a novel site to 1) produce robust population estimates from an understudied habitat, and 2) improve understanding of niche partitioning strategies in a modified carnivore guild.

Using the spotted hyaena (*Crocuta crocuta*) as a model species, **Chapter Two** reviews the current survey methodologies for estimating the population density of large carnivores. I advocate the wider application of spatial capture-recapture (SCR) techniques to estimate spotted hyaena density and provide recommendations for adopting these methods. In **Chapter Three** I provide a summary of the decline in protected area health and large carnivore populations in Malawi, before providing an overview of KNP and the sites' importance to regional conservation efforts. I build on this in **Chapter Four**, using camera trap surveys and SCR modelling to estimate leopard (*Panthera pardus*) and spotted hyaena density in KNP between 2016 and 2018. Using a novel spatial partial identity model (SPIM), I also address the issue of uncertainty in individual identification from camera trap data. Density estimates were low across survey years, compared to estimates from sub-Saharan Africa, for both leopard (1.9 ±0.19 SD adults/100km^2) and spotted hyaena (1.15 ±0.42 SD adults/100km^2). In addition, the presence of lion (*Panthera leo*) and wild dog (*Lycaon pictus*) is limited to dispersing individuals, highlighting the degradation of the protected area and the wider loss to the carnivore guild in KNP.

In **Chapter Five**, using a combination of co-detection modelling, time-to-event analyses, and temporal activity patterns from camera trap data, I examine the spatiotemporal dynamics of leopard and spotted hyaena in KNP. I find that detection of leopard and spotted hyaena is significantly associated with the detection of preferred prey and competing carnivores, increasing the likelihood of species interaction. In addition, female leopards display temporal partitioning from both intra- and inter-specific competitors, which may affect overall fitness and result in increased exposure to sources of anthropogenic mortality. Using scat analysis techniques, **Chapter Six** compares the dietary niche overlap, as a proxy for intraguild competition, of leopard and spotted hyaena in KNP. Results show that leopard and spotted hyaena share relatively high levels of dietary overlap (Pianka's overlap = 0.65), providing further evidence of the potential for interspecific competition between the two species.

This study provides the first robust population estimates for leopard and spotted hyaena in KNP and evidence of a range of niche partitioning strategies adopted by large carnivores in a modified carnivore guild. The low population density estimates for leopard and spotted hyaena are a cause for conservation concern. These concerns are exacerbated by the mutual drivers of spatiotemporal behaviour, the high levels of dietary overlap, and low prey densities, which increase the risk of exploitation and interference competition and could have negative consequences for population demographics. Therefore, increasing prey populations will be essential to minimise levels of interspecific competition between large carnivores. In addition, continued monitoring of population density and intraguild dynamics will be critical for assessing the efficacy of ongoing conservation initiatives in KNP and other protected areas in Malawi under similar levels of anthropogenic pressure.

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Zikomo kwambiri!

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List of abbreviations used

AP – African Parks

DNPW – Department of National Parks and Wildlife Malawi

GLMM – Generalised Linear Mixed Model

IFAW – International Fund for Animal Welfare

KNP – Kasungu National Park

MZTFCA – Malawi Zambia Transfrontier Conservation Area

NNP – Nyika National Park

PA – Protected Area

PWA – Parks and Wildlife Assistant

SCR – Spatial capture-recapture

SPIM – Spatial partial identity model

VMWR – Vwaza Marsh Wildlife Reserve

THE STATUS AND BEHAVIOURAL ECOLOGY OF LARGE CARNIVORES IN A HUMAN-IMPACTED MIOMBO WOODLAND

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CHAPTER ONE

Introduction

CHAPTER ONE: Introduction

1.1 The role of large carnivores

The order Carnivora consists of 250 terrestrial species that inhabit every major habitat on Earth and perform a critical role in regulating ecosystems (Hunter, 2018). Despite occurring at naturally low densities, carnivores are essential for maintaining biodiversity and ecosystem function by controlling herbivores and mesopredators through top-down interactions (Ripple *et al.* 2014; Hoeks *et al.* 2020). Indeed, large carnivores are historically valued for their role in managing herbivore populations (Fretwell, 1977; Oksanen *et al.* 1981). However, there is a growing body of literature indicating that large carnivores play a pivotal role in the delivery of wider ecosystem services (Schmitz *et al.* 2010; Letnic *et al.* 2012; Ford *et al.* 2014; Atkins *et al.* 2019), whilst also providing economic and social benefits on a global scale, particularly in the developing world (Naidoo *et al.* 2011; Ripple *et al.* 2014; Macdonald, C. *et al.* 2017; Braczkowski *et al.* 2018).

1.1.1 Ecological role

Whilst direct predation from large carnivores is a key regulator of prey populations (Dobson *et al.* 2006), predators also affect prey demography, and wider ecosystem function, through the consequences of prey risk avoidance strategies (Creel & Christianson, 2008; Schmitz *et al.* 2010). For example, the presence of large carnivores in an environment creates a “landscape of fear”, where prey species adopt antipredator behavioural responses to minimise predation risk (Brown *et al.* 1999; Preisser *et al.* 2005). In these ecosystems, prey species either entirely avoid or minimise exposure time in resource-rich habitats, where the risk of predation is heightened (Creel *et al.* 2005; Laundré *et al.* 2010). These areas of suppressed browsing and grazing buffer lower trophic levels, preventing overconsumption from large herbivores and increasing heterogeneity in plant and tree species (Kuijper *et al.* 2013; Suraci *et al.* 2016; le

Roux *et al*. 2018). The resulting diversity of plant and tree species creates a gradient of food availability and vegetation cover, integral to managing predation risk and maintaining ecosystem function on a wider scale (Schmitz *et al*. 2010; le Roux *et al*. 2018). The loss of carnivores from an ecosystem often results in herbivore populations increasing and coincides with a reduction in risk-avoidance behaviour. Over time this can lead to trophic cascades that have wide-ranging impacts on prey and plant communities (Ripple *et al*. 2001; Terborgh & Estes, 2010; Ford *et al*. 2014; Winnie & Creel, 2017; Atkins *et al*. 2019). These trophic cascades have been observed in numerous landscapes, including the United States where the decline of cougar (*Puma concolor*) populations led to higher densities of mule deer (*Odocoileus hemionus*) and resulted in greater browsing intensity, increased bank erosion and decreased riparian biodiversity (Ripple & Beschta, 2006). Similarly, in Mozambique where civil war led to a widespread collapse in large carnivore populations, the diet and spatial use of bushbuck (*Tragelaphus sylvaticus*) was altered by the absence of predators, leading to changes in plant community structure and the suppression of common food plants (Atkins *et al*. 2019).

Similar to the suppression of prey populations through risk-avoidance behaviours, large carnivores also limit the impact of mesopredators (mammalian carnivores of intermediate body size) on an ecosystem through intraguild competition (Prugh *et al*. 2009; Ripple *et al*. 2013; Newsome *et al*. 2017). The extirpation, or extensive population decline, of large carnivores from an ecosystem can lead to “mesopredator release”, whereby mesopredator numbers increase substantially in the absence of larger apex predators (Crooks & Soulé, 1999). The removal of large carnivores often means that mesopredators can achieve persistently high densities and, without the regulating effect of apex predators, this can drive the decline or extinction of prey populations; therefore, destabilising community structure and disrupting ecosystem services (Rayner *et al*. 2007; Beschta & Ripple, 2009; Brashares *et al*. 2010; Gordon *et al*. 2017). For example, Cunningham *et al*. (2018) reported that the extensive decline of the

Tasmanian devil (*Sarcophilus harrisii*) population, from a species-specific transmissible disease, led to increased foraging and scavenging opportunities for feral cats (*Felis catus*). Reduced suppression of feral cats has broad implications for protecting native vertebrate species, as feral cats are a key cause of species decline (Woinarski *et al.* 2015), whilst slower consumption of carrion increases the prevalence of disease-causing bacteria and potential risk of disease transmission in wildlife and livestock (Cunningham *et al.* 2018).

The integral role that large carnivores play in ecosystem services means that large carnivores can also be regarded as indicator species for ecosystem health (Cardillo *et al.* 2005; Morrison *et al*. 2007). The naturally low densities of large carnivores, combined with their sensitivity to ecosystem disruption (e.g., habitat alteration, poisoning events, poaching and anthropogenic disturbance), often means that the disappearance of large carnivores from an environment is a precursor to wider biodiversity loss (Redford, 2005; Sergio *et al*. 2006; Kittle *et al*. 2017). For instance, Burton *et al*. (2011) highlighted the decline of lion (*Panthera leo*) observations in Mole National Park, Ghana, as an indicator of broader decline, both in the protected area and across the wider region. Conversely, in ecosystems where large carnivores have been restored, they are often attributed with aiding habitat restoration (Kuijper *et al.* 2013; Beschta & Ripple, 2015), suppressing mesopredator and invasive species density (Derham *et al*. 2018; Sheehy *et al*. 2018) and contributing to the return of essential resources (e.g., carrion) and scavenger diversity (Wilmers *et al*. 2003; Sievert *et al*. 2018). Population monitoring of large carnivores and effective conservation management of the large carnivore guild, therefore, has the potential to prevent biodiversity loss, regulate ecosystem services and act as an indicator of overall environmental health (Sergio *et al*. 2006; Dalerum *et al*. 2008; Ripple *et al*. 2014).

1.1.2 Economic and social role

Alongside the ecological merits of large carnivore presence, these species also provide economic and social benefits through a variety of direct and indirect methods (Ripple *et al.* 2014). Likely the most common and direct way in which large carnivores provide economic value to a landscape, is tourism (Lindsey *et al*. 2007; Skibins *et al*. 2013). Due to their iconic nature and popularity in mainstream culture, the simple presence of large carnivores can provide economic benefits for tourism (Di Minin *et al*. 2013; van der Meer, Badza & Ndhlovu, 2016). For example, jaguar (*Panthera onca*) ecotourism in the Brazilian Pantanal was estimated to generate a gross annual income close to US$7 million (Tortato *et al.* 2017), whilst the reintroduction of lions to Pilanesberg National Park, South Africa, generated US$9 million per year for the regional economy (McNeely, 2000). In addition, sustainable trophy hunting can provide a vital source of income when conducted under a regulated and evidence-based framework (IUCN, 2016; Booth *et al.* 2020). For instance, sustainable hunting of lion and leopard (*Panthera pardus*) in the Savé Valley Conservancy, Zimbabwe, generated over US$3 million in gross income over a four-year period (Funston *et al*. 2013). As tourism and hunting are often significant contributors to local and national economies, the loss of carnivores and associated revenue can have a considerable impact on livelihoods (Dickman *et al*. 2011; Mossaz *et al*. 2015; IUCN, 2016).

Large carnivore presence can also have indirect benefits for local economies and social welfare, including benefits to human health and pastoralism (O'Bryan *et al*. 2018). Previous research has highlighted that by predating stray dogs, leopards occupying the densely populated areas around Mumbai, India, provide valuable public health benefits by reducing dog bite incidents and rabies transmission, whilst saving local authorities US$18,000 per year in sterilisation and vaccination costs (Braczkowski *et al*. 2018). In agricultural landscapes, where large carnivores are often persecuted, there are positive aspects of human-carnivore coexistence that are often overlooked (Ripple *et al*. 2014; O'Bryan *et al*. 2018). For example, suppression of mesopredators and regulation of prey populations by large carnivores, as discussed previously, have been shown to reduce crop raiding (Brashare *et al*. 2010; Taylor *et al*. 2016; Thinley *et al*. 2018). For instance, Taylor *et al*. (2016) found that the presence and abundance of large carnivores in African protected areas was a more effective strategy for mitigating crop-raiding by baboons (*Papio* spp.) than human hunting of crop-raiders or changes in crop quality. Crop-raiding can have wide-ranging implications, particularly in developing countries, as financial income is lost (often leading to alternative livelihoods being sought, including bushmeat poaching; Lindsey *et al*. 2013a) and human livelihoods are impacted as children are forced to miss school to defend crops from attack (Mackenzie *et al.* 2015). Top-down control of mesopredators and prey populations by large carnivores is, therefore, an important tool for mitigating human-wildlife conflict (Taylor *et al*. 2016). Furthermore, by reducing disease prevalence in ungulate populations (by targeted predation of infected prey), large carnivores actively mitigate disease outbreaks that can be passed on to domestic livestock and cause great expense to agricultural industries and pastoralists (Packer *et al*. 2003; Ostfeld & Holt, 2004; Tanner *et al.* 2019).

Despite their potential benefits to agricultural landscapes, the presence of large carnivores in pastoral environments, or bordering protected areas, is often controversial and the negative impacts have been well documented (e.g., Woodroffe *et al.* 2005; Morehouse & Boyce, 2011; Kissui *et al*. 2019). Livestock depredation is the primary source of human-carnivore conflict and, as livestock loss has financial ramifications, it impacts the quality of peoples' livelihoods (Kissui *et al*. 2019). For example, the average cost of livestock depredation per farmer in a Namibian conservancy was US$2,848 and, as average expenditure was US$1,708 per annum, continued livestock loss is likely to have severe financial implications (Verschueren *et al*. 2020). The continued growth of human populations, combined with the decline in protected area health and habitat fragmentation, means increasing levels of human-carnivore conflict are predicted (Inskip & Zimmermann, 2009). Therefore, despite the positive aspects of large carnivores in an economic and social context, there is a need for long-term solutions to mitigate human-carnivore conflict that are beneficial for people and wildlife (Dickman *et al*. 2011).

1.2 Global decline of large carnivores

Although large carnivore presence has wide-ranging ecosystem benefits, many large carnivores have experienced significant population declines and the continued reduction of their geographic ranges (Ripple *et al*. 2014; Wolf & Ripple, 2018). As a result of these global trends, 80% of large carnivore species are now undergoing population declines and 64% of these species are threatened with extinction (Wolf & Ripple, 2018). Continued global alteration and fragmentation of habitats (Segan *et al*. 2016; Powers & Jetz, 2019) has resulted in large carnivores occupying, on average, only 47% of their historical geographical range (Ripple *et al*. 2014). In some cases, such as the Ethiopian wolf (*Canis simensis*), range contraction is as high as 99% of the species' historical range (Wolf & Ripple, 2017).

Decline in large carnivore populations can be attributed to numerous factors, including habitat destruction (Ripple *et al*. 2014; Espinosa *et al*. 2018), loss of natural prey (Wolf & Ripple, 2016; Sandom *et al*. 2018), direct and indirect persecution (St John *et al*. 2018; Knox *et al*. 2019; Loveridge *et al*. 2020), reduced habitat connectivity (McClure *et al*. 2017; Pitman *et al*. 2017) and increased conflict with humans (Treves & Karanth, 2003; Henschel *et al*. 2011; Broekhuis *et al*. 2017). These threats vary among species and populations, with some threats occurring in localised areas of a species geographic range, whilst other limiting factors may extend beyond a species' range, thereby preventing recolonisation (Ripple *et al*. 2014). Furthermore, the increasing pressures of climate change (Johnson *et al*. 2018; Rabaiotti &

Woodroffe, 2019) and human population growth (Geldmann *et al*. 2014; Jones *et al*. 2018) are likely to further intensify the risks posed to threatened large carnivores over time.

The causes of large carnivore declines are often concurrent with global biodiversity loss, however, they are exacerbated for large carnivores due to their susceptibility to anthropogenic disturbance and habitat alteration (Cardillo *et al*. 2005; Maxwell *et al*. 2016). Most large carnivores occur at relatively low population densities, whilst their slow reproductive cycles and low infant survival rates make them highly susceptible to persecution and unable to quickly respond to population decline (Cardillo *et al*. 2005; Ripple *et al*. 2014). Furthermore, their wide-ranging behaviour and high food requirements, compounded by increasing human population densities and encroachment into protected areas, bring large carnivores into further conflict with humans and livestock, leading to increased persecution and vulnerability to extinction (Broekhuis *et al*. 2017; O'Neil *et al*. 2020).

Owing to their naturally low densities and extensive ranging behaviour, large carnivores require substantial areas of contiguous, high-quality habitat for populations to persist (Di Minin *et al*. 2016; Wolf & Ripple, 2017). Isolated protected areas alone are often ineffective for large carnivore protection, with species requiring vast networks of connected habitat to ensure sufficient resource availability, maintain gene flow and alleviate the pressures of intraguild competition (Crooks *et al*. 2011; Lamb *et al*. 2020; Naude *et al*. 2020). However, large carnivores are particularly sensitive to the growing pressure of anthropogenic activities (e.g., livestock farming, poaching, infrastructure development) at protected area boundaries (Woodroffe & Ginsberg, 1998; Balme, Hunter & Slotow, 2010; Watson *et al*. 2014). Increased exposure to the risks of anthropogenic disturbance at reserve edges act as population sinks for large carnivores (Woodroffe & Ginsberg, 1998; Veldhuis *et al*. 2019). For example, jaguar density was up to 18 times higher in the core areas of Yasuní Biosphere Reserve, Ecuador, when compared to edge areas that were exposed to access roads and human settlements

(Espinosa *et al*. 2018). The negative effects of anthropogenic pressure at reserve edges can also impact natal dispersal, blocking immigration and potentially leading to inbreeding within populations (e.g., Riley *et al*. 2014; Naude *et al*. 2020). If the detrimental impact of edge effects and population sinks cannot be balanced with reproductive rates and successful dispersal events, then carnivore populations can rapidly decline (Woodroffe & Ginsberg, 1998). For example, a collapse in the lion population in Gonarezhou National Park, Zimbabwe, was suspected to be from hazardous edge effects, including luring animals outside park boundaries for trophy hunting and the increased risk of snaring incidents closer to reserve edges (Groom *et al*. 2014).

1.3 Large carnivore responses to anthropogenic disturbance

In areas of high human encroachment and intensive poaching, carnivores are known to face extirpation (Woodroffe, 2000; Henschel *et al*. 2005; Atkins *et al*. 2019). As human populations rise, and anthropogenic pressures increase on protected areas, they create both biotic and abiotic challenges that impact carnivores negatively (Šálek *et al.* 2015). The extent to which large carnivores can persist in human-impacted landscapes differs between species and is largely dependent on the scale at which they interact with humans and their ability to adopt behavioural responses (Cardillo *et al.* 2005). For example, leopards across Africa and Asia can persist at relatively high densities, even in unprotected, human-dominated areas (Athreya *et al.* 2013; Jacobson *et al*. 2016). As solitary generalists, exhibiting a diverse and adaptable dietary niche, leopards have a greater tolerance for persisting in the complex matrix of human-dominated landscapes (Braczkowski *et al*. 2012; Athreya *et al*. 2016; Kumbhojkar *et al.* 2020). In comparison, social, group-living large carnivores, such as African wild dogs (*Lycaon pictus*), and larger-bodied species, such as tigers (*Panthera tigris*) and lions, often struggle to adapt in areas of increased human disturbance (Karanth *et al*. 2011b; Everatt *et al.* 2019; O'Neil *et al*. 2020). These species have a greater reliance on large ungulate prey (Karanth *et al*. 2004; Hayward & Kerley, 2005) and, therefore, when the abundance of natural prey is depleted, they are likely to target livestock or increase their ranging behaviour, with both responses heightening the risk of exposure to anthropogenic sources of mortality (Fahrig & Rytwinski, 2009; Lindsey *et al*. 2017; Everatt *et al*. 2019).

1.3.1 Spatiotemporal behaviour

Increasing rates of anthropogenic disturbance can result in large carnivores altering their spatial use and temporal activity, often with the aim of maximising avoidance of human features and activities (Sévêque *et al*. 2020). Human activity has been observed to alter the spatiotemporal activity of several large carnivores, including cougars (Suraci *et al*. 2019), lions (Oriol-Cotterill *et al*. 2015), Amur leopards (*P. pardus orientalis*; Yang *et al*. 2018), spotted hyaenas (*Crocuta crocuta*; Kolowski *et al*. 2007) and brown bears (*Ursus arctos*; Parres *et al*. 2020). However, modifying spatiotemporal responses, and shifts away from natural patterns of activity, can have consequences for individual fitness, community dynamics and population persistence (Gaynor *et al*. 2018). For example, Amur tigers (*Panthera tigris altaica*) in areas of higher anthropogenic use reduced handling time and meat consumption on kills, whilst abandoning 63% of kills due to disturbance from human activity (Kerley *et al*. 2002). The development of human infrastructure can also impact carnivore space use, often bringing carnivores into further conflict with humans or increasing exposure to sources of mortality (Barrueto *et al*. 2014). For example, despite sufficient prey availability and forest cover, Thompson *et al*. (2020) found that jaguar space use was significantly reduced in areas closer to human settlements, with consequences for dispersal and functional connectivity between populations. In addition, some aspects of human-altered landscapes, such as road networks, provide easy travel corridors and are used to delineate territories and aid social communication through scent marking sites (Rafiq *et al*. 2020a). This behaviour can increase the likelihood of vehicle collision, and Kerley *et al*. (2002) found that survivorship and reproductive success were significantly reduced when Amur tiger habitat use incorporated primary road networks.

1.3.2 Interspecific competition and guild dynamics

Whilst large carnivores may alter their spatiotemporal dynamics to avoid interaction with anthropogenic disturbance, the behaviour of one species is often part of an intricate community structure that can be impacted when species alter patterns of activity (Sévêque *et al*. 2020). In most ecosystems, the behavioural ecology and spatial distribution of carnivores is driven by competition for available resources and the risk of intraguild predation (Palomares & Caro, 1999; Linnell & Strand, 2000; Caro & Stoner, 2003). Subordinate carnivores can reduce the detrimental effects of competition by diverging their use of one or more niche axes: spatially, adjusting their habitat use and home range size to limit encounters with dominant predators (e.g., Karanth *et al*. 2017; Marneweck *et al*. 2019); temporally, modifying their activity patterns to reduce times of overlap with competitors (e.g., Santos *et al*. 2019; Rasphone *et al*. 2020); and trophically, utilising different food resources (e.g., Hayward & Kerley, 2008). By partitioning their use of these three dimensions, complex carnivore communities with similar ecological requirements can facilitate coexistence (Caro & Stoner, 2003; Chesson & Kuang, 2008).

When the spatiotemporal behaviours of one or more species are influenced by anthropogenic disturbance, it can cause significant alterations to guild dynamics and, potentially, lead to population decline (Gaynor *et al*. 2018; Manlick & Pauli, 2020; Wilson *et al.* 2020). These more subtle and complex behavioural responses to anthropogenic disturbance have not received the same level of scientific investigation as the more direct implications of human impact, such as population decline and localised extirpation (Wang *et al.* 2015; Frey *et al*. 2020). However, detecting these subtle shifts in large carnivore behaviour may provide early indicators of species decline and allow more pre-emptive conservation management decisions (Frey *et al.* 2020; Wilson *et al.* 2020). Shifts in guild dynamics and niche partitioning have been observed in multiple landscapes and can have cascading effects on ecosystem health (Kuijper *et al*. 2016; Gaynor *et al*. 2018). For example, grey wolves (*Canis lupus*) in the Rocky Mountains increased their nocturnal activity in relation to disturbance and this, in turn, resulted in coyotes (*Canis latrans*) exhibiting higher levels of diurnal activity and expanding their spatial range (Frey *et al*. 2020). This could facilitate a form of mesopredator release, with coyotes benefiting from a reduction in top-down control and potentially increasing dietary overlap with other diurnal mesopredators (Frey *et al*. 2020).

In addition to changing large carnivore dynamics through the alteration of species behaviour, human disturbance can lead to shifts in community dynamics by altering the composition of the guild itself (Heim *et al*. 2019). Large carnivores vary in their adaptability to anthropogenic disturbance, with rates of population decline often differing between species. Apex predators (e.g., lion, tiger) are unlikely to have evolved mechanisms for facilitating coexistence with other dominant predators (i.e., humans) and, as a result, are more likely to find adaptation to human-dominated landscapes challenging (Everatt *et al*. 2019). This can lead to increased rates of population decline for dominant species, for instance the lion population in Liuwa Plains, Zambia, declined to one individual, whilst the spotted hyaena population remained stable, likely due to their greater tolerance of human disturbance (M'soka *et al.* 2016). However, by altering the community assemblage and resulting shifts in activity and niche partitioning between competitors, essential ecosystem processes, such as top-down regulation or interference competition, can be impacted (Wang *et al*. 2015; Frey *et al*. 2020). For example, intensive pastoralist activity surrounding Rajaji National Park, India, led to a collapse in the competitively-dominant tiger population and, in turn, an increase in the subordinate leopard population (Harihar *et al*. 2011). However, upon removal of the surrounding pastoralist community, the tiger population almost doubled in size, increasing competition with leopards. This shift in guild dynamics resulted in leopard density declining by almost 80% over five years, whilst increased competition for resources resulted in leopard diet shifting to livestock depredation (Harihar *et al.* 2011).

1.3.3 Diet and prey preference

Poaching and trophy hunting can alter the abundance of available prey inside and outside protected areas (Lindsey *et al*. 2013a; Wolf & Ripple, 2016). Large carnivores are frequently impacted by unsustainable offtake of ungulate species, as the species targeted by poachers and hunters overlap with the weight range of large carnivore preferred prey (Henschel *et al*. 2011; Darimont *et al.* 2015; Wolf & Ripple, 2016). A global synthesis of available studies revealed that humans harvested shared prey at a rate of 1.9 times higher than all other predators combined (Darimont *et al.* 2015). The density and distribution of prey are often strong drivers of carnivore abundance (Rabelo *et al*. 2019; Ash *et al*. 2020; Searle *et al*. 2020) and how large carnivores respond to prey depletion is often indicative of their ability to persist in the face of wider anthropogenic change. In areas where prey species are exploited at unsustainable levels, large carnivores may be forced to target alternative sources of prey. For instance, Persian leopard (*Panthera pardus saxicolor*) in Iran were found to utilise wild boar (*Sus scrofa*) at higher levels than elsewhere across their range, as religious beliefs meant poachers avoided hunting *suidae* species (Ghoddousi *et al*. 2017). Whilst this adaptation aided leopard persistence, the reduction in dietary niche breadth and increased risk of hunting dangerous prey could still have long term impacts on population viability (Ghoddousi *et al*. 2017).

Most carnivores display some degree of dietary breadth, however, there is growing evidence that the decline in large prey species is resulting in a shift towards smaller prey and dietary niche contraction (Wolf & Ripple, 2016; Creel *et al*. 2018). The depletion of larger prey, and resulting increase in dietary overlap between carnivore species, can have wide ranging implications for conservation management. A review of large carnivore studies by Khorozyan *et al*. (2015) revealed that beyond a minimum threshold for prey biomass, livestock predation increases significantly. This, in turn, increases the likelihood of retaliatory killing and lowers tolerance of large carnivore presence (van Eeden *et al*. 2018; LeFlore *et al*. 2019). In addition, increased dietary overlap between dominant and subordinate competitors can lead to higher rates of interspecific competition, potentially limiting subordinate carnivores (e.g., African wild dog, cheetah *Acinonyx jubatus*) that facilitate coexistence through niche partitioning (Dröge *et al*. 2017; Creel *et al*. 2018). There may also be negative impacts incurred on energetic fitness, group survival and reproduction of carnivores when smaller prey items are targeted that are below optimal weight ranges, although this subject requires further investigation (Carbone *et al*. 1999; Woodroffe *et al*. 2007; Creel *et al*. 2018).

1.4 Lack of population data for large carnivores and challenges for data collection

Although there is a growing body of literature highlighting the global decline of large carnivore populations, the implementation of effective management strategies to combat this decline are reliant on robust and accurate population assessments (Balme, Hunter & Slotow, 2009; Tobler & Powell, 2013). Providing reliable estimates whilst establishing methodologies and analytical frameworks from which baseline assessments of population stability can be quantified, is crucial for effective monitoring and informing conservation priorities (Green *et al*. 2020). Despite their ecological, economic and social benefits, there are large areas where estimates of population size and ecological information are still lacking for large carnivores (Bauer *et al*. 2015; Popescu *et al*. 2016; Jędrzejewski *et al*. 2018). For example, recent studies have highlighted the lack of accurate population estimates available for cheetah (Durant *et al*. 2017), jaguar (Jędrzejewski *et al*. 2018), leopard (Jacobson *et al*. 2016), lion (Braczkowski *et al*. 2020a) and snow leopard (*Panthera uncia*; Alexander *et al*. 2015; Suryawanshi *et al*. 2019) across their geographic ranges.

Obtaining robust density estimates for large carnivores is challenging (Burton *et al*. 2015; Devens *et al*. 2018). Many of these species are cryptic, solitary and wide-ranging, making data collection time-consuming and costly (Balme, Hunter & Slotow, 2009; Burton *et al*. 2015; Midlane *et al*. 2015). Furthermore, naturally low densities of large carnivores often result in limited sample sizes, making inference difficult and subject to wide margins of error (Gardner *et al*. 2010; Royle *et al*. 2014). For instance, over a period of 17,204 trap nights and 14 camera trap surveys, Murphy *et al*. (2018) only recorded an average of 3.42 fosa (*Cryptoprocta ferox*) individuals per survey. In the absence of accurate and/or recent estimates, conservation practitioners are often consigned to using anecdotal evidence or best guesses to inform conservation management decisions (Rodrigues *et al*. 2006; Balme *et al*. 2014; Jędrzejewski *et al*. 2018). In some cases, such as tiger populations in India, even where intensive survey efforts are undertaken to assess population trends, there are concerns over sampling methods and the precision of data used to inform conservation policy decisions (Harihar *et al*. 2017; Gopalaswamy *et al*. 2019).

1.4.1 Existing survey techniques

Various techniques have been employed globally to estimate the abundance and density of carnivores, each with their own limitations (Wilson & Delahay, 2001; Balme, Hunter & Slotow, 2009; Midlane *et al*. 2015; Dröge *et al*. 2020). These techniques include the use of indirect signs, such as spoor and faecal counts (Webbon *et al*. 2004; Henschel *et al*. 2020), prey availability (Karanth *et al*. 2004; Hayward *et al*. 2007), questionnaire surveys (Mésochina *et al*. 2010), and more direct techniques, such as density estimates derived from the home ranges of collared animals (Simcharoen *et al.* 2008; Devens *et al.* 2018), distance sampling (Hounsome *et al.* 2005; Durant *et al.* 2011) and acoustic playback surveys (Cozzi *et al.* 2013; Midlane *et al.* 2015). Critique of these methods and the efficacy of monitoring techniques is a central topic in conservation biology, as the most robust methods for estimating density are continually sought (Wilson & Delahay, 2001; Karanth *et al.* 2011a; Hayward *et al.* 2015).

Whilst there is a general consensus that precise and robust estimates of population size are best obtained through long-term, intensive studies employing recently developed techniques, such as spatial capture-recapture modelling or genetic sampling, these considerations often have to be balanced with logistical and budgetary restraints (Bischof *et al.* 2020; Dröge *et al.* 2020). This trade-off between the precision of estimates and survey considerations, combined with the wide-ranging, cryptic behaviour of large carnivores, often means that indirect census techniques are employed (Jhala *et al.* 2011; Aebischer *et al.* 2020; Henschel *et al.* 2020). These methods are often cheaper to conduct and, as they do not rely on direct observation, can produce larger sample sizes (Balme, Hunter & Slotow, 2009; Funston *et al.* 2010). However, the use of indirect survey techniques, most notably track counts, are increasingly questioned as issues surrounding the precision of estimates, analytical approaches and detection probability, continue to be raised (Hayward *et al.* 2015; Stephens *et al.* 2015; Gopalaswamy *et al.* 2019; Dröge *et al.* 2020). These issues are exemplified by the ongoing debate over nationwide tiger surveys in India, where the use of indirect survey methods (track/faecal counts) is met with widespread criticism as spurious trends in tiger density continue to be reported (Karanth *et al.* 2011a; Harihar *et al.* 2017; Gopalaswamy *et al.* 2019). The issue of effective monitoring and the limitations of survey methods are discussed further in Chapter Two, using a case study on spotted hyaena (see pages 31-67).

1.4.2 The emergence of camera trapping and spatial capture-recapture

In recent years, the use of camera traps for density estimation has become increasingly popular (Burton *et al*. 2015; Agha *et al.* 2018; Green *et al.* 2020). The method's minimal disturbance, combined with less labour-intensive survey requirements and the growing accessibility of equipment, has seen camera trapping become a preferred and rigorous method for density estimation, particularly for species that can be individually identified (Balme, Hunter & Slotow, 2009; Rovero & Zimmerman, 2016; Apps & McNutt, 2018). In addition to advancements in technology, which have improved camera trap performance (i.e., trigger speed, image quality) and product costs (Meek & Pittet, 2012), there have been developments in data management and image recognition software (Young *et al*. 2018). These factors have increased the feasibility, scale and potential applications of camera trapping for wildlife research, particularly for cryptic large carnivores (Forrester *et al*. 2017; Agha *et al*. 2018).

Alongside technological and practical advances in camera trapping, analytical frameworks from which estimates of population density can be derived have also seen continued development (Karanth & Nichols, 1998; Rowcliffe *et al.* 2008; Efford & Fewster, 2013; Royle *et al*. 2014). Density estimation from camera trapping, such as with capture–recapture modelling, has become an increasingly integral process in wildlife ecology and species management (Kays & Slauson, 2008; Royle & Gardner, 2011). Early investigations using camera trap arrays to estimate population size were restricted to species uniquely identifiable from their pelage patterns and relied on closed model capture-recapture methods (Karanth & Nichols, 1998, Trolle and Kéry, 2003; Royle *et al*. 2009). Whilst capture-recapture modelling establishes the basic principles of photographic capture-recapture, identifying individuals from photographic captures and using the associated time and date stamp to form individual capture histories, these models do not incorporate the spatial component of density estimation (Royle *et al*. 2014). Therefore, capture-recapture models fail to account for spatially explicit biological processes (i.e., individual movement) or the spatial distribution of the trap array (Royle *et al.* 2018; Green *et al.* 2020). The exclusion of a spatial context from capture-recapture models results in critical limitations, most notably limiting the ability to precisely define an effective area sampled, thereby making density estimation an arbitrary process (Royle *et al.* 2018). In addition, individual encounter probability and trap-level variation infer spatial processes. For example, individuals on the periphery of a trapping grid have a lower probability of capture and heterogeneity in these processes is not accounted for in the capture-recapture framework (Karanth & Nichols, 1998; Efford, 2004).

Spatial capture-recapture (SCR) models build on the technical limitations of conventional capture-recapture, incorporating the spatial information associated with individual capture histories and sampling devices to generate an explicit model of individual distribution across a defined state space (Efford, 2004; Royle *et al.* 2014; Sutherland *et al*. 2019). By relating the spatial context of individual encounters to explicit descriptions of spatial structure, whilst allowing for the integration of additional sources of data relating to spatial use (e.g., telemetry data) and landscape features (e.g., prey density, elevation), SCR provides a flexible framework to investigate ecological concepts, such as demography (Braczkowski *et al*. 2020b), resource selection (Broekhuis *et al*. 2020) and landscape connectivity (Sun *et al*. 2017). This flexible framework, combined with the potential for wide geographic sampling ranges and continued technological improvements, makes SCR modelling an important development in density estimation from camera trapping (Green *et al*. 2020).

The application of SCR with camera trapping data has steadily increased over the last decade (Agha *et al*. 2018; Green *et al.* 2020) and has become the standard method for estimating population density for multiple species of conservation concern (Royle *et al.* 2018, Sollmann, 2018). This is particularly true for carnivores, with a review of camera trapping and SCR analysis by Green *et al*. (2020) finding that almost 91% of published articles relating to density estimation were focused on carnivores. These studies have provided some of the first reported population estimates for threatened carnivore species (e.g., Kane *et al.* 2015; Suryawanshi *et al*. 2019). The development of SCR and advances in camera trapping have, therefore, provided conservation practitioners with a framework for robust assessment of carnivore populations, although this has largely focused on species that are individually identifiable to date, and the continued application and growing reliance on these methods is expected to continue (Burton *et al*. 2015).

Recent studies have highlighted key assumptions within the analytical framework of SCR, particularly in its application to camera trap data (Royle *et al.* 2018; Green *et al.* 2020; Johansson *et al*. 2020). The most common issue when SCR models are applied to camera trapping data, is uncertainty regarding individual identification and the misclassification of photographs (Alexander *et al*. 2015; Augustine *et al*. 2018; Johansson *et al*. 2020). Individuals within a study population are often identified by variation in their unique pelage patterns (e.g., spots or stripes; Figure 1.1); however, these markings can often be difficult to differentiate, and the process of individual identification can be further hampered by issues such as, poor photograph quality, change in pelage patterns over time and partial identity (Foster & Harmsen, 2012; Augustine *et al*. 2018). Erroneous identification of sampled individuals can alter population estimates: if observers misidentify known individuals as new individuals then these additional capture histories will inflate population estimates, and vice-versa if new individuals are incorrectly identified as known individuals. Johansson *et al*. (2020) highlighted the potential for observer error using a captive snow leopard population, with 12.5% of all capture occasions misclassified and the resulting density estimates inflated on average by 35%. This potentially common issue has led to speculation that, despite advances in SCR modelling, there could be widespread overestimation of threatened species (Foster & Harmsen, 2012; Choo *et al*. 2020; Johannson *et al*. 2020).

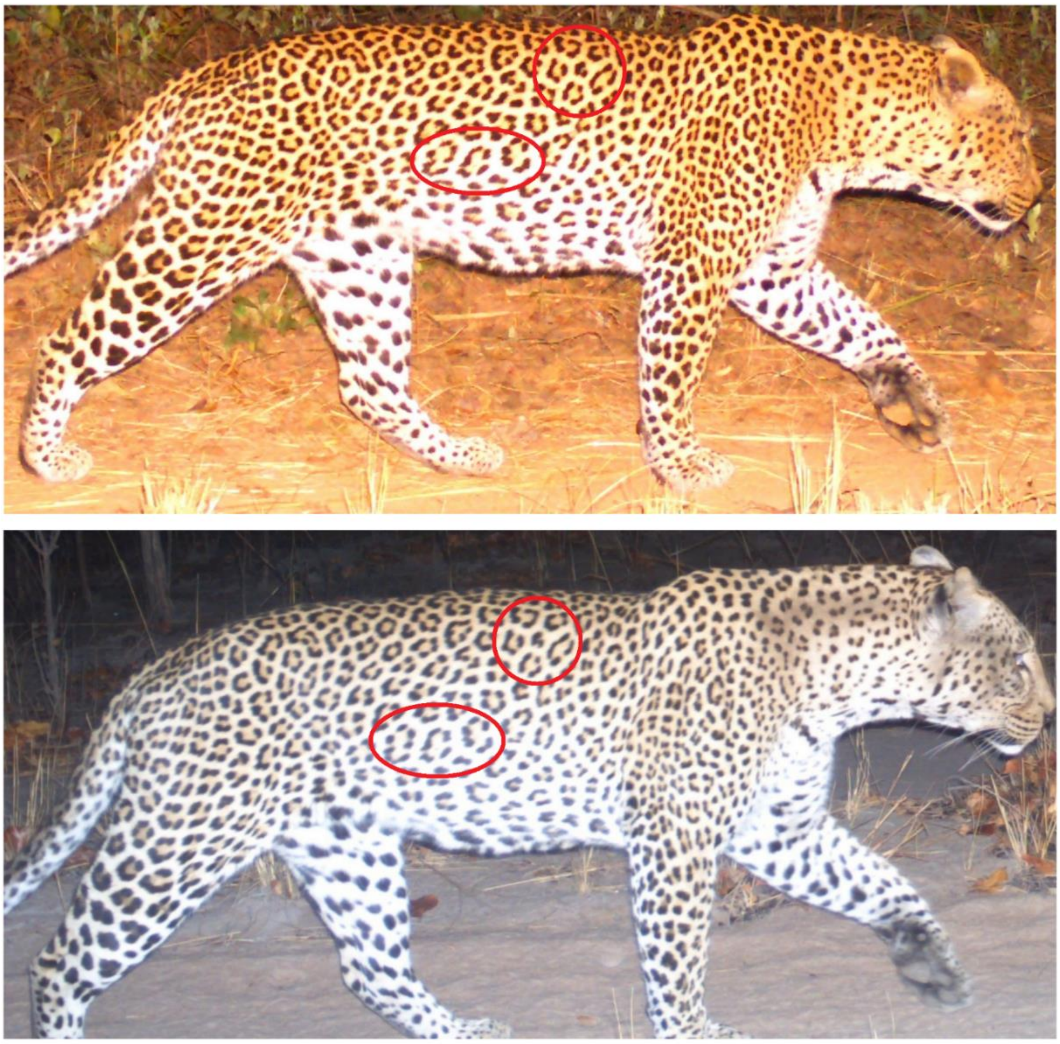


Figure 1.1. An example of individual recognition from unique pelage patterns. Here the unique spot patterns of a male leopard are compared, and two identifying features are highlighted (red circles).

A recent review of SCR models and camera trapping by Green *et al*. (2020) also highlighted that the precision of density estimates using SCR techniques was limited, as less than a quarter of published studies reported high precision (coefficient of variation ≤ 20%) in their density estimates. These findings could limit the ability of SCR modelling to identify linear trends in density over time, with the likelihood of detecting population decline reduced when the precision of estimates is lowered (Green *et al*. 2020). However, it should be noted that estimates from SCR modelling often produce a higher degree of precision than most conventional methods, such as track counts and home range density estimation (e.g., Elliot & Gopalaswamy, 2017; Devens *et al*. 2018; Dröge *et al*. 2020). Furthermore, the benefits of individual recognition over multiple surveys, which are overlooked in indirect methods, provide additional metrics and early indicators of population decline, such as reduced survival rates and skewed sex ratios (Braczkowski *et al*. 2020b; Harihar *et al*. 2020).

1.4.3 Camera trapping and behavioural research

The recent technological and analytical advances in camera trapping have also provided novel opportunities for quantifying behavioural traits and interspecific interactions for large carnivores (Rowcliffe *et al*. 2014; Frey *et al*. 2020). Aspects of large carnivore behaviour, such as daily activity levels, habitat use, movement (i.e., home range estimation) and spatiotemporal partitioning, that can be difficult to quantify in field studies, can all be investigated using camera traps and are becoming increasingly popular (Burton *et al*. 2015; Caravaggi *et al*. 2017). Previously employed methods for studying animal behaviour, for example, direct observations or VHF/GPS telemetry, have significant disadvantages when analysing behaviour, including limited sample sizes, the use of invasive techniques (e.g., live animal capture) and expensive operating costs (Hebblewhite & Haydon, 2010). In contrast, remote camera trapping provides a non-invasive opportunity for studying population and community-level processes, often across larger spatial and temporal scales than would be feasible with other methods (Burton *et al*. 2015; Cusack *et al*. 2017; Frey *et al*. 2020).

1.5 Decline of large carnivores in Africa and the need for population assessment

Throughout Africa, both inside and outside protected areas, there is a growing imbalance between large carnivore and human populations (Woodroffe, 2000; Jones *et al*. 2018). Across landscapes, populations of apex predators (e.g., lion, leopard, spotted hyaena, African wild dog, cheetah) are suffering substantial declines, due to poaching (Lindsey *et al*. 2013a; Wolf & Ripple, 2016), habitat loss (Riggio *et al*. 2013; Pitman *et al*. 2017), human-wildlife conflict

(Mkonyi *et al.* 2017; LeFlore *et al.* 2019) and disease (Woodroffe & Ginsberg, 1999; Canning *et al.* 2019). Simultaneously, human population density and population growth are increasing annually across Africa (Gerland *et al.* 2014). The expansion of anthropogenic impacts puts additional strain on protected areas, as encroachment on habitats and human-induced mortality increase (Hansen *et al.* 2013; Jones *et al.* 2018; Everatt *et al.* 2019).

Large carnivores have suffered substantial range contractions across Africa, on average losing 68.16% of their historical range (range = 27.2% - 93.7%, Wolf & Ripple, 2017). This is of great concern for the conservation management of large carnivores, as populations are increasingly restricted to protected area networks (Bauer *et al.* 2015; Pacifici *et al.* 2020). For example, the lion population across Africa has lost ~75% of its original habitat, and viable populations are now restricted to only a few large, protected areas, with all but four African countries observing a decline in population numbers (Riggio *et al.* 2013; Bauer *et al.* 2015). In many protected areas, common sources of prey, such as ungulates, are also targeted for the bushmeat trade (Lindsey *et al.* 2013a; Lindsey *et al.* 2017). This trade further intensifies the pressures on large carnivores, as carnivore prey preference overlaps significantly with target species for bushmeat poaching (e.g., Henschel *et al.* 2011), often forcing predators outside protected areas in search of prey and into further conflict with humans.

Whilst the continued decline of large carnivore populations in Africa is widely acknowledged, large areas across the continent lack baseline data on population status, interspecific interactions, and ecological requirements (Bauer *et al.* 2015; Jacobson *et al.* 2016; Durant *et al.* 2017). This issue is particularly relevant in Africa, with Martin *et al.* (2012) highlighting that, based on land area, Africa is the second most understudied global region in terms of ecological research. This paucity of data on population status and ecological interactions, limits the efficacy of conservation initiatives at all levels (Delsink *et al.* 2013; Henschel *et al.* 2014). In addition, previous reviews have highlighted discrepancies between areas where research effort has been focused and those in most urgent need of assessment (Balme *et al.* 2014; Pototsky & Cresswell, 2020). For instance, Henschel *et al.* (2014) observed that of the 463 articles available on African lion up until 2005, there was not a single article that focused solely on the critically endangered West African population. The omittance of these data from large portions of the continent are largely due to logistical, financial, and political constraints (Pototsky & Cresswell, 2020). For example, civil war has meant that the population status of African wild dogs in Angola has only recently been updated for the first time in forty years (Overton *et al*. 2020), whilst logistical and financial difficulties meant that regionwide density estimates for lions in West Africa were also overlooked until recently, hampering effective management (Henschel *et al*. 2014).

The paucity of accurate population data and ecological information for large carnivores across entire countries, major habitats and individual protected areas has hindered effective conservation management at all levels (Ray *et al*. 2005; Pitman *et al*. 2015). For instance, density estimates produced by Martin & de Meuleneur (1988) for African leopard across their range are still used in several countries (e.g., Mozambique, Namibia, Tanzania) to set hunting quotas (Strampelli *et al*. 2018). However, the estimates of Martin & de Meulenuer (1988) have been widely reported as inaccurate due to their model's reliance on rainfall data and the omittance of key factors regarding leopard population dynamics, such as human-induced mortality and prey availability (Norton, 1990; Balme *et al.* 2010). Furthermore, recent studies have highlighted discrepancies between estimates used for justifying hunting quotas and the current status of leopard populations in corresponding protected areas (Strampelli *et al*. 2018; Trouwborst *et al.* 2020). Similar issues relating to the paucity of reliable data, standardised methods, and the efficacy of associated conservation policies, have been highlighted for lion (Lindsey *et al*. 2013b; Macdonald, D.W. *et al*. 2017; Braczkowski *et al*. 2020a), cheetah (Weise *et al*. 2017) and wild dog (Nicholson *et al*. 2020) across their geographic ranges.

Interspecific interactions and avoidance behaviour within the large carnivore guild play an integral role in maintaining ecosystem function and regulating trophic communities (Caro & Stoner, 2003; Ripple *et al*. 2014). The ecological impact and potential for cascading ecosystem effects are particularly strong in Africa, as the large carnivore guild is still relatively intact in comparison to most other parts of the world (Dröge *et al*. 2017). Yet, largely due to their cryptic nature and naturally low abundance, relatively little is known about niche partitioning and interspecific interactions between the African carnivore guild across large sections of their range and in diverse community assemblages (Havmøller *et al.* 2020b; Rafiq *et al.* 2020b). The extent to which large carnivores can display behavioural plasticity, adapting their position along niche axes to facilitate intraguild coexistence in response to shifting environmental factors, differs between species (Dröge *et al*. 2017; Everatt *et al*. 2019; Vogel *et al*. 2019). As pressure on African ecosystems intensifies, from sources such as resource availability (Rich *et al*. 2017; Creel *et al.* 2018), human activity (Gaynor *et al.* 2018; Green & Holekamp, 2019) and climate change (Rabaiotti & Woodroffe, 2019), further changes in spatiotemporal behaviour, diet and guild dynamics are predicted (Tilman *et al.* 2017; Shamoon *et al*. 2018). Understanding community dynamics, and the potential impact that shifts in these dynamics may have at a population level is, therefore, important for informing conservation management decisions and predicting potential alterations in community structure from changing environmental factors (Rafiq *et al*. 2020b).

Without robust data on which to base management decisions, and the ability to effectively monitor population trends and identify drivers of decline, the continued reduction of carnivore populations across large sections of their geographical range will likely continue. There is, therefore, a need for further investigation into the status of regional carnivore populations, estimating population density alongside levels of interspecific competition and ecological requirements, to promote a shift towards evidence-based conservation management (Sutherland *et al*. 2004; Balme *et al*. 2014; Durant *et al*. 2017).

1.6 Aims of study

This thesis has two distinct research themes: 1) the need for effective population monitoring of large carnivores at all levels of conservation management, and 2) examining levels of interspecific competition and mechanisms of coexistence in a large carnivore guild impacted by human disturbance (Figure 1.2). This study will assess the population status and intraguild dynamics between large carnivores in Kasungu National Park (KNP), Malawi, a miombo woodland and a site experiencing high anthropogenic disturbance. Further justification of study site selection and rationale is provided in **Chapter Three**. These data will be used to implement effective conservation management in KNP and can also be used as baseline data to inform conservation strategies across Malawi and miombo woodlands in south-central Africa. As one of the last viable protected areas in Malawi, effective management and protection of large carnivore populations in KNP is a regional conservation priority.

This PhD thesis aims to:

1. **Critically evaluate the current survey techniques for estimating spotted hyaena density and provide recommendations for improved population monitoring.** In **Chapter Two** I will review the current literature on spotted hyaena population estimates, evaluate available survey techniques and make recommendations to improve future estimates and population monitoring across the species' range.
2. **Estimate the density of large carnivore populations in KNP, Malawi, using a spatial partial identity model in a spatial capture-recapture framework.** In **Chapter Four** I estimate the density and conservation status of large carnivore populations in KNP. These estimates are novel at a local, national, and international

scale, as the first leopard density estimates for KNP, Malawi and a miombo woodland habitat. Estimates of the population status of spotted hyaena and other large carnivore species are the first published estimates for KNP and Malawi.

3. **Analyse the spatiotemporal dynamics of the remaining large carnivore populations in KNP and identify the drivers of habitat use.** In **Chapter Five** I quantify the spatiotemporal dynamics between the remaining leopard and spotted hyaena populations in KNP. In the absence of other resident members of the large carnivore guild, this chapter considers how interspecific competition and intraguild dynamics may be altered and considers the potential conservation implications of adapting spatiotemporal behaviours.
4. **Determine the diet of leopard and spotted hyaena and assess levels of dietary overlap as a proxy for interspecific competition.** In **Chapter Six** I aim to quantify the level of dietary overlap between leopard and spotted hyaena in KNP, whilst providing an initial insight into the dietary composition of both large carnivores. Large mammal species have declined in KNP, due to poaching pressure, and this chapter assesses the potential for interspecific competition when prey availability is reduced.

1.7 Structure of thesis

Using the spotted hyaena as a model species, **Chapter Two** investigates the issues highlighted in sections 1.4 and 1.5 and evaluates the existing survey techniques to estimate large carnivore density. As the most abundant large carnivore in Africa, with an extensive geographic range, spotted hyaena are a good model species that exemplify the issues facing the wider carnivore guild. I review the literature available on spotted hyaena population estimates and critically evaluate the efficacy of current survey techniques for estimating population density. I advocate the greater utilisation of SCR methods and a unified framework to provide robust population estimates to effectively guide conservation management and policy decisions for the species.

In **Chapter Three** I introduce my study site, KNP, Malawi, and provide a wider background on Malawi and miombo woodlands. Miombo woodland is the primary habitat in KNP and a habitat for which data is lacking on large carnivore population density and behavioural ecology. Malawi is under intense pressure from anthropogenic disturbance, with a high human population density and a reliance on natural resources. I provide a summary of the decline in both protected area health and large carnivore populations in Malawi, before providing an overview of KNP and its importance to regional conservation efforts.

Chapter Four estimates population density for leopard and spotted hyaena in KNP between 2016 and 2018. In this chapter I provide the first published density estimates for both leopard and spotted hyaena in Malawi, whilst also providing the first estimates of leopard density in a miombo woodland habitat. I present evidence on the current status of other large carnivores in KNP, notably the presence of dispersing lion and African wild dog. I evaluate the use of the spatial partial identity model (SPIM) for providing robust density estimates comparable to conventional SCR models. This study is the first to apply SPIM in an African ecosystem and one of the first published applications of this novel technique since its inception (Augustine *et al*. 2018). I show that SPIM offers improvement for estimating density where individual identity is not always certain from single flank images, offering a preferable analytical framework to address the common issue of uncertain identity in camera trap datasets.

Chapter Five assesses the spatiotemporal dynamics of the remaining leopard and spotted hyaena populations in KNP. Leopard and spotted hyaena persist at similar low densities in KNP, and in the absence of a resident lion population, I examine the intraguild dynamics of the remaining large carnivore guild and the drivers of habitat use. I show that the presence of leopard and spotted hyaena is driven by the presence of preferred prey species and this increases the likelihood of interaction between the large carnivore guild. In addition, I present further evidence of leopard temporal sexual segregation, a finding that has only recently been identified in the literature by Havmøller *et al.* (2020b). Examination of temporal activity rates suggests that female leopards are active for almost 20% longer of the daily cycle than sympatric carnivores, an observation that may have implications for individual fitness and survival rates.

In **Chapter Six** I examine the diet of both leopard and spotted hyaena in KNP and assess the dietary overlap between the two species. Building on the results from **Chapter Five**, which assesses the level of interaction between leopard and spotted hyaena along the two niche axes of space and time, this chapter looks at the remaining niche axis, resource partitioning. Dietary segregation is a common strategy to facilitate coexistence in carnivore guilds where guild members cannot avoid spatiotemporal interaction (e.g., du Preez *et al.* 2017). This chapter reports the first insight into the dietary ecology of both species in KNP, whilst adding to the limited literature on dietary partitioning in sites of reduced prey abundance and high levels of anthropogenic disturbance.

I conclude the thesis with **Chapter Seven**, synthesising the results of Chapters 2-6 and assessing the findings of these studies in the wider context of the existing literature. This chapter highlights some of the issues concerning large carnivore population recovery in KNP and considers potential management solutions to aid in species recovery. I provide recommendations for future monitoring of carnivore populations in KNP, whilst advocating similar research to be undertaken across the understudied protected areas of Malawi.

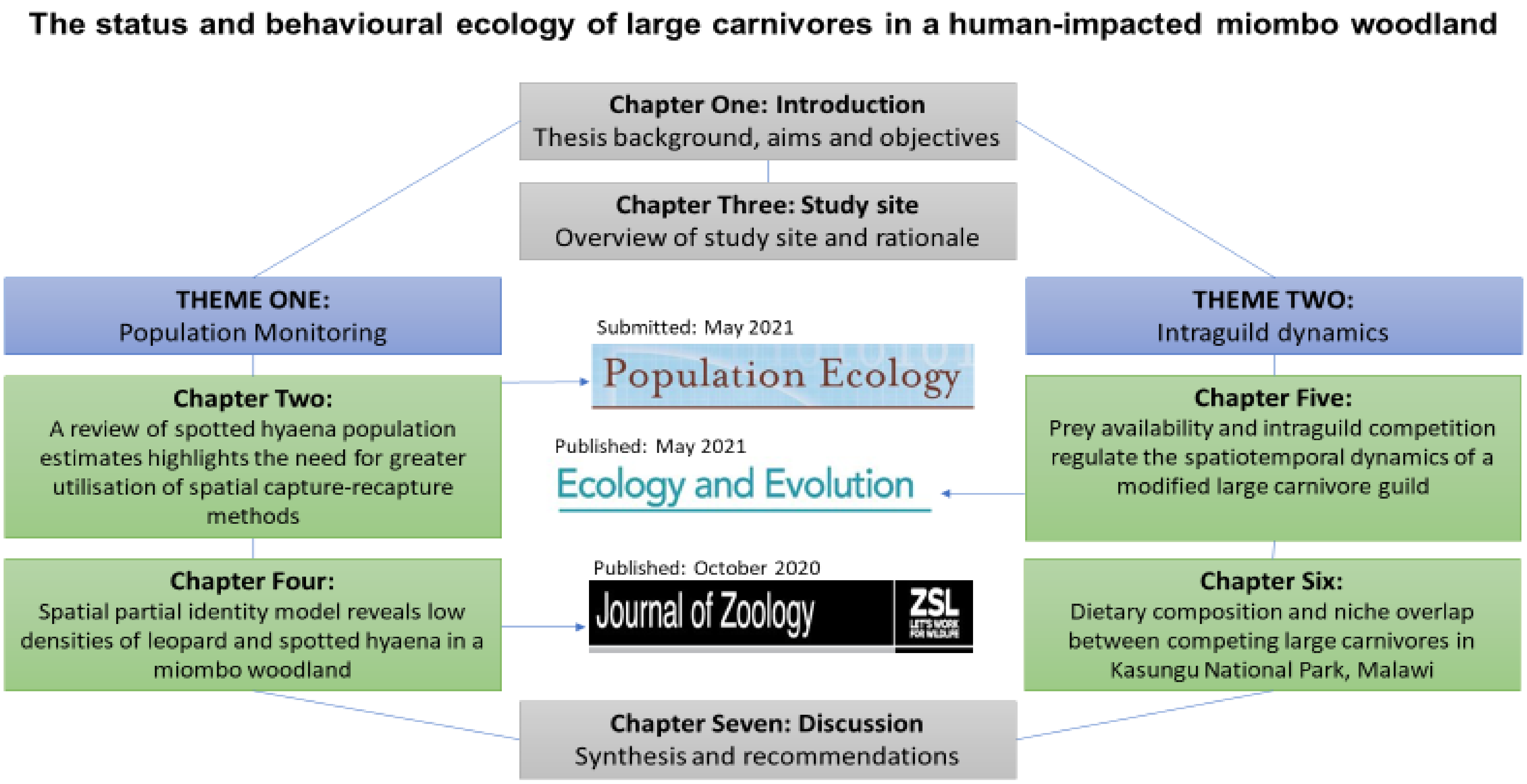
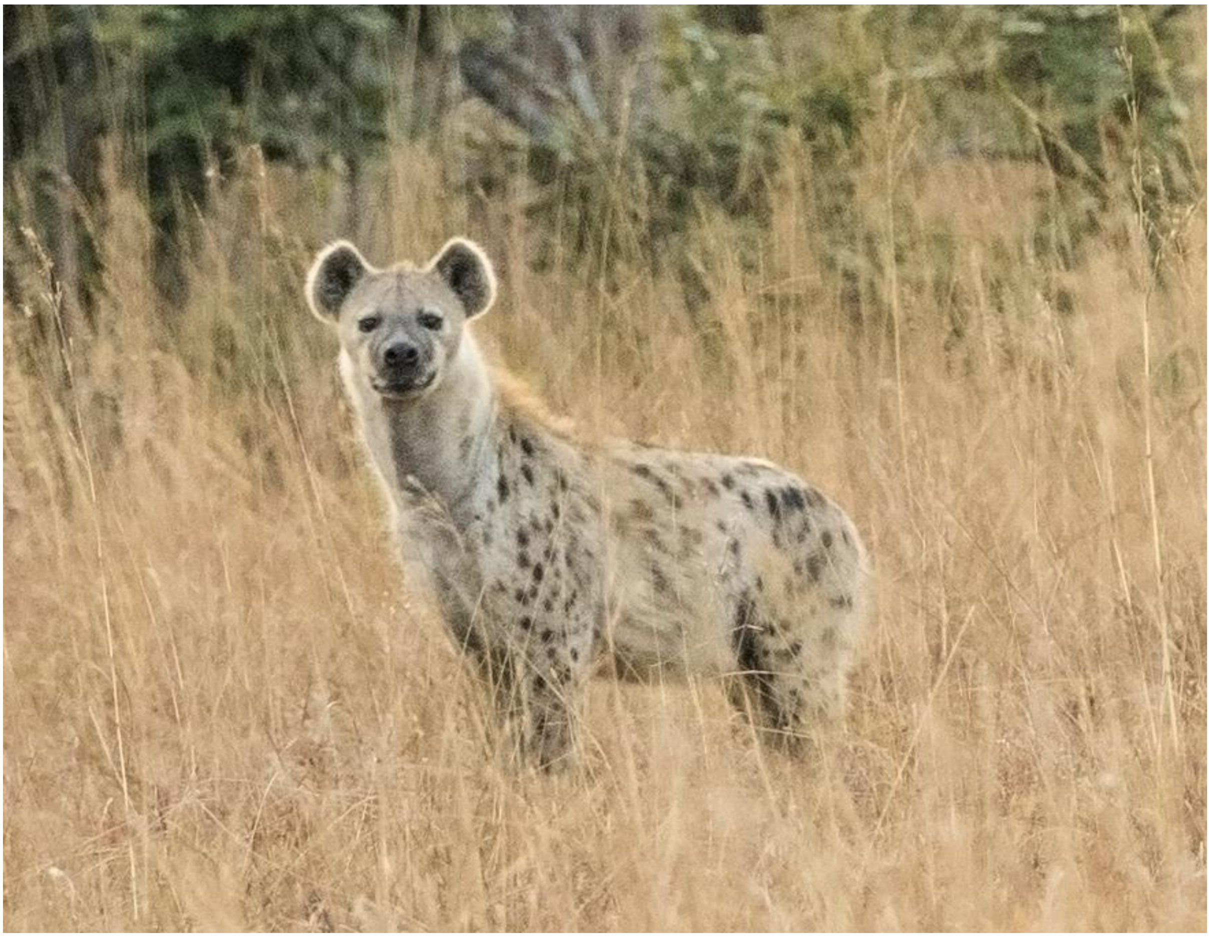


Figure 1.2. A schematic diagram highlighting the structure of the thesis. Chapters that have been accepted or submitted for publication are displayed, along with respective journal outlets.

CHAPTER TWO

A review of spotted hyaena population estimates highlights the need for greater utilisation of spatial capture-recapture methods



CHAPTER TWO: A review of spotted hyaena population estimates highlights the need for greater utilisation of spatial capture-recapture methods

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Cover image: A spotted hyaena responding to a call-in in Kasungu National Park, Malawi. **Photo credit:** Owen Slater.

Keywords

camera trapping, carnivore conservation, Crocuta crocuta, density estimation, Malawi, Panthera pardus, spatial capture–recapture

Abstract

As apex predators with a regulating effect on interspecific competitors and prey demographics, monitoring of spotted hyaena (*Crocuta crocuta*) population trends can provide a reliable indicator of ecosystem health. Robust estimates of population density are, therefore, critical for effective conservation management. However, the ability of current survey techniques to monitor large carnivore population trends effectively are increasingly questioned. This has led recent studies to advocate increased application of spatial capture-recapture (SCR) methods to estimate population density for large carnivores. Therefore, we reviewed the literature regarding methods used to estimate population density for spotted hyaena between 2000 and 2021. Our review found that SCR methods are currently underutilised for estimating spotted hyaena density, with only six published studies (12% of articles assessed) using an SCR approach. Call-in surveys were the most frequently used method, featuring in 43% of studies. However, 59% of studies that used call-in surveys could not estimate a site-specific calibration index. The calibration index estimates the distance and rate at which the focal species responds to audio lures and, as response rates are impacted by site-specific ecological and environmental factors, studies that could not calibrate this index are likely inaccurate. Further application of SCR techniques will allow more robust estimation of spotted hyaena density, reducing the wide confidence margins and potential overestimation that limit inference from existing survey methods. We advocate the use of SCR techniques to produce further estimates of spotted hyaena density and improve conservation management decisions.

2.1 Introduction

Robust population estimates play a pivotal role in the implementation of effective conservation management strategies, reintroduction efforts and monitoring schemes (Hayward *et al*. 2015). As large carnivore populations continue to experience wide-scale declines (Ripple *et al*. 2014), robust methods for assessing density and population trends must be at the forefront of evidence-based conservation management (Hayward *et al*. 2015; Elliot & Gopalaswamy, 2017). However, accurate data are often lacking for large carnivores, due to their cryptic behaviour and naturally low densities (Balme, Hunter & Slotow, 2009; Elliot & Gopalaswamy, 2017). In addition, available estimates are often outdated, overestimated or subject to wide confidence intervals (Braczkowski *et al.* 2020a). The paucity of reliable data can impact the management of target species and, inadvertently, have a cascading effect on the management of other vulnerable species. For example, intraguild competition can have a detrimental effect on threatened or reintroduced carnivores, such as cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*), so reliable density estimates for sympatric large carnivores can provide a valuable metric for reintroduction success (Darnell *et al.* 2014; Weise *et al*. 2015).

2.1.1 Spotted hyaena: indicators of ecosystem health

Spotted hyaena (*Crocuta crocuta*) are widespread, social carnivores that occupy a broad range of habitats in sub-Saharan Africa, from sparse deserts to montane woodlands and suburban areas (Holekamp *et al*. 2012; Yirga *et al*. 2014). As the most abundant large carnivore in Africa (Watts & Holekamp, 2008), spotted hyaena are routinely overlooked as a species of conservation concern. However, the spotted hyaena is often maligned and subject to high levels of persecution, particularly outside protected areas (Bohm & Höner, 2015). In addition, threats such as loss of natural prey, human-wildlife conflict and susceptibility to wire snaring and poisoning, are contributing to declines in spotted hyaena populations across Africa (Frank *et al*. 2011; Bohm & Höner, 2015; Wolf & Ripple, 2016; Loveridge *et al*. 2020). Loveridge *et al.*

(2020) highlighted that wire-snaring is a particular conservation concern, with spotted hyaena representing 92% of large carnivore snaring records in the Zimbabwean region of the Kavango-Zambezi Transfrontier Conservation Area and, as such, the species' conservation status warrants further attention.

Spotted hyaena density varies greatly across their geographic range, from 0.85/100km^2 in arid environments (Fouché *et al.* 2020) up to 165/100km^2 in prey-rich East African savanna ecosystems (Watts & Holekamp, 2008). As a dominant member of the large carnivore guild, spotted hyaena play an integral role in ecosystem services by regulating prey numbers, providing carrion for scavengers, and influencing carnivore dynamics through interspecific competition (Périquet *et al.* 2015; Green *et al.* 2018). Furthermore, spotted hyaena exhibit high levels of behavioural plasticity that enable them to persist in landscapes where other carnivores cannot compete (Holekamp & Dloniak, 2010; Green *et al* 2019). High behavioural plasticity makes spotted hyaena good models for assessing environmental change and monitoring wider ecosystem health (Trinkel, 2009; Green *et al.* 2018; Green *et al.* 2019). For example, increasing spotted hyaena population density can be an early indicator of competitive release from the regulating effect of competition with lions (*Panthera leo*) and signify declining trends in sympatric carnivores (M'soka *et al.* 2016; Green *et al.* 2018).

2.1.2 Current methods limit inference

Uncertainty regarding estimates of population size or density often stems from underlying issues with the survey methodologies employed for large carnivores. The challenges associated with surveying elusive, wide-ranging and often nocturnal large carnivores, combined with the need for rapid and cost-effective survey methods, has led to extensive use of index-calibrated methods to survey large carnivores (Mills *et al.* 2001; Funston *et al.* 2010; Winterbach *et al.* 2016). Index-calibrated methods assume a stable linear relationship between a measurable index (e.g., number of tracks or scats per km searched) and true population density (Funston *et al*. 2010) and, as these methods tend not to rely on direct observations, they are quicker and cheaper to conduct than more labour-intensive methods such as camera trapping or search-encounter techniques (Balme, Hunter & Slotow, 2009; Midlane *et al.* 2015).

In Africa, the use of two index-calibrated methods, track counts and call-in surveys, have frequently been employed to estimate density for spotted hyaena and other large carnivores (Croes *et al.* 2011; Aebischer *et al.* 2020; Henschel *et al.* 2020). However, the capacity of index-calibrated methods to account for variance in detection probability and spatial heterogeneity, whilst overestimating the precision of the putative index to successfully predict true density, has led to concerns that these methods produce spurious estimates and wide error margins (Gopalaswamy *et al.* 2015; Belant *et al.* 2019; Dröge *et al.* 2020). In some cases, confidence intervals do not include the true population size (Belant *et al*. 2019; Dröge *et al*. 2020) or are wide enough that inferences on population trends would be negligent as a basis for conservation management decisions (e.g., Bouché *et al.* 2016; Bauer *et al.* 2017). Consequently, numerous authors have cautioned against the widespread application of index-calibrated methods to infer population trends and inform management and policy decisions (e.g., Rosenblatt *et al.* 2014; Gopalaswamy *et al.* 2015; Hayward *et al.* 2015; Dröge *et al.* 2020).

Call-in surveys, whereby acoustic lures (i.e., prey distress sounds or carnivore social calls) are played from a calling station and a calibration response index applied to estimate population size from the response rate (Mills *et al.* 2001), are commonly used to survey spotted hyaena and lion populations. Despite the popularity of this method, call-in surveys have several limitations that reduce the precision and inference of results (Elliot & Gopalaswamy, 2017; Dröge *et al*. 2020). The calibration index is a key assumption in call-in surveys that determines the distance at which animals respond to the acoustic lure (see Mills *et al*. 2001 for a description of the required experiment). Conducting call-in calibration experiments is difficult in dense habitats or areas where animals are not well habituated (Bauer, 2007; Cozzi *et al.* 2013). As a result, researchers are often reliant on previous calibration estimates that may not accurately reflect their study site or population and, consequently, impact the precision of results (Kirsten *et al*. 2017). Furthermore, attempts to estimate response radius in areas of low density and restricted access can add further time constraints and financial costs, with potentially negative consequences for habituation (Midlane *et al.* 2015).

2.1.3 Emergence of spatial capture-recapture

In the last two decades, spatial capture-recapture (SCR) modelling has emerged as a reliable and robust technique from which to estimate population density (Efford, 2004; Borchers & Efford, 2008; Royle, Fuller & Sutherland, 2018). SCR methods utilise the spatial information associated with individual encounter history data to model the movement and distribution of individuals across a defined state space (Royle *et al*. 2014). The incorporation of a spatially explicit framework distinguishes SCR from conventional capture-recapture models, thereby addressing the challenges of buffering, heterogeneity in detection probability and trap-level variation that limited inference from traditional capture-recapture studies (Royle *et al.* 2014). SCR methods are commonly associated with camera trap data, where individuals are often identified through their unique pelage patterns, although these models can also be applied to DNA sampling, acoustic surveys and search-encounter methods, and have been used to estimate density for a wide-range of global taxa (e.g., Sutherland *et al*. 2016; Sun *et al*. 2017; López-Bao *et al*. 2018; Balme *et al*. 2019). As SCR models have developed to incorporate additional covariates (e.g., age and sex; Sollmann *et al*. 2011) and supplementary data (e.g., movement data from radio/GPS collars; Royle *et al*. 2013), the use of SCR has become the standard method for obtaining reliable population estimates for many species with unique identification features (Royle, Fuller & Sutherland, 2018). Despite the growing application and sophistication of SCR models, recent studies have highlighted that SCR approaches have been underutilised for multiple large carnivore species, including lions (Braczkowski *et al.* 2020a), snow leopards (*Panthera uncia*; Alexander *et al.* 2015; Sharma & Singh, 2020) and wolves (*Canis lupus*; López-Bao *et al*. 2018).

In this study we review and critically assess the literature on spotted hyaena population estimates and survey methodologies by 1) evaluating the survey methods used to estimate spotted hyaena density and their geographical distribution; 2) discussing the limitations of current spotted hyaena survey methodology; and 3) highlighting the potential for future utilisation of SCR methods, whilst identifying possible survey considerations within the SCR framework for estimating spotted hyaena density.

2.2 Materials and Methods

We followed the protocol of Braczkowski *et al*. (2020a) to conduct our literature review and searched for peer-reviewed articles on two comprehensive databases: Web of Science and Google Scholar. We used the following keyword combinations to search for peer-reviewed literature: “spotted hyaena” AND “density” OR “population size” OR “numbers”. We then repeated this process, replacing the keyword “spotted hyaena” with “*Crocuta crocuta*” (accounting for the English/US spelling hyaena/hyena) and the same density keyword variations. To remove bias in our search we limited the date range from 2000 to 2020, as SCR models were only developed towards the end of the 20th Century (Royle *et al*. 2014). We checked all search pages for the Web of Science results but limited our Google Scholar results to the first 100 articles. All articles were inspected, and excluded where: 1) there were no population estimates, 2) previous or unpublished estimates of density or population size were cited; and/or 3) the survey method used was not explicitly stated. For studies that matched our criteria, we recorded the survey method used to estimate population size or density and calculated the total proportion of articles each method featured in. Table 2.1 provides definitions of survey methods documented in the literature to estimate spotted hyaena density. For studies that used call-in survey methods we also recorded if the study was able to calibrate a site-specific response rate.

We assessed the spatial coverage of published estimates to determine any geographical preference for individual survey techniques. We recorded the country of each study and calculated the total number of studies per country. We documented the survey method used in each study and, using the geographic regions documented by the African Union (African Union, 2020), calculated the total number of times each method was used per region.

Table 2.1. Definitions of survey methods used to estimate spotted hyaena density and key literature that details each methodology.

Survey method	**Definition**	**Key literature**
Call-in survey	Audio lures (prey distress calls and/or carnivore social calls) are played through loudspeakers to attract large carnivores. The number of responding individuals are recorded and a calibration index applied, whereby the maximum distance a species will respond from is calculated.	Mills *et al*. 2001; Ferreira & Funston, 2016.
Track count	Surveys are often road based and consist of driving transects at slow speeds. Tracks encountered are identified to species level, from which track density per 100km is calculated. Previously estimated models for substrate type and species (see key literature) are then applied to predict true density.	Funston *et al*. 2010; Winterbach *et al*. 2016
Spatial capture-recapture (SCR)	SCR models make use of the spatial location of encounter history data to determine an individual's activity centre and uses these data to estimate the density of activity centres across a precisely defined polygon, known as the state space, which contains the trap array. Can be applied to several types of trapping data, e.g., camera trapping, DNA sampling, mist netting, cover boards/refugia.	Borcher & Efford, 2008; Royle *et al*. 2014

Capture-recapture	Individually unique identifiers (e.g., pelage patterns, ear tags) are used to gather encounter history data. Abundance estimates are calculated based on the number of individuals captured and frequency of recaptures. Density can then be obtained by estimating an effective trapping area and dividing the abundance estimate by the sampled area.	Otis *et al*. 1978; Karanth & Nichols, 1998
Distance sampling	Fixed-width transect surveys are conducted where target animals encountered are recorded, along with distance and angle from transect intercept. Density can then be calculated by modelling a fitted detection function, that can predict detection probability as a function of distance from the transect line.	Buckland *et al*. 2015
Total count	Population size is estimated by counting all observed individuals over a specified length of time. Counts can use individual identification to limit the effect of double counting.	Gese, 2001

2.3 Results

We reviewed 144 published studies on spotted hyaena from 18 African countries, in 49 different journals. We identified 51 studies, in 25 journals, that contained population estimates and detailed how these estimates were obtained (Appendix I).

2.3.1 Preferred methods for population estimates

Overall, six survey methods were used to estimate spotted hyaena population density. Of the 52 studies assessed, 50 used one survey method (96% of studies) and two used mixed methods. Call-in surveys were the most frequently used method, featuring in 43% of the articles assessed (n = 22 studies; Figure 2.1). Of the 22 studies that used call-in methods, over half (59%) were unable to undertake their own calibration experiments to estimate site-specific response distances of spotted hyaena. Index-calibrated methods (call-in surveys and track counts) were used in 63% of studies (n = 33 studies). SCR methods were used in six studies, 12% of articles, with only one study published prior to 2019. Camera traps were used to estimate spotted hyaena density in five of the six SCR studies, with a search-encounter method used in one study. Of the six studies that used SCR methods, five of these studies had a multi-species focus, estimating density for spotted hyaena and at least one other species.

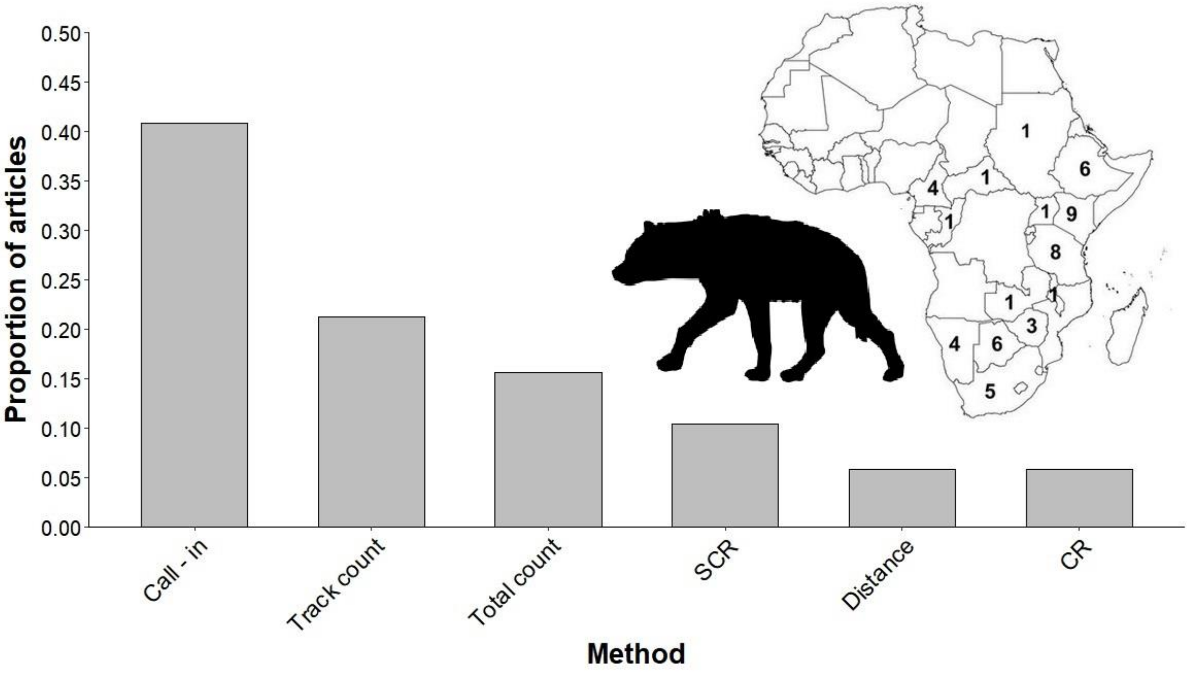

Figure 2.1. Survey methods used to obtain estimates of spotted hyaena density or population size and the proportion of reviewed articles that applied each survey method. Insert map shows the location of published studies from sub-Saharan Africa and the number of studies from each country where estimates were available.

2.3.2 Spatial coverage of survey methods

Density estimates were available for spotted hyaena populations in 14 African countries, representing 36% of spotted hyaena range states. Studies from East (49% of studies) and Southern (39% of studies) Africa accounted for the majority of available estimates (Table 2.2). There were six studies (12%) from the Central African region and no population estimates from West Africa. Call-in surveys or track counts were the most frequently used methods in all three regions (East, Central and Southern) where studies had been conducted. All population estimates using total counts and distance sampling were from East Africa, specifically in Kenya and Tanzania. Five of the six population estimates derived from SCR methods were conducted in Southern Africa.

Table 2.2. Number of times individual survey methods were used to estimate spotted hyaena density and/or population size by region and country. Individual survey methods include call-ins, track counts (Track), total counts of individuals (Total), Distance sampling (Distance), Spatial Capture-Recapture (SCR) and Capture-Recapture (CR). Note that the total number of times methods were used here (n = 54) is larger than the number of published studies found in the review (n = 51 studies) as two studies used multiple methods.

	Method					
Region/Country	**Call-in**	**Track**	**Total**	**Distance**	**SCR**	**CR**
East Africa	12	1	8	3	1	-
Ethiopia	6	-	-	-	-	-
Kenya	1	1	5	1	1	-
Sudan	1	-	-	-	-	-
Tanzania	3	-	3	2	-	-
Uganda	1	-	-	-	-	-
Southern Africa	7	8	-	-	5	2
Botswana	2	3	-	-	3	-
Malawi	-	-	-	-	1	-
Namibia	1	1	-	-	1	1
South Africa	3	2	-	-	-	-
Zambia	-	-	-	-	-	1
Zimbabwe	1	2	-	-	-	-
Central Africa	3	3	-	-	-	1
Cameroon	2	2	-	-	-	-
Central African Republic	1	1	-	-	-	-
Republic of Congo	-	-	-	-	-	1
TOTAL	22	12	8	3	6	3

2.4 Discussion

Here we found that SCR methods are currently underutilised for estimating spotted hyaena density, compared to other available methods. However, with five of the six studies using SCR methods published since 2019, this may indicate a growing change in preferred survey methodology. Despite the increase in SCR-derived estimates for spotted hyaena, the number of published studies utilising SCR methods is still relatively low when compared to sympatric carnivores. For example, ~55% of published studies estimating leopard (*Panthera pardus*) density in sub-Saharan Africa, since 2000, used SCR methods (see Appendix II). Spotted hyaena population estimates are also limited to only 14 out of 39 African countries where the species is resident (Bohm & Höner, 2015), which evidences that just under two-thirds of range states lack baseline density estimates. Since spotted hyaena density varies considerably between habitats and with levels of anthropogenic disturbance (Yirga *et al*. 2017; Fouché *et al*. 2020), there is a need for increased reporting of population estimates from understudied regions to inform local conservation management.

2.4.1 Addressing issues with current survey methodologies

Our review indicates that call-in surveys are the most frequently used method for estimating spotted hyaena density. However, calculating a site-specific calibration index to estimate response radius remains a significant challenge. This is highlighted here as over half the published studies were unable to conduct site-specific calibration experiments. In addition, some authors acknowledged that their calibration indices were unreliable and subject to wide confidence limits, owing to small sample sizes (e.g., Ogutu *et al*. 2005). Studies that could not conduct their own calibration experiment often relied on the estimates of Mills *et al*. (2001). A lack of animal habituation and logistical feasibility were often cited as key reasons for not undertaking the calibration experiment. Site-specific differences in habitat structure, competing carnivore densities and anthropogenic disturbance are likely to affect the local response rate of spotted hyaena. Subsequently, it is unlikely these frequently cited calibration indices are widely applicable and corresponding estimates are likely to be inaccurate.

Call-in surveys can also suffer from issues with habituation. For example, Belant *et al*. (2016) found that lions quickly become habituated to audio lures and habituation levels are not reduced by temporal and spatial variation in calls. As a result, calibration experiments may lower species response rates during survey periods. Habituation from repeated call-in surveys could also impact response rates over multi-season surveys, with a lower response rate potentially leading to incorrect assumptions of population decline over time (Belant *et al*. 2016). In addition, response rate to acoustic lures can also be reduced in areas where competing carnivore densities are skewed, or human activity is prevalent (Midlane *et al*. 2015; Kirsten *et al*. 2017). For example, areas of high lion density can limit the response rate of spotted hyaena (Kiffner *et al*. 2007; Kirsten *et al*. 2017), whilst cautious behaviour in areas of increased human disturbance can mean responding individuals are still potentially missed (Bauer, 2007). As such, call-in surveys are often of limited value for multi-species surveys and can be inaccurate in low density areas, where population estimates are often most urgently required.

Call-in surveys are an effective tool for confirming the presence of spotted hyaena, and other large carnivores, in understudied regions where conservation efforts have been restricted. For example, the presence of spotted hyaena and lion in Dinder National Park, Sudan, were recently confirmed through call-in surveys (Mohammed *et al.* 2019). Furthermore, we recognise that call-in surveys are beneficial for obtaining population estimates in areas that are logistically challenging for other survey methods, such as camera trapping. This is highlighted in our review by the sole use of call-in surveys in Ethiopia, where studies were conducted in peri-urban areas that would make the use of other survey techniques difficult (Yirga *et al.* 2014; Yirga *et al*. 2017). Where call-in surveys are conducted, we suggest efforts are made to identify responding individuals (Trinkel, 2009). However, we appreciate that identifying and documenting individuals at call-in surveys is difficult with cautious animals and low visibility habitats (Bauer, 2007). The collection of individual encounter data at call-in surveys would allow these data to be analysed in an SCR framework (Elliot & Gopalaswamy, 2017) if surveys were repeated, thereby improving precision, avoiding double counting, and accounting for imperfect detection. Going forward, we recommend that call-in surveys either adopt an SCR approach to data collection or the survey method is employed as an initial step to confirm species presence.

Track counts were the second most popular method for estimating spotted hyaena density and were represented in almost a quarter of all published articles. Despite the popularity of track counts, derived population estimates often have wide confidence intervals and overstated precision (Elliot & Gopalaswamy, 2017; Belant *et al*. 2019; Dröge *et al*. 2020). Low precision stems from unmodelled detection probability and oversimplification of the variance in the relationship between track density and true population density in the initial linear equation (Gopalaswamy *et al*. 2015; Hayward *et al*. 2015; Dröge *et al*. 2020). Dröge *et al*. (2020) argued that track counts do not comply with IUCN guidelines for population monitoring, as estimates may not be accurate enough to monitor population trends over time. In addition, track counts are reliant on standardised methods and assumptions. A key assumption is that all animals in the surveyed region have the same probability of detection, regardless of environmental (e.g., prey availability, interspecific competition) or anthropogenic (increased human activity) variability (Elliot & Gopalaswamy, 2017; Henschel *et al*. 2020). In the case of spotted hyaena, this assumption is difficult to meet, with spotted hyaena behaviour known to be influenced by human activity (Boydston *et al.* 2003; Belton *et al.* 2016), areas of increased prey availability and competition with lions (Périquet *et al.* 2015). Violating the assumption of equal detection results in underestimation of density (Henschel *et al.* 2020), with knock on effects for conservation management decisions. It is, therefore, difficult to make a strong case for the future use of track count surveys to monitor spotted hyaena populations.

When analysed in an occupancy framework track counts are efficient and cost-effective for gathering large carnivore presence/absence data, including spotted hyaena. The limitations of track count data are better incorporated into model inference within occupancy models as they account for imperfect detection and allow the use of covariates to model heterogeneity in site-use estimates (MacKenzie *et al*. 2017). Track count data have provided valuable insights into the distribution and drivers of site use for multiple large carnivore species in Africa (e.g., Everatt *et al.* 2014; Henschel *et al*. 2016; Petracca *et al*. 2019) and we encourage further use of occupancy models over index-calibrated density estimates (Dröge *et al.* 2020). However, efforts to estimate density from occupancy models are cautioned against due to variability in spatial use and home-range utilisation (Link *et al.* 2018; Rogan *et al.* 2019).

Distance sampling and total count methods were used in 11 studies to estimate spotted hyaena density or population size, all of which were from Kenya and Tanzania, notable for their wide-open grasslands and high visibility (Durant *et al.* 2011; Farr *et al*. 2019). Whilst these surveys were able to estimate spotted hyaena density, these models are reliant on open habitats and the study species being reasonably habituated to human presence (Durant *et al*. 2011). Furthermore, studies that conducted distance sampling in Kenya and Tanzania were able to observe spotted hyaena during daylight hours (Durant *et al.* 2011). Often spotted hyaena are more nocturnal in areas of anthropogenic disturbance (Kolowski *et al*. 2007). As such, the wider applicability of distance sampling and total counts appears limited, with low capture success in areas of reduced visibility (e.g., dense woodlands) and/or high levels of anthropogenic disturbance making robust estimates unlikely, or requiring intensive survey effort (e.g., Thorn *et al*. 2010; Burton *et al.* 2011). With ≥ 60 observations recommended for robust estimates from distance sampling (Buckland *et al*. 2015), and reliable data on observed distance and angle necessary, these methods are not applicable across a considerable area of the spotted hyaena’s geographical range.

Total counts were used in long-term studies in Kenya and Tanzania to assess temporal changes in demography and population size (Höner *et al.* 2005; Green *et al.* 2018). Whilst direct counts employed for spotted hyaena did incorporate individual identification, allowing for more robust estimates of population size and avoidance of double counting, the time and effort required for direct counts is better combined with long-term behavioural studies (Gese, 2001). Certainly, if the aim of conservation practitioners is to compare population trends between sympatric carnivores, total counts are not a replicable model as the survey method is not viable for more cryptic species, such as leopard and cheetah.

2.4.2 Towards robust estimates with SCR

The development of SCR models has overcome several of the issues that limit inference from conventional survey methods for spotted hyaena. Most notably, the incorporation of detection probability and survey effort into SCR models improves the precision of estimates, compared to the wide error margins associated with index-calibrated methods (Broekhuis & Gopalaswamy, 2016; Braczkowski *et al.* 2020a). However, a recent review by Green *et al.* (2020) found that some SCR density estimates from camera trapping lacked the necessary precision for monitoring population trends over time, with precision increasing when more individuals from the study population were captured. Inference from large carnivore survey methods is often hampered by naturally low densities and small sample sizes, leading to inaccuracies or cautious estimation of population size (Bauer, 2007; Winterbach *et al.* 2016). As small sample sizes are common in spotted hyaena studies (e.g., Mohammed *et al.* 2019; Fouché *et al.* 2020; Davis *et al.* 2021), by extracting the individual and spatial information from encounter history data, SCR models can be used to make effective use of limited datasets and produce statistically robust estimates (Royle *et al*. 2014; Royle, Fuller & Sutherland, 2018). Furthermore, by accounting for the spatial location of captures, SCR models allow for estimation of fine-scale variation in density across landscapes (Gopalaswamy *et al*. 2012). Covariates of interest (e.g., prey density, illegal activity) can also be included in SCR models to investigate potential drivers of spatial distribution, providing a more comprehensive understanding of species density and distribution, thereby informing conservation management (Broekhuis & Gopalaswamy, 2016; Ramesh *et al*. 2017).

Current preferred survey methods for spotted hyaena fail to capitalise on the benefits of individual identification, which can provide additional metrics for assessing population health (Braczkowski *et al*. 2020a). Information on animal movement, sex ratios and survival rates are embedded within individual encounter history data (Karanth *et al.* 2006). Key indicators of population decline, or recovery, can be assessed by monitoring key parameters derived from individual identification (Harmsen *et al*. 2017; Brackzkowski *et al*. 2020a). For example, Duangchantrasiri *et al*. (2016) used survival rates from repeated SCR surveys to determine the efficacy of increased law enforcement efforts for tiger (*Panthera tigris*) population recovery. Using sex-specific movement parameters and calculated sex ratios derived from SCR estimates, Braczkowski *et al*. (2020b) highlighted increased home range movements and male-biased sex ratios as early indicators of potential collapse in lion population numbers.

In addition, the SCR approach is flexible, lending itself to direct (e.g., search-encounter; Broekhuis & Gopalaswamy, 2016) and indirect (e.g., camera trapping; Rich *et al*. 2019) methods, allowing researchers to select appropriate methodologies for their study site and population. As spotted hyaena occupy a diverse array of habitats and display varying behavioural responses to anthropogenic disturbance (Belton *et al*. 2016; Yirga *et al.* 2017), the flexibility of applying SCR models to individual encounter history data provides a standardised framework to monitor the species throughout their range. For example, the open grassland habitats of East Africa would be appropriate for search-encounter methods, as spotted hyaena are regularly encountered in daylight hours and distance sampling techniques are a viable approach. Furthermore, the dense vegetation and high levels of human disturbance documented in countries, such as Cameroon (Croes *et al.* 2011; Kirsten *et al.* 2017), would benefit from applying SCR models to frequently used indirect methods, like camera trapping or DNA sampling.

SCR methods have been widely applied to estimate felid densities across Africa, with camera trap surveys routinely used to obtain encounter history data (e.g., Brassine & Parker, 2015; Kane *et al*. 2015; Balme *et al*. 2019). Spotted hyaena are widely distributed across sub-Saharan Africa and are likely caught as bycatch on camera trap surveys undertaken for sympatric carnivores (e.g., Williams *et al.* 2020). However, spotted hyaena population estimates are rarely reported from these surveys, despite data occasionally being used as covariates to make inferences about the behaviour or density of the focal species (e.g., Ramesh *et al*. 2017; Balme *et al*. 2019). Of the six studies using SCR methods to estimate spotted hyaena density, 83% of studies had a multi-species focus (e.g., O'Brien & Kinnaird, 2011; Rich *et al*. 2019; Davis *et al*. 2021; Vissia *et al*. 2021). Thereby highlighting that SCR estimates for spotted hyaena can be obtained from camera trap grids with a multi-species focus. Increased reporting of spotted hyaena density, from studies where they may have been previously overlooked, would be beneficial for the conservation management of spotted hyaena and interspecific competitors.

One of the limitations of an SCR approach is the cost of equipment and/or survey effort (Balme, Hunter & Slotow, 2009; Rafiq *et al.* 2019; Braczkowski *et al.* 2020a). We acknowledge that call-in surveys and track counts are often cheaper to conduct (Balme, Hunter & Slotow, 2009). However, the improvements in precision and benefits of individual identification for long-term population monitoring means that SCR-derived estimates can provide a greater balance of accuracy and cost-effectiveness (Balme, Hunter & Slotow, 2009; Braczkowski *et al.* 2020a).

In addition, the multi-species SCR approaches of both Rich *et al*. (2019), using camera traps, and Rafiq *et al*. (2019), using tourist photographic records, demonstrate the ability of SCR techniques to survey multiple large carnivore species simultaneously, thereby optimising survey costs. In areas where there is high tourism demand, the citizen science approach of Rafiq *et al*. (2019) has shown that SCR estimates are obtainable at considerably reduced costs. Where a citizen science approach is not possible, a viable option for reducing camera trap survey costs is the utilisation of spatial partial identity models (Augustine *et al*. 2018) which can produce robust SCR estimates from partial identity samples obtained using single camera trap stations, instead of the conventional dual camera survey design (Davis *et al.* 2021).

Sexing spotted hyaena, particularly from camera trap images, could be a potential constraint of SCR methods for estimating spotted hyaena density. Sex-specific variation in space use and movement result in differences in detection probability and, where possible, should be incorporated into candidate models (Sollmann *et al*. 2011). However, movement patterns between male and female spotted hyaena are known to differ (Boydston *et al*. 2005; Kolowski *et al*. 2007) and the species is notoriously difficult to sex. Therefore, incorrect classification could result in skewed sex ratios and reduced accountability for heterogeneity in the observation process. Consequently, any attempt to incorporate sex-specific variation should be reliant on agreement between multiple trained observers or, in the case of long-term research projects, the incorporation of maintained identification databases to ascertain sex. Alternatively, aging spotted hyaena based on their spot patterns and coat wear is relatively easy (e.g., age groupings in M’soka *et al*. 2016). As movement patterns also vary between age groups in spotted hyaena (Boydston *et al.* 2005), the incorporation of age classes into SCR models could improve model inference whilst accounting for variation in detection probability.

A key assumption of SCR models is that individual activity centres are uniformly and independently distributed over the state space (a region that incorporates the study area and a defined buffer which includes all potential activity centres for sampled individuals; Royle *et al*. 2014). However, this assumption is often violated in social, group-living carnivores (e.g., lions, wolves), potentially influencing precision and affecting the underlying state process model (Bischof *et al*. 2020). As spotted hyaena are social carnivores, living in clans ranging from 5-90 individuals (Holekamp *et al*. 2012), these assumptions represent a possible source of bias in SCR-derived estimates. Despite their close-knit social groups, spotted hyaena display fission-fusion dynamics, whereby clan members are often found alone or in smaller subgroups that are subject to compositional change, and, as such, individual encounter history data is often collected. For example, Stratford *et al*. (2019) found that 62% of recorded camera trap images of spotted hyaena were lone individuals. As individual movements represent a large proportion of encounter history data, the impact on precision and interval coverage will likely be reduced (see Bischof *et al*. 2020). Indeed, simulations by Lopez-Bao *et al*. (2018) have shown that SCR models can provide reliable outputs for species violating assumptions of dependence in activity centres. However, further development of SCR models that can incorporate fission-fusion dynamics and group association into the state point process are required (Elliot & Gopalaswamy, 2017; Bischof *et al*. 2020).

2.5 Conclusions

Call-in surveys and track counts are currently the preferred methods for estimating spotted hyaena density. However, the efficacy of these methods has recently been questioned for long-term population monitoring (Gopalaswamy *et al*. 2015; Dröge *et al*. 2020; Elliot *et al*. 2020). In comparison, SCR methods have the potential to monitor population change and assess trends in survival (by including individual identification and movement parameters), whilst incorporating environmental attributes (e.g., prey density) and demographic covariates (Karanth *et al*. 2006; Braczkowski *et al*. 2020b). Index-calibrated methods account for almost two-thirds of available spotted hyaena estimates but often overestimate density or are subject to wide confidence intervals, creating uncertainty in population size and stability (Braczkowski *et al*. 2020a; Dröge *et al*. 2020). We argue that there should be greater concern for the status of spotted hyaena populations across Africa and increased survey efforts for understudied populations. Similar to recent calls for greater utilisation of SCR methods in the conservation management of lion (Braczkowski *et al*. 2020a) and snow leopard (Sharma & Singh, 2020) populations. Here we recommend adoption of an SCR approach to estimate spotted hyaena density, providing a unified framework for population monitoring across the species' geographic range.

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CHAPTER THREE

Study site and background

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3.1 Malawi

Malawi is a landlocked country situated in south-central Africa, bordered by Tanzania, Zambia, and Mozambique (Figure 3.1). It is classified amongst the world's least-developed countries (FAO, 2013a), with 89.4% of the country living below the $3.10/day line (OPHI, 2020) and an economy heavily based on agriculture. Malawi has a total land area of 94,276km^2, relatively small in comparison to other African countries. However, it also has one of the highest population densities in Africa that continues to grow annually (192/people per km^2; World Bank Group, 2019). Malawi had an estimated population of 18.6 million people in 2019 and this is projected to double by 2038 (World Bank Group, 2020).

A large proportion of the population relies on subsistence farming, for both income and food security, with 84% of the population living in rural areas (Schaafsma *et al.* 2018). Subsistence farming practices are impacted by climatic factors, such as drought and flooding, resulting in frequent food insecurity issues with more than one-third of the country unable to meet daily calorie requirements (Ecker & Qaim, 2011; Conway *et al*. 2015). As the population of Malawi continues to grow, wide-scale conversion of land for agriculture has increased outside protected areas (Schaafsma *et al*. 2018; van Velden *et al*. 2020). Furthermore, over 97% of Malawian households are reliant on illegally and unsustainably sourced biomass for domestic cooking and heating energy (Republic of Malawi, 2019). Conversion of land for agriculture and reliance on wood for fuel has resulted in Malawi experiencing the highest deforestation rate in Africa (Mapulanga & Naito, 2019). Widespread deforestation has exasperated food security risks, with continuing degradation of natural habitats reducing soil fertility and increasing the risk of flooding (Republic of Malawi, 2010).

Figure 3.1. A map of Malawi, indicating the main cities and towns and its location within south-central Africa. Inset map shows the location of Malawi within Africa.

3.2 Miombo woodlands

The predominant forest cover in Malawi is miombo woodland (Gondwe *et al*. 2019). A seasonally dry tropical woodland, miombo woodlands are characterised by trees of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, and perform key ecological functions, such as carbon storage and nutrient cycling, in sub-Saharan Africa (Frost, 1996; Walker & Desanker, 2004). Miombo woodlands form an extensive range across East and Central Southern Africa, covering approximately 2.7 million km^2 (Figure 3.2) and making up 10% of the continent's vegetation cover (Ribeiro *et al*. 2012; Gondwe *et al*. 2019). Covering ten African nations, these woodlands extend from Angola in the west to Mozambique and Tanzania in the east. Miombo woodlands are considered one of the world's richest biodiversity hotspots and have been identified as one of five global wilderness areas that should be prioritised for conservation (Mittermeier *et al*. 2003). However, as human population densities increase and the demand for land conversion for agriculture intensifies, widespread deforestation of miombo woodlands continues at an extensive rate (Walker & Desanker, 2004; Bone *et al*. 2016; Gondwe *et al*. 2019). In Malawi, the annual rate of deforestation is between 1.0 - 2.8% (Republic of Malawi, 2010), with Bone *et al*. (2016) estimating that, between 1972 and 2009, 36% of the country's forest cover was lost.

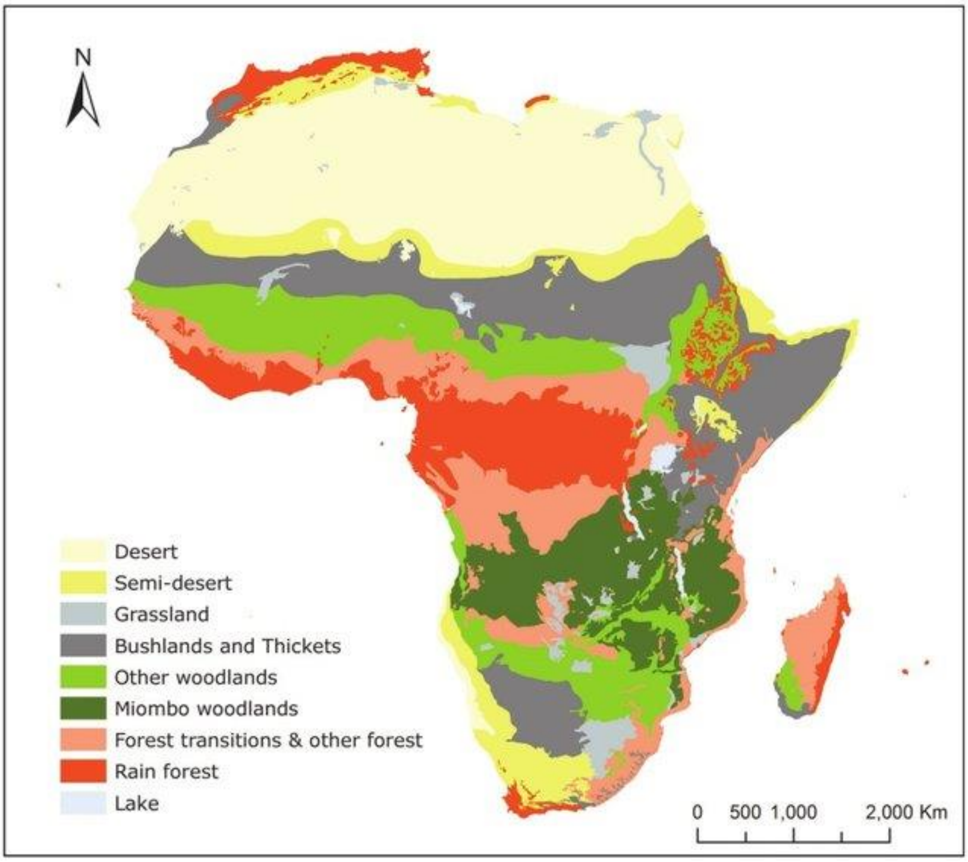

Figure 3.2. Key African vegetation zones with miombo woodlands displayed in dark green. Miombo woodland covers approximately 2.7 million km^2. (Source: Ribeiro et al. 2012).

Despite the habitat's extensive range, there is a paucity of available data on population estimates for large carnivores, and wildlife populations in general, within miombo woodlands (Frost, 1996; Caro, 1999; Balme *et al*. 2007; Hardouin *et al*. 2020; Strampelli *et al*. 2021). This is potentially due to the challenges associated with surveying miombo woodlands, with high tree density, thick canopy cover and tall seasonal grasses often making direct observation and site accessibility challenging (Caro, 1999; Kiffner *et al.* 2013; Hambrecht *et al.* 2019). In addition, the typically low biomass and density of large mammal species, compared to savanna communities, could also mean that miombo woodlands have been overlooked as a habitat of conservation importance (Frost, 1996; Waltert, Meyer & Kiffner, 2009). For example, miombo woodlands support only 20-30% of the ungulate biomass of savanna habitats with comparable rainfall (Frost, 1996). Subsequently, the lack of baseline estimates of large carnivore density in miombo woodlands makes species monitoring difficult and hampers effective conservation management.

3.3 Decline in protected area health in Malawi

There are currently 99 protected areas (PAs) in Malawi, including five national parks and four wildlife reserves, accounting for almost 23% of the terrestrial land area (World Bank Group, 2018). However, severe under-funding, combined with high rates of deforestation and increasing anthropogenic pressures caused by a growing population, have resulted in wide-scale declines in wildlife populations (Munthali & Mkanda, 2002; Lindsey *et al.* 2018; Briers-Louw *et al*. 2019; van Velden *et al*. 2020). As one of the poorest African nations, the national parks and PAs have been severely underfunded over recent decades (Munthali & Mkanda, 2002). Waterland *et al*. (2015) reported that the Department of National Parks and Wildlife Malawi (DNPW) had an annual budget of US$315,000 in 2014, approximately one-third of the department's estimated minimum funding requirement (US$1,050,000). To put this into context, Packer *et al*. (2013) estimated that a budget between US$500/year and US$2,000/year per km^2 of protected area is required to conserve large carnivores effectively. With the combined size of Malawi's five national parks being approximately 7,045km^2, a minimum budget of US$3,522,500/year would be required in the national parks alone. These financial limitations have led to a widespread shortage of resources and equipment that has restricted the ability of DNPW to maintain park security and manage wildlife populations effectively (Munthali & Mkanda, 2002). For example, it was estimated that less than 10% of Parks and Wildlife Assistants (PWAs) had access to basic patrolling equipment (i.e., boots, water bottles, weapons and ammunition), whilst access to critical resources such as vehicles and computers were limited, or items were not in a functioning state (Waterland *et al*. 2015).

This lack of infrastructure and resources has resulted in PAs being subject to high levels of poaching and habitat destruction that have resulted in population declines and localised extirpations (Abbot & Homewood, 1999; Munthali & Mkanda, 2002; Staub *et al.* 2013; Sievert *et al*. 2018). For example, black rhinoceros (*Diceros bicornis*) and cheetah were declared extinct in Malawi by the 1990s, although both have subsequently been reintroduced (Bhima & Dudley, 1996; Sievert *et al.* 2018). Malawi is also considered to be a hub for illegal wildlife crime activity, with wildlife populations inside Malawian PAs targeted for bushmeat poaching and the country used as a transit hub for neighbouring states (Waterland *et al.* 2015; van Velden *et al*. 2020). Outside PAs, the consumption and utilisation of wildlife has been unregulated by authorities, resulting in the depletion of many large mammal species, and isolating remaining populations inside PAs (Munthali & Mkanda, 2002). For instance, between 1986 and 1996, 7,083 large mammals were officially reported to have been killed in Malawi, of which 22% were illegally poached inside PAs and 78% were killed for animal control outside PAs (Munthali, 1998). In addition, arable land comprises more than 40% of the total land area of Malawi (FAO, 2013b; Figure 3.3), leaving the majority of PAs isolated and restricting animal movements and gene flow (Munthali & Mkanda, 2002).

In recent years, the situation has begun to improve in some PAs across Malawi, with growing investment from local and international conservation organisations. For example, a public-private partnership between the international non-governmental organisation African Parks (AP) and DNPW has seen AP take over management of four PAs in Malawi (Majete Wildlife Reserve, Liwonde National Park, Nkhotakota Wildlife Reserve, Mangochi Forest Reserve) and invest heavily in park security, community initiatives and the re-establishment of wildlife populations (Briers-Louw *et al.* 2019; van Velden *et al.* 2020). In addition, amendments to the National Parks and Wildlife Act in 2017, which substantially increased the penalties for wildlife crime and coincided with expanded national efforts to prevent illegal poaching, has strengthened attempts to protect PAs in Malawi. However, with only ~16% of protected land under private partnerships, and after decades of underfunding, the conservation efforts needed to restore Malawi’s PAs are sizeable.

3.4 Conservation status and threats to large carnivores in Malawi

Large carnivores have been the subject of widespread persecution in Malawi, particularly outside PAs. For example, Mésochina *et al.* (2010) reported that between 2006 and 2010 the equivalent of 20% of the Malawi lion population was eliminated by official Problematic Animal Control operations. Recent estimates have highlighted the widespread decline of lion populations in Malawi, with the nationwide population estimated at only 25 (Chardonnet, 2002) and, more recently, 34 (Mésochina *et al.* 2010) individuals. The decline in the Malawi lion population is indicative of a wider decline in large carnivore populations across the country, for which most PAs are data deficient. Consumption of illegally sourced bushmeat is common in Malawi, reaching up to almost 40% of the population, and this has a considerable impact on remaining prey bases (van Velden *et al.* 2020). As the loss of wild prey is a key driver of carnivore decline (Jacobson *et al.* 2016; Wolf & Ripple, 2016), it is likely a significant contributing factor to population losses in Malawi. Coinciding with high rates of bushmeat

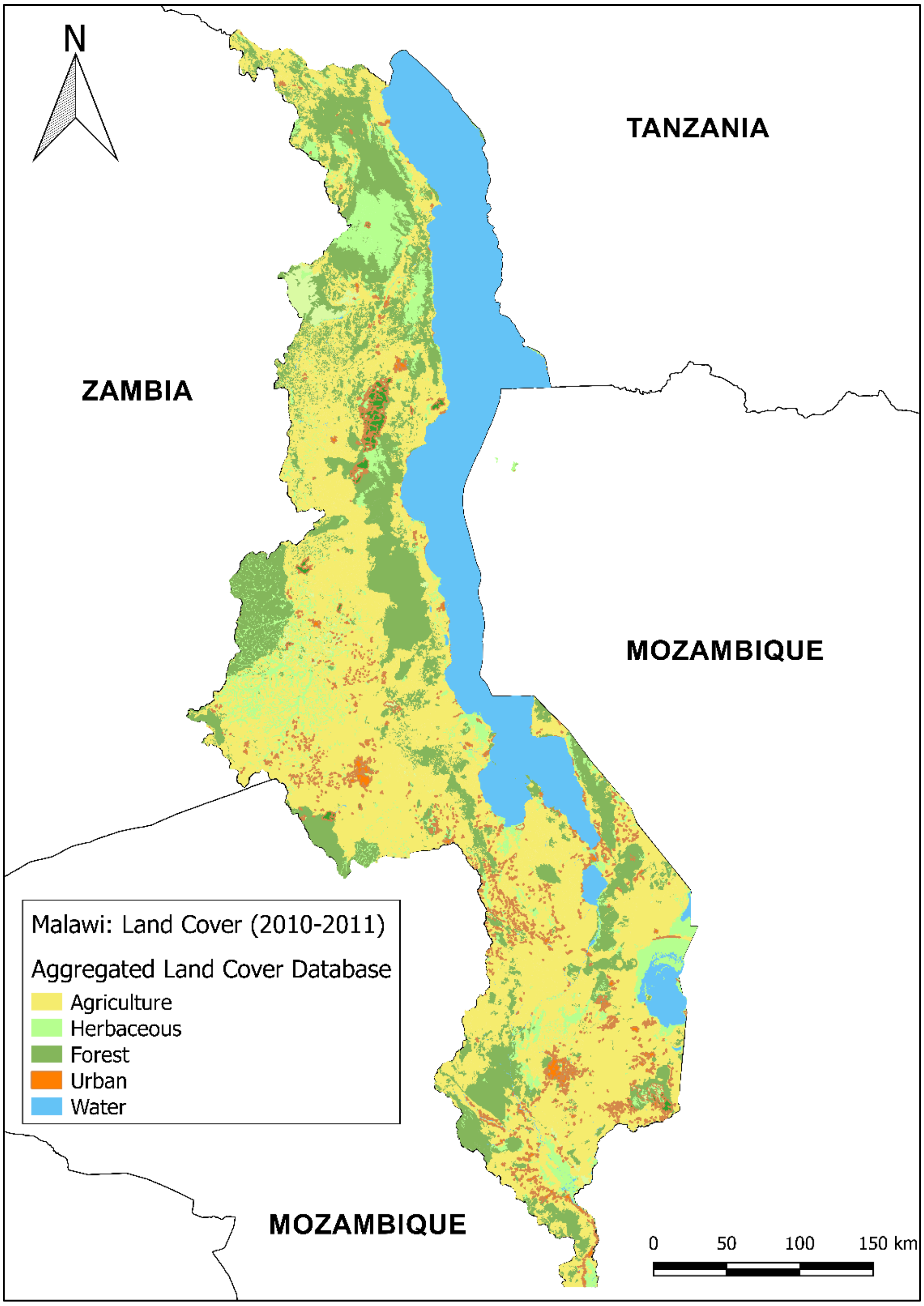

Figure 3.3. Map showing land cover in Malawi (2010-2011). Agricultural land cover is prominent outside of protected forested areas and limits habitat connectivity. (Data source: FAO, 2013b).

poaching, the use of illegal wire snares for poaching ungulate species is common in Malawian PAs (Mésochina *et al.* 2010). For example, since AP took over management of Liwonde National Park in 2015 they have removed over 40,000 snares from the park (African Parks, 2021). Wire snares have been identified as a key cause of carnivore decline across Africa (Becker *et al*. 2013; Loveridge *et al.* 2020), and anecdotal evidence suggests that they have caused similar declines in Malawi (Figure 3.4). Habitat fragmentation and human-wildlife conflict have also contributed to large carnivore decline, as high human population densities surrounding PAs, and a continuing decline in forest cover (Gondwe *et al*. 2019), means that carnivores moving outside PAs are increasingly likely to encounter conflict (for example, Figure 3.5).

Figure 3.4. An example of anecdotal evidence indicating the impact of wire snares on large carnivores in Malawi. Here a spotted hyaena in Kasungu National Park can be seen with a wire snare around its neck.

The issue of habitat fragmentation and landscape connectivity is likely exacerbated in Malawi due to the size of PAs, with only three PAs larger than 1,000km^2 (Nyika National Park, 3,200km^2; Kasungu National Park, 2,316km^2; Nkhotakota Wildlife Reserve, 1,800km^2). Indeed, the size and relative isolation of Malawian PAs has been considered a limiting factor in the recovery of cheetah and wild dog populations in Malawi (DNPW, 2011). Large carnivores have extensive range requirements (Wolf & Ripple, 2018; Noonan *et al.* 2020), with their high energetic demands often meaning they move beyond reserve boundaries and come into further conflict with humans (Woodroffe & Ginsberg, 1998; Farhadinia *et al.* 2018). Shifts in prey availability and environmental productivity can result in these ranging behaviours expanding (Loveridge *et al*. 2009) and the impact of edge effects is often amplified in smaller PAs (Balme *et al.* 2010; Noonan *et al.* 2020). This is potentially a key factor in the decline of large carnivore populations in Malawi. For example, all large carnivores, besides spotted hyaena, were believed to be extirpated from Liwonde National Park (580km^2; Sievert *et al.* 2018). Whilst it has been speculated that Nyika National Park (Malawi's largest PA) is the only area where a viable leopard population remains (Purchase *et al*. 2007; Briers-Louw *et al*. 2019).

There is, however, a paucity of empirical data on the status and population density of large carnivores in Malawi, and conservation research has received little attention (Purchase *et al.* 2007). In general, it is widely acknowledged that large carnivores have experienced significant declines across Malawi and, with the exception of spotted hyaena, remaining populations of large carnivores are thought to be restricted to PAs (Mésochina *et al.* 2010; Briers-Louw *et al.* 2019). For example, in the Lower Shire Valley, large felids (i.e., lion and leopard) were restricted to Majete Wildlife Reserve by the 1970s and were considered extirpated from the region by the 1990s (Briers-Louw *et al*. 2019). However, the extent of these declines across Malawi is difficult to determine, as neither historic nor current population estimates are widely available or are subject to anecdotal evidence. As large carnivores can act as indicator species for wider ecosystem health (Dalerum *et al.* 2008), estimating the current status of large carnivores in PAs across Malawi would be beneficial to assess ecosystem health and establish baseline estimates to evaluate the success of ongoing conservation initiatives.

Figure 3.5. A leopard killed outside KNP in 2015, highlighting the problem that large carnivores face when moving outside protected areas. The leopard was less than 2km from the Kasungu National Park boundary. Image credit: Daniel Grove.

3.5 Kasungu National Park

This study was conducted in Kasungu National Park (KNP), Malawi (central coordinates S12.9092°, E33.1689°), a 2,316km^2 legally-protected area that encompasses a large part of the Kasungu Plateau. KNP forms part of the 30,621km^2 Malawi Zambia Transfrontier Conservation Area (MZTFCA; Figure 3.6) that is of importance for biodiversity conservation in the Central Zambezian Miombo Woodland Ecoregion. The MZTFCA consists of Kasungu National Park, Nyika National Park and Vwaza Marsh Game Reserve in Malawi and Lukusuzi National Park, North Luangwa National Park and several game management areas in Zambia. KNP and Lukusuzi National Park, Zambia, form the Kasungu/Lukusuzi Transfrontier Area, allowing dispersal of wildlife species between the two parks.

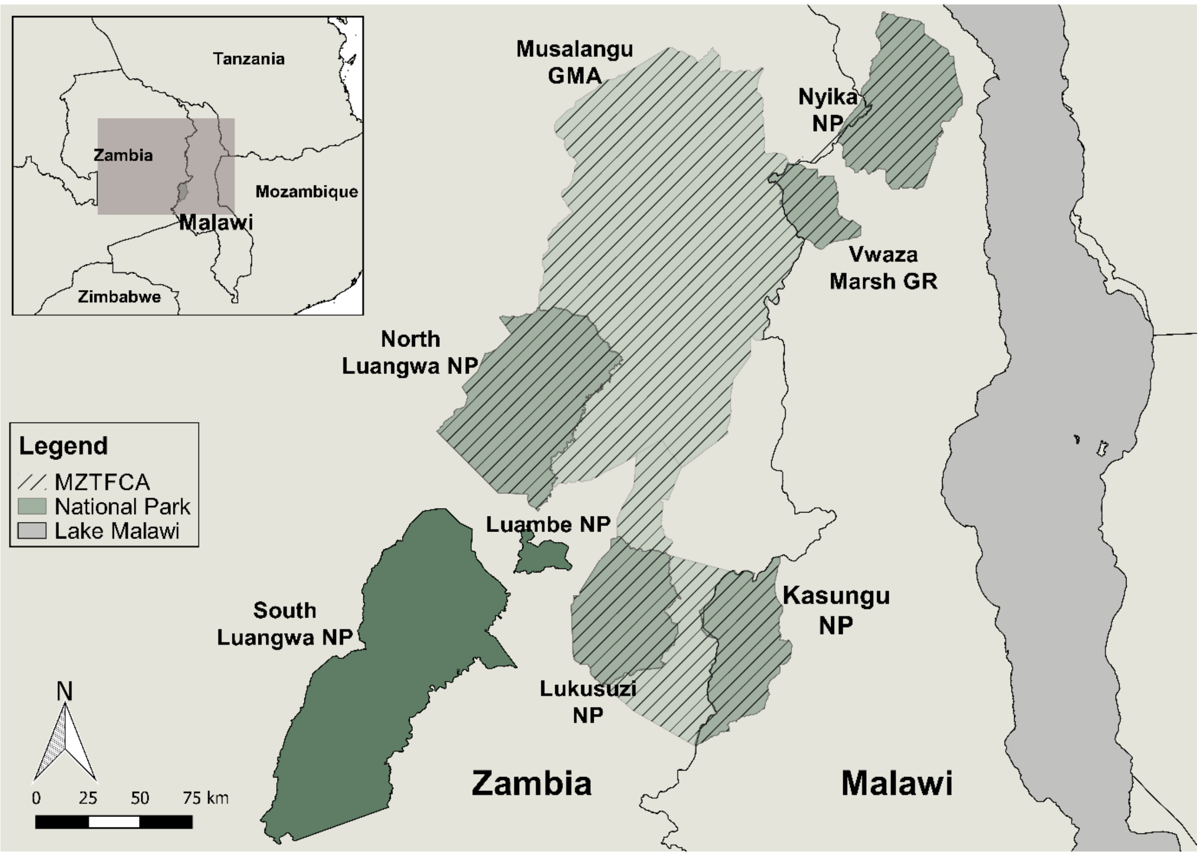

Figure 3.6. Map showing the location of Kasungu National Park and its position within the wider Malawi Zambia Transfrontier Conservation Area (MZTFCA). Inset displays the location of the MZTFCA in south-central Africa.

KNP is dominated by miombo woodland, comprising *Brachystegia* and *Julbernardia* spp. (Bhima *et al.* 2003). Three main rivers flow through the park (Dwangwa, Lingadzi and Liziwazi) that form an extensive river network and drainage system that intersperses closed canopy miombo woodland with seasonally wet grassland areas and isolated rocky inselbergs. The altitude ranges between 1,000m and 1,500m, and the mean annual rainfall is 780mm, with most rainfall occurring during the wet season between October and April (Bhima *et al.* 2003). KNP is largely unfenced, with the only erected fencing in the south-east of the park in a state of disrepair and bordered by unprotected land in both Malawi and Zambia. The area surrounding KNP consists of subsistence farming, charcoal burning and tobacco production, which is beginning to encroach into the protected area along park boundaries (Bhima *et al.* 2003). No human settlements, besides national park authorities (operating from ten ranger camps inside the park), are permanently based in KNP and trophy hunting is not permitted in the park.

Like other Malawian PAs, KNP has suffered from a lack of funding and resources that has resulted in high rates of poaching and a subsequent decline in wildlife populations (Munthali & Mkanda, 2002). A review of illegal wildlife crime in Malawi by Waterland *et al.* (2015) highlighted this lack of infrastructure, with only 46 PWAs deployed in KNP in 2014, tasked with covering an area of 2,316km^2. This critical lack of on-the-ground presence has made historic law enforcement in KNP ineffective, with poachers able to target areas where patrols are unable to cover regularly (Waterland *et al.* 2015). The negative consequences of limited infrastructure and resources are exemplified by the decline in the KNP elephant (*Loxodonta africana*) population which, during the last aerial survey in 2014, was estimated to be just 46 individuals (Macpherson, 2015). This is a decline of over 94% in just over two decades, with 800 individuals estimated in 1993 (Bell *et al.* 1993; Bhima *et al.* 2003). The situation in KNP has been improved in recent years with the assistance of the International Fund for Animal

Welfare (IFAW), who have increased PWA numbers, provided PWA training, improved park fencing and increased financial and logistical support (IFAW, 2021).

Historically, the large carnivore guild (lion, leopard, spotted hyaena, wild dog and cheetah) were known to be present in KNP (Nowell & Jackson, 1996; Woodroffe *et al*. 1997; Mills & Hofer, 1998 De Garine-Wichatitsky *et al.* 2001). However, it is believed that large carnivore populations have generally declined in KNP over recent decades. The lion population in KNP was estimated to be 40 individuals in the late 1980s (Morris, 2006 in Mésochina *et al*. 2010) but has undergone a significant decline, with a review by Mésochina *et al.* (2010) estimating a population of just 6 lions in the park. However, this estimate was based on anecdotal evidence from questionnaire surveys. Between 2006 and 2010, PWAs only reported seeing lion a maximum of once a year in KNP (Mésochina *et al*. 2010). Both Purchase *et al*. (2007) and Mésochina *et al*. (2010) hypothesised that lion presence in KNP was likely restricted to transient individuals from the Luangwa Valley, although information on lion movements is lacking for the region. Cheetah were known to be present in KNP until the late 1980s, with KNP representing the last remaining cheetah population in Malawi (DNPW, 2011). This population has since been declared extirpated, with no cheetah observed in KNP for over twenty years (DNPW, 2011; Durant *et al*. 2015). It is believed that wild dogs are still present in KNP, with an estimated population of 14 individuals (Woodroffe & Sillero-Zubiri, 2020). This population has fluctuated over recent years, as noted by Woodroffe *et al.* (1997), but at least one pack was observed in 2011 and seen in subsequent years, with the population considered transient across the MZTFCA (DNPW, 2011). Spotted hyaena and leopard are both known to be present in KNP, although information on population estimates and trends is lacking (Bohm & Höner, 2015; Jacobson *et al*. 2016). Purchase *et al*. (2007) stated that leopard populations appeared to be declining across other PAs in Malawi, including their extirpation from three PAs in the southern region, and that their status in KNP was unknown.

Large herbivores have also experienced significant declines, with widespread poaching in the early 2000s resulting in remaining populations of several large mammal species (e.g., zebra *Equus quagga*, eland *Taurotragus oryx* and buffalo *Syncerus caffer*) being translocated to Liwonde National Park, Malawi, as their safety could not be guaranteed in KNP (Munthali & Mkanda, 2002). Munthali & Mkanda (2002) raised concerns that by removing animals from already small populations there was a significant chance of inbreeding depression and further decline in large mammal populations in KNP. Aerial surveys conducted in 2014 add further evidence that large mammal populations are still significantly reduced in KNP, with reduced total counts of all species assessed since the previous survey (Macpherson, 2015). Whilst robust data on population estimates for large mammals are lacking for KNP, the decline in prey abundance has been considered a key limiting factor, preventing the recovery or reintroduction of large carnivore populations in the park (Mésochina *et al*. 2010; DNPW, 2011).

The perceived decline in large carnivore populations in KNP, combined with the loss of natural prey and the general decline in protected area health, means assessing the status of remaining large carnivores in KNP should be a conservation priority for Malawi. As the second largest protected area in Malawi, and with wider connectivity to the MZTFCA, KNP is an important site for large carnivore conservation in the region. In addition, data gathered in KNP may be representative of wider species decline across Malawi, with most Malawian PAs under similar environmental pressures and miombo woodland the primary habitat across the country. Data from KNP can, therefore, act as a baseline for monitoring carnivore populations and wider ecosystem health in KNP, whilst also providing metrics that can be used in comparison to assess the status of other PAs across Malawi.

Localised extirpation of lion populations is expected to increase over the coming decades, with the species predicted to survive in only the largest PAs across Africa and in small, intensively managed, fenced reserves (Bauer *et al*. 2015). Subsequently, the localised loss of the lion population in KNP could offer a novel opportunity to test theories on guild dynamics and interspecific competition between remaining competitors (notably leopard and spotted hyaena). Alongside the broader socio-ecological issues of high human population density, habitat loss and declining prey populations, the issues facing KNP and Malawi are indicative of wider issues across Africa. Therefore, KNP could offer insights into how species respond to anthropogenic disturbance and alterations to the carnivore guild, whilst informing predictions for conservation management under increasing levels of environmental change.

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CHAPTER FOUR

Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland

CHAPTER FOUR: Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland

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Abstract

Decline in global carnivore populations has led to increased demand for assessment of carnivore densities in understudied habitats. Spatial capture-recapture (SCR) is used increasingly to estimate species densities, where individuals are often identified from their unique pelage patterns. However, uncertainty in bilateral individual identification can lead to the omission of capture data and reduce the precision of results. The recent development of the two-flank spatial partial identity model (*SPIM*), offers a cost-effective approach which can reduce uncertainty in individual identity assignment and provide robust density estimates. We conducted camera trap surveys annually between 2016 and 2018 in Kasungu National Park, Malawi, a primary miombo woodland and a habitat lacking baseline data on carnivore densities. We used *SPIM* to estimate density for leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*) and compared estimates with conventional SCR methods. Density estimates were low across survey years, when compared to estimates from sub-Saharan Africa, for both leopard (1.9 ± 0.19 SD adults/100km^2) and spotted hyaena (1.15 ± 0.42 SD adults/100km^2). Estimates from *SPIM* improved precision compared to analytical alternatives. Lion (*Panthera leo*) and wild dog (*Lycaon pictus*) were absent from the 2016 survey, but lone dispersers were recorded in 2017 and 2018, and both species appear limited to transient individuals from within the wider transfrontier conservation area. Low densities may reflect low carrying capacity in miombo woodlands or be a result of reduced prey availability from intensive poaching. We provide the first leopard density estimates from Malawi and a miombo woodland habitat, whilst demonstrating that *SPIM* is beneficial for density estimation in surveys where only one camera trap per location is deployed. The low density of large carnivores requires urgent management to reduce the loss of the carnivore guild in Kasungu National Park and across the wider transfrontier landscape.

4.1 Introduction

Density estimation is an important tool for monitoring wildlife populations, which is critical for effective conservation management (Sollmann *et al*. 2011; Balme *et al.* 2019). Despite the ecological, economic and social importance of carnivores, basic data on population density and distribution are lacking across large areas of their geographic range (Ripple *et al.* 2014; Bauer *et al*. 2015; Jacobson *et al.* 2016). This is particularly true in Africa, despite well-reported declines across the continent (Ripple *et al*. 2014; Di Minin *et al*. 2016; Wolf & Ripple, 2016). With increasing anthropogenic pressures, rising human populations and high rates of poaching, the need for rapid status assessments in understudied areas is critical for carnivore conservation management and identification of species at high risk of decline (Jacobson *et al*. 2016; Rosenblatt *et al*. 2016; Elliot & Gopalaswamy, 2017).

Obtaining robust density estimates for carnivores which are cryptic, wide-ranging and often solitary, is challenging (Balme *et al*. 2009a; Sollmann *et al*. 2011). Various techniques have been employed to estimate carnivore abundance and density, each with their own limitations (Balme *et al*. 2014; Midlane *et al.* 2015; Rogan *et al*. 2019). In recent years, density estimates derived from camera trapping, e.g., using capture–recapture modelling, have become increasingly important in wildlife ecology and species management (Royle *et al*. 2014; Rovero & Zimmerman, 2016). The development of spatial capture-recapture (SCR) models, incorporating the spatial location of captures and an explicit model of individual distribution across space, has resolved initial problems with capture-recapture modelling and allows more robust and accurate density estimation (Efford, 2004; Royle *et al*. 2009; Sollmann *et al*. 2011).

Whilst SCR methods are among the most robust methods for density estimation, the fundamental requirement for all captured individuals to be identified with certainty is not always achievable (Link *et al*. 2010; Augustine *et al*. 2018; Augustine *et al*. 2019; Johansson *et al*. 2020). For example, when camera trap arrays are used to survey individually identifiable animals, common practice is to deploy two camera traps at each sampling location, ensuring both sides of the animal are photographed for bilateral identification (Henschel & Ray, 2003). However, in situations where field conditions are limited by circumstances, such as topography, financial resources, malfunctioning equipment or poor image quality, photographs of only one side may be available (Wang & Macdonald, 2009; McClintock *et al*. 2013; Alonso *et al*. 2015; Augustine *et al.* 2018). This leads to partial identification of some, or all, of the study population (Foster & Harmsen, 2012; McClintock *et al*. 2013). In these circumstances, researchers are often forced to omit data from analyses (e.g., Wang & Macdonald, 2009; Alonso *et al*. 2015; Rosenblatt *et al.* 2016; Strampelli *et al*. 2020; Mohamed *et al.* 2021), leading to the loss of valuable recapture data, and, potentially, introducing significant bias (Madon *et al*. 2011; Augustine *et al*. 2018).

The recent development of spatial partial identity models (SPIMs; Augustine *et al*. 2018) offers an analytical alternative to conventional SCR for partially identified datasets, allowing the use of a larger proportion of recaptures, whilst reducing the negative bias associated with individual heterogeneity in capture probability (Augustine *et al*. 2018; Augustine *et al*. 2019). SPIMs use a Markov Chain Monte Carlo (MCMC) algorithm to reconstruct the true capture histories probabilistically, like previously developed partial identity models (McClintock *et al.* 2013). These partial identity models differ, however, as SPIMs incorporate the spatial location of individual captures to associate latent samples probabilistically, thereby reducing uncertainty in identity assignment (Augustine *et al.* 2018; Augustine *et al.* 2019). As uncertainty regarding partial identity samples is reduced, this allows for better estimation of density and movement parameters that are key to the SCR framework. Like conventional SCR methods, further variables including age, sex and morphological differences, can be incorporated into SPIMs to resolve partial identities further and improve precision (Augustine *et al*. 2019).

Miombo woodland is the dominant vegetation type across south-central Africa, totalling 2.7 million km^2 (Frost, 1996), yet baseline data on carnivore densities are lacking for this habitat type (Balme *et al*. 2007; Stein *et al.* 2016), and as a result species management may be ineffective. Malawi is predominantly covered by miombo woodland but is lacking robust assessments of large carnivore density which, consequently, hampers effective species management that could be used as an exemplar for other countries across south-central Africa. Malawi is experiencing some of the highest rates of environmental degradation, climate change and deforestation in Africa, due to high population density (Stevens & Madani, 2016) and increasing population growth (United Nations, 2019). Therefore, the paucity of carnivore density estimates within miombo woodlands, combined with increasing anthropogenic impacts, makes assessment of large carnivore populations in Malawi a conservation priority for effective species management in the region.

In this study we estimate large carnivore density in Kasungu National Park (KNP), Malawi, using a spatial partial identity model in a spatial capture-recapture framework. KNP comprises miombo woodland that has been impacted by high rates of anthropogenic pressures, including poaching, which has severely reduced numbers of natural prey (Munthali & Mkanda, 2002; Bhima *et al*. 2003). The study presents the first robust estimate of leopard (*Panthera pardus*) density in a miombo woodland, alongside spotted hyaena (*Crocuta crocuta*, hereafter hyaena) density, and highlights the status of other large carnivore populations in this regionally important protected area. We discuss the implications of our findings for the management of carnivores in KNP, the potential for wider inference across miombo woodlands and the application of SPIMs for camera trap surveys.

4.2 Materials and Methods

4.2.1 Study area

The study was conducted in KNP, Malawi (central coordinates S12.9092°, E33.1689°; Figure 4.1), a 2,316km^2 legally protected area that encompasses a large part of the Kasungu Plateau. KNP is largely unfenced, with the only erected fencing in the south-east of the park in a state of disrepair and bordered by unprotected land in both Malawi and Zambia. KNP forms part of the 30,621km^2 Malawi Zambia Transfrontier Conservation Area (MZTFCA), that is of importance for biodiversity conservation in the Central Zambezian Miombo Woodland Ecoregion. KNP and Lukusuzi National Park, Zambia, form the Kasungu/Lukusuzi Transfrontier Area allowing dispersal of wildlife species between the two parks.

KNP is dominated by miombo woodland, comprising *Brachystegia* and *Julbernardia* spp. (Bhima *et al.* 2003). Three main rivers flow through the park (Dwangwa, Lingadzi and Liziwazi) that form an extensive river network and drainage system that intersperses closed canopy miombo woodland with seasonally wet grassland areas and isolated rocky inselbergs. The altitude ranges between 1,000m and 1,500m and mean annual rainfall is 780mm, with most rainfall occurring during the wet season between November and April (Bhima *et al*. 2003). The area surrounding KNP consists of subsistence farming, charcoal burning and tobacco production, which is beginning to encroach into the protected area along park boundaries (Bhima *et al.* 2003). No human settlements, besides national park authorities (operating from ten ranger camps inside the park), are permanently based in KNP and trophy hunting is not permitted in the park.

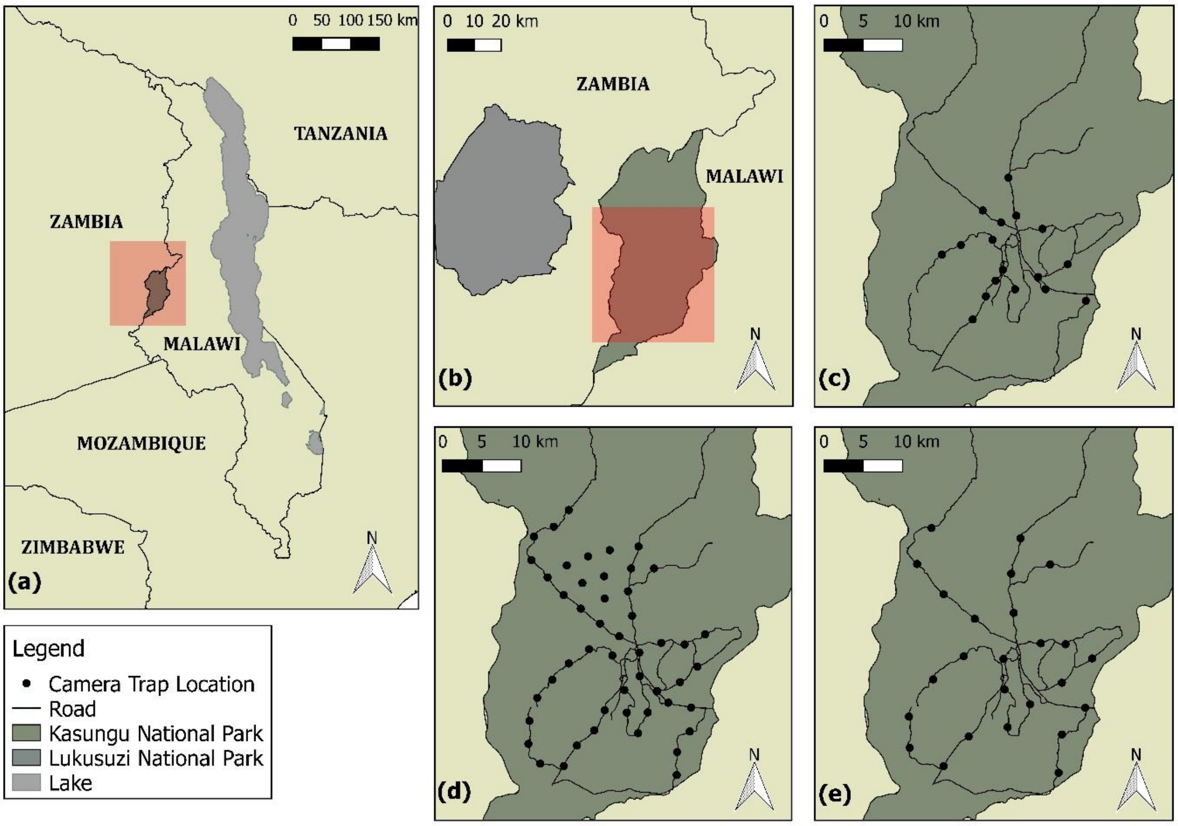

Figure 4.1. Map showing (a) the location of Kasungu National Park (KNP) within Malawi and (b) the location of KNP with reference to Lukusuzi National Park, Zambia, and an overview of the area covered for camera trap surveys represented in; (c) camera trap locations for the 2016 survey, (d) camera trap locations for the 2017 survey and (e) camera trap locations for the 2018 survey.

Historically, large carnivores (lion (*Panthera leo*), leopard, hyaena, wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*)) were known to be present in KNP (Nowell & Jackson, 1996; Woodroffe *et al*. 1997; Mills & Hofer, 1998). However, all have experienced declines in the past three decades, with cheetah declared extirpated (Durant *et al*. 2015) and an estimated fourteen wild dogs (Woodroffe & Sillero-Zubiri, 2020) and five lions (Mésochina *et al*. 2010) reported from anecdotal accounts and questionnaire surveys. African elephants (*Loxodonta africana*) declined from approximately 2,000 individuals in 1977 to 117 individuals in 2003, due to poaching (Bhima *et al*. 2003). Black rhinoceros (*Diceros bicornis*) were declared extinct in KNP in 1985 (Bhima & Dudley, 1996) and all other large herbivores present in the park are believed to have suffered population reductions, due to illegal hunting, though data are lacking (Munthali & Mkanda, 2002; Bhima *et al*. 2003).

4.2.2 Camera trapping

Camera trap surveys were undertaken during the dry season (May to October) in 2016, 2017 and 2018. Surveys were not completed during the wet season due to limited road access and tall grass causing multiple false triggers. A combination of motion-activated white flash camera traps (Cuddeback Models C and F; Cuddeback Inc., Wisconsin, USA) and infrared cameras (Bushnell Trophy Cam HD; Bushnell Corporation, Kansas, USA), were used during all surveys. Infrared cameras were partly used in 2016 and 2017, due to limited numbers of white flash cameras being available. All cameras used in 2018 were white flash. One camera trap was used at each sampling location to maximise the area surveyed with the limited numbers of cameras available, with 17, 50 and 25 trapping locations used per year, respectively (Fig. 1).

Each trapping location was surveyed for 90 days in 2016 and 2018. In 2017, cameras were deployed at locations for 60 days then redeployed in new locations for a further 60 days, totalling 120 days of survey. These were considered adequate survey lengths for assuming demographic closure and to ensure suitable numbers of photographic captures for large carnivores (Royle *et al*. 2014; Dupont *et al*. 2019).

We used a maximum camera spacing of 3-5km (Devens *et al*. 2018; Strampelli *et al*. 2020) to select camera locations prior to deployment, with placement focused on the KNP road network. No home range estimates are available for large carnivores in KNP, but a maximum spacing of 5km ensured that there were no gaps in the array large enough to encompass an average adult female leopard home range (30km^2; Braczkowski *et al*. 2016). As female leopard home ranges are smaller than those of male leopards and hyaena, this spacing was considered adequate for both species. We focused placement on roads in KNP, as carnivores are known to utilise road networks (Swanepoel *et al.* 2015; Braczkowski *et al*. 2016) and previous pilot data showed capture success was greater on roads than random placement. Final camera positions were selected as close to the pre-determined points as possible and chosen based on evidence of carnivore presence or in suitable habitat to maximise the probability of photographic captures (Henschel & Ray, 2003). Although the trap array size and camera locations differed each year, due to logistical reasons, SCR models are generally considered more robust to these changes than conventional capture-recapture models (Sollmann *et al*. 2011; Braczkowski *et al.* 2016). Cameras were mounted on trees approximately 40-60cm above the ground and two metres from the road or game trail and operated continuously, with one image taken per trigger, and the minimum delay possible for each model. Each camera trap was visited every 10-14 days to download images, check batteries and ensure all cameras remained operational, in accordance with standard camera trap survey procedures (Henschel & Ray, 2003).

4.2.3 Density estimation and statistical analyses

Individual leopard and hyaena were identified from photographs using their unique pelage patterns (Henschel & Ray, 2003). A database was maintained of identified individuals, with partial (single-flank) or complete (two-flank) identities, to build capture histories for SCR analysis. We initially identified individuals from left flank captures for both species, due to higher numbers of identified left flank individuals recorded during preliminary surveys. Complete identities were added where flanks were certain to come from the same individual (from baited stations outside of survey time, live captures, dual camera trap stations and multiple passes of a single camera trap). Leopards were sexed by visual determination of external genitalia, presence of the dewlap, frontal bossing and overall body size (Henschel & Ray, 2003; Devens *et al*. 2018). Any dependent cubs (determined by body size and/or simultaneous capture with an adult female) were excluded from analyses, due to their inclusion leading to inflated density estimates and violating independent capture probabilities (Balme *et al*. 2019). Sexing was not possible for hyaena due to difficulties in determining sex from external genitalia and body size. Capture histories were developed for spatial captures and trap effort, with each day (24 hours) treated as a separate sampling occasion (Goldberg *et al*. 2015). Trap effort was measured through a binary matrix of active-inactive days, to improve estimates of detection probability, and included the spatial location of each camera station.

Density was modelled using the package *SPIM* (Augustine, 2018) in R v.3.5.2 (R Development Core Team, 2018), to resolve the complete identity of individuals from single-flank samples probabilistically (see Augustine *et al*. 2018 for complete description of spatial partial identity model). A Bernoulli observation model was fitted and, for MCMC simulations, a single chain of 50,000 iterations per single session analysis was undertaken, with a burn-in of 1,000 iterations and data augmentation of 100-130 individuals for leopard and 125-250 for spotted hyaena. Analyses were conducted with an increasing buffer width from 10,000 to 25,000 metres (leopard) and 10,000 to 40,000 metres (hyaena), using 5,000 metre increments, until density estimates stabilised (Chase-Grey *et al*. 2013; Devens *et al*. 2018). Point estimates were calculated using the posterior mode and 95% intervals estimated using the highest posterior density interval. Model convergence of MCMC samples was assessed by examining trace plots and histograms for each parameter. Simulations were undertaken separately for each species and survey year, instead of incorporating a multi-session model, as this process is not currently implemented in the *SPIM* package.

For comparison with *SPIM*, density estimates were modelled using the Bayesian package *SPACECAP* v1.1.0 (Gopalaswamy *et al.* 2012) in R v.3.5.2. Common practice with partial identities is to use the flank with the greater number of captures for density estimates (e.g., Rosenblatt *et al*. 2016: Strampelli *et al*. 2020), therefore, we developed single-flank capture histories for each year and species using the flank with the higher number of identifiable photos.

In addition, we modelled the capture histories where both flanks were known with certainty for each species and included, separately, the partial left and right flank images, for which we did not have complete identities. We then averaged the two, both-side plus partial sample models to attain mean density estimates for each species and year. We then compared the single-side and averaged both-side density estimates against the *SPIM* output and measured the 95% credible interval width to assess any gain in precision from using *SPIM*. Wherever possible, we kept MCMC settings as close to simulations in *SPIM* as possible, to aid comparison, and fitted a half-normal detection function, the trap response function and Bernoulli's encounter model. We used a 1km^2 pixel area to represent potential home range centres. Chain convergence was assessed using the Geweke diagnostic test, where z-scores between -1.6 and 1.6 imply convergence was achieved. Model fit was also determined from Bayesian p-values provided in the *SPACECAP* output, with p-values close to 0.05 and 1 suggesting inadequate fit.

4.3 Results

4.3.1 Camera trap surveys

A total of 17, 50 and 25 cameras were deployed in KNP during 2016, 2017 and 2018, respectively, at 92 locations across the three years (Table 4.1). Total sampling effort was 5,990 trap nights with an average camera trap spacing of 3.35km (±0.94 SD) across all survey periods.

Camera trap surveys yielded 274 leopard captures with an average of 91 (±37.54 SD) per year, ranging from 48 in 2016 to 114 in 2018. Using unique pelage patterns, 40 individual leopards (29 females, 8 males, 3 unsexed) were identified in KNP over the three survey years from left flank spot patterns (Table 4.2), of which 17 were complete identities (where both left and right flank were certified from the same individual). A further 14 leopards (all female), for which right side flank information could not be linked to a left side flank, were included in the analyses to be resolved by the two-flank *SPIM* model. In addition, five dependent cubs, from four different females, were captured across survey years and were excluded from the analyses.

Surveys yielded a total of 346 hyaena captures, with an average of 115 (±44.56 SD) per year, ranging from 64 in 2016 to 144 in 2017. Thirty-three individual hyaena were identified during the survey period from their left flank spot patterns, of which 19 were complete identities where both flanks were known. Seventeen unresolved right flank identities were also included in the analyses to be resolved by the two-flank *SPIM* models.

Table 4.1. Summary of camera trap sampling effort between 2016-2018 in Kasungu National Park, Malawi. Survey duration is the time-period of the survey, with date showing the months surveyed in each year. The number of camera trap stations, total trap nights (calculated as the total number of nights camera traps were effectively working during the survey), mean and standard deviation of trap nights per camera and average camera trap spacing (km) is also given per survey year.

Sample year	Survey duration (days)	Date	Camera trap stations	Total trap nights	Mean trap nights per camera (± SD)	Average camera spacing (± SD)
2016	90	May - August	17	1283	73 ± 16.85	2.83 ± 1.08
2017	120	June - October	50	2630	52.6 ± 11.99	2.78 ± 0.31
2018	90	June - September	25	2077	83.1 ± 15.41	4.43 ± 0.59

Table 4.2. Capture success rates for leopard and spotted hyaena across three years of camera trap surveys in Kasungu National Park, Malawi. Number of identified individuals for each year includes individuals identified in previous years but excludes right-flank individuals that could not be linked to already known individuals. Capture rate is defined as the total number of captures, divided by trap nights and multiplied by 100.

Sample Year	Total leopard captures	No. of identified leopards	Leopard capture rate (%)	Total hyaena captures	No. of identified hyaenas	Hyaena capture rate (%)
2016	48	9	3.7	64	13	5
2017	112	18	4.2	144	18	5.4
2018	114	23	5.5	138	25	6.6

4.3.2 Density estimation

Using *SPIM* the highest leopard density estimate for KNP was 2.11 adults/100km^2 in 2016 (Table 4.3), with an overall mean density estimate (derived from individual estimates from each survey year) of 1.9 (±0.19 SD) adults/100km^2 (95% CI = 1.48 – 2.92/100km^2). Density estimates from *SPIM* increased credible interval precision by 48, 40 and 68%, respectively, compared to the single-flank analyses. Credible intervals from *SPIM* also outperformed the averaged two-flank density estimates by 9% in 2018 and 35% in both 2017 and 2016, respectively. The average value of σ (the spatial scale parameter that determines the rate at which detection probability decreases with distance between an activity centre and a trap) was 3,447 (±684 SD) metres. Buffer width stabilised at 15,000m for each survey year and the average state space was 2,361 km^2 (±571 SD). Diagnostic statistics and trace plots suggested model fit and convergence was achieved in all models run in *SPIM* and *SPACECAP* (Table S1).

The highest density estimate for spotted hyaena in KNP was 1.62 adults/100km^2 in 2018 (Table 4.4), with an overall mean density estimate of 1.15 (±0.42 SD) adults/100km^2 (95% CI = 0.72 – 1.82/100km^2). The single-flank and both-flank plus partial identity models for 2016 did not converge in *SPACECAP* and were excluded from the model list. Density estimates obtained in *SPIM* increased credible interval precision by 27 and 25%, respectively, in comparison to the single-flank models. Estimates from *SPIM* and the averaged two-flank models produced similar results and levels of precision in 2018 and 2017. The spatial scale parameter, σ, was larger for hyaena than leopard, with an average value of 5,768 (±586 SD) metres. Buffer width stabilised at 20,000m in 2017 and 2018 and 40,000m in 2016. Average state space size was 4,952km^2 (±2134 SD). Diagnostic statistics and trace plots suggested model fit and convergence was sufficient for all other models run in *SPIM* and *SPACECAP* (Appendix III).

Table 4.3. Posterior summaries of model parameters for leopards in Kasungu National Park from the spatial partial identity model (SPIM) compared with the single-flank model with the higher number of captures (Single) and the mean estimate from the both plus partial left side (B+L) and both plus partial right side (B+R) data sets.

Year	Model	D ± SD (95% CI)	(D) CI width	σ ± SD	λ_0 ± SD
2018	SPIM	1.77 ± 0.30 (1.35 – 2.54)	1.19	3954 ± 343	0.012 ± 0.002
	Mean (B+L, B+R)	2.22 ± 0.36 (1.65 – 2.86)	1.31	5195 ± 621	0.010 ± 0.003
	Single	2.65 ± 0.63 (1.65 – 3.94)	2.29	4628 ± 888	0.006 ± 0.003
2017	SPIM	1.81 ± 0.33 (1.21 – 2.50)	1.29	3718 ± 340	0.010 ± 0.002
	Mean (B+L, B+R)	2.09 ± 0.42 (0.90 – 2.87)	1.97	4910 ± 729	0.006 ± 0.003
	Single	2.21 ± 0.61 (1.20 – 3.35)	2.15	3741 ± 708	0.008 ± 0.004
2016	SPIM	2.11 ± 0.79 (1.87 – 3.71)	1.84	2669 ± 554	0.009 ± 0.003
	Mean (B+L, B+R)	1.80 ± 1.15 (0.72 – 3.54)	2.82	5115 ± 1806	0.006 ± 0.005
	Single	3.38 ± 1.71 (0.86 – 6.68)	5.82	4127 ± 2670	0.006 ± 0.004

D is the density per 100 km^2 with standard deviation (±SD) and 95% credible intervals (95% CI); σ is the detection function spatial scale parameter; and λ_0 is the detection function baseline encounter rate. The width of credible intervals for D is measured to assess any gain in precision from using SPIM.

Table 4.4. Posterior summaries of model parameters for spotted hyaena in Kasungu National Park from the spatial partial identity model (SPIM) compared with the single-flank model with the higher number of captures (Single) and the mean estimate from the both plus partial left side (B+L) and both plus partial right side (B+R) data sets.

Year	Model	*D* ± SD (95% CI)	(*D*) CI width	σ ± SD	λ_0 ± SD
2018	SPIM	1.62 ± 0.27 (1.17 – 2.26)	1.09	5192 ± 391	0.011 ± 0.002
	Mean (B+L, B+R)	2.15 ± 0.31 (1.67 – 2.78)	1.11	5971 ± 546	0.013 ± 0.003
	Single	2.40 ± 0.41 (1.66 – 3.16)	1.5	5560 ± 791	0.007 ± 0.002
2017	SPIM	1.01 ± 0.24 (0.61 – 1.47)	0.86	5749 ± 687	0.006 ± 0.001
	Mean (B+L, B+R)	1.29 ± 0.24 (0.93 – 1.75)	0.82	7989 ± 1441	0.005 ± 0.001
	Single	1.43 ± 0.32 (0.93 – 2.07)	1.14	6999 ± 1722	0.005 ± 0.002
2016	SPIM	0.81 ± 0.44 (0.38 – 1.74)	1.36	6364 ± 2653	0.007 ± 0.004

D is the density per 100 km^2 with standard deviation (±SD) and 95% credible intervals (95% CI); σ is the detection function spatial scale parameter; and λ_0 is the detection function baseline encounter rate. The width of credible intervals for D is measured to assess any gain in precision from using SPIM.

4.3.3 Capture rates for other large carnivores

Other large carnivores were rarely encountered during surveys. Cheetah were not recorded in any survey year. In 2017 one male lion and one male wild dog were recorded. The lion (likely the same individual from diagnostic features) was recorded on 11 sampling occasions at 8 camera locations, whilst the wild dog was captured at 7 camera locations on 9 sampling occasions. Through unique pelage patterns it was confirmed that all images were of the same individual wild dog. In 2018 the same individual wild dog was recorded on 9 sampling occasions at 6 camera locations. Lion presence was not recorded during the 2018 survey.

4.4 Discussion

4.4.1 Leopard density

The spatial partial identity model produced the first successful density estimates for a leopard population in Malawi and for a primary miombo woodland habitat. We estimated a mean density of 1.9 (±0.19 SD) adults/100km^2 in KNP, with minor variation between the three years suggesting a stable trend in leopard density. Prior to this study, there were no estimates of leopard density from a primary miombo woodland habitat, with the only published estimate from a mosaic of five habitats where a single area of miombo woodland was surrounded by Afromontane forest and Afrotropical rainforest (Havmøller *et al*. 2019). Our estimates indicate leopard density in KNP is low, in comparison to studies from elsewhere in sub-Saharan Africa, and comparable to leopard densities in human-impacted areas (e.g., 2.49 leopards/100km^2, Balme *et al.* 2010; 2.7 leopards/100km^2, Henschel *et al*. 2011; 1.18 leopards/100km^2, Devens *et al*. 2021) and more arid environments (e.g., 1.5 leopards/100km^2, Stander *et al.* 1997; 1.0 leopards/100km^2, Stein *et al*. 2011; 1.2 leopards/100km^2, Edwards *et al*. 2016).

The majority of Malawian protected areas (PAs) are under similar environmental pressures to KNP, with bushmeat poaching and habitat loss prevalent (van Velden *et al*. 2020) and miombo woodland the predominant forest cover (Gondwe *et al.* 2019). Our leopard density estimate for KNP can, therefore, be used as a baseline for PAs in Malawi. However, we encourage further survey efforts to understand the Malawi leopard population status and trends, which has received little conservation attention to date. The Malawi leopard population is thought to be largely restricted to PAs and reintroduction efforts have already been needed to restore leopard populations in Majete Wildlife Reserve (Briers-Louw *et al*. 2019). As one of only three PAs in Malawi that is over 1,000km^2 in size, KNP likely represents one of the few areas where a viable leopard population can persist in Malawi at these low densities. Therefore, the KNP leopard population requires active conservation management to understand and mitigate threats and increase population numbers.

Despite wide habitat tolerance and resilience to anthropogenic threats, habitat specialisation is likely to translate to important differences in leopard population density across landscapes (Balme *et al*. 2007). Miombo woodlands are regarded as relatively poor habitats for large mammals, with low biomass density and nutrient-poor soils, and this may reflect naturally low leopard densities (Frost, 1996; Waltert, Meyer & Kiffner, 2009). The potential for naturally low densities in miombo woodlands is likely further exacerbated in KNP by the decline in prey populations, a factor that has been identified as a key driver of leopard population decline (Henschel *et al.* 2011; Jacobson *et al*. 2016). However, as our results are from a single survey area, it is difficult to make inferences about the optimality of KNP and other miombo woodlands for leopard populations. Other regions, such as the miombo woodlands of southern Tanzania, where the size of protected areas is greater and substantial populations of large carnivores are known to be present (Abade *et al*. 2018; Havmøller *et al*. 2019), may hold higher densities of leopard and further surveys in these regions would allow for greater understanding of the importance and potential of miombo woodlands for leopards.

4.4.2 Spotted hyaena density

We estimated a mean hyaena density of 1.15 (±0.42) adults/100km^2 in KNP. Our estimate is comparatively low to other reported densities across sub-Saharan Africa (e.g., 89 hyaena/100km^2, Höner *et al.* 2005; 94 hyaena/100km^2, Watts & Holekamp, 2008; 52 hyaena/100km^2, M'soka *et al*. 2016) and is over 95% lower than the only previously reported density of 31 hyaena/100km^2 from a miombo woodland (Creel & Creel, 2002). Hyaena density in KNP is the lowest reported in a woodland habitat to date and is comparable to density estimates from arid environments (0.9 hyaena/100km^2, Mills, 1990; 2 hyaena/100km^2, Trinkel & Kastberger, 2005) and those recorded in Majete Wildlife Reserve, Malawi (2.62 hyaena/100km^2, Briers-Louw, 2017). However, Majete Wildlife Reserve benefits from higher levels of protection compared to KNP and hyaena prey species have been reintroduced over the past decade (Briers-Louw *et al*. 2019). It is likely that hyaena are found at low densities across Malawi, but whether these low densities are naturally occurring or due to the decline in protected area health over previous decades is difficult to ascertain due to a lack of previous estimates.

The reduction in large mammal numbers (Munthali & Mkanda, 2002; Bhima *et al*. 2003) and the decline of competing carnivore populations in KNP suggests a period of high anthropogenic disturbance that is likely to have reduced large carnivore densities. The persistence of hyaena and leopard is potentially due to both species displaying higher levels of behavioural plasticity than other large carnivores, with a wide dietary niche and greater tolerance of human-impacted landscapes (Hayward, 2006; Hayward *et al.* 2006). Despite these high levels of behavioural plasticity, the near extirpation of competing large carnivores and reduction in natural prey is likely to result in increased levels of competition between remaining leopard and hyaena populations (M'soka *et al*. 2016).

Hyaena are competitively dominant over leopard (Balme *et al*. 2019), with at least 10% of leopard kills lost to hyaenas and the higher rates of kleptoparasitism suffered by female leopards known to negatively affect reproductive success (Balme *et al*. 2017). Leopard and hyaena are found at similar densities in KNP and with the loss of competing carnivores, most notably lion, and the reduction in natural prey, further research is needed to assess how this affects interspecific competition between the remaining large carnivore guild (Hayward & Slotow, 2009; M'soka *et al*. 2016). This is crucial to future management of large carnivore persistence in KNP and other areas of high anthropogenic disturbance (M'soka *et al*. 2016; Abade *et al*. 2018).

Prey availability is known to influence hyaena population density (Höner *et al*. 2005; Périquet *et al*. 2015). Therefore, securing the remaining prey base and allowing prey populations to recover in KNP should encourage the hyaena population to recover naturally (M'soka *et al*. 2016). High rates of reproductive success for hyaena in the absence of a resident lion population and the benefits of increased clan size for food acquisition (Kruuk, 1972) and cub survival (Watts & Holekamp, 2009) could lead to a rapid increase in the KNP hyaena population. Comparatively, leopard reproductive success is often naturally low (Balme *et al*. 2013) and further influenced by bottom-up processes in low productivity habitats (Stander *et al*. 1997) and in populations below carrying capacity (Owen *et al*. 2010). A growth in the hyaena population could, therefore, potentially lead to increased competition between the remaining carnivore guild and a subsequent decline in the KNP leopard population. Consequently, any conservation management interventions (such as increased law enforcement efforts or prey reintroduction/supplementation) in KNP should be closely monitored through annual camera trap surveys (Balme *et al*. 2009b).

4.4.3 Lion and wild dog presence

Our results suggest that both lion and wild dog are no longer resident in KNP, highlighting the degradation of the protected area. It is likely that lion and wild dog in KNP are dispersing individuals, potentially from nearby populations in Zambia, as connectivity between Malawian PAs is largely restricted by high human population density and loss of forest cover (Gondwe *et al*. 2019). The presence of dispersing lion and wild dog in 2017 and 2018 demonstrates the ability of carnivores to move through the MZTFCA, a cause for optimism for future conservation management of the region. However, increasing anthropogenic pressure on dispersal corridors and protected area networks in Zambia may jeopardise future dispersal efforts (Watson *et al*. 2014), highlighting the need for increased planning and continued international collaboration to protect these corridors and the ecological functionality of the wider region. Furthermore, securing, and increasing, the remaining prey base in KNP is vital to support future dispersers and promote natural recolonisation or potential reintroduction efforts.

4.4.4 Application of SPIM and survey considerations

This study provides further evidence that the *SPIM* package can provide robust density estimates, comparable to conventional SCR methods, whilst improving precision for partial identity samples (Augustine *et al*. 2018; Greenspan *et al*. 2020). As SCR methods are widely used to inform conservation management, and partial identity is a common problem for researchers, any gain in precision should be of broad interest (Augustine *et al*. 2018; Johansson *et al*. 2020). Our results show that in comparison with single-flank estimates, often the preferred and more conservative approach for partial identity samples, *SPIM* improves the precision of density estimates. We, therefore, recommend the use of *SPIM* for studies deploying single camera stations or studies where partial identities constitute a large proportion of the data.

Difficulties in sexing hyaena meant that sex could not be included as a covariate, which may have influenced our density estimates. However, the relatively small sample size for each survey year would have resulted in only a minor influence on sex-specific parameters and we are, therefore, confident in our estimates (Efford & Mowat, 2014; Mohamed *et al.* 2021). Similarly, for leopard, the small sample size of males to females (one male in 2016, four in 2017) would likely have resulted in minimal difference in sex-specific parameters. Comparative studies with relatively small sample sizes for male and female individuals have found that the null model, whereby sex-specific parameters (detection rate and spatial scale) are not incorporated into model inference, had the highest model support, or produced similar estimates to other analytical methods (Chase-Grey *et al.* 2013; Devens *et al*. 2018; Balme *et al*. 2019; Strampelli *et al*. 2020).

Whilst dual camera trap survey stations still provide the most accurate and effective way of collecting recapture data for complete identities of large carnivores, the development of *SPIM* (Augustine, 2018) and similar packages for partially identified datasets (McClintock, 2015), allows alternative survey design considerations for conservation management (Augustine *et al*. 2018; Farhadinia *et al.* 2019). Robust, and often rapid, density estimates are key for species management (Bauer *et al.* 2015; Jacobson *et al*. 2016) and *SPIM* provides a cost-effective and accurate method for analysing camera trap data that deviates from the conventional dual camera trap survey design (Augustine *et al.* 2018). The potential to survey a protected area using half the number of camera traps used in conventional designs is highly advantageous for protected area managers, the majority of whom have limited budgets (Mansourian & Dudley, 2008). The use of *SPIM* also allows a wider survey area to be used, when camera numbers are limited, resulting in a greater proportion of the population being sampled (Foster & Harmsen, 2012; Greenspan *et al*. 2020; Mohamed *et al.* 2021).

Populations perceived to be at low densities are often in the most urgent need of assessment and require intensive survey efforts (Balme *et al*. 2009a; Sollmann *et al.* 2011). The potential gains in precision from using *SPIM* are greater for populations at low density, where single-flank captures can be linked with increased certainty, and *SPIM* could, therefore, be beneficial to future survey efforts (Augustine *et al*. 2018). We recommend that the trade-offs between dual and single camera stations are considered on a case-by-case basis but the use of *SPIM* offers a novel solution to issues with camera trap survey design and analysis (Augustine *et al*. 2018; Greenspan *et al*. 2020). We suggest further camera trapping efforts to estimate large carnivore populations in miombo woodlands and other understudied regions, coupled with the use of *SPIM* where necessary, to provide robust estimates for effective conservation management.

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CHAPTER FIVE

Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild

CHAPTER FIVE: Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild

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Abstract

Effective conservation management requires an understanding of the spatiotemporal dynamics driving large carnivore density and resource partitioning. In African ecosystems, reduced prey populations and the loss of competing guild members, most notably lion (*Panthera leo*), are expected to increase levels of competition between remaining carnivores. Consequently, intraguild relationships can be altered, potentially increasing the risk of further population decline. Kasungu National Park (KNP), Malawi, is an example of a conservation area that has experienced large-scale reductions in both carnivore and prey populations, leaving a resident large carnivore guild consisting of only leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*). Here we quantify the spatiotemporal dynamics of these two species and their degree of association, using a combination of co-detection modelling, time-to-event analyses, and temporal activity patterns from camera trap data. Detection of leopard and spotted hyaena was significantly associated with the detection of preferred prey and competing carnivores, increasing the likelihood of species interaction. Temporal analyses revealed sex-specific differences in temporal activity, with female leopard activity patterns significantly different to those of spotted hyaena and male conspecifics. Heightened risk of interaction with interspecific competitors and male conspecifics may have resulted in female leopards adopting temporal avoidance strategies to facilitate co-existence. Female leopard behavioural adaptations increased overall activity levels and diurnal activity rates, with potential consequences for overall fitness and exposure to sources of mortality. As both species are currently found at low densities in KNP, increased risk of competitive interactions, that infer a reduction in fitness, could have significant implications for large carnivore demographics. Protection of remaining prey populations is necessary to mitigate interspecific competition and avoid further alterations to the large carnivore guild.

5.1 Introduction

Global environmental change is driving the decline in large carnivore populations and can be attributed to numerous factors, including habitat destruction, loss of natural prey, reduced landscape connectivity and human-wildlife conflict (Ripple *et al*. 2014; Wolf & Ripple, 2016). Rising anthropogenic impacts increase pressure on species interactions through the loss of complex carnivore guilds, declines in natural prey and shrinking protected area networks (Jones *et al*. 2018; Sévêque *et al*. 2020). These factors can distort carnivore dynamics and ecosystem function through increased competition for resources (Creel *et al*. 2018; Manlick & Pauli, 2020), reduced suppression of mesocarnivores (Brook *et al*. 2012; Prugh & Sivy, 2020), shifts in spatial use (Carter *et al*. 2019; Parsons *et al*. 2019) and changes in survival rates for dominant and subordinate competitors (M'soka *et al*. 2016; Elbroch & Kusler, 2018). These alterations in community assemblage and species dynamics can result in cascading trophic effects (Finke & Denno, 2005; Suraci *et al*. 2016; Winnie & Creel, 2017). As large carnivore dynamics have a key regulating effect on density and resource partitioning (Dröge *et al*. 2017; Groom *et al*. 2017), understanding their ecological and anthropogenic drivers is critical for effective conservation management (Davis *et al*. 2018; Sévêque *et al*. 2020).

The spatiotemporal dynamics of large carnivores have been widely investigated across sub-Saharan Africa (e.g., Hayward & Slotow, 2009; Dröge *et al*. 2017; Balme *et al*. 2019; Rafiq *et al*. 2020b). However, few studies have examined the spatiotemporal dynamics of these species in habitats where competing guild members, most notably lion (*Panthera leo*), have been extirpated (M'soka *et al*. 2016). Lions are often the dominant competitor in African carnivore guilds, but due to their preference for larger prey items (>200kg; Hayward & Kerley, 2005), tendency for livestock predation, and social nature, they are often at greater risk of localised extinction than other large carnivores (Everatt *et al*. 2019), such as leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*, hereafter hyaena). In the absence of lions, interference competition between remaining members of the carnivore guild is predicted to intensify, which could lead to changes in dynamics and increase the risk of population decline (Périquet *et al.* 2015; M'soka *et al.* 2016). Large carnivore behaviour is further driven by "bottom-up" processes, of which the abundance and distribution of preferred prey are primary regulators (Hayward *et al*. 2007; Wolf & Ripple, 2016). As large carnivores often share a degree of dietary overlap, any decline in prey abundance is also likely to disturb species dynamics through increased competition for food or the concentration of carnivore activity in areas of higher prey availability (Creel *et al*. 2018).

How, and if, these altered environments impact species' mechanisms of spatial use and temporal activity warrants further investigation. Malawi, in south-central Africa, offers a unique opportunity to study carnivore dynamics. Widespread persecution and the depletion of large prey species has led to the localised loss of resident lion populations, with the species restricted to either infrequent dispersing males or small isolated populations in fenced reserves (Mésochina *et al*. 2010; Briers-Louw *et al.* 2019; Davis *et al.* 2021). Malawi has one of the highest population densities in Africa (186 people/km^2; National Statistical Office, 2019), with 80% of the population dependent on natural resources (e.g., firewood) and agriculture for income, heating, and food security (Yaron *et al*. 2011; Schaafsma *et al*. 2018). Subsequently, Malawi has the highest deforestation rate in Africa (Mapulanga & Naito, 2019), whilst protected areas have been subject to widespread subsistence poaching (van Velden *et al*. 2020). Kasungu National Park (KNP) is a model example of a protected area in Malawi that has experienced these declines in carnivore and prey populations (Munthali & Mkanda, 2002; Davis *et al*. 2021). As the second-largest protected area in Malawi, comprised of miombo woodland, the primary habitat type across the country (Gondwe *et al*. 2019), and subject to the same environmental pressures as other reserves, KNP is a novel site to a) test theories on resource and guild-based competition, and b) understand how species respond to anthropogenic disturbance.

The loss of a resident lion population means that leopard and hyaena are the two dominant competitors in KNP. Both leopard and hyaena are known to display wide habitat preferences, have diverse diets, and persist in areas of high human disturbance (Holekamp & Dloniak, 2010; Jacobson *et al*. 2016). These behavioural traits allow leopard and hyaena to survive in areas where other apex predators cannot (Green *et al*. 2018; Loveridge *et al*. 2020). Localised extirpation of lion populations is expected to increase over the coming decades, with the species predicted to survive in only the largest protected areas across Africa and in small, intensively managed, reserves (Bauer *et al*. 2015). Consequently, understanding carnivore dynamics in areas of anthropogenic disturbance is important for predicting future alterations in carnivore guilds (Rafiq *et al.* 2020b). The intraguild dynamics of leopard and hyaena in KNP can, therefore, act as a model to inform conservation management under increasing levels of environmental change.

Spatiotemporal dynamics between leopard and hyaena are complex, with findings varying between habitats and carnivore community assemblages. The availability of preferred prey is known to significantly influence the presence of both species (Périquet *et al*. 2015; Balme *et al*. 2019; Searle *et al.* 2020). In addition, leopard kills are subject to high levels of kleptoparasitism from hyaena (Balme *et al*. 2017a), which is known to affect reproductive success in female leopards (Balme *et al*. 2013). Hyaena are also a direct source of leopard mortality (Swanepoel *et al*. 2015). In some ecosystems, kleptoparasitism has resulted in leopard adopting either spatial (Ramesh *et al*. 2017; Comley *et al*. 2020) or temporal (Havmøller *et al*. 2020b) avoidance strategies, although Ramesh *et al*. (2017) suggested that the spatial avoidance between leopard and hyaena was due to lion presence. Leopards also exhibit behavioural adaptations (i.e., tree-caching and dietary plasticity) to facilitate coexistence with hyaena (Balme *et al.* 2019; Briers-Louw & Leslie, 2020). However, the spatiotemporal dynamics of leopard and hyaena are often overlooked (Vanak *et al*. 2013; Rafiq *et al.* 2020b), particularly in ecosystems where the carnivore guild has been depleted due to anthropogenic disturbance. The lack of understanding of coexistence strategies between leopard and hyaena in such area's limits conservation management.

We used data from camera trapping surveys to investigate the spatiotemporal dynamics of leopard and hyaena in KNP, a protected miombo woodland habitat where these species are the only remaining members of the large carnivore guild. We applied co-detection modelling (Cusack *et al*. 2017; Balme *et al.* 2019), time-to-event analyses (Cusack *et al*. 2017) and temporal overlap comparisons (Rowcliffe *et al.* 2014) to evaluate the impact of a range of interspecific, ecological, and anthropogenic parameters on carnivore activity. Availability of preferred prey has previously been highlighted as a significant driver of leopard and hyaena presence (Périquet *et al*. 2015; Searle *et al*. 2020), and accordingly, we predict that, a) detection of both species will increase in relation to prey detectability, b) this will result in significant rates of co-detection between leopard and hyaena, and c) the potential for high levels of spatial overlap between leopard and hyaena will result in leopard adopting temporal avoidance mechanisms to facilitate coexistence and avoid competition.

5.2 Materials and Methods

5.2.1 Study site

KNP (central coordinates S12.9092°, E33.1689°; Figure 5.1) is a 2,316km^2 protected area in the central region of Malawi. KNP is dominated by miombo woodland, consisting of *Brachystegia* and *Julbernardia* spp. (Bhima *et al*. 2003). Closed canopy miombo woodland is interspersed with seasonally wet grassland areas (locally known as dambos) and isolated rocky inselbergs. The altitude ranges between 1,000 and 1,500m, and mean annual rainfall is 780mm (Bhima *et al*. 2003).

In the early 2000s poaching was so prolific that populations of several remaining prey species were moved from KNP to Liwonde National Park, Malawi, as their survival could no longer be guaranteed in KNP (Munthali & Mkanda, 2002). Consequently, KNP has experienced a significant decline in large mammal (Munthali & Mkanda, 2002; Bhima *et al*. 2003) and carnivore populations (Davis *et al*. 2021). Lions, once known residents in KNP, are now restricted to dispersing individuals from the wider Malawi-Zambia Transfrontier Conservation Area (Mésochina *et al*. 2010; Davis *et al*. 2021) and cheetahs (*Acinonyx jubatus*), also previously known residents, have been extirpated (IUCN/SSC, 2015). Whilst lions are not strictly extirpated from KNP, they are not present at levels that would have an influence on the guild dynamics of resident carnivore populations. Leopard and hyaena are the only remaining resident large carnivore species in KNP, with densities in 2018 estimated at 1.77 leopard/100km^2 and 1.62 hyaena/100km^2 (Davis *et al*. 2021).

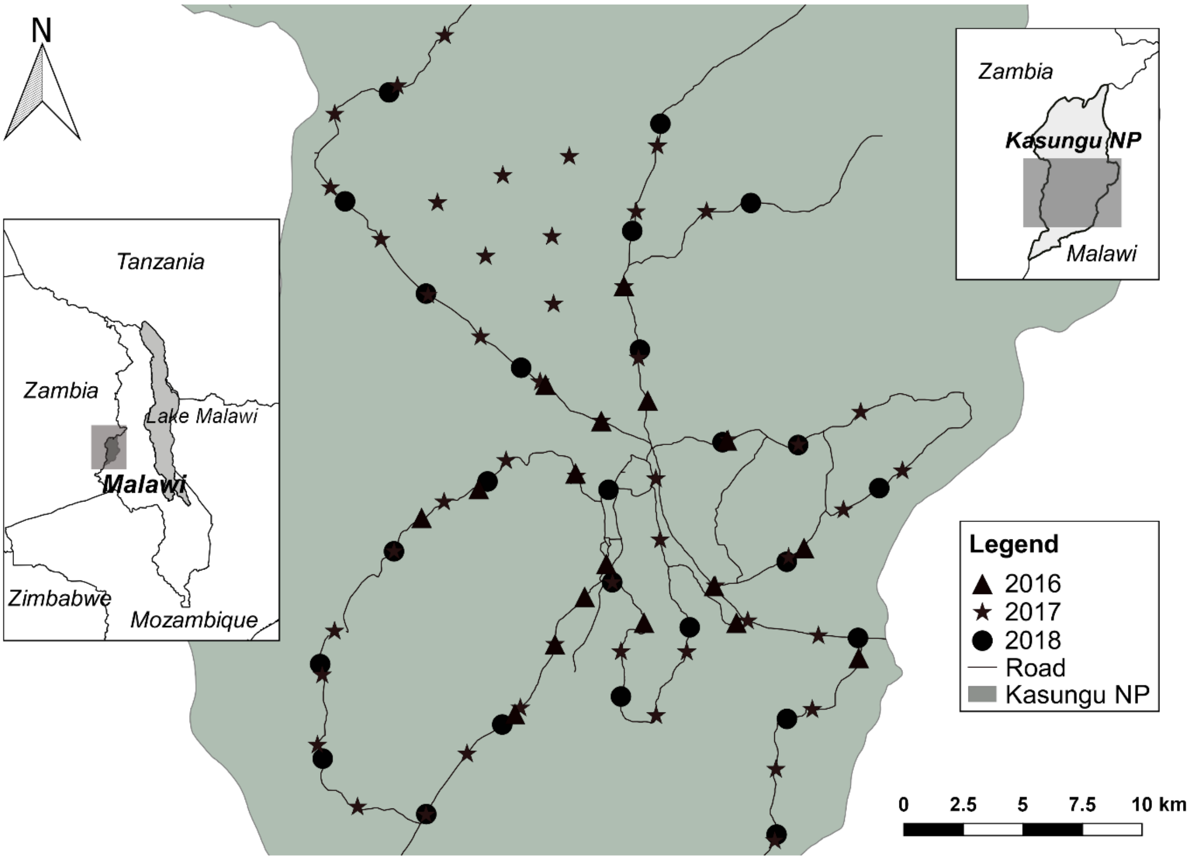


Figure 5.1. Camera trap locations for surveys conducted in 2016, 2017 and 2018 in Kasungu National Park, Malawi. Inset maps show the area covered within Kasungu National Park and the location of Malawi within sub-Saharan Africa.

5.2.2 Camera trap surveys

Data were collected from camera trap surveys lasting 90-120 days between May and October over a three-year period (2016-2018; Figure 5.1). To maximise the detection probability of large carnivores, roads and major trails were prioritised for camera placement (Cusack *et al.* 2015; Davis *et al.* 2021). One camera was deployed per station and stations were checked regularly to maintain camera function and data collection. All images were catalogued to species level and individual leopards were sexed using criteria outlined in Henschel & Ray (2003).

5.2.3 Co-detection modelling

We used a co-detection modelling approach to assess predictors of leopard and hyaena detection (Cusack *et al*. 2017; Balme *et al*. 2019). Due to high rates of naïve occupancy for both species, data were unsuitable for co-occupancy analysis. The co-detection approach allowed the use of data from all survey years. We measured the detection and non-detection of leopard and hyaena as a binary response variable ("1" for detection, "0" for non-detection) for each camera trap station, using an occasion length of five days per sampling event. We chose the five-day sampling event to correspond with the timeframe for the time-to-event analysis (described below) and the low detection rates of both focal species resulting in zero inflation with a one-day sampling occasion. Binary responses were modelled as a function of different combinations of detection covariates using binomial generalised linear mixed-effect models (GLMM's; Bolker *et al*. 2009; Cusack *et al*. 2017).

Based on evidence from previous studies, we selected five covariates that could impact the likelihood of detection for both leopard and hyaena, incorporating interspecific, environmental, and anthropogenic factors (Table 5.1). We measured prey detection from camera trap data as a binary response variable and assumed that prey species selected differed for leopard and hyaena. As leopard diet in KNP has not been assessed, we selected known leopard prey species from a similar habitat type (Havmøller *et al*. 2020a), or species for which we had anecdotal evidence (from camera traps and opportunistic kill sites) of predation in KNP. The following were included as leopard prey species: common duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus sylvaticus*), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), yellow baboon (*Papio cynocephalus*), porcupine (*Hystrix africaeaustralis*) and savanna hare (*Lepus victoriae*). Preliminary diet analysis for spotted hyaena in KNP identified common duiker, bushpig, savanna hare, warthog, bushbuck and kudu (*Tragelaphus* *strepsiceros*) as the most frequent prey species and, as such, these species were selected for the hyaena prey covariate (Carnivore Research Malawi, *unpublished data*).

Vegetation cover, hunting strategy and landscape features can all impact carnivore detection rates, as predators select areas optimal for increased prey density, heightened vulnerability to predation and their preferred hunting method (i.e., denser cover for ambush, open habitat for endurance; Balme *et al*. 2007; Watts & Holekamp, 2009). We used a binary variable for habitat type (Strampelli *et al*. 2018), where each camera site was designated as either “open”, where at least one side of the trail was bordered by open grassland, or “closed”, where both sides of the trail were bordered by miombo woodland.

For distance-based covariates (i.e., distance to water, distance to park border) the Euclidian distance (km) between each camera trap and the chosen feature were extracted in QGIS v.2.18.16 (QGIS Development Team, 2020). As KNP has no buffer zone and no continual fencing, distance to park border was selected as a suitable covariate to test for human disturbance. Clearance for agricultural land and the lack of a buffer zone means human settlements often begin at the KNP park boundary (Munthali & Mkanda, 2002). We reasoned that distance to park border was, therefore, a suitable covariate to incorporate both the impact of edge effects (Woodroffe & Ginsberg, 1998) and the proximity to human settlements (Balme *et al*. 2010).

GLMM’s were conducted in R v.3.6.3 (R Development Core Team, 2020), using package ‘lme4’ (Bolker *et al.* 2009). We removed one camera trap that malfunctioned shortly after being set from the analyses. There was no significant collinearity ($r < 0.5$ for all pairwise comparisons) between continuous covariates and, therefore, none were excluded from model selection. We aggregated data from all survey years and included year as a random effect to compensate for temporal variability. Camera station ID was also fitted as a random effect to control for repeated measures between sites (Cusack *et al*. 2017). All possible combinations of detection covariates were modelled for both leopard and hyaena, with only selected prey species differing between model sets (see Appendix IV for full candidate lists). We used an Information Theoretic Approach whereby models were ranked on their Akaike Information Criterion (AICc, corrected for small sample sizes) and models with ΔAICc < 2 considered to have strong support and selected for model averaging (Burnham & Anderson, 2002). From the final set of candidate models (ΔAICc < 2), average β-coefficient estimates were obtained using the 'MuMIn' package (Barton, 2020). Individual covariates were deemed significant when 85% confidence limits did not pass through zero, following Arnold (2010). The importance of individual covariates for predicting large carnivore detection were assessed using the summed model weights (Σw) of all models in the final candidate set. There was no evidence of overdispersion ($\hat{c} > 1.1$) across models, which was calculated as the ratio of the sum of the squared Pearson residuals to the residual degrees of freedom (Harrison, 2014).

Table 5.1. Detection covariates, with sampling range and mean, hypothesised to affect the likelihood of detection for leopard and spotted hyaena in Kasungu National Park, Malawi. The hypothesised effect on large carnivore detection is indicated, alongside supporting evidence for the predicted effect.

Covariate	Source	Sampling range (mean)	Hypothesised effect	Supporting evidence
Hyaena detection	Camera trap	1 (detection) 0 (non-detection)	- [a]	Swanepoel *et al*. 2015; Balme *et al*. 2017a
Leopard detection	Camera trap	1 (detection) 0 (non-detection)	+ [b]	Balme *et al*. 2017a
Distance to water (km)	GIS	0.03 – 10.45 (3.35)	+	Watts & Holekamp 2009; Havmøller *et al*. 2019
Distance to park border (km)	GIS	0.78 – 14.38 (7.99)	-	Woodroffe & Ginsberg, 1998; Balme *et al*. 2010
Preferred prey detection	Camera trap	1 (detection) 0 (non-detection)	+	Höner *et al*. 2005 ; Balme *et al*. 2019
Habitat type*	Observation	1 (open) 0 (closed)	- [a] + [b]	Balme *et al*. 2007; Watts & Holekamp 2009

[a] Effect on leopard detection

[b] Effect on hyaena detection

*hypothesised effect is based on habitat openness

5.2.4 Time-to-event analysis

We used time-to-event analyses to examine leopard and hyaena response to sympatric carnivores and preferred prey species across survey seasons (Cusack *et al*. 2017; Balme *et al.* 2019). Prey species were kept as defined for co-detection modelling. For each reference detection (defined as a photographic capture of a chosen species, e.g., leopard), we calculated the minimum time to capture the species of proximal interest (e.g., hyaena) at the same camera station. Any occasion where a reference detection was followed by another detection of the reference species was removed from the analyses. The calculated times between reference and proximal detections were then aggregated into 24-hour sampling intervals, with interval limits of five days before or after the reference detection (n = 10 days). For each 24-hour interval (n = 10 intervals) we then calculated an observed detection probability by dividing the number of proximal detections in each interval period by the total number of detections in the survey year for the species of proximal interest.

Expected distributions of proximal detection were randomly simulated by sampling activity patterns and capture rates of the proximal species, to generate new dates and times, which were then compared to the original, unchanged, reference detections (Cusack *et al*. 2017). From 1000 random iterations of proximal detection, we obtained expected values of detection probability for each 24-hour interval, which were then compared to the observed probability using standard two-tailed permutation tests, using the package ‘ade4’ (Dray & Siberchicot, 2020). Analyses could not be conducted for the 2016 survey, or between leopard sexes, as sample sizes were too small.

5.2.5 Temporal activity

Camera trap images from all survey years were used to estimate daily activity levels (percentage of time spent active over the 24-hour daily cycle) and degree of temporal overlap between large carnivore species and, for leopard, between individual sexes. Data for both large carnivore species were combined across survey years for the final analyses. We tested data for each species (and individual sexes for leopard) for differences between survey years to ensure no bias between individual years (Appendix V). To determine if activity patterns were significantly different to a random distribution over the circadian cycle, we performed a Hermans-Rasson test (Landler, Ruxton & Malkemper, 2019) on temporal data for both leopard and hyaena, using the package 'CircMLE' (Fitak & Johnsen, 2017). We used the time and date stamp from all photographic captures to determine animal activity. All models were fitted to clock time as surveys were conducted during the same survey period (between May-October each year) and daylight variance is limited at latitudes below 20° (Vazquez *et al.* 2019). To reduce bias and overrepresentation of activity at certain times of the day, only one photographic capture was used for analysis when time stamps were within 30 minutes of each other, unless unique pelage patterns confirmed different individuals were photographed. We performed analyses when species presented a minimum of thirty images accumulated in each survey year, as small sample sizes can bias activity estimations and misrepresent activity levels (Rowcliffe *et al*. 2014). We conducted analyses using the 'overlap' (Meredith & Ridout, 2016) and 'activity' (Rowcliffe, 2019) packages in R v3.6.3 (R Development Core Team, 2020).

Overall activity (i.e., the distribution of animal activity throughout the day) was estimated using the Kernel circular density function in 'activity' (Rowcliffe *et al.* 2014; Santos *et al.* 2019). Overlap of activity was quantified using the coefficient of overlap (Δ), which varies from 0 (no overlap) to 1 (complete overlap) (Santos *et al*. 2019). The Δ_4 estimator was used for all species included in the analyses as all sample sizes were ≥ 75 and Δ_4 is considered the most robust estimator for this sample size (Ridout & Linkie, 2009; Meredith & Ridout, 2014). To estimate confidence intervals for activity levels we simulated 10,000 smoothed bootstrap samples. Pairwise comparisons of bootstrapped activity patterns were then tested for significant differences in the ‘activity’ package, using a Wald statistic on a chi-square distribution with one degree of freedom (Rovero & Zimmermann, 2016).

5.3 Results

5.3.1 Camera trap results

We completed 5,990 camera trap nights across 92 camera trap stations in KNP between 2016 and 2018, with 702 photographic captures of large carnivore species and 854 of prey species (Table 5.2). Sufficient sample sizes for temporal analyses were recorded for leopard and hyaena (> 30 captures in each survey year). The presence of one sub-adult male lion was recorded in 2017, whilst one wild dog was recorded in 2017 and again in 2018 (determined by a unique pelage pattern), confirming the absence of resident lion and wild dog populations in KNP.

Table 5.2. List of species detected and yearly and total counts from camera trap surveys between 2016 and 2018 in Kasungu National Park, Malawi. Capture totals are provided for all large carnivores recorded and the prey species of leopard and spotted hyaena that were chosen for spatiotemporal analyses.

Order	Scientific name	Common name	2016 captures	2017 captures	2018 captures	Total captures
Carnivora	*Panthera pardus*	Leopard	48	116	115	279
	Crocuta crocuta	Spotted hyaena	113	148	133	394
	Panthera leo	Lion	0	11	0	11
	Lycaon pictus	African wild dog	0	9	9	18
Artiodactyla	*Sylvicapra grimmia*	Common duiker	22	42	63	127
	Tragelaphus sylvaticus	Bushbuck	4	7	7	18
	Tragelaphus strepsiceros	Greater kudu	1	6	17	24
	Phacochoerus africanus	Warthog	4	9	12	25
	Potamochoerus larvatus	Bushpig	13	48	36	97
Lagomorpha	*Lepus victoriae*	Savanna hare	25	110	45	180
Rodentia	*Hystrix africaeaustralis*	Cape porcupine	24	166	158	348
Primates	*Papio cynocephalus*	Yellow baboon	5	23	7	35

5.3.2 Co-detection analyses

Leopard

Four models (ΔAICc < 2) were selected from the final set of 11 candidate models (combined AICc weights >0.95) for model averaging (Table 5.3). There was no evidence of overdispersion ($\hat{c}$ = 0.90) in the most parametrised model. Detection of prey (β = 0.443 ± 0.162, 85% CI = 0.210 – 0.676), proximity to water (β = 0.311 ± 0.110, 85% CI = 0.152 – 0.470) and detection of hyaena (β = 0.310 ± 0.178, 85% CI = 0.053 – 0.567) were positive predictors of leopard detection. Prey detection and proximity to water were the best predictors of leopard detection (Σw = 1.0 for both).

Hyaena

Five models (ΔAICc < 2) were identified for model averaging from the final set of 22 candidate models (AICc weights >0.95; Table 5.4). There was no evidence of overdispersion ($\hat{c}$ = 0.93) in the most parametrised model. Detection of prey (β = 0.366 ± 0.163, 85% CI = 0.131 – 0.601) and leopard (β = 0.303 ± 0.182, 85% CI = 0.041 – 0.566) were positive predictors of hyaena detection and both terms had high model support (preferred prey, Σw = 1.00; leopard, Σw = 0.78).

Table 5.3. Model selection for binomial generalised linear mixed models predicting the likelihood of leopard detection at camera stations in Kasungu National Park, Malawi, across all survey years (2016, 2017 and 2018) during a given 5-day sampling occasion. Models were ranked according to Akaike weights (W_i) based on the Akaike Information Criterion for small samples (AICc), cumulative model weight is also presented (Cum. W_i). Models with AICc differences (ΔAICc) < 2 were averaged and β-coefficient estimates, with associated standard error (SE ±), 85% confidence limits and summed model weights (Σw) presented.

Model	K^a	AICc	ΔAICc	W_i	Cum. W_i	Log likelihood
Hyaena + Prey + Water	6	1120.34	0.00	0.31	0.31	-554.13
Prey + Water	5	1121.38	1.05	0.18	0.49	-555.67
Hyaena + Prey + Water + Habitat	7	1121.91	1.58	0.14	0.63	-553.91
Hyaena + Prey + Water + Border	7	1122.34	2.00	0.11	0.74	-554.12
Prey + Water + Habitat	6	1123.01	2.68	0.08	0.82	-555.47
Prey + Water + Border	6	1123.37	3.03	0.07	0.89	-555.65
Hyaena + Prey + Water + Border + Habitat	8	1123.90	3.57	0.05	0.94	-553.89
Prey + Water + Border + Habitat	7	1124.98	4.64	0.03	0.97	-555.44
Hyaena + Water	5	1125.96	5.63	0.02	0.99	-557.96
Hyaena + Prey	5	1126.85	6.51	0.01	1.00	-558.40

Parameter	β-coefficient	SE ±	Lower 85%	Upper 85%	Σw (%)
Prey*	0.443	0.162	0.210	0.676	1.0
Water*	0.311	0.110	0.152	0.470	1.0
Hyaena*	0.310	0.178	0.053	0.567	0.75
Border	0.017	0.108	-0.138	0.172	0.19
Habitat	-0.144	0.223	-0.465	0.177	0.15

* Indicates parameter had a significant effect on leopard detection as 85% confidence limits exclude zero.

[a] number of parameters in the model.

Table 5.4. Model selection for binomial generalised linear mixed models predicting the likelihood of hyaena detection at camera stations in Kasungu National Park, Malawi, across all survey years (2016, 2017 and 2018) during a given 5-day sampling occasion. Models were ranked according to Akaike weights (W_i) based on the Akaike Information Criterion for small samples (ΔAICc), cumulative model weight is also presented (Cum. W_i). Models with AICc differences (ΔAICc) < 2 were averaged and β-coefficient estimates, with associated standard error (SE ±) and 85% confidence limits presented. Only the ten highest ranking models are presented here.

Model	**K^a**	**AICc**	**ΔAICc**	**W_i**	**Cum. W_i**	**Log likelihood**
Prey + Leopard	5	1245.60	0.00	0.19	0.19	-617.78
Prey	4	1246.48	0.87	0.12	0.31	-619.22
Prey + Leopard + Habitat	6	1247.08	1.47	0.09	0.40	-617.50
Prey + Leopard + Border	6	1247.35	1.75	0.08	0.48	-617.64
Prey + Leopard + Water	6	1247.50	1.89	0.07	0.55	-617.71
Prey + Habitat	5	1247.97	2.37	0.06	0.61	-618.96
Prey + Border	5	1248.18	2.58	0.05	0.66	-619.07
Prey + Water	5	1248.44	2.84	0.05	0.71	-619.20
Leopard	4	1248.75	3.14	0.04	0.75	-620.36
Prey + Leopard + Habitat + Water	7	1248.88	3.27	0.04	0.79	-617.39

Parameter	**β-coefficient**	**SE ±**	**Lower 85%**	**Upper 85%**	**Σw (%)**
Prey*	0.366	0.163	0.131	0.601	1.00
Leopard*	0.303	0.182	0.041	0.566	0.78
Habitat	0.178	0.247	-0.178	0.533	0.16
Border	0.060	0.121	-0.114	0.235	0.14
Water	-0.041	0.120	-0.213	0.131	0.13

*Indicates parameter had a significant effect on hyaena detection as 85% confidence limits exclude zero.

[a] number of parameters in the model.

5.3.3 Time-to-event analysis

Leopard-hyaena

Compared to expected detection probability distributions, hyaena were more likely to be detected in the 24 hours after a leopard event during the 2017 survey ($p < 0.05$; Figure 5.2). In 2017, leopard capture events were significantly more likely when hyaena had been captured in the previous 24 ($p < 0.01$) and 48 ($p < 0.05$) hours. In the 2018 survey there was no significant bias in detection shown by either species.

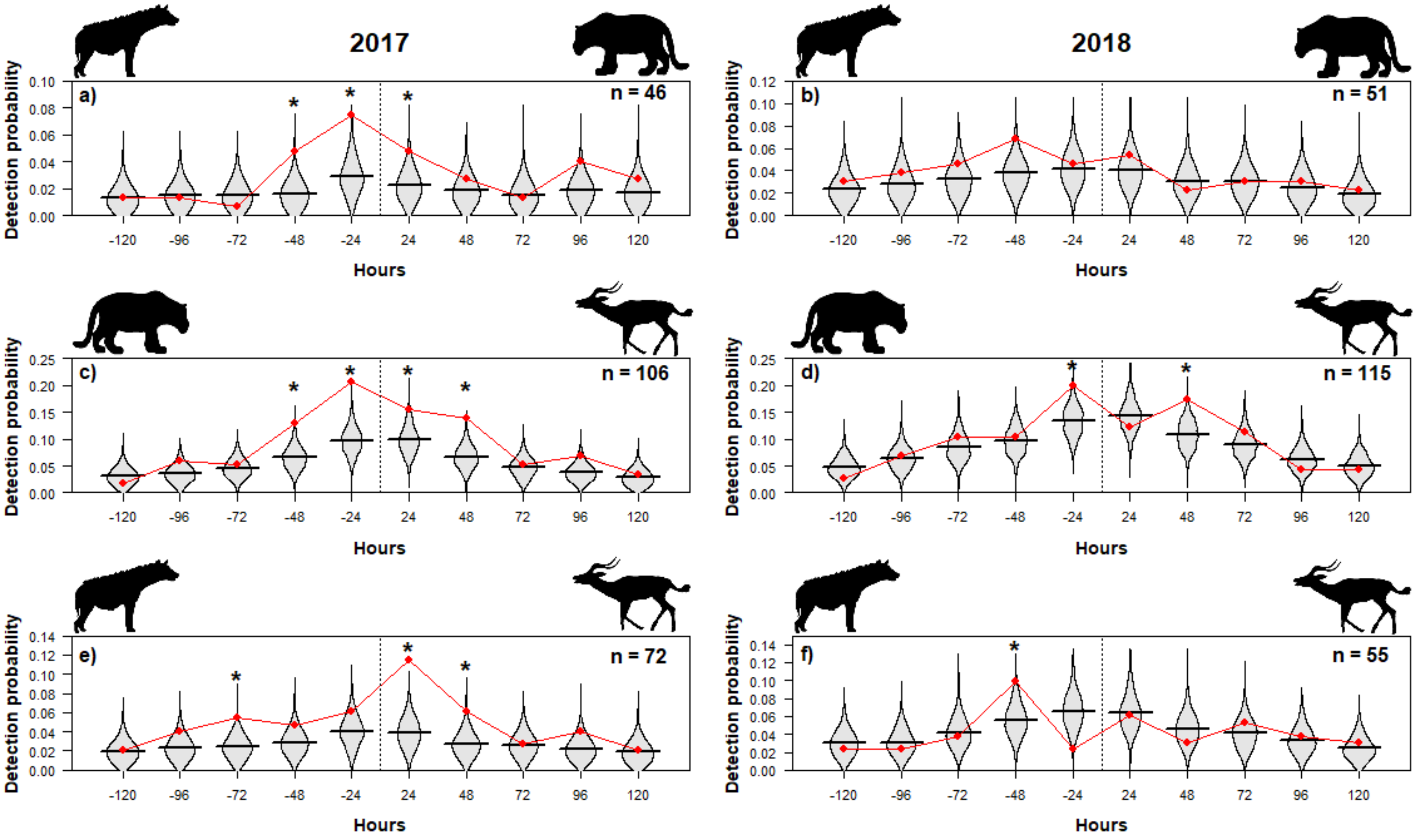
Leopard-prey

Leopard detections were higher 24 ($p < 0.05$; Fig. 2) and 48 ($p < 0.001$) hours after, and 24 and 48 hours (both $p < 0.001$) before a prey detection in 2017. Leopard detections were significantly higher 24 hours ($p < 0.05$) before and 48 hours ($p < 0.05$) after a prey detection in 2018.

Hyaena-prey

Hyaena response to a prey detection was comparable to leopard response in the 2017 survey, with increased detections 24 ($p < 0.001$; Fig. 2) and 48 ($p < 0.05$) hours after prey species detections. Hyaena detections were higher within 72 hours ($p < 0.05$) before a prey detection in 2017. Hyaena detections were higher than expected within 48 hours ($p < 0.05$) before prey species detection in 2018.

Figure 5.2. The observed (red) and expected (grey) probability of detecting hyaena after a leopard capture in 2017 (a) and 2018 (b), leopard after a prey species capture in 2017 (c) and 2018 (d) and, hyaena after a prey species capture in 2017 (e) and 2018 (f), at the same sampling site within five days before and after in Kasungu National Park, Malawi. Asterisks (*) above expected distributions, obtained from 1000 random simulations of capture events for the corresponding species, indicate days for which observed detection rates were significantly different ($p < 0.05$) to expected values. Sample sizes, from which observed detection probabilities were calculated, are given for each year.



5.3.4 Temporal activity

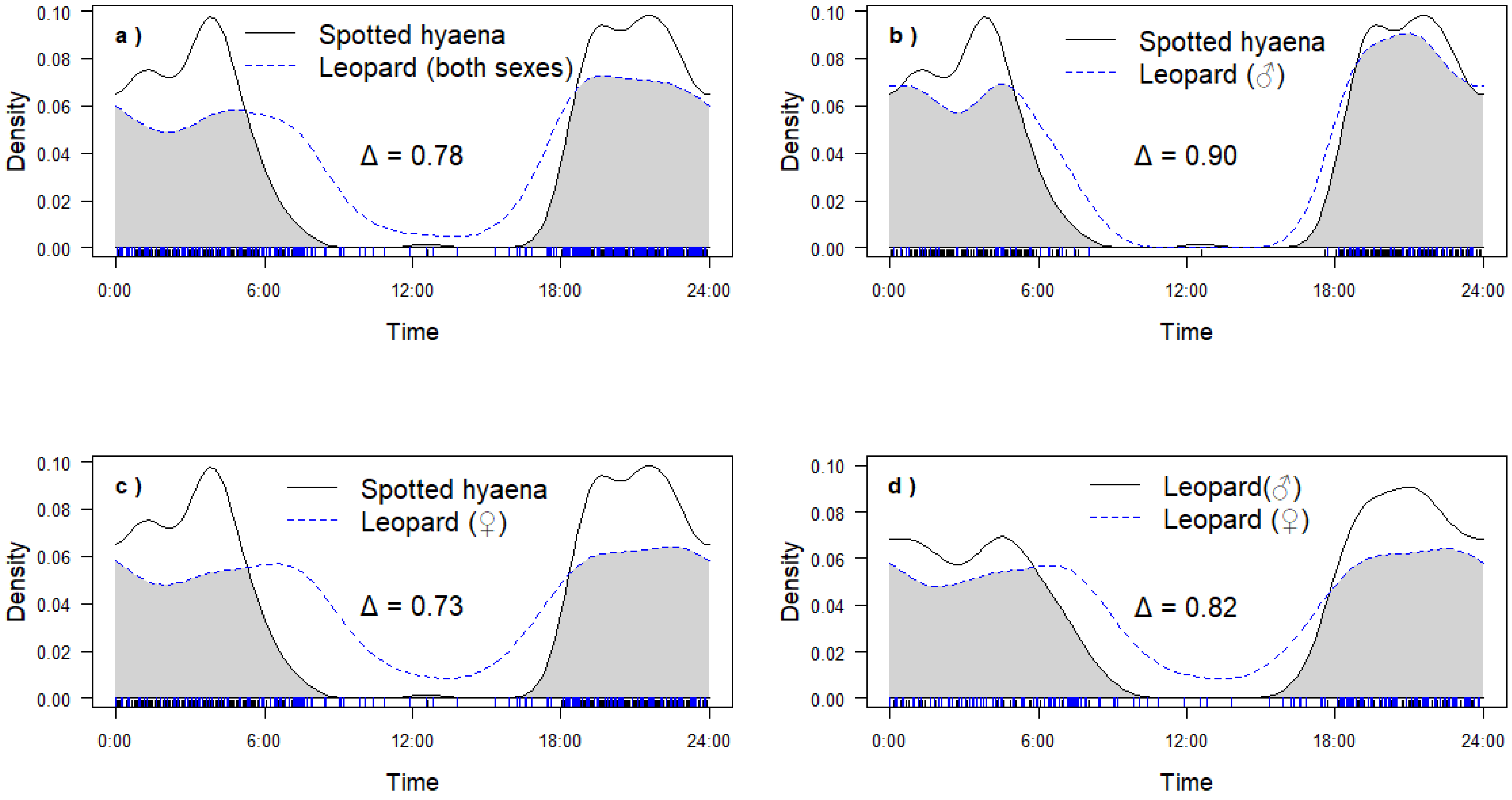
Overall activity (estimated proportion of time spent active over the daily cycle) was 0.57 (SE = 0.05) for leopard (both sexes), 0.46 (SE = 0.06) for male leopard, 0.65 (SE = 0.06) for female leopard and 0.42 (SE = 0.03) for hyaena (Table 5.5). The Hermans-Rasson test confirmed that both leopard and hyaena had activity patterns that were significantly different from random ($p < 0.001$ for all; Appendix VI). We observed an overlap average of $\Delta = 0.78$ for leopard-hyaena, $\Delta = 0.9$ for male leopard-hyaena, $\Delta = 0.73$ for female leopard-hyaena and $\Delta = 0.82$ for male leopard-female leopard (Figure 5.3). The lowest coefficient of overlap observed was between female leopard and hyaena. Leopard showed higher levels of diurnal activity with peaks at dawn and dusk, whilst hyaena showed higher levels of strictly nocturnal activity, with peaks before dawn and after dusk.

Table 5.5. Estimates of proportion of time active for large carnivore species in Kasungu National Park, Malawi, estimated from the distribution of camera trapping photos over the daily cycle. N is the number of photographic captures and Estimate is the overall activity with standard error (SE) and 95% confidence intervals (95% CI).

Species	***N***	**Estimate**	**SE**	**95% CI**
Leopard (both sexes)[*]	273	0.573	0.048	0.473 – 0.659
Leopard (♂)	77	0.459	0.056	0.312 – 0.525
Leopard (♀)	170	0.649	0.056	0.504 – 0.723
Spotted hyaena	385	0.423	0.027	0.359 – 0.465

[*] Includes images of leopards that could not be sexed but identified to species level.

Figure 5.3. Temporal overlap in activity patterns between a) spotted hyaena and leopard (both sexes); b) spotted hyaena and male leopard; c) spotted hyaena and female leopard; d) male and female leopard. Temporal activity patterns are compiled from surveys conducted in Kasungu National Park, Malawi, between 2016 and 2018. Coefficient of overlap (Δ) for each pairwise comparison is displayed, and shaded areas represent temporal overlap.



There was a 15% difference in overall temporal activity levels between leopard (both sexes) and hyaena in KNP (Wald $\chi^2 = 7.39$, df = 1, $p < 0.01$, Table 5.6). However, when individual leopard sexes were compared with hyaena, there was only a 4% difference in overall activity levels between male leopard and hyaena (Wald $\chi^2 = 0.34$, df = 1, p = *0.55).* Female leopards were active for 23% more of the daily cycle than hyaena *(*Wald $\chi^2 = 13.05$, df = 1, $p < 0.001$) and nearly 20% more active than male leopards (Wald $\chi^2 = 5.76$, df = 1, $p < 0.05$).

Table 5.6. Estimates of difference in activity between large carnivore species in Kasungu National Park, Malawi, from the distribution of camera trapping photos over the diel activity schedule. Bootstrapped activity patterns, with 10,000 smoothed bootstrap samples, were compared using Wald statistic (W) on a chi-square distriubtion with one degree of freedom in order to test for significance (P) at the 5% level.

Species Interaction	**Difference**	**SE**	***W***	***P***
Leopard (both sexes) – Spotted hyaena	0.151	0.055	7.39	0.007
Leopard (♂) – Leopard (♀)	0.190	0.079	5.763	0.016
Leopard (♂) – Spotted hyaena	0.037	0.062	0.346	0.556
Leopard (♀) – Spotted hyaena	0.227	0.063	13.048	< 0.001

5.4 Discussion

Spatiotemporal dynamics play an important role in facilitating coexistence between the large carnivore guild, yet little is known about these dynamics in human-altered landscapes (Sévêque *et al.* 2020). In protected areas where anthropogenic disturbance disrupts community structure, competition between remaining carnivores is predicted to increase (Périquet *et al.* 2015). We explored spatiotemporal partitioning between leopard and hyaena in a modified guild where they are the only competing large carnivores, providing a novel habitat in which to test theories on guild dynamics. Our results indicate that prey availability and the presence of competing carnivores positively influence the spatiotemporal dynamics of both leopard and hyaena. In the absence of a resident lion population and the depleted prey base in KNP, these shared drivers of spatiotemporal behaviour increase the likelihood of costly interactions and could have negative consequences for large carnivore demographics.

Our findings show that prey detection is a significant predictor of detection for both hyaena and leopard, supporting our predictions and in accordance with previous studies (Höner *et al.* 2005; Périquet *et al*. 2015; Ramesh *et al*. 2017; Searle *et al.* 2020). Leopard detection was also explained by proximity to water, as observed in previous studies (Balme *et al.* 2007; Havmøller *et al*. 2019). This finding supports our hypothesis that leopard space-use is primarily driven by prey presence in KNP, as prey species are commonly associated with riparian areas, and these areas provide adequate cover for the leopards' preferred ambush technique (Balme *et al*. 2007). Confirming our prediction, co-detection and time-to-event analyses showed a mutually positive influence between hyaena and leopard, as recorded by Balme *et al*. (2019). Given their competitive dominance and propensity for kleptoparasitism (Balme *et al*. 2017a), the influence of leopard presence on hyaena space-use likely indicates the additional benefits of high spatiotemporal overlap for hyaena. In similar areas of Africa, where prey abundance is depleted, there is evidence that dietary overlap increases between large carnivores (Creel *et al*. 2018). As prey presence was a significant predictor of leopard and hyaena detection, it may be that both species are responding to the same environmental cue (i.e., prey availability) resulting in increased co-detection rates.

The high spatial overlap of leopard and hyaena in KNP, combined with mutual drivers of detection, is likely to increase interaction between the two species. Despite the inherent risk of interaction with dominant competitors (i.e., lion and hyaena), previous studies have shown that intraguild competitors often have little bearing on leopard spatiotemporal dynamics (Balme *et* al. 2017b; Miller *et al*. 2018; Strampelli *et al.* 2018; Rafiq *et al*. 2020b). In the absence of spatiotemporal responses, leopards are often reliant on behavioural adaptability, such as tree-caching and dietary plasticity, to support intraguild coexistence (Voigt *et al*. 2018; Balme *et al*. 2019). In KNP this is evident for male leopards, as we recorded high temporal overlap between male leopard and hyaena. This finding challenges our prediction that both leopard sexes would display temporal avoidance of hyaena, as observed by Havmøller *et al.* (2020b). In contrast, female leopards displayed different temporal activity patterns to hyaena. Kleptoparasitism from hyaena has been shown to negatively impact reproductive success of female leopard and female leopards suffer higher rates of kleptoparasitism, compared to males (Balme *et al*. 2017a). As such, increased interaction with hyaenas presents a greater risk for female leopards and could explain the temporal partitioning. Furthermore, male leopards are more likely to display tree-caching behaviour than female conspecifics (Stein *et al*. 2015; Balme *et al*. 2017a), which could facilitate greater coexistence with hyaena. Tree-caching would be less effective for female leopard due to the threat of intraspecific kleptoparasitism (Balme *et al*. 2017a) and this could lead female leopards to adopt the additional mechanism of temporal partitioning found in this study (Miller *et al*. 2018).

Our results support Havmøller *et al*. (2020b), who recorded temporal differences between leopard sexes and increased levels of female diurnal activity compared to males. These findings highlight the importance of incorporating sex into pairwise behavioural comparisons. Increased interaction with male conspecifics heightens the risk of kleptoparasitism and infanticide for female leopards and observed temporal differences could be a mechanism to minimise these costly encounters (Balme *et al*. 2013; Swanepoel *et al*. 2015; Balme *et al*. 2017c). Miller *et al*. (2018) hypothesised that temporal segregation between leopard and interspecific competitors could increase at sites of reduced prey abundance, due to higher rates of resource sharing, which may explain the sex-specific and interspecific differences in temporal activity observed here. In addition, female leopards can exhibit wider dietary niches than male conspecifics, often displaying more opportunistic feeding strategies and predating on smaller-bodied prey items (e.g., Voigt *et al.* 2018). The wider dietary plasticity of female leopards could be an additional mechanism to facilitate coexistence and further investigation of leopard sex-specific dietary specialisation in KNP would improve our knowledge of intraguild dynamics and niche partitioning strategies.

Female leopard daily activity levels were 19% to 23% higher than those of male leopard and hyaena. These extended periods of diel activity may increase the likelihood of interaction with intraguild competitors and anthropogenic threats (e.g., road traffic, human activity), thus heightening exposure to potential sources of mortality (Rizzuto *et al.* 2018; Havmøller *et al.* 2020b). The greater energetic costs imposed by higher activity levels may reduce reproductive success and overall fitness (Wilmers *et al.* 2017; Rizzuto *et al.* 2018), creating cascading demographic effects. Further research is required to assess the potential impacts of intraguild competition and depleted prey on female leopard fitness and reproductive success.

There was no effect of proximity to park boundary or habitat type on detection of leopard or hyaena. These findings highlight the ability of both species to persist throughout the protected area, which is encouraging for local conservation management. We acknowledge that the coarse scale on which habitat was assessed here may not be sufficient to identify fine-scale habitat preferences. Previous studies have highlighted the higher tolerance of hyaena (Mkonyi *et al.* 2018) and leopard (Strampelli *et al.* 2018; Petracca *et al.* 2019) to human presence, compared to other large carnivores (Everatt *et al.* 2019). Our results provide further evidence of the species' adaptability in areas of close proximity to human settlement. However, our temporal analyses suggest that hyaena activity is largely restricted to nocturnal movements, which is considered an early response to high levels of human disturbance (Kolowski *et al.* 2007; Holekamp & Dloniak, 2010).

We acknowledge that our results are restricted to KNP and further efforts to quantify spatiotemporal behaviours in modified carnivore guilds would be beneficial to inform carnivore conservation management in human-altered landscapes. Malawi offers an interesting avenue for such studies, as several protected areas have seen similar reductions in large carnivore and prey populations (Mésochina *et al*. 2010; van Velden *et al*. 2020). In this study, camera trap placement was focused on roads and trails to optimise capture rates for large carnivores. Despite this, we are confident our findings are representative of carnivore habitat use in KNP, as road systems play an integral role in carnivore space use (Rafiq *et al*. 2020a). In addition, since large carnivore densities are low in KNP (Davis *et al*. 2021), it is also the only viable, non-invasive method for gathering large amounts of data to quantify carnivore behaviour (Rowcliffe *et al*. 2014). However, the use of road networks could have reduced prey species capture rates, as these areas increase exposure to predation risk and human activity, potentially underrepresenting aspects of observed predator-prey interaction (Oriol-Cotterill *et al*. 2015; Havmøller *et al*. 2020b).

Camera trap density and length of sampling occasion for co-detection and time-to-event models could have reduced precision of estimates. Whilst overall detections were similar for leopard and hyaena in 2017 and 2018, interactive behaviours may be underrepresented in 2018 as only half the number of camera trap sites were deployed, due to logistical reasons. Although aggregating detection events into larger bins may impact the accuracy of parameter estimates (as models are sensitive to changes in temporal scale; see Cusack *et al*. 2017), this practice is commonly used for large carnivores that have naturally low detection rates (e.g., Abade *et al*. 2018; Strampelli *et al*. 2018). Future studies could look to increase the density of camera traps deployed to yield higher capture rates and this may allow for shorter temporal scales to be used. However, given the low densities of large carnivores in KNP it is unlikely that an occasion length shorter than 24-hours could be applied. The deployment of GPS collars with high sampling rates, as in Rafiq *et al*. (2020b), could be of greater benefit to gather fine-scale data on carnivore activity and encounter rates.

Improved law enforcement efforts and ongoing reintroductions of prey species could increase prey abundance in KNP (IFAW, 2020). Under these conditions, and with the absence of a competing lion population, hyaena numbers could quickly rise, as observed by M'soka *et al*. (2016) in Liuwa Plains, Zambia. Conversely, leopard population recovery is gradual and reproductive success is naturally low (Balme *et al*. 2013; Balme *et al*. 2017c). Increased hyaena clan size would have direct benefits for food acquisition and hyaena cub survival (Höner *et al*. 2005), potentially exacerbating current levels of interspecific competition. In response to increased competition, leopards are likely to adapt their spatiotemporal behaviour and may switch to smaller prey items (du Preez *et al*. 2017; Comley *et al*. 2020) or be forced into sub-optimal habitat (e.g., low prey abundance, edge habitats; Vanak *et al*. 2013). Additional behavioural adaptations could have negative consequences for population recovery. For example, Comley *et al*. (2020) hypothesised that the decreasing leopard population in Selati Game Reserve, South Africa, was attributable to high levels of interspecific competition with the resident, much larger, hyaena population. As such, close monitoring of large carnivore densities and intraguild dynamics is required in KNP to assess the impact of ongoing conservation initiatives.

We have shown that leopard and hyaena coexist in KNP, with male leopard and hyaena showing significant spatiotemporal overlap, whilst female leopards exhibit temporal partitioning to mitigate potential interactions with intra-and-interspecific competitors. Whether the behavioural responses of female leopards are sufficient to maintain reproductive success and long-term population viability, is unknown. Our results show that prey occurrence is a significant predictor of leopard and hyaena detection. Therefore, protecting remaining prey populations should be a management priority to conserve the resident carnivore guild. Further understanding of the drivers of spatiotemporal behaviours can help alleviate the challenges caused by changing niches and shifts in carnivore community dynamics (Rafiq *et al*. 2020b). As protected areas are subject to increasing levels of anthropogenic disturbance (Jones *et al.* 2018), further research of large carnivore spatiotemporal dynamics will be imperative to maintain carnivore coexistence and to implement effective long-term conservation strategies.

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CHAPTER SIX

Dietary composition and niche overlap between competing large carnivores in Kasungu National Park, Malawi

CHAPTER SIX: Dietary composition and niche overlap between competing large carnivores in Kasungu National Park, Malawi

Abstract

Intraguild competition is a key mechanism that can shape large carnivore community structure by suppressing subordinate competitors and altering niche partitioning strategies, potentially impacting population demographics. Large carnivores often compete for similar resources and assessing dietary overlap within carnivore guilds can be a reliable indicator of interspecific competition. Loss of natural prey, primarily from unsustainable human offtake, is a key factor in species decline and can heighten levels of competition between competing carnivores, as resources become increasingly limited. In Kasungu National Park (KNP), Malawi, the carnivore guild has been altered by high levels of anthropogenic disturbance, leading to reduced prey availability and a resident carnivore guild consisting of only leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*). Using scat analysis techniques, the dietary composition and level of niche overlap between leopard and spotted hyaena were assessed. Leopard and spotted hyaena shared a high degree of dietary overlap between prey species ($O_{ab} = 0.65$), whilst leopard showed a greater level of dietary specialisation. Dietary overlap and the potential for exploitation competition was higher for prey species within the small (< 19kg) and large (> 80kg) prey weight ranges ($O_{ab} > 0.95$ for both). However, leopard and spotted hyaena utilised different prey species within the medium (19-80kg) prey weight range, thus reducing levels of competition. These results suggest there is strong potential for exploitation and interference competition between leopard and spotted hyaena, which could have a limiting effect on large carnivore population density. A focus on restoring large mammal prey populations in KNP will help to mitigate levels of interspecific competition and reduce the potential for exploitation competition between large carnivores.

6.1 Introduction

Interspecific competition is an important component of ecosystem functionality that can alter community structure, species distribution and population dynamics (Caro & Stoner, 2003; Chesson & Kuang, 2008; Prugh & Sivy, 2020). For example, within carnivore guilds, competitive interaction with dominant guild members can have deleterious effects on subordinate carnivores, such as reduced individual fitness, lower reproductive rates, and population suppression (Palomares & Caro, 1999; Prugh *et al*. 2009). To reduce the potential for competitive interaction with dominant guild members, and the associated negative costs of competition, subordinate carnivores typically exhibit niche differentiation (Schoener, 1974). By partitioning their use of one or more niche axes (space, time and resource availability; Schoener, 1974), subordinate carnivores can facilitate coexistence with sympatric competitors (Sévêque *et al*. 2020).

Where sympatric carnivores display spatiotemporal overlap, access to shared resources may be limited and, in large carnivore communities, this resource is often food. In response to exploitative competition with dominant guild members, subordinate competitors may exhibit dietary niche segregation and utilise different food resources (Schoener, 1983). Resource partitioning can limit the impact of competition, however, diverging use of any of the three niche axes can have implications for the survival and fitness of subordinate carnivores (du Preez *et al*. 2017). For example, dietary segregation can force subordinate carnivores to predate smaller, sub-optimal prey, with potential implications for overall fitness and group dynamics (Hayward & Kerley, 2008). In addition, resource partitioning can be further altered by anthropogenic disturbance (Smith *et al*. 2018; Manlick & Pauli, 2020; Sévêque *et al*. 2020), whereby a human-induced reduction in resource availability, such as the offtake of natural prey, can affect levels of intraguild competition, as carnivore guilds are forced to compete for increasingly limited resources (Creel *et al*. 2018). For example, increasing use of small prey items by lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*, hereafter hyaena) limited the potential for niche partitioning by cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*) populations in Liuwa Plains, Zambia (Dröge *et al*. 2017).

Large carnivores have experienced widespread population and geographic range declines over the last two centuries, largely due to increasing anthropogenic threats (Ripple *et al.* 2014; Ceballos *et al*. 2015; Wolf & Ripple, 2017). The local extirpation, or depletion, of natural prey from an environment, often caused by unsustainable human offtake, has been identified as a key factor in large carnivore population decline (Wolf & Ripple, 2016; Sandom *et al.* 2018). Due to the high metabolic demands associated with large body size, large carnivores require abundant mammalian prey to persist in an environment (Carbone & Gittleman, 2002; Creel *et al*. 2018). The reliance of carnivores on large prey has further driven population declines, with significant prey depletion either leading to localised extirpations (e.g., Maisels *et al*. 2001; Burton *et al*. 2011), or forcing carnivores to search for alternative food sources, often resulting in increased livestock predation (Khorozyan *et al*. 2015; Khan *et al*. 2018). Determining large carnivore dietary composition is, therefore, crucial for their effective conservation management and key to assessing their adaptability in the face of continuing environmental change (Havmøller *et al*. 2020).

Here, the diets of sympatric leopard (*Panthera pardus*) and hyaena populations in Kasungu National Park (KNP), Malawi, are compared to determine the level of dietary niche overlap between the two species, as a proxy for intraguild competition. The dietary niche breadth of leopard and hyaena is diverse (Hayward, 2006; Hayward *et al*. 2006), and this dietary adaptability, combined with flexible hunting strategies and behavioural plasticity, has helped both species to persist in areas where other large carnivores have been extirpated (e.g., Loveridge *et al.* 2020). In most environments, hyaena and leopard are part of a wider carnivore guild that is competing for resources (e.g., Hayward & Kerley, 2008; Creel *et al*. 2018; Briers-

Louw & Leslie, 2020), but in KNP this carnivore guild has been depleted, with the loss of resident lion, cheetah and wild dog populations (Mésochina *et al*. 2010; IUCN/SSC, 2015; Davis *et al*. 2021a). In addition, prey availability has been reduced in KNP through unsustainable levels of illegal poaching (Munthali & Mkanda, 2002; Mésochina *et al*. 2010). Previous studies have highlighted that a reduction in prey abundance, particularly of larger-bodied prey species, can result in increased dietary overlap and reduced dietary niche breadth (Creel *et al*. 2018). As leopard and hyaena populations are known to be found at low densities in KNP (Davis *et al*. 2021a), determining if this reduction in prey abundance has impacted prey choice and dietary overlap is important for local conservation management.

The dietary ecology of large carnivores has been well-studied in parts of east and southern Africa where the carnivore guild is largely intact (e.g., Hayward & Kerley, 2008; du Preez *et al*. 2017; Broekhuis *et al*. 2018; Comley *et al*. 2020). However, further information is needed on dietary overlap and interspecific competition between sympatric carnivores in disturbed and understudied habitats (Breuer, 2005; Rduch, 2016; Creel *et al*. 2018). The breakdown of carnivore community assemblages and decline of prey abundance is predicted to increase across African protected areas, as anthropogenic pressures continue to grow (Wolf & Ripple, 2016; Jones *et al*. 2018; Sandom *et al*. 2018). Information on intraguild competition and dietary ecology in these human-disturbed environments will, therefore, be important for local conservation management and of wider relevance as these issues become more pertinent in African ecosystems. Using scat analysis techniques, this study assesses dietary composition and overlap between leopard and hyaena in KNP, a human-disturbed ecosystem with reduced prey availability and a modified carnivore guild. It is predicted that, a) leopard and hyaena will exhibit a high level of dietary overlap, and b) dietary overlap will be higher in the medium-sized (19-80kg) prey weight group, as both leopard and hyaena preferentially select for prey in this weight range (Hayward, 2006, Hayward *et al*. 2006).

6.2 Materials and Methods

6.2.1 Study area

The study was conducted in KNP, a 2,316km^2 legally protected area in the Central Region of Malawi. KNP is largely comprised of miombo woodland (*Brachystegia* and *Julbernardia* spp.), which is interspersed with a network of seasonally wet grasslands and isolated rocky inselbergs. Mean annual rainfall is 780mm, falling between November and April. Leopard and hyaena are found at similar density in KNP, with recent estimates of 1.77 leopard/100km^2 and 1.62 hyaena/100km^2 (Davis *et al*. 2021a). Prey populations in KNP have been subject to high levels of subsistence poaching, which has reduced prey abundance (Munthali & Mkanda, 2002). For example, an aerial survey conducted in 2014 estimated a 95% decline in buffalo (*Syncerus caffer*) numbers since 1992 and a 97% decline in the zebra (*Equus quagga*) population over the same time-period, with the zebra population estimated at just six individuals (Macpherson, 2015).

6.2.2 Scat collection and analysis

Scats from large carnivores were collected between May 2016 and January 2018 in KNP (Figure 6.1). For each sample collected, the species, location and date were recorded. Scats were identified based on diameter, segmentation, colour, shape, and presence of associated field signs (e.g., tracks), using the specifications in Stuart & Stuart (2000). Three methods were used to collect carnivore scats: opportunistic collection, walked transects and, for hyaena, monitoring of known latrine sites. Opportunistic collection of faecal samples along roads and trails was conducted throughout the study period (May 2016 – January 2018). Ten walked transects of 5km in length were designed to search the KNP road network for scats that could be overlooked whilst driving. The KNP road network was targeted for walked transect search protocols as large carnivores frequently use road systems as communication hubs (Rafiq *et al.*

2020). Hyaena scats were also collected at latrine and den sites, which were visited periodically throughout the study period.

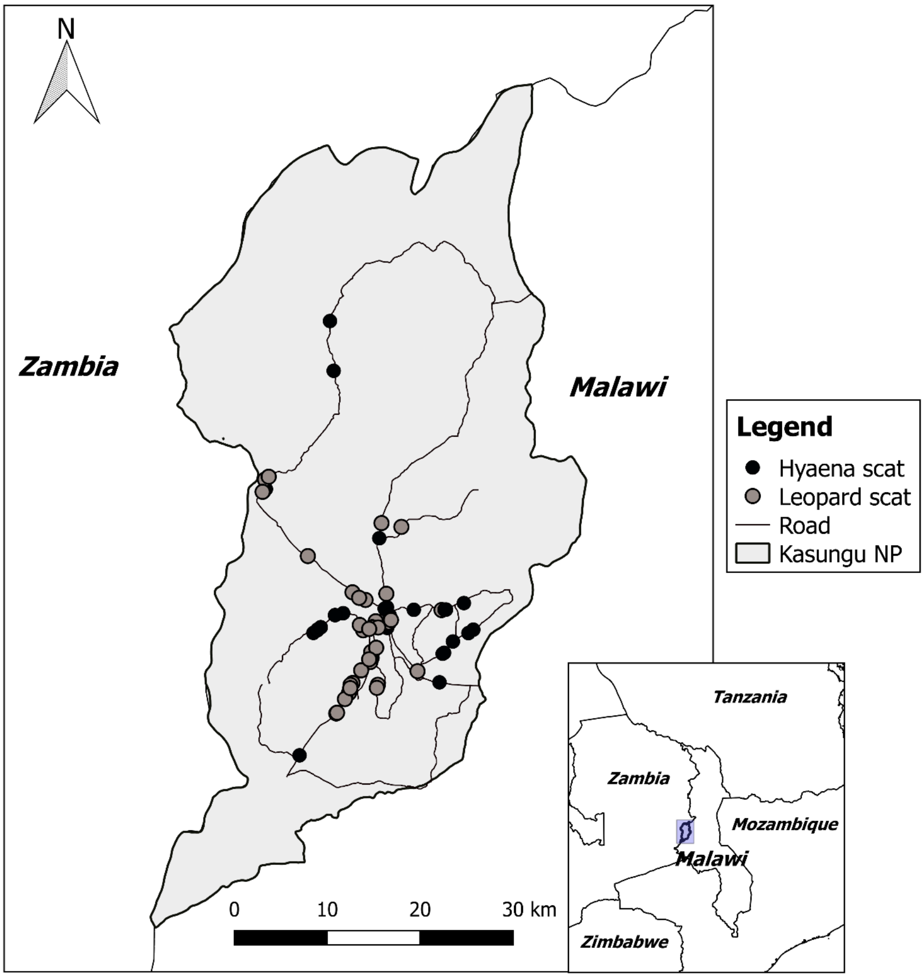

Figure 6.1. Map of Kasungu National Park, Malawi, indicating the location of all analysed scats (n = 79) collected for the assessment of leopard and spotted hyaena diet.

Faecal samples were sun-dried for 24 hours, before being soaked in warm water until malleable. Samples were washed over a sieve until the water ran clear, then the remaining contents were air-dried for at least 24 hours. Ten hairs from each scat were selected at random, with hairs spread across a grid and a random number generator used to select individual hairs from sampled squares. All samples were identified microscopically from their cuticle imprint, using the techniques developed by Keogh (1983). Microphotographs at 40x magnification were taken at the base, middle and end of each follicle. Cuticle patterns were then identified to species level using the reference guide developed by Beveridge & van den Hoogen (2013) and from samples opportunistically collected from carcasses during the study period by Carnivore Research Malawi. Identifying bushpig (*Potamochoerus larvatus*) and warthog (*Phacochoerus africanus*) samples to species-level can be challenging from cuticle images, as cuticles are similar in structure (Beveridge & van den Hoogen, 2013). Therefore, these two species were considered as family *suidae* spp. to avoid misidentification. All leopard samples were identified following the same protocol to species-level by Carnivore Research Malawi and received as secondary data. For hyaena, cuticle images were sent to the author and subsequently identified to species-level.

6.2.3 Dietary composition and biomass

Leopard and hyaena dietary composition were determined using three methods: frequency of occurrence (FO), corrected frequency of occurrence (CFO) and relative biomass (R). FO was calculated as the number of occurrences of a single prey item divided by the total number of occurrences of all prey items (Klare *et al*. 2011). However, as FO can overestimate the importance of certain prey items, a CFO was calculated to account for multiple prey items occurring in a single scat (Henschel *et al*. 2005; Klare *et al*. 2011). CFO assigns a weighting of one to each scat, which is then split by the number of prey species identified per scat. For example, if four prey items were found in a scat then a weighting of 0.25 would be applied to each species present. CFO for each prey species is then expressed as a percentage by dividing the total occurrence across scats by the number of scats available (Karanth & Sunquist, 1995).

Variation in the size of selected prey can limit inference from frequency of occurrence methods and overestimate the importance of smaller prey items in carnivore diet (Henschel *et al*. 2005; Klare *et al*. 2011). Estimating biomass consumption is, therefore, recommended over conversion factors, particularly for carnivores with diverse diets (Chakrabarti *et al.* 2016; Lumetsberger *et al.* 2017). Previous studies have used linear regression models to estimate biomass consumption, often applying the model developed by Ackerman *et al*. (1984) for pumas (*Puma concolor*). However, failure to account for physiological constraints and carnivore feeding behaviour in these early biomass models led to significant bias and inaccuracies in biomass estimation (Wachter *et al*. 2012; Lumetsberger *et al*. 2017). Therefore, the non-linear biomass model developed by Chakrabarti *et al.* (2016) from lion and leopard feeding trials was used to calculate biomass consumed per scat:

$$Y = 0.033 - 0.025\exp^{-4.284\,(X/Z)}$$

where Y is the mass of prey consumed per collectable scat, X is the mean prey body mass, and Z is the mean carnivore body mass. As no correction factors have been developed to calculate biomass consumption for hyaena, and hyaena are similar in body-size to lion and leopard, the biomass model of Chakrabarti *et al.* (2016) was also used for hyaena calculations.

Prey weights were calculated using 75% of the average adult female weight, derived from Kingdon (2015), as recommended in Hayward *et al.* (2007) and Chakrabarti *et al*. (2016). Mean carnivore body masses for leopard and hyaena were also derived from Kingdon (2015). The method provided in Chakrabarti *et al.* (2016) was used to calculate biomass consumed per scat (Y), total biomass consumed ($B = Y$ x CFO) and relative biomass ($R = (B/\Sigma B)$ x 100). Prey preference was not investigated here as reliable population estimates were not available for all prey species in KNP, with poor visibility limiting the efficacy of aerial counts for cryptic species (e.g., bushbuck, *Tragelaphus scriptus*) and low prey density resulting in limited sample sizes for ground transects.

6.2.4 Dietary overlap and niche breadth

Dietary overlap was determined using Pianka's (1973) index:

$$O_{ab} = \frac{\sum_n P_{ia} P_{ib}}{\left(\sum P_{ia}^2 \, P_{ib}^2\right)^{\frac{1}{2}}}$$

where O_{ab} is the degree of dietary overlap between species a and b; P_{ia} is the relative frequency of the prey item *i* found in the scat of species a; P_{ib} is the relative frequency of the prey item *i* found in the scat of species b; and *n* is the total number of prey items in a predator scat. The resulting values range from 0 (no overlap) to 1 (complete overlap) and, in accordance with similar studies of large carnivore diet, overlap is considered to be biologically significant when values exceed 0.60 (Mbizah *et al*. 2012; Comley *et al*. 2020). The degree of dietary overlap between leopard and hyaena was estimated for both the relative occurrence of all prey species and prey weight groups, using the classification of Pitman *et al*. (2012): small (< 19kg), medium (19-80 kg) and large (> 80 kg). Pianka's index was calculated using the package 'spaa' (Zhang, 2016) in R v4.0.1 (R Core Development Team, 2020).

Dietary niche breadths were calculated using Levins' index (Levins, 1968), standardised by Hurlbert (1978):

$$B_s = \frac{((1/\sum P_i^2) - 1)}{(\mathrm{n} - 1)}$$

where P_i is the proportion of occurrence of each prey item *i* in predator diet *P*, and *n* is the number of prey taxa. B_s ranges from zero to one, with lower values indicating a more specialised diet and higher values indicating generalist diets.

6.3 Results

A total of 151 (leopard, n = 41; hyaena, n = 107) large carnivore faecal samples were collected in KNP between May 2016 and January 2018, of which 79 were available for analyses (leopard, n = 39; hyaena, n = 40). Faecal accumulation curves showed that 90% of all prey species found in samples were detected after analysing 22 scats for both leopard and hyaena (Figure 6.2). Identification of hair samples was not possible in <1% and 12.75% of leopard and hyaena scats, respectively.

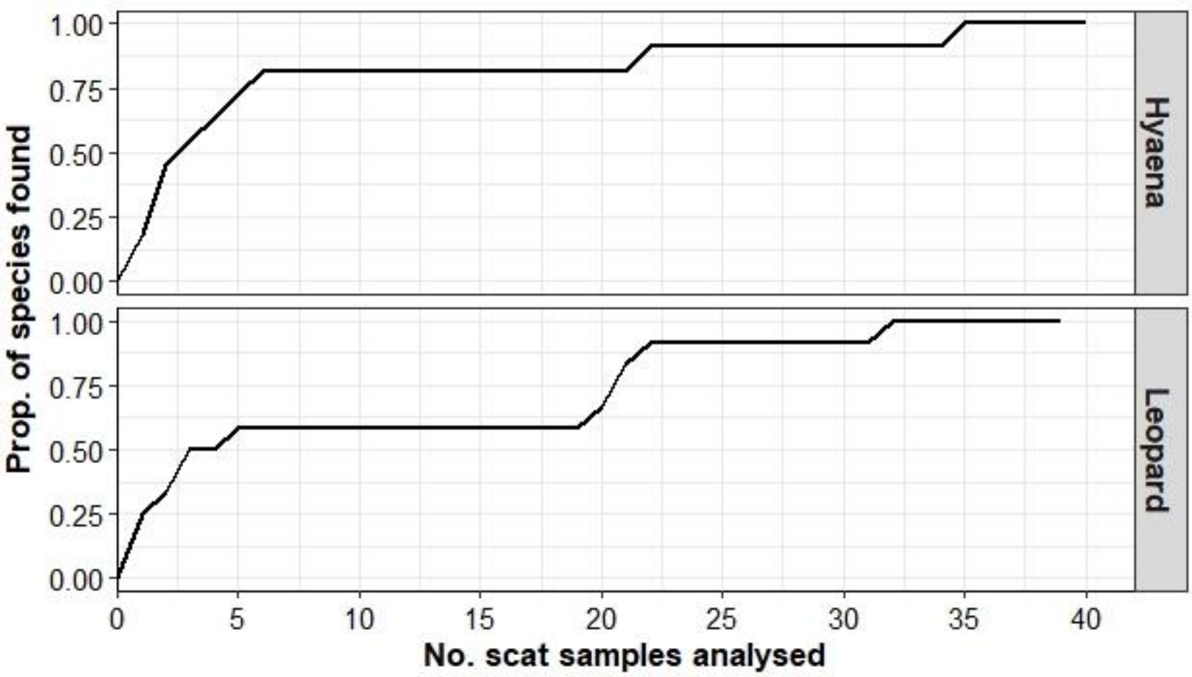

Figure 6.2. Cumulative curves showing the proportion of species identified from scat analysis for leopard and hyaena in Kasungu National Park, Malawi.

6.3.1 Dietary composition and biomass

Twelve different prey items were recorded in leopard faecal samples, with a mean of 3.13 (SD ± 1.10) prey items per sample. Based on CFO, the most frequently found prey items in leopard diet were common duiker (25.51%; Table 6.1), bushbuck (21.72%), puku (18.46%) and kudu (16.77%). 11 different prey items were recorded in hyaena faecal samples, with a mean of 2.65

(SD ± 0.92) prey items per sample. The most frequently identified prey items for hyaena, based on CFO, were kudu (25.43%), *suidae* spp. (21.05%) and common duiker (21.25%).

Biomass calculations revealed that over 80% of leopard diet was comprised of bushbuck (23.06%; Table 6.1), common duiker (21.79%), puku (20.49%) and kudu (18.93%). For hyaena, kudu (28.71%), *suidae* spp. (22.78%), common duiker (16.80%) and reedbuck (11.18%) comprised approximately 80% of the biomass consumed. Medium-sized prey were the most important prey size group for leopard, contributing 46.25% of the biomass consumed (Figure 6.3). For hyaena, the medium (40.48%) and large (40.52%) prey size groups contributed equally to biomass consumption.

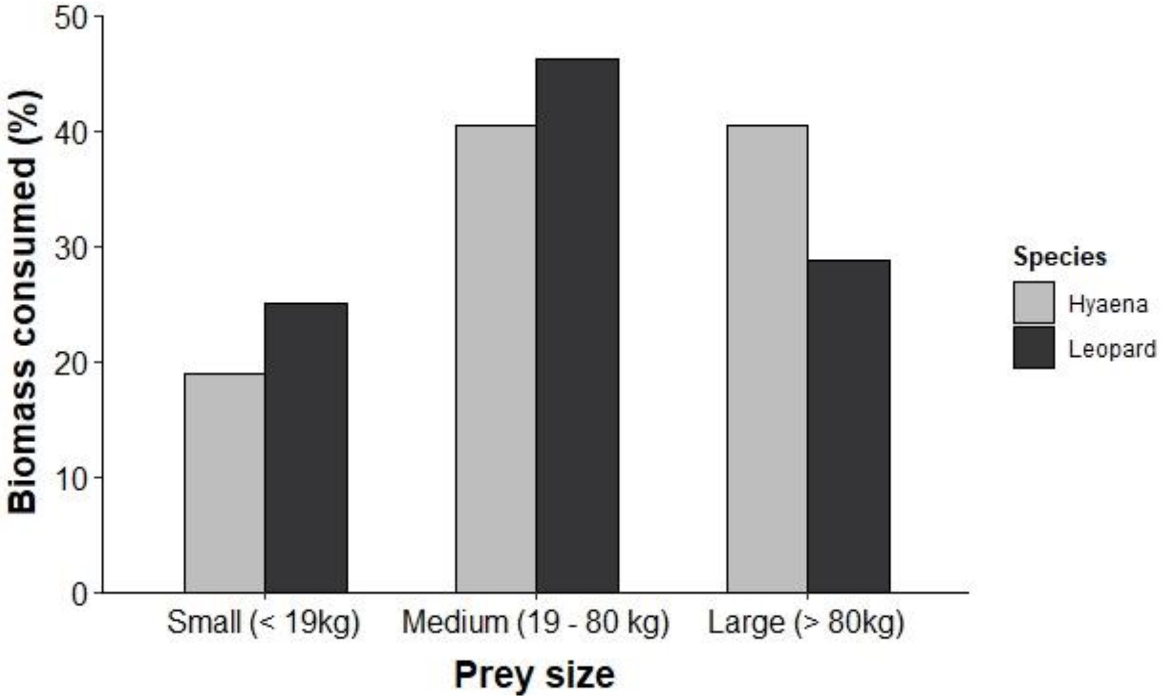

Figure 6.3. The contribution (%) of prey size groups to the diet of leopard and spotted hyaena in Kasungu National Park, Malawi, based on relative biomass consumed. The prey size classes used were taken from Pitman *et al.* (2012).

Table 6.1. Frequency of occurrence (FO) and corrected frequency of occurrence (CFO) of prey species found in faecal samples of leopard and spotted hyaena in Kasungu National Park, Malawi. Biomass calculations, based on the models of Chakrabarti et al. (2016), are also presented, where Y is the biomass consumed per scat, B is the total biomass consumed in kg, and R is the relative contribution of individual prey items to overall biomass consumption.

	Leopard (n = 39)					**Spotted hyaena (n = 40)**				
Prey Species	FO (%)	CFO (%)	Y	B (kg)	R (%)	FO (%)	CFO (%)	Y	B (kg)	R (%)
Bushbuck, *Tragelaphus sylvaticus*	29.82	21.72	1.65	35.73	23.06	4.89	5.48	1.94	10.64	5.60
Common duiker, *Sylvicapra grimmia*	26.74	25.51	1.32	33.77	21.79	21.55	21.25	1.50	31.91	16.80
Dwarf mongoose, *Helogale parvula*	1.54	2.10	0.45	0.95	0.61	-	-	-	-	-
Eland, *Taurotragus oryx*	-	-	-	-	-	4.89	4.23	2.14	9.07	4.78
Elephant, *Loxodonta africana*	-	-	-	-	-	0.29	1.25	2.15	2.68	1.41
Kudu, *Taurotragus strepsiceros*	17.48	16.77	1.75	29.33	18.93	23.28	25.43	2.14	54.53	28.71
Puku, *Kobus vardonii*	14.91	18.46	1.72	31.75	20.49	0.29	0.83	2.07	1.72	0.91
Rodentia spp.	0.26	0.44	0.77	0.34	0.22	-	-	-	-	-
Sable, *Hippotragus niger*	4.88	8.69	1.75	15.20	9.81	5.75	4.98	2.14	10.68	5.62
Savanna hare, *Lepus victoriae*	0.26	0.44	0.71	0.31	0.20	4.02	3.75	0.81	3.04	1.60
Southern reedbuck, *Redunca arundinum*	0.26	0.64	1.66	1.11	0.71	8.33	10.18	2.09	21.25	11.18
Suidae spp.	0.26	0.44	1.65	0.75	0.49	26.44	21.05	2.06	43.27	22.78
Vervet monkey, *Chlorocebus pygerythrus*	-	-	-	-	-	0.29	1.25	0.92	1.15	0.60
Yellow baboon, *Papio cynocephalus*	2.57	2.97	1.12	3.41	2.20	-	-	-	-	-
Goat, *Capra hircus*	1.03	1.49	1.51	2.32	1.50	-	-	-	-	-

6.3.2 Dietary overlap and niche breadth

Across all prey items, dietary composition overlapped significantly between leopard and hyaena (O_{ab} = 0.65). When dietary composition was split by prey size groups, leopard and hyaena displayed significant levels of overlap for small (O_{ab} = 0.97) and large (O_{ab} = 0.95) prey items, but dietary overlap was lower for medium-sized prey species (O_{ab} = 0.22). In total there were eight prey species found in both leopard and hyaena faecal samples: four species were preyed on exclusively by leopard and three by hyaena. Leopard exhibited a lower dietary niche breadth (B_s = 0.33) than hyaena (B_s = 0.43), indicating that leopard had a more specialised diet.

6.4 Discussion

Resource partitioning and niche differentiation are important strategies that allow carnivore communities to coexist (Caro & Stoner, 2003). For example, dietary partitioning is a common strategy that may facilitate sympatry between competing carnivores, reducing the potential for interspecific competition (du Preez *et al.* 2017). Nevertheless, competition for resources can increase levels of intraguild competition, which can be exacerbated when prey abundance is depleted, and, subsequently, amplifies incidents of direct interaction (Harihar *et al.* 2011). The results of this study confirmed the prediction that leopard and hyaena shared a significant level of dietary overlap in KNP (O_{ab} = 0.65). Contrary to our prediction, overlap between leopard and hyaena was lower for medium-sized prey items (O_{ab} = 0.22), with both predators utilising different prey species within this weight range. Dietary overlap was considerably higher in small (≤ 19kg) and large (> 80kg) prey weight groups (O_{ab} > 0.95 in both), increasing the potential for exploitation competition.

Dietary overlap between leopard and hyaena in KNP was in accordance with recorded levels in another Malawian protected area, Majete Wildlife Reserve (O_{ab} = 0.61; Briers-Louw & Leslie, 2020). Although, in contrast with other studies across the species' range, overall estimates of dietary overlap in KNP were lower than previous comparisons (e.g., $O_{ab} = 0.91$ in both Mbizah *et al*. 2012 and Comley *et al.* 2020). Chapter Five has previously shown that the spatiotemporal dynamics of leopard and hyaena in KNP are positively associated with the presence of prey and competing carnivores, thus increasing the likelihood of interaction (Davis *et al*. 2021b). The findings of Chapter Six, therefore, add further evidence of potentially high levels of competition between the two species. Increased competition for prey can lead to greater levels of interference and exploitation competition between predators (Harihar *et al.* 2011; Périquet *et al*. 2015) and have direct consequences on population density, behaviour and survival (e.g., Mondal *et al*. 2012). As the dominant competitor, hyaena are a key source of kleptoparasitic behaviour across the leopards' range and are responsible for stealing up to 10% of leopard kills (Balme *et al*. 2017). Kleptoparasitism can have negative effects on reproductive success and individual fitness (Krofel *et al*. 2012; Balme *et al*. 2017), whilst direct interaction with hyaenas is a source of mortality in leopard populations (Swanepoel *et al.* 2015). Subsequently, the potential for increased levels of competition and interaction between remaining leopard and hyaena populations in KNP is a cause for conservation concern.

Despite high levels of dietary overlap, large carnivores can often mitigate intraguild competition by preferentially selecting prey in different weight groups (e.g., Andheria *et al.* 2007; du Preez *et al*. 2017). Consumption of medium-sized (19-80kg) prey comprised over 40% of the total biomass in both leopard and hyaena diet, however, the two carnivores utilised different prey species within this weight range, thus reducing levels of dietary overlap. Kudu were an important large-bodied prey item for both leopard and hyaena and was the only species >80kg that contributed more than 10% of the consumed biomass to the diet of either carnivore. In previous studies, hyaena have preferentially selected larger prey items (e.g., Hayward, 2006; Briers-Louw & Leslie, 2020). Therefore, increasing the abundance and diversity of larger prey species should be a management priority to mitigate interspecific competition between hyaena and leopard. The recent reintroduction of waterbuck (*Kobus ellipsiprymnus*), a preferred prey of hyaena in previous studies (e.g., Rduch, 2016; Briers-Louw & Leslie, 2020), and the supplementation of other large mammal species in KNP (IFAW, 2020) should be seen as important first steps in this process.

Bushbuck and common duiker were the most frequently selected prey by leopard in KNP, in accordance with the preferred prey species identified in a range-wide study by Hayward *et al.* (2006). The more specialised diet and narrower niche breadth of leopard, compared to hyaena, also concurs with the findings of recent studies (e.g., Briers-Louw & Leslie, 2020; Comley *et al*. 2020). In some human-disturbed environments where prey has been depleted, leopard have been found to switch to smaller-bodied prey species, such as rodents (e.g., Henschel *et al*. 2011; De Luca & Mpunga, 2018; Havmøller *et al.* 2020). However, the greater contribution of medium-sized prey to leopard diet, observed in this study, implies that this dietary switch has not occurred in KNP. Nevertheless, the importance of puku (average prey mass (kg): 47.25) in the leopard's diet could be a result of geographic bias in scat sample collection. As puku prefer wetland and riverine habitats (Rduch & Jentke, 2021), the species is restricted to a core area of KNP centred around the permanent water at Lifupa Dam (Macpherson, 2015). Subsequently, puku are unlikely to feature in the diet of individual leopards outside of this core area, particularly leopards occupying territories around the boundaries of KNP. Future studies would benefit from increased sampling efforts around the park edges to improve estimates of dietary composition.

Across their geographic range, hyaena prefer medium- to large-bodied prey in the 56-182kg weight category (Hayward, 2006; Holekamp & Dloniak, 2010). As medium- and large-bodied prey items contributed equally to the relative biomass consumption in hyaena diet in KNP, our results are largely in accordance with the range-wide review of Hayward (2006). The high occurrence of kudu and suidae spp. also corresponds with previous findings in Malawian protected areas (Briers-Louw & Leslie, 2020), miombo woodlands (Rduch, 2016) and across the species' geographic range (Hayward, 2006; Mbizah *et al*. 2012; Comley *et al*. 2020). The wider dietary niche breadth of hyena in KNP, compared to the resident leopard population, highlights the more unselective and flexible nature of hyaena predation, as observed in Hayward (2006) and Périquet *et al*. (2015). Whilst hyaena predation strategies are often adaptable, small prey items are not as frequently selected as other prey weight ranges (Holekamp & Dloniak, 2010). For example, Rduch (2016) and Comley *et al*. (2020) found that hyaena did not consume any prey items below 30kg in weight. In this study, small prey items comprised a significant proportion of consumed biomass in hyaena diet (~20%). This may indicate an increased reliance on small prey items in KNP, as has been observed in other studies where prey abundance has been depleted (e.g., Creel *et al*. 2018). There was a significant level of dietary overlap with leopard for small prey items (O_{ab} = 0.97), with common duiker representing the majority of biomass consumed by hyaena within this weight range. As common duiker is a key prey species for leopard in KNP, further utilisation of small prey could increase levels of interspecific competition between the two species.

The total number of scats available for analyses in this study could have limited inference. For example, Trites and Joy (2005) recommended a minimum sample size of 59 faecal samples to broadly describe a species' site-specific diet. However, previous studies have found that ~30 samples are sufficient to detect most prey items (e.g., Breuer, 2005) and as both sample sizes reached an asymptote, this study was adequate for providing an initial insight into dietary composition and overlap. Whilst all scats were collected and identified to criteria frequently used in dietary studies, there is potential for scats to be misidentified at species level (Morin *et al*. 2016). For example, Havmøller *et al*. (2020) used similar criteria to identify leopard scats in Tanzania through DNA metabarcoding, finding that 27.5% of collected samples originated from hyaena and serval (*Leptailurus serval*) or could not be identified to species level.

Misidentification of samples could lead to incorrect conclusions regarding prey preference or dietary niche breadth, potentially misinterpreting species' dietary adaptability or levels of interspecific competition (Morin *et al*. 2016). As hyaena samples in our study were primarily collected from latrine sites, it is unlikely that these could be misidentified as leopard scats. In addition, the absence of other large carnivores (i.e., lion) in KNP means it is unlikely that hyaena faecal samples were incorrectly identified. However, it is acknowledged that, despite the use of standardised criteria, the issue of misidentification could limit inference from leopard scats, with both caracal (*Caracal caracal*) and serval present in KNP. It is recommended that future studies utilise the DNA metabarcoding approach of Havmøller *et al*. (2020), where logistical and financial restraints allow, to minimise the risk of incorrect scat classification and improving the certainty with which prey remains can be identified.

Recent studies have indicated that leopard diet shows varying levels of specialisation, both between sexes and at the individual level (Voigt *et al*. 2018; Balme *et al*. 2020). Female leopards often demonstrate a wider dietary niche than male conspecifics but are more reliant on small prey items (Voigt *et al*. 2018). In contrast, male leopards often display a greater degree of specialisation and a preference for larger prey items (Pitman *et al*. 2013; Balme *et al*. 2020). Both foraging tactics, individual specialisation and targeting of smaller prey, can have negative consequences for population health. For example, Balme *et al*. (2020) found that males with more specialised diets occupied territories with fewer females, whilst cub productivity and survival to independence was lower than in areas with more generalist males. In addition, hunting smaller prey items can have implications for individual fitness and energy expenditure, as animals are forced to hunt more frequently, whilst balancing metabolic demands (Carbone *et al*. 2007; Creel *et al*. 2018). The low leopard population density in KNP (Davis *et al*. 2021a) and observed sex-specific temporal partitioning (Davis *et al*. 2021b), means that further research into dietary specialisation between leopard sexes could be beneficial to future conservation management. These data could be collected using satellite collars on leopards and the investigation of GPS clusters of locations to identify kill sites (Martins *et al.* 2011; Pitman *et al.* 2014). However, these methods are often limited by small sample sizes and are biased towards larger prey items (Jansen *et al.* 2019). Alternatively, stable isotype analysis from whisker samples could be used (see Voigt *et al.* 2018) to determine sex-specific dietary specialisation. However, as both methods require live capture, their use in KNP could be logistically challenging and result in limited sample sizes.

This study has shown that there is a high degree of dietary overlap between leopard and hyaena and provides a valuable understanding of large carnivore dietary ecology and overlap in KNP. These findings provide further evidence that interspecific competition between remaining carnivore populations could have negative consequences for local conservation management. Although, it should be noted that a high degree of dietary overlap does not necessarily translate into increased levels of competition (Mbizah *et al.* 2012). Nevertheless, measures of dietary overlap do provide indirect evidence that competition is likely within the carnivore guild and, as direct measures of competition are often difficult to quantify in cryptic carnivore species, these metrics are often the only viable option to inform management decisions (Vanak & Gompper, 2009; Rduch, 2016). Ongoing efforts in KNP to restore large mammal prey populations and mitigate prey depletion (IFAW, 2020) will help to alleviate the pressures of interspecific competition observed in this study. Continued monitoring of large carnivore diets in KNP is recommended, as these data can provide a valuable indicator for levels of interspecific competition. Further research into individual specialisation and leopard sex-specific diets will help to inform local conservation management and provide a wider insight into leopard dietary adaptation in human-disturbed environments.

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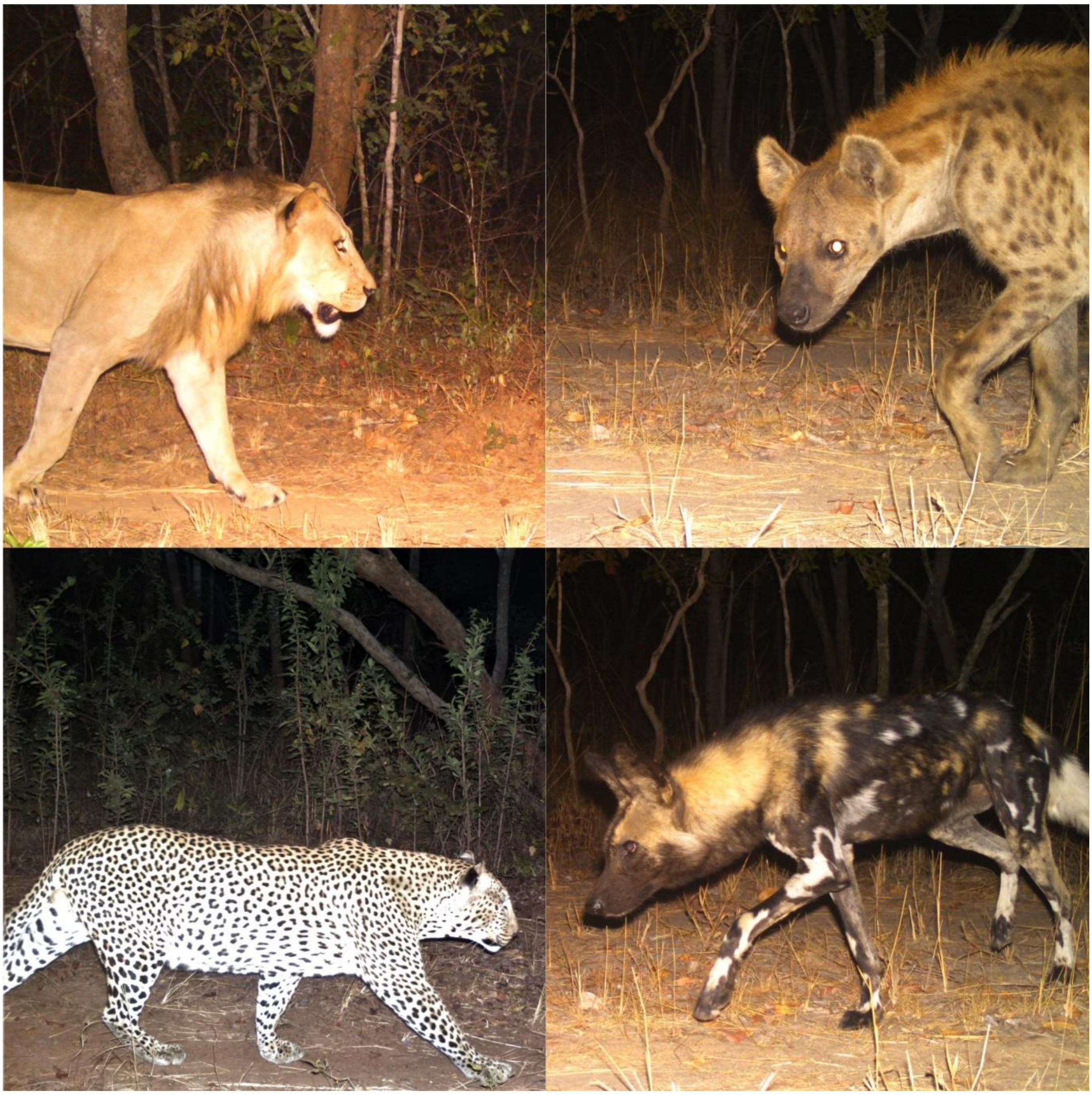
CHAPTER SEVEN

Discussion



CHAPTER SEVEN: Discussion

7.1 Synopsis

Large carnivores play an integral role in maintaining biodiversity and ecosystem functioning, whilst providing positive economic and social effects, such as tourism revenue and public health benefits (Ripple *et al*. 2014; O'Bryan *et al*. 2018). However, the continued decline in protected area health (Jones *et al*. 2018), increasing levels of human disturbance (Darimont *et al*. 2015) and the vulnerability of large carnivores to environmental change (Cardillo *et al*. 2005) mean that they have suffered substantial population decline and geographic range contraction (Ripple *et al*. 2014; Di Minin *et al*. 2016). Despite widespread acknowledgement of large carnivore population decline, robust assessments of population density and guild dynamics are crucially lacking, particularly in areas of high human disturbance where these data are often most needed (Jacobson *et al*. 2016; Elliot & Gopalaswamy, 2017; Rafiq *et al*. 2020b). Subsequently, studies that investigate the status and behavioural ecology of large carnivores in the context of elevated anthropogenic disturbance are necessary to inform effective conservation management (Balme *et al*. 2014; Sévêque *et al*. 2020).

This thesis helps to fill two knowledge gaps identified as priorities for large carnivore conservation, 1) provide robust estimates of large carnivore population density in areas identified as data deficient, and 2) investigate large carnivore guild dynamics in areas of increased human disturbance. In **Chapter Two**, using spotted hyaena as a model species, I have provided a novel assessment of current survey methodologies for estimating large carnivore population density and provided a comprehensive argument for improving range-wide population estimates through greater utilisation of SCR methods. **Chapter Three** has summarised the issues threatening protected areas in Malawi and provided a rationale for the selection of KNP as a study site. **Chapter Four** highlights the application of SCR to large carnivores and provides novel estimates of both spotted hyaena and leopard density in KNP. Density estimates for spotted hyaena and leopard are the first for KNP and, for leopard, the first estimates in Malawi and a miombo woodland habitat, thereby addressing a key knowledge gap in the leopards' geographic range. These baseline density estimates are a crucial first step for continued monitoring of large carnivore populations in KNP, providing an important metric for evaluating the impact of ongoing conservation initiatives. In addition, the application of SPIM (Augustine *et al*. 2018) in **Chapter Four**, addresses the issue of uncertainty in individual identification from single-station camera trap surveys, advocating the wider use of SPIM in areas that are currently data deficient for large carnivores. **Chapters Five** and **Six** have provided a valuable first insight into the intraguild dynamics of leopard and spotted hyaena in KNP, across the three niche axes of space, time and resource partitioning. The interspecific dynamics between leopard and spotted hyaena have previously been identified as an overlooked area of large carnivore dynamics (Vanak *et al*. 2013; Rafiq *et al.* 2020b) and, in the absence of a resident lion population, KNP has provided a novel site to investigate guild dynamics and behavioural responses to anthropogenic disturbance.

In this chapter I will discuss the conservation implications and potential avenues for further research identified from this study, both in KNP and across the wider landscape.

7.2 Status of large carnivores in KNP and the need for wider survey efforts

7.2.1 Leopard density

Chapter Four produced the first leopard density estimates for KNP, Malawi and a miombo woodland habitat. Between 2016 and 2018, leopard density was estimated at 1.9 (± SD 0.19) individuals/100km^2, representing one of the lowest recorded density estimates for leopard in sub-Saharan Africa (Table 7.1). Leopard density in KNP is comparable to human-impacted landscapes and low-productivity habitats (e.g., Henschel *et al.* 2011; Devens *et al*. 2018; Mann *et al*. 2020). However, as the KNP estimates are from a single survey area, and are the first in a miombo woodland, it is difficult to make inferences as to why estimates are low in KNP. Nevertheless, based on prior knowledge of the underlying drivers of leopard density and distribution, it is possible to make some predictions as to the underlying causes of the low estimates found in KNP. Habitat productivity is thought to be a key driver of leopard density (Balme *et al.* 2007; Jacobson *et al*. 2016) and miombo woodlands are a relatively low-productivity habitat, supporting ungulate biomasses at only 20-30% of comparable savanna habitats with similar rainfall levels (Frost, 1996). Thus, leopard density in miombo woodlands is likely to be lower than comparable savanna habitats, where most available leopard density estimates are recorded. In addition, decline of wild prey is recognised as a major threat to leopard populations across their geographic range (Jacobson *et al*. 2016). For example, loss of wild prey to bushmeat hunters in the Congo Basin caused a 78% reduction in leopard population density in areas under the most intense poaching pressure (Henschel *et al*. 2011). Consequently, although leopard populations are likely to exist at naturally low densities in miombo woodlands, the observed decline of sympatric carnivores and large mammal populations in KNP (Munthali & Mkanda, 2002; Mésochina *et al*. 2010) suggests that anthropogenic pressures, such as bushmeat poaching and habitat loss, have contributed to the low leopard density. Protecting remaining prey species and increasing large mammal populations is, therefore, a key step in recovering the KNP leopard population.

Table 7.1. Published leopard density estimates (per 100km^2), using SCR methods, from sub-Saharan Africa between 2010-present. The habitat type and protected status of the study site are provided, and estimates are in order from highest to lowest. Estimates from this study are in bold.

Study Site	Density	Protected area?	Habitat	Reference
Okonjima Nature Reserve, Namibia	14.51	Yes	Acacia thornveld	Noack et al. (2019)
Mpala Ranch, Laikipia County, Kenya	12.03	No	Bushland/open woodland	O'Brien & Kinnaird (2011)
Sabi Sands Game Reserve, South Africa	11.8	Yes	Savanna/woodland	Balme et al. (2019)
Phinda Game Reserve, South Africa	11.25	Yes	Savanna/woodland	Balme et al. (2010)
Western Soutpansberg, South Africa	10.73	No	Montane woodland	Chase Grey et al. (2013)
Western shores, St Lucia, South Africa	8.4	Yes	Coastal savanna	Ramesh et al. (2017)
Farm matrix, Waterberg Biosphere, South Africa	6.59	No	Mountain bushveld	Swanepoel et al. (2015)
Multiple (24) sites across South Africa	6.3[a]	Yes	Mixed habitats	Rogan et al. (2019)
Serengeti National Park, Tanzania	5.57[b]	Yes	Savanna/woodland	Allen et al. (2020)
Lapalala Wilderness, South Africa	5.35	Yes	Mountain bushveld	Swanepoel et al. (2015)
Bubye Valley Conservancy, Zimbabwe	5.28	Yes	Savanna/woodland	du Preez et al. (2014)
Welgevonden Game Reserve, South Africa	4.56	Yes	Mountain bushveld	Swanepoel et al. (2015)
Udzungwa Mountains, Tanzania	4.22	Yes	Mixed woodlands	Havmøller et al. (2019)
Western Soutpansberg, South Africa	3.65	No	Montane woodland	Williams et al. (2017)
Phinda Game Reserve, South Africa	3.53[b]	Yes	Savanna/woodland	Braczkowski et al. (2016)
Bubye Valley Conservancy, Zimbabwe	2.79	Yes	Savanna/woodland	du Preez et al. (2014)
Xonghile GR, Mozambique	2.6	Yes	Sandveld	Strampelli et al. (2021)
Non-protected land, South Africa	2.49	No	Savanna/woodland	Balme et al. (2010)
Kasungu National Park, Malawi	**1.9**	**Yes**	**Miombo woodland**	**This study**
Ndumo Game Reserve, South Africa	1.6	Yes	Savanna/woodland	Ramesh et al. (2017)
Little Karoo, South Africa	1.26	Both	Semi-arid fynbos	Mann et al. (2020)
Western Cape, South Africa	1.18	Both	Mixed habitats	Devens et al. (2021)
Eastern/Western Cape, South Africa	0.95[a]	Both	Mixed habitats	Devens et al. (2018)

[a] Mean density across multiple sites; [b] Mean density from multiple estimates.

Encouragingly, despite the low population density in KNP, the minor variation between survey years suggests a stable trend in leopard density. I acknowledge that a three-year survey period is a relatively short time-period to make inferences on populations trends, however, previous studies have identified significant trends in leopard density across similar temporal scales. For example, using annual camera trap surveys, Williams *et al*. (2017) found that leopard density in the Soutpansberg Mountains, South Africa, decreased by 44% within a four-year survey period. Despite the apparent stable leopard density in KNP, the low-density estimate for leopard is of conservation concern, as the population is susceptible to stochastic events, poaching and other conflict with humans. KNP has been subject to high levels of historic poaching (Bhima *et* al. 2003; Macpherson, 2015) and evidence of both leopard poaching and other anthropogenic mortality were observed during the study (Figure 7.1). Leopard reproductive success is often naturally low and, as a result, population recovery can be a gradual process (Balme *et al*. 2013). However, increasing the prey populations and improving law enforcement should help to recover the KNP leopard population. In addition, further research assessing leopard survival rates and potential threats are advised. The loss of resident leopard populations from two PAs in Malawi, namely Majete Wildlife Reserve and Liwonde National Park (Briers-Louw *et al*. 2019), should serve as a warning that, despite their adaptability and resilience to anthropogenic threats, there is a risk of localised extirpation if conservation management cannot address the causes of decline.

Figure 7.1. Evidence of leopard poaching and anthropogenic mortality in KNP. A) Two leopard skins that were recovered by KNP law enforcement in 2016. Image credit: Mike Labuschagne. B) Leopard killed in a village bordering KNP after killing livestock and attacking community members. Image credit: Amanda Harwood.

Data from this thesis are the first empirical estimates for a leopard population in Malawi and challenge assumptions made by Martin and de Meulenuer (1988), who modelled previously published leopard estimates and mean annual rainfall to predict leopard densities across sub-Saharan Africa. Using this predictive modelling approach, Martin and de Meulenuer (1988) estimated an average density of 0.10 leopards/km^2 (10 leopards/100km^2) in miombo woodlands and a country-wide population of 4,530 leopards in Malawi. The overly simplistic modelling approach and accompanying estimates have been widely rejected in literature (Norton, 1990; Jenny, 1996) for omitting critical factors, such as anthropogenic mortality and prey availability, from the model and relying on the assumption that leopards occur at maximum potential densities in all available habitats (Balme *et al.* 2010). Results of this thesis add further evidence that these estimates need to be revised and, whilst Malawi does not have a trophy hunting industry, other countries (e.g., Tanzania/Mozambique) that comprise miombo woodland habitat and have been subject to high levels of anthropogenic disturbance, still utilise the Martin and de Meulenuer (1988) estimates to set trophy hunting quotas (Strampelli *et al.* 2020). Unsustainable trophy hunting is a primary threat to leopard populations (Jacobson *et al.* 2016) and a paucity of local population data is a key factor limiting the ability to set sustainable quotas (Balme *et al.* 2010). The results of **Chapter Four** suggest that the leopard density estimate of Martin and de Meulenuer (1988) for Malawi and miombo woodlands is likely to be inaccurate. I suggest that further surveys be conducted in miombo woodlands to encourage informed decision-making and provide evidence-based results for use in conservation management strategies (Balme *et al.* 2014; Strampelli *et al.* 2021).

7.2.2 Spotted hyaena density

Chapter Four estimated spotted hyaena density between 2016 and 2018 to be 1.15 (± SD 0.42) individuals/100km^2, providing the first density estimate for KNP. Density estimates between survey years suggest a minor increase in the KNP spotted hyaena population between 2016 and 2018. As highlighted in **Chapter Two**, SCR models have not been used to estimate spotted hyaena density as widely as they have for other sympatric and individually identifiable carnivores, such as leopard. Subsequently, the estimates presented here are some of the first to use SCR methods (Table 7.2). The estimates from this study are some of the lowest spotted hyaena density estimates in the available literature, comparable to arid environments (e.g., Fouché *et al*. 2020; Table 7.2) and considerably lower than the only previously reported density of 31 hyaena/100 km^2 from a miombo woodland (Creel & Creel, 2002). Prey availability has a strong regulating effect on spotted hyaena demographics and, where prey populations decrease, there is often a subsequent decline in spotted hyaena abundance (Périquet *et al*. 2015). For example, a 70% decline in the spotted hyaena population size in Ngorongoro Crater, Tanzania, between the mid-1960s and mid-1990s, was attributed to a substantial decline in preferred prey (Höner *et al*. 2005). Therefore, it is likely that the reduction in prey populations in KNP (Munthali & Mkanda, 2002; Macpherson, 2015) has limited the population density of spotted hyaena. As previously recommended, restoring and protecting prey populations in KNP will be the most effective measure to increase spotted hyaena density.

Table 7.2. Spotted hyaena density estimates (per 100km^2), using SCR methods, from sub-Saharan Africa. The habitat type and protected status of the study site are provided. Estimates from this study are in bold.

Study Site	Density	Protected Status?	Habitat	Reference
Central Tuli Block, Botswana	14.9	Yes	Riverine woodlands	Vissia et al. (2021)
Moremi Game Reserve, Botswana	10.1	Yes	Savanna grassland/mopane woodland	Rich et al. (2019)
Moremi Game Reserve and management areas, Botswana	6.5[a]	Yes	Acacia and mopane woodlands	Rafiq et al. (2019)
Mpala Ranch, Kenya	4.93	No	Savanna woodland	O’Brien & Kinnaird (2011)
Majete Wildlife Reserve, Malawi	2.69	Yes	Savanna woodland	Briers-Louw (2017)
Kasungu National Park, Malawi	**1.15**	**Yes**	**Miombo woodland**	**This study**
Tsauchab River Valley, Namibia	0.85	No	Arid savanna	Fouche et al. (2020)

[a] approximate density estimated from figure - actual estimate not provided.

Chapter Four has added further evidence that estimates of multiple species are possible from camera trap surveys, in accordance with previous studies (O’Brien & Kinnaird, 2011; Rich *et al*. 2019). As highlighted in **Chapter Two**, camera trap surveys have been routinely used to estimate density for felid species. However, the use of SCR techniques to estimate spotted hyaena density, or provide estimates for multiple species, from camera trapping surveys has not been as widely adopted. For example, Green *et al*. (2020) found that 82% of density estimates in camera trap surveys were of felids and 91.6% of studies focused on only one species. In accordance with the recommendations in **Chapter Two**, I advocate that further efforts are made to report density estimates for multiple species when using camera trap survey techniques. In particular, SCR models have been underutilised for estimating spotted hyaena density and increased reporting of spotted hyaena density from camera trap surveys would be beneficial for the species' conservation management. As spotted hyaena are widely distributed across Africa, and often occur at higher densities than sympatric carnivores (Watts & Holekamp, 2008; Rich *et al.* 2019), there is scope for increased reporting of density estimates from camera trap surveys, where the species could previously have been overlooked.

Wire-snaring is a popular method used by bushmeat poachers to catch wild prey (Mudumba *et al*. 2021) and, as highlighted in **Chapter Three**, the method is prevalent in Malawian PAs. However, due to their non-selective nature, the deployment of wire snares can result in significant levels of by-catch and are increasingly viewed as a key source of mortality for large carnivores (Becker *et al*. 2013; Loveridge *et al.* 2020; Mudumba *et al*. 2021). For example, one in five adult male lions in South Luangwa National Park, Zambia, have been recorded as snared (Becker *et al.* 2013). This study recorded evidence of snared spotted hyaena in every survey year (Figure 7.2) and, therefore, it is likely that wire-snaring represents an important threat to large carnivores in KNP. Wire-snaring appears to be a particular threat to spotted hyaena, with spotted hyaena representing 92% of large carnivore snare records in the Zimbabwean section of the Kavango-Zambezi Transfrontier Conservation Area (Loveridge *et al*. 2020). Although there was no evidence of leopard being caught in wire snares in KNP, this could be due to their smaller body size, which makes it harder to break out of snares at the trap site (Loveridge *et al*. 2020). There were insufficient data to investigate the demographic impacts of wire-snaring on the KNP spotted hyaena population, and further investigation into the effect of snaring by-catch on large carnivores would be beneficial, along with research into the spatial and temporal trends of wire-snaring activity. In addition, the recruitment of additional law enforcement personnel in KNP (IFAW, 2020) should allow more intensive snare patrols, which would help clear existing snares and assist in the identification of snaring hotspots to inform effective protocols.

Figure 7.2. Evidence of wire-snare injuries on spotted hyaena during A) 2015; B) 2016; C) 2017, and D) 2018. Note that left-sided spot patterns on images A-C are of different individuals, indicating that wire-snare injuries are prevalent in the population.

7.2.3 Status of other large carnivores

The results of **Chapter Four** suggest that lion and wild dog are no longer resident in KNP. Historic populations of lion and wild dog are known to have occurred in KNP (Woodroffe *et al*. 1997; Mésochina *et al*. 2010), suggesting a period of high anthropogenic disturbance that resulted in the loss of these resident populations. Lion and wild dog are both sensitive to anthropogenic disturbance, with their wide-ranging behaviour, dependency on large-bodied prey and social structure limiting their behavioural flexibility (Everatt *et al*. 2019; Creel *et al*. 2020). This limited ability to persist in anthropogenically-impacted landscapes, when compared to leopard and spotted hyaena, could explain the decline of lion and wild dog populations in KNP.

Evidence collected in this study of a single male lion in 2017 and the same individual wild dog in 2017 and 2018, highlights the potential for dispersing individuals to move through the MZTFCA. Wild dogs require vast areas of connected habitat and often exhibit long-range dispersal events (e.g., Davies-Mostert *et al*. 2012; Cozzi *et al*. 2020), with such movements facilitating recolonisation and supporting viable populations at national and international scales (Creel *et al*. 2020). Similarly, dispersal is key to maintaining genetic diversity in the Zambian lion population, one of the few remaining strongholds for the species (Curry *et al*. 2019). I recommend that protection of the dispersal corridor between KNP and Lukusuzi National Park, Zambia, is prioritised to ensure that connectivity between KNP and the wider MZTFCA is maintained. Connectivity to the MZTFCA is critical to encourage recolonisation in KNP and, alongside ongoing initiatives to restore prey populations and improve law enforcement, could help to recover large carnivore populations in KNP. In addition, further information on the status of large carnivores in Lukusuzi National Park would be beneficial, as the park is largely data deficient and represents the key link between KNP and the wider network of Zambian PAs.

7.2.4 Application of SPIM

The use of SPIM in **Chapter Four**, to estimate density for leopard and spotted hyaena resulted in improved levels of precision. Compared to single-flank analyses, SPIM increased credible interval precision for leopard and spotted hyaena by 52% and 26%, respectively. Partial identity is a common problem for researchers (e.g., Rosenblatt *et al*. 2016; Mohamed *et al*. 2019; Strampelli *et al*. 2020) and, as density is a key metric used to inform conservation management decisions, any gain in precision should be of broad interest. In areas of low population density, single-flank captures can be linked with increased certainty (Augustine *et al*. 2018). Consequently, the benefits of SPIM are greater for large carnivore populations found at low densities, which are often populations in human-disturbed environments or areas in need of intensive conservation management. Furthermore, a review of SCR estimates from camera trapping methods by Green *et al*. (2020) suggested that researchers should try to maximise the number of individuals captured during surveys to increase the precision of estimates. SPIM could be a valuable tool in this respect, allowing researchers to deploy one camera per station, instead of the conventional dual-camera setup. This would effectively double the potential survey area that can be covered and, subsequently, sample a wider proportion of the study population. Estimating density for species of conservation concern is often hampered by the financial cost of robust survey methods (e.g., Alonso *et al*. 2015) and/or the difficulty of removing captured individuals from datasets that are already sparse (e.g., Mohamed *et al*. 2019). Therefore, SPIM offers potential solutions to common methodological and analytical problems (Augustine *et al.* 2018). I recommend the use of SPIM for studies where partial identities constitute a large proportion of the sampled population, or as a solution to logistical and/or financial limitations relating to camera trap deployment.

Large carnivores often exhibit sex-specific variation in space-use and detectability (e.g., Swanepoel *et al*. 2015; Fabiano *et al*. 2020) and previous studies have shown that incorporating this variability into SCR models can improve inference (Sollmann *et al*. 2011). In addition, further covariates of interest (e.g., prey availability) can be incorporated into SCR analyses to estimate within-patch variation in density (Ramesh *et al*. 2017; Allen *et al*. 2020). However, it is not currently possible to incorporate these additional models in SPIM, with only the null model, where detection rate and space use are constant, available in the *SPIM* package. As such, researchers should consider the trade-off between addressing the problem of partial identity in sampled individuals and utilising the additional suite of demographic and environmental covariates that can be modelled in more conventional SCR packages. However, if partial identities constitute a large proportion of available samples, it is advisable to focus on producing a robust density estimate, rather than drawing potentially unreliable inferences from additional analyses where individual identities are left unresolved. It should also be noted that the SPIM package was only recently developed, and it is intended that additional models incorporating covariates of interest, open populations and multiple sessions will be added over time (B. Augustine, pers. comm.).

7.2.5 The need for wider survey efforts

The estimates in **Chapter Four** are the first density estimates for KNP and represent an important baseline for future conservation monitoring in the region. However, the majority of Malawian PAs are still lacking data on the status of large carnivore populations and would benefit from research to establish baseline density estimates. Alongside KNP, Nyika National Park (NNP) and Vwaza Marsh Wildlife Reserve (VMWR), in the northern region of Malawi, comprise the Malawian section of the MZTFCA. Of the protected areas in Malawi with the highest protected status (national parks and game reserves), NNP and VMWR represent 39% of the total protected land in Malawi. Comprising a significant portion of protected habitat in Malawi and representing vital connectivity links to Zambia and the wider MZTFCA, both NNP and VMWR are, therefore, important PAs for large carnivore conservation. However, the two PAs have been the subject of limited conservation research, particularly for large carnivores. Similar to KNP, miombo woodland is the dominant habitat in VMWR and NNP (at lower levels). Both PAs also have a similar carnivore guild to KNP, with resident populations of leopard and spotted hyaena and evidence of dispersing lion (Byrne *et al.* 2019; Harwood *et al.* 2019; African Lion Database, 2020). Subsequently, NNP and VMWR offer important opportunities to, a) establish further baseline density estimates in Malawian PAs that are currently data deficient and of significant conservation value, b) provide additional density estimates in the understudied miombo woodland habitat, and c) further test the theories presented in this thesis on intraguild dynamics in a modified carnivore guild.

NNP would also represent a feasible study site to test recommendations presented in **Chapter Two** regarding the application of SCR models to call-in data to produce spotted hyaena density estimates. As SCR models are reliant on individual identification, the challenge of identifying spotted hyaena at call-in stations is a potential barrier to this novel survey technique, as spotted hyaena can be cautious when approaching call-in stations (e.g., Bauer, 2007; Kirsten *et al.* 2017). Whilst individual identification from call-in sites has been documented before (see Trinkel, 2009), to my knowledge, the application of SCR models to call-in data has not been tested. The open landscape of the Nyika plateau and personal observation of spotted hyaena response to audio playbacks in NNP could provide optimal conditions for trialling this novel method. A camera trap survey conducted simultaneously would be beneficial for comparing

SCR estimates from both methods, whilst also providing density estimates for leopard and other carnivores in NNP.

7.3 Intraguild dynamics in KNP

Niche partitioning between intraguild competitors (e.g., lion, leopard, spotted hyaena) requires further investigation, as contrasting results continue to emerge from different habitats (e.g., Hayward & Slotow, 2009; Balme *et al.* 2019; Havmøller *et al.* 2020b; Rafiq *et al.* 2020b). The localised loss of the resident lion population in KNP has offered a novel opportunity to test theories on guild dynamics and interspecific competition between remaining competitors, which is predicted to intensify and impact population demographics when community assemblage is altered (e.g., Périquet *et al.* 2015; M'soka *et al.* 2016). In addition, increased understanding of the spatiotemporal dynamics between leopard and spotted hyaena has been identified as a key knowledge gap in large carnivore guild dynamics (e.g., Rafiq *et al.* 2020b).

In **Chapter Five**, using a combination of co-detection modelling, time-to-event analyses, and temporal activity patterns from camera trap data, I have shown that detection of leopard and spotted hyaena is positively associated with the detection of preferred prey and competing carnivores. Mutual drivers of spatiotemporal behaviour increase the likelihood of interaction between leopard and spotted hyaena, and the heightened risk of interaction with intra- and inter-specific competitors could explain the additional temporal partitioning behaviour displayed by female leopards in this study. The estimates of dietary overlap presented in **Chapter Six** provide further evidence of potentially high levels of interspecific competition between leopard and spotted hyaena in KNP. The results of **Chapter Six** show that leopard and spotted hyaena share a significant level of dietary overlap (O_{ab} = 0.65). Dietary overlap was considerably higher in small (≤ 19kg) and large (> 80kg) prey weight groups ($O_{ab} > 0.95$ in both), increasing the potential for interference and exploitation competition in these prey weight ranges. However, this was mitigated, to some extent, by the utilisation of different prey species within the medium-sized (19-80kg) prey weight range, causing a reduction in dietary overlap ($O_{ab} = 0.22$).

7.3.1 Conservation implications of intraguild dynamics

The results of **Chapters Five** suggest that bottom-up factors (i.e., prey availability) have a regulating effect on large carnivore spatiotemporal behaviour in KNP, a finding that is in accordance with recent studies (e.g., Miller *et al*. 2018; Sogbohossou *et al*. 2018; Balme *et al*. 2019). Furthermore, the results of **Chapter Six** highlight that almost two-thirds of leopard and spotted hyaena dietary composition overlap. Subsequently, as overlap is high along the three niche axes, there is a risk of exploitative and interference competition between leopard and spotted hyaena. Shared drivers of spatiotemporal behaviour and competition for prey may represent points of inter-and intra-specific carnivore conflict, which could have negative consequences on density and survival (Caro & Stoner, 2003; Dröge *et al*. 2017). As both leopard and spotted hyaena are found at low densities in KNP, as highlighted in **Chapter Four**, the potential for high levels of intraguild competition may be a limiting factor in population recovery efforts, particularly for leopard as the subordinate competitor (Allen *et al*. 2020).

Previous studies have found that spotted hyaena have a strong competitive influence on leopard populations. For example, spotted hyaena were found to have a greater influence than lion on leopard ecology in both Sabi Sands (Balme *et al*. 2017; Balme *et al*. 2019) and Selati (Comley *et al*. 2020) Game Reserves, South Africa. As habitat generalists, spotted hyaena are often ubiquitous across PAs, making spatial avoidance of spotted hyaena difficult for competing carnivores (Balme *et al*. 2019). This seems apparent in KNP, with spotted hyaena detected on 83% of camera traps between 2016 and 2018 and the detection of both leopard and spotted hyaena associated with the presence of similar preferred prey species and competing carnivores

(Davis *et al.* 2021b). Instead, leopards often utilise tree-caching (hoisting and consuming their prey in trees) to reduce the risk posed by kleptoparasitism (Balme *et al*. 2017), and this may be a strategy used by leopards in KNP to mitigate competition with spotted hyaena. This hypothesis seems more probable for male leopards, who displayed a higher level of temporal overlap with spotted hyaena than female conspecifics in KNP, and are known to hoist more kills than female leopards (Balme *et al*. 2017). However, the extent to which leopards exhibit hoisting behaviour varies between populations and the degree to which tree-caching is used in KNP is unknown (Sunquist & Sunquist, 2002; Balme *et al*. 2017). In addition, tree-caching can still incur food costs and a potential loss of individual fitness. For example, Tarugara *et al*. (2021) found that spotted hyaena were present at 82% of leopard feeding events and the presence of spotted hyaena caused leopards to reduce their feeding time.

Detecting behavioural responses, such as alterations in spatial use or activity patterns, are often the first measurable reactions that animals show to anthropogenic disturbance and may be used as an early indicator of environmental stress (Ordiz *et al.* 2014; Gaynor *et al.* 2018). The increased levels of diurnal activity displayed by female leopards in **Chapter Five**, compared to male conspecifics and spotted hyaena, is in accordance with Havmøller *et al.* (2020b) and is only the second time sex-specific variation in activity has been documented for a leopard population. Furthermore, overall activity rates (time active over the diel cycle) for female leopards were ~20% higher than other large carnivores in KNP. These findings are interesting when compared to temporal activity in other large carnivore populations, where a shift towards nocturnal behaviour and a reduction in overall activity is often observed in areas of human disturbance and increased interspecific competition (e.g., Kolowski *et al.* 2007; Gaynor *et al*. 2018; Patten *et al*. 2019; Frey *et al*. 2020).

As highlighted in **Chapter Five**, the additional mechanism of temporal partitioning adopted by female leopards could have negative consequences for individual fitness and population demographics. For example, the higher rates of diurnal activity observed in female leopards could risk further exposure to sources of anthropogenic mortality, such as road traffic accidents, and increased levels of human interaction (Havmøller *et al*. 2020b). Increased rates of adult mortality are often implicated in population sinks and ecological traps (e.g., Balme, Hunter & Slotow, 2010; van der Meer *et al.* 2013) and, as such, further research into the demographic effects of female leopard spatiotemporal behaviour in KNP would be beneficial.

Niche partitioning and adaptive responses to interspecific competition often entail a food cost, such as reduced foraging time or limited access to certain prey sources (Oriol-Cotterill *et al*. 2015; Hertel *et al*. 2016). Previous research has shown that leopard diets can be sex-specific (Voigt *et al*. 2018; Balme *et al*. 2020) and vary between habitats (Hayward *et al*. 2006; Havmøller *et al.* 2020a). **Chapter Five** has indicated that female leopards adapt their temporal behaviour in KNP, likely to minimise intra-and interspecific competition, and this could have implications on diet and foraging behaviour that were not identified in **Chapter Six**. For instance, diurnal hunting and increased exposure to higher levels of human activity can result in reduced handling time of prey items (e.g., Kerley *et al*. 2002) and can lead predators to increase kill rates, inferring higher energetic costs, to compensate for reduced consumption (Smith *et al.* 2015). Whilst **Chapter Six** was able to provide a first insight into the composition and dietary overlap of leopard and spotted hyaena in KNP, further investigation into leopard sex-specific foraging behaviour would increase our knowledge of dietary strategies in leopard populations under environmental and interspecific pressures.

7.3.2 Potential for competitive release of spotted hyaena population

Current levels of interspecific competition and strategies for niche partitioning may be mitigated, in part, by the low densities of both leopard and spotted hyaena in KNP. Low population densities of competing carnivores have been suggested in previous studies (e.g., Creel & Creel 1996; Karanth *et al*. 2017; Hardouin *et al*. 2021) as a contributing factor that limits the pressure of interspecific competition. As discussed in **Chapters Four** and **Five**, ongoing conservation initiatives to boost prey populations and increase law enforcement efforts in KNP (IFAW, 2020) could provide the optimal conditions for competitive release of the spotted hyaena population. Previous studies have shown that spotted hyaena populations can fluctuate with prey availability (e.g., Höner *et al*. 2005; Périquet *et al*. 2015), and increased prey abundance also has benefits for cub survival and food acquisition (Watts & Holekamp, 2009). In addition, lions often have a regulating effect on spotted hyaena populations, with exploitation and interference competition from lions limiting spotted hyaena clan size (Périquet *et al*. 2015). The effect of competitive release from lions has been documented in previous studies (see M'soka *et al*. 2016 and Green *et al*. 2018), with these studies suggesting that high densities of spotted hyaena were attributable to the decline of lion populations and reduction in interspecific competition. Therefore, it is possible that similar population trends will be seen in KNP, if the causes of spotted hyaena population decline (i.e., reduced prey availability, direct/indirect poaching pressure) can be addressed and the presence of lion in KNP remains limited.

Predicting the impact of this hypothesised competitive release on sympatric carnivores and interspecific competition is difficult, as the impact on wider carnivore guild dynamics has yet to be investigated. However, the findings in **Chapter Five**, that the spatiotemporal dynamics of both leopard and spotted hyaena are driven by the presence of preferred prey and competing carnivores, suggest that an increase in the spotted hyaena population would have negative consequences for the KNP leopard population. Further evidence to support this theory can be found in Comley *et al.* (2020), who suggested that the declining leopard population in Selati Game Reserve, South Africa, was attributable to increased competition from spotted hyaena, with spotted hyaena found at a density almost four-times that of leopard. Consequently, continued monitoring of large carnivore demographics and intraguild dynamics in KNP are necessary to evaluate the impact of ongoing conservation initiatives. I recommend that camera trap surveys are continued annually to monitor large carnivore densities, assess population trends and analyse how spatiotemporal dynamics develop. Furthermore, PAs across Africa are predicted to come under increasing anthropogenic pressures, and similar reductions in the large carnivore guild are expected (e.g., the loss of lion from many PAs; Bauer *et al.* 2015). Monitoring of large carnivore dynamics in KNP may, therefore, provide valuable insights that are applicable to wider conservation management, as guild dynamics are altered, and could help inform conservation efforts in PAs undergoing similar periods of recovery.

7.3.3 Assessing seasonal variability in niche partitioning

One limitation of the findings in **Chapters Five** and **Six** is that seasonal variability in niche partitioning was unaccounted for. In a review by Sévêque *et al.* (2020), only 28% of studies accounted for seasonal variation in niche partitioning, however, 75% of the studies that did account for seasonal variability found that it altered carnivore dynamics. Recent studies by Amorós *et al.* (2020) and Périquet *et al.* (2021) have found seasonal variation in the interspecific dynamics of lion and spotted hyaena and, therefore, it is possible that there are seasonal differences in the dynamics between leopard and spotted hyaena in KNP. Previous studies have found that interference competition and niche partitioning between the African large carnivore guild increases during the dry season, when resources are often scarcer (e.g., Vanak *et al*. 2013; Périquet *et al.* 2021). As this study primarily covered the dry season in KNP it is, therefore, conceivable that the niche partitioning strategies exhibited are to facilitate coexistence when competition and risk of interaction is most intense. Tall seasonal grasses and limited road access means that camera trapping is logistically difficult to undertake in KNP during the wet season and results in limited sample sizes (pers. obs.). Therefore, incorporating seasonal variation into future studies would likely entail the deployment of VHF or satellite collars, similar to studies by Vanak *et al*. (2013) and Périquet *et al*. (2021). However, the financial costs for a collaring study would likely be higher than a camera trap survey (e.g., Caravaggi *et al*. 2017) and, given the low densities of leopard and spotted hyaena in KNP, could also result in small sample sizes.

7.4 Summary of recommendations

Chapter Seven has reviewed the findings of this study and the conservation implications for KNP and the wider region. A summary of the recommendations and potential avenues for future research in KNP and the wider region are as follows:

- Continued monitoring of large carnivore population densities and intraguild dynamics in KNP are necessary to evaluate the efficacy of ongoing conservation management strategies (e.g., IFAW, 2020) and the potential impact of these initiatives on carnivore demographics. Efforts to increase prey populations in KNP and improve law enforcement efficacy should provide a more secure habitat for large carnivores. As previously discussed, these conditions could be beneficial for the spotted hyaena population in KNP and lead to competitive release in the absence of a resident lion population. Competitive release of spotted hyaena would likely be detrimental to the KNP leopard population, whilst skewed carnivore demographics could also have negative consequences for dispersing carnivores or potential reintroductions (e.g., Weise *et al*. 2015). I recommend that annual camera trap surveys are undertaken to closely monitor carnivore demographics. Annual surveys would allow close monitoring of changes in density, whilst additional metrics that could hint at population changes (e.g., skewed sex ratios, increased movement parameters; Braczkowski *et al*. 2020) could also be monitored.

- Maintaining a sufficient prey base in KNP will be an important tool for mitigating the potentially negative consequences of interspecific competition between leopard and spotted hyaena. Initial efforts to supplement and reintroduce prey species in KNP began in 2020 (IFAW, 2020) and the continued restoration of these prey populations is vital to large carnivore recovery. In addition, the depleted prey base in KNP has been identified as a key limiting factor in potential reintroduction efforts of other large carnivores (i.e., lion, Mésochina *et al*. 2010; cheetah and wild dog, DNPW, 2011). Continued restoration of prey populations in KNP will, therefore, be beneficial to any potential reintroduction initiatives.
- Further research on individual/sex-specific dietary specialisation, survival, and encounter rates of the KNP leopard population would be beneficial to future conservation management. The findings of this study have highlighted that the spatiotemporal responses of female leopards to conspecific and interspecific competitors could have implications of conservation concern. In addition, recent studies (Voigt *et al.* 2018; Balme *et al.* 2020; Havmøller *et al*. 2020a) have demonstrated individual, sex-specific, and habitat-specific variation in leopard dietary preferences, and further investigation of these issues in human-disturbed landscapes would help inform wider conservation management.
- With PWA numbers increasing in KNP (IFAW, 2020), additional snare deployment teams would be beneficial to remove existing snares within the park. Snares were

observed on spotted hyaena in all three survey years (2016-2018) and further research on the demographic impact of wire-snaring would be beneficial. Snares also represent a threat to dispersing carnivores, that exhibit wide ranging behaviour (e.g., Fattebert *et al*. 2013; Cozzi *et al*. 2020), and prey populations (Mudumba *et al*. 2021). Consequently, the removal of existing snares would help to increase prey populations and safeguard dispersing carnivores from the wider MZTFCA.

- Connectivity between KNP, Lukusuzi National Park (Zambia) and the wider MZTFCA must be maintained to facilitate the dispersal of large carnivores. Anthropogenic activity around national parks and game management areas in Zambia has been shown to restrict the movement of large carnivores (Lindsey *et al*. 2014; Rosenblatt *et al*. 2014), whilst habitat connectivity between Zambian PAs is also in decline (Watson *et al*. 2015). As leopard have also been documented to range over vast areas when dispersing (e.g., Fattebert *et al*. 2013), maintaining connectivity will be vital for all large carnivores in KNP. In addition, increased collaboration between Malawian and Zambian authorities would be beneficial when formulating conservation strategies.
- Surveys to evaluate the status and population density of large carnivores in the other PAs of Malawi are crucially needed, as most PAs are data deficient and evidence-based conservation management is, therefore, limited. This study has highlighted NNP and VMWR as two sites that should be prioritised, as these PAs have transfrontier links and cover an extensive area that is optimal for large carnivore conservation. However, forest reserves in Malawi, that do not receive the same level of legal protection as national parks and game reserves, that are still known to contain small populations of large carnivores, such as Mangochi Forest Reserve, should also be prioritised for assessment.

7.5 Conclusions

Results from this study are indicative of wider large carnivore population decline and help to support a growing body of literature highlighting that concern for large carnivore conservation is growing (Ripple *et al*. 2014; Di Minin *et al*. 2016; Jacobson *et al*. 2016; Sandom *et al*. 2018). Encouragingly, alongside this thesis, large carnivore populations in understudied habitats are beginning to receive greater conservation attention (e.g., Strampelli *et al.* 2018; Harris *et al.* 2019; Havmøller *et al*. 2019; Mohammed *et al.* 2019; Petracca *et al.* 2019; Braczkowski *et al.* 2020a). Addressing these knowledge gaps, whilst applying robust survey techniques, will ensure that conservation decision-making is driven by evidence-based data on population status and localised threats (Hayward *et al.* 2015; Braczkowski *et al*. 2020b). In addition, further efforts to understand large carnivore guild dynamics, the drivers of spatiotemporal use, and prey preferences in human-disturbed landscapes, will become increasingly relevant as anthropogenic change continues to modify ecosystems and alter community assemblages (Dirzo *et al*. 2014; Sandom *et al.* 2017).

The review of spotted hyaena survey methods, presented in this thesis, has made a comprehensive argument for a unified SCR framework under which reporting of spotted hyaena populations can be improved. This study has provided important baseline density estimates for leopard and spotted hyaena in an understudied area of the species' geographic range, and highlighted the status of other large carnivore guild members in KNP. These findings have demonstrated the use of SPIM and the applicability of these novel models to resolve issues of uncertainty in camera trap data, whilst increasing the precision of density estimates. As SPIM is most applicable to areas of low population density, it is hoped that SPIM can be further utilised in understudied and disturbed habitats, where logistical and financial limitations may have previously restricted efforts to survey large carnivores (Davis *et al.*

2021a). The intraguild dynamics described in this thesis have highlighted the potential for increased interaction and competition for resources between sympatric competitors and the possible conservation implications of these interactions (Davis *et al*. 2021b). The findings of this study indicate that the current intraguild dynamics in KNP are likely to have negative consequences for leopards, and in particular female leopards. Therefore, further research into leopard behavioural responses and levels of individual fitness will benefit conservation management. Furthermore, there is a pressing need to expand survey efforts in other PAs in Malawi and establish similar baseline estimates of large carnivore density, whilst improving knowledge of guild dynamics in these human-disturbed environments.

The human population of Malawi is predicted to double within the next twenty years (World Bank, 2020). Subsequently, large carnivore populations and Malawian PAs are likely to come under increasing anthropogenic pressures. The current status of large carnivore populations in KNP, the second largest protected area in Malawi and a site of importance to the wider transfrontier landscape, is of conservation concern (Davis *et al*. 2021a). The recovery of large carnivore populations is often a gradual process, owing to their slow life-history traits (Ripple *et al*. 2014). As such, the window to protect and restore large carnivores in KNP is diminishing. However, the strengthening of environmental laws, continued investment by local and international conservation organisations, and ongoing restoration efforts, will hopefully help to secure KNP and increase large carnivore populations. The results of this study act as a first insight into the status and behavioural ecology of large carnivores in KNP, and provide important metrics from which the efficacy of ongoing conservation initiatives can be measured. Large carnivores can offer a crucial indicator of protected area health and provide valuable ecosystem services (Ripple *et al*. 2014). Consequently, their continued monitoring, both in KNP and across Malawi, should be an integral component of future conservation management efforts.

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Appendices

Appendix I

Table A1. Literature reviewed on spotted hyaena (*Crocuta crocuta*) population estimates and survey methods used since 2000.

Authors	**Journal**	**Year**	**Title**	**Method**	**Country**
Aebischer, T. et al.	Biological Conservation	2020	Apex predators decline after an influx of pastoralists in former Central African Republic hunting zones	Mixed (Track count/call up)	Central African Republic
Ahlswede, S. et al.	African Journal of Ecology	2019	Using the Formozov–Malyshev–Pereleshin formula to convert mammal spoor counts into density estimates for long-term community-level monitoring	Track count	Namibia
Bauer, H.	African Journal of Ecology	2007	Status of large carnivores in Bouba Ndjida National Park, Cameroon	Call up	Cameroon
Bauer, H. et al.	African Journal of Ecology	2015	Large carnivore abundance in the Benoue Ecosystem, North Cameroon	Track count	Cameroon
Cozzi, G. et al.	Biodiversity Conservation	2013	Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation	Call up	Botswana
Creel, S. & Creel, N.M.	Book	2002	The African Wild Dog	Call up	Tanzania
Croes, B.M. et al.	Biological Conservation	2011	The impact of trophy hunting on lions (Panthera leo) and other large carnivores in the Bénoué Complex, northern Cameroon	Track count	Cameroon
Davis, R.S. et al.	Journal of Zoology	2020	Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland	SCR	Malawi
Dunnink, J.A. et al.	Oryx	2019	A socio-ecological landscape analysis of human-wildlife conflict in northern Botswana	Track	Botswana
Durant, S.M. et al.	Journal of Applied Ecology	2011	Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania	Distance sampling	Tanzania
Farr, M.T. et al	Ecological Applications	2019	Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives	Distance sampling	Kenya

Ferreira, S.M. & Funston, P.J.	African Journal of Wildlife Research	2016	Population estimates of spotted hyaenas in the Kruger National Park, South Africa	Call up	South Africa
Fewster, R.M.	Biometrics	2011	Variance Estimation for Systematic Designs in Spatial Surveys	Distance sampling	Tanzania
Fouché, J. et al.	African Journal of Ecology	2020	Density estimates of spotted hyaena (Crocuta crocuta) on arid farmlands of Namibia	SCR	Namibia
Funston, P.J. et al.	Journal of Zoology	2010	Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance.	Track count	South Africa
Funston, P.J. et al.	PLoS One	2013	Insights into the Management of Large Carnivores for Profitable Wildlife-Based Land Uses in African Savannas	Track	Zimbabwe
Graf, J.A. et al.	Acta Theriologica	2009	Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park, South Africa	Call up	South Africa
Green, D.S. et al.	Biodiversity Conservation	2019	Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions	Total counts	Kenya
Green, D.S. et al.	Philosophical Transactions B	2019	Can hyena behaviour provide information on population trends of sympatric carnivores?	Total counts	Kenya
Groom, R.J. et al	Oryx	2014	Surveys of lions Panthera leo in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse	Call up	Zimbabwe
Henschel, P. et al.	African Journal of Ecology	2020	Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor	Track count	Kenya
Henschel, P. et al.	Journal of Mammalogy	2014	The status of savanna carnivores in the Odzala-Kokoua National Park, northern Republic of Congo	Capture recapture	Republic of Congo
Höner, O.P. et al.	Journal of Animal Ecology	2012	The impact of a pathogenic bacterium on a social carnivore population	Total counts	Tanzania
Höner, O.P. et al.	Journal of Animal Ecology	2002	The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism	Total counts	Tanzania
Höner, O.P. et al.	Oikos	2005	The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena	Total counts	Tanzania
Keeping, D.	Animal Conservation	2014	Rapid assessment of wildlife abundance: estimating animal density with track counts using body mass–day range scaling rules	Track count	South Africa
Keeping, D. et al.	Biological Conservation	2018	Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana	Track count	Botswana

Kiffner, C. et al.	African Journal of Ecology	2007	Response of lions (Panthera leo LINNAEUS 1758) and spotted hyaenas (Crocuta crocuta ERXLEBEN 1777) to sound playbacks	Call up	Tanzania
Kirsten, I. et al.	African Journal of Ecology	2017	Lion (Panthera leo) and spotted hyena (Crocuta crocuta) abundance in Bouba Ndjida National Park, Cameroon; trends between 2005 and 2014	Call up	Cameroon
Mbise et al.	Global Ecology and Conservation	2020	Do carnivore surveys match reports of carnivore presence by pastoralists? A case of the eastern Serengeti ecosystem	Call up	Tanzania
Mbizah, M.M. et al.	South African Journal of Wildlife Research	2012	Diet of four sympatric carnivores in Save Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (Lycaon pictus)	Track count	Zimbabwe
Mills, M.G.L. et al.	Animal Conservation	2001	Estimating the size of spotted hyaena (Crocuta crocuta) populations through playback recordings allowing for non-response	Call up	South Africa
Mohammed, A.A. et al.	African Journal of Ecology	2019	Lion and spotted hyaena abundance in Dinder National Park, Sudan	Call up	Sudan
M'soka, J. et al.	Biological Conservation	2016	Spotted hyaena survival and density in a lion depleted ecosystem: The effects of prey availability, humans and competition between large carnivores in African savannahs	Mark-resight	Zambia
O'Brien, T.G. & Kinnaird, M.F.	Ecological Applications	2011	Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid	SCR	Kenya
Ogutu, J.O. et al.	Journal of Zoology	2005	The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya	Call up	Kenya
Ogutu, J.O. et al.	PLoS One	2017	Wildlife Population Dynamics in Human-Dominated Landscapes under Community-Based Conservation: The Example of Nakuru Wildlife Conservancy, Kenya	Total counts	Kenya
Omoya, E.O. et al.	Oryx	2013	Estimating population sizes of lions Panthera leo and spotted hyaenas Crocuta crocuta in Uganda's savannah parks, using lure count methods	Call up	Uganda
Rafiq, K. et al.	Current Biology	2019	Tourist photographs as a scalable framework for wildlife monitoring in protected areas	Mixed (SCR, track, call in)	Botswana
Rich, L.N. et al	Biological Conservation	2019	Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data	SCR	Botswana
Stratford, K. et al.	African Journal of Ecology	2019	Dyadic associations reveal clan size and social network structure in the fission–fusion society of spotted hyaenas	Capture recapture	Namibia

Trinkel, M.	Canadian Journal of Zoology	2009	A keystone predator at risk? Density and distriubtion of the spotted hyena (Crocuta crocuta) in the Etosha National Park, Namibia	Call up	Namibia
Vissia et al.	Journal of Zoology	2021	Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana	SCR	Botswana
Watts, H.E. & Holekamp, K.E.	Journal of Mammalogy	2009	Ecological Determinants of Survival and Reproduction in the Spotted Hyena	Total counts	Kenya
Watts, H.E. & Holekamp, K.E.	Journal of Zoology	2008	Interspecific competition influeces reoroduction in spotted hyenas	Total counts	Kenya
Yirga, G. et al.	Mammalian Biology	2013	Spotted hyena (Crocuta crocuta) coexisting at high density with people in Wukro district, northern Ethiopia	Call up	Ethiopia
Yirga, G. et al.	Momona Ethiopian Journal of Science	2014	Status of Lion (Panthera leo) and Spotted Hyena (Crocuta crocuta) in Nechisar National Park, Ethiopia	Call up	Ethiopia
Yirga, G. et al.	Mammalian Biology	2014	Local spotted hyena abundance and community tolerance of depredation in human-dominated landscapes in Northern Ethiopia	Call up	Ethiopia
Yirga, G. et al.	Mammalian Biology	2017	Densities of spotted hyaena (Crocuta crocuta) and African golden wolf (Canis anthus) increase with increasing anthropogenic influence	Call up	Ethiopia
Yirga, G. et al.	European Journal of Wildlife Research	2011	Peri-urban spotted hyena (Crocuta crocuta) in northern Ethiopia: diet, economic impact, and abundance	Call up	Ethiopia
Yirga, G. et al.	Wildlife Research	2015	Spotted hyena (Crocuta crocuta) concentrate around urban waste dumps across Tigray, northern Ethiopia	Call up	Ethiopia

Appendix II

Table A2. Literature reviewed on leopard (*Panthera pardus*) population estimates and methods used to estimate density in sub-Saharan Africa between 2000 and 2021.

Authors	Year	Title	Journal	Method	Country
Aebischer et al.	2020	Apex predators decline after an influx of pastoralists in former Central African Republic hunting zones	Biological Conservation	Track	CAR
Allen et al.	2020	Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti	Biodiversity and Conservation	SCR	Tanzania
Balme et al.	2019	Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality	Population Ecology	SCR	South Africa
Balme et al.	2009	Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (Panthera pardus) population	Biological Conservation	CR	South Africa
Balme et al.	2010	Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa	Animal Conservation	CR	South Africa
Balme et al.	2009	Evaluating Methods for Counting Cryptic Carnivores	Journal of Wildlife Management	CR/Track/GPS	South Africa
Bauer et al.	2015	Large carnivore abundance in the Benoue Ecosystem, North Cameroon	African Journal of Ecology	Track	Cameroon
Boast & Houser	2012	Density of large predators on commercial farmland in Ghanzi, Botswana	South African Journal of Wildlife Research	Track	Botswana
Braczkowski et al.	2016	Scent Lure Effect on Camera-Trap Based Leopard Density Estimates	PLoS One	SCR/CR	South Africa
Chapman & Balme	2010	An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture–recapture models	South African Journal of Wildlife Research	CR	South Africa

Chase Grey et al.	2013	Evidence of a High Density Population of Harvested Leopards in a Montane Environment	PLoS One	SCR	South Africa
Croes et al.	2011	The impact of trophy hunting on lions (Panthera leo) and other large carnivores in the Bénoué Complex, northern Cameroon	Biological Conservation	Track	Cameroon
Davis et al.	2020	Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland	Journal of Zoology	SCR	Malawi
Devens et al.	2021	Estimating leopard density across the highly modified human-dominated landscape of the Western Cape, South Africa	Oryx	SCR	South Africa
Devens et al.	2018	Counting the spots: The use of a spatially explicit capture–recapture technique and GPS data to estimate leopard (Panthera pardus) density in the Eastern and Western Cape, South Africa	African Journal of Ecology	SCR/GPS	South Africa
du Preez et al.	2014	To bait or not to bait: A comparison of camera-trapping methods for estimating leopard Panthera pardus density	Biological Conservation	SCR	Zimbabwe
Dunnink et al.	2019	A socio-ecological landscape analysis of human–wildlife conflict in northern Botswana	Oryx	Track	Botswana
Edwards et al.	2016	Leopard density estimates from semi-desert commercial farmlands, south-west Namibia	African Journal of Ecology	CR	Namibia
Funston et al.	2013	Insights into the Management of Large Carnivores for Profitable Wildlife-Based Land Uses in African Savannas	PLoS One	Track	Zimbabwe
Funston et al.	2010	Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance	Journal of Zoology	Track	South Africa/Zimbabwe
Havmoller et al.	2019	Reserve size and anthropogenic disturbance affect the density of an African leopard (Panthera pardus) meta-population	PLoS One	SCR	Tanzania
Henschel et al.	2020	Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor	African Journal of Ecology	Track	Kenya
Henschel et al.	2011	Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters	African Journal of Ecology	SCR	Gabon

Keeping	2014	Rapid assessment of wildlife abundance: estimating animal density with track counts using body mass–day range scaling rules	Animal Conservation	Track	South Africa
Keeping et al.	2018	Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana	Biological Conservation	Track	Botswana
Mann et al.	2020	A leopard's favourite spots: Habitat preference and population density of leopards in a semi-arid biodiversity hotspot	Journal of Arid Environments	SCR	South Africa
Maputla et al.	2013	Calibrating a camera trap–based biased mark–recapture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa	African Journal of Ecology	CR	South Africa
Miller et al.	2018	Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition	Journal of Animal Ecoogy	SCR	South Africa
Noack et al.	2019	Leopard Density Estimation within an Enclosed Reserve, Namibia Using Spatially Explicit Capture-Recapture Models.	Animals	SCR	Namibia
O'Brien and Kinnaird	2011	Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid	Ecological Applications	SCR	Kenya
Rafiq et al.	2019	Tourist photographs as a scalable framework for wildlife monitoring in protected areas	Current Biology	SCR/Track	Botswana
Ramesh et al.	2017	Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator	Ecology and Evolution	SCR	South Africa
Rich et al.	2019	Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data	Biological Conservation	SCR	Botswana
Rogan et al.	2019	The influence of movement on the occupancy–density relationship at small spatial scales	Ecosphere	SCR	South Africa

Rosenblatt et al.	2016	Effects of a protection gradient on carnivore density and survival: an example with leopards in the Luangwa valley, Zambia	Ecology and Evolution	CR	Zambia
Searle et al.	2021	Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape	Biological Conservation	SCR	Tanzania
Stein et al.	2011	Leopard population and home range estimates in north-central Namibia	African Journal of Ecology	CR	Namibia
Strampelli et al.	2020	Leopard Panthera pardus density in southern Mozambique: evidence from spatially explicit capture–recapture in Xonghile Game Reserve	Oryx	SCR	Mozambique
Swanepoel et al.	2015	Density of leopards Panthera pardus on protected and non-protected land in the Waterberg Biosphere, South Africa	Wildlife Biology	SCR	South Africa
Swanepoel et al.	2015	Functional Responses of Retaliatory Killing versus Recreational Sport Hunting of Leopards in South Africa	PLoS One	SCR	South Africa
Tarugara et al.	2019	Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (Panthera pardus) population	Global Ecology and Conservation	CR	Zimbabwe
Williams et al.	2017	Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management	Royal Society Open Science	SCR	South Africa

* Methods: Capture-recapture (CR); use of GPS/satellite/VHF collars (GPS); Spatial capture-recapture (SCR); Track count surveys (Track).

Appendix III

Table A3. Geweke diagnostic statistics and Bayes p-values generated in *SPACECAP* for the single-flank and both plus partial sample models for leopard and spotted hyaena in Kasungu National Park, Malawi.

Year	Model	sigma	lam0	beta	psi	N	Bayes P-value
2018	Leopard - Single	0.65	-1.16	1.29	1.69	1.52	0.55
	Leopard - Both + Left	-0.93	0.72	-0.36	-0.73	-0.61	0.78
	Leopard - Both + Right	0.36	-0.76	0.88	0.87	0.73	0.83
	Hyaena – Single	-0.01	0.19	-0.44	-0.37	-0.27	0.75
	Hyaena - Both + Left	1.06	-0.53	0.51	0.61	0.01	0.9
	Hyaena - Both + Right	0.7	0.05	-0.33	-1.55	-1.53	0.87
2017	Leopard – Single	-1.57	0.56	-0.39	-0.48	-0.42	0.65
	Leopard - Both + Left	0.81	-1.03	1.43	1.15	1.47	0.74
	Leopard - Both + Right	0.8	-0.22	0.11	0.2	-0.05	0.76
	Hyaena – Single	1.04	-0.47	0.11	-1.23	-1.23	0.54
	Hyaena - Both + Left	-0.42	0.61	0.19	-0.34	-0.23	0.62
	Hyaena - Both + Right	1.16	-1.57	0.95	-0.49	-0.7	0.63
2016	Leopard - Single	-0.61	-1.09	0.09	0.66	0.68	0.59
	Leopard - Both + Left	-0.1	0.8	-1.08	-0.8	-0.82	0.63
	Leopard - Both + Right	1.51	-1.28	1.06	-1.58	-1.55	0.71

Appendix IV

Table A4.1. Overall summaries of binomial generalised linear mixed models predicting the likelihood of leopard detection at camera stations in Kasungu National Park, Malawi, across all survey years (2016, 2017 and 2018) during a given 5-day sampling occasion. Each model log-likelihoods (logLik), number of parameters (K), delta AICc (ΔAICc), AICc weight (Wi), and cumulative AICc weights (Cum. Wi) are presented.

Model	***K***	**AICc**	**ΔAICc**	***W*i**	**Cum. *W*i**	**Log likelihood**
Hyaena + Prey + Water	5	1117.88	0.00	0.29	0.29	-553.91
Prey + Water	4	1118.88	1.00	0.17	0.46	-555.42
Hyaena + Prey + Water + Habitat	6	1119.47	1.59	0.13	0.59	-553.70
Hyaena + Prey + Water + Border	6	1119.86	1.98	0.11	0.70	-553.89
Prey + Water + Habitat	5	1120.51	2.64	0.08	0.78	-555.23
Prey + Water + Border	5	1120.85	2.97	0.06	0.84	-555.40
Hyaena + Prey + Water + Border + Habitat	7	1121.44	3.56	0.05	0.89	-553.67
Prey + Water + Border + Habitat	6	1122.47	4.59	0.03	0.92	-555.20
Hyaena + Water	4	1123.57	5.69	0.02	0.94	-557.77
Hyaena + Prey	4	1124.37	6.49	0.01	0.95	-558.17
Water	3	1124.94	7.06	0.01	0.96	-559.46
Hyaena + Water + Habitat	5	1125.26	7.38	0.01	0.97	-557.60
Hyaena + Water + Border	5	1125.32	7.44	0.01	0.98	-557.63
Prey	3	1125.32	7.44	0.01	0.99	-559.65
Hyaena + Prey + Border	5	1126.20	8.32	0.01	1.00	-558.08
Hyaena + Prey + Habitat	5	1126.37	8.49	0.00	1.00	-558.16
Water + Border	4	1126.66	8.78	0.00	1.00	-559.31
Water + Habitat	4	1126.67	8.79	0.00	1.00	-559.32
Hyaena + Water + Border + Habitat	6	1126.96	9.08	0.00	1.00	-557.44
Prey + Border	4	1127.13	9.25	0.00	1.00	-559.55
Prey + Habitat	4	1127.32	9.45	0.00	1.00	-559.65
Hyaena + Prey + Border + Habitat	6	1128.19	10.31	0.00	1.00	-558.06
Water + Border + Habitat	5	1128.35	10.47	0.00	1.00	-559.15
Prey + Border + Habitat	5	1129.13	11.25	0.00	1.00	-559.54
Hyaena	3	1130.32	12.44	0.00	1.00	-562.15
Hyaena + Border	4	1131.80	13.92	0.00	1.00	-561.88
Hyaena + Habitat	4	1132.33	14.45	0.00	1.00	-562.15
Border	3	1133.04	15.16	0.00	1.00	-563.51
Habitat	3	1133.61	15.73	0.00	1.00	-563.80
Hyaena + Border + Habitat	5	1133.80	15.92	0.00	1.00	-561.87
Border + Habitat	4	1135.04	17.16	0.00	1.00	-563.50

Table A4.2. Overall summaries of binomial generalised linear mixed models predicting the likelihood of spotted hyaena detection at camera stations in Kasungu National Park, Malawi, across all survey years (2016, 2017 and 2018) during a given 5-day sampling occasion. Each model log-likelihoods (logLik), number of parameters (K), delta AICc (ΔAICc), AICc weight (Wi), and cumulative AICc weights (Cum. Wi) are presented.

Model	***K***	**AICc**	**ΔAICc**	W_i	**Cum.** W_i	**Log likelihood**
Leopard + Prey	4	1243.14	0.00	0.18	0.18	-617.55
Prey	3	1244.02	0.88	0.11	0.29	-619.00
Leopard + Prey + Habitat	5	1244.61	1.47	0.09	0.38	-617.28
Leopard + Prey + Border	5	1244.88	1.75	0.07	0.45	-617.42
Leopard + Prey + Water	5	1245.02	1.89	0.07	0.52	-617.49
Prey + Habitat	4	1245.51	2.37	0.05	0.57	-618.74
Prey + Border	4	1245.72	2.59	0.05	0.62	-618.84
Prey + Water	4	1245.98	2.84	0.04	0.66	-618.97
Leopard	3	1246.29	3.16	0.04	0.70	-620.14
Leopard + Prey + Water + Habitat	6	1246.40	3.27	0.03	0.73	-617.17
Leopard + Prey + Habitat + Border	6	1246.41	3.27	0.03	0.76	-617.17
Leopard + Prey + Water + Border	6	1246.77	3.63	0.03	0.79	-617.35
Prey + Habitat + Border	5	1247.26	4.13	0.02	0.81	-618.61
Prey + Water + Habitat	5	1247.41	4.27	0.02	0.83	-618.68
Leopard + Habitat	4	1247.62	4.48	0.02	0.85	-619.79
Prey + Water + Border	5	1247.68	4.54	0.02	0.87	-618.81
Leopard + Border	4	1247.96	4.83	0.02	0.89	-619.97
Leopard + Prey + Water + Habitat + Border	7	1248.20	5.06	0.01	0.90	-617.05
Leopard + Water	4	1248.23	5.10	0.01	0.91	-620.10
Habitat	3	1249.01	5.87	0.01	0.92	-621.49
Prey + Water + Habitat + Border	6	1249.16	6.02	0.01	0.93	-618.54
Border	3	1249.28	6.15	0.01	0.94	-621.63
Leopard + Habitat + Border	5	1249.35	6.22	0.01	0.95	-619.65
Leopard + Water + Habitat	5	1249.47	6.34	0.01	0.96	-619.71
Water	3	1249.66	6.52	0.01	0.97	-621.82
Leopard + Water + Border	5	1249.90	6.76	0.01	0.98	-619.92
Habitat + Border	4	1250.69	7.56	0.00	1.00	-621.33
Water + Habitat	4	1250.96	7.82	0.00	1.00	-621.46
Leopard + Water + Habitat + Border	6	1251.20	8.07	0.00	1.00	-619.57
Water + Border	4	1251.27	8.14	0.00	1.00	-621.62
Water + Habitat + Border	5	1252.64	9.50	0.00	1.00	-621.29

Appendix V

Table A5.1. Estimates of difference in activity between years and sexes for leopard in Kasungu National Park, Malawi. Bootstrapped activity patterns, with 10,000 smoothed bootstrap samples, were compared using Wald statistic (*W*) on a chi-square distriubtion with one degree of freedom in order to test for significance (*P*) at the 5% level.

Species Interaction	**Difference**	**SE**	***W***	***P***
Leopard (both sexes) 2016 – Leopard (both sexes) 2017	0.09	0.10	0.79	0.37
Leopard (both sexes) 2016 – Leopard (both sexes) 2018	<0.001	0.10	<0.001	0.99
Leopard (both sexes) 2017 – Leopard (both sexes) 2018	-0.09	0.09	1.11	0.29
Leopard (male) 2016 – Leopard (male) 2017	0.04	0.14	0.09	0.76
Leopard (male) 2016 – Leopard (male) 2018	0.04	0.14	0.09	0.76
Leopard (male) 2017 – Leopard (male) 2018	<0.001	0.10	<0.001	0.99
Leopard (female) 2016 – Leopard (female) 2017	-0.09	0.12	0.63	0.43
Leopard (female) 2016 – Leopard (female) 2018	-0.10	0.11	0.75	0.39
Leopard (female) 2017 – Leopard (female) 2018	-0.002	0.11	<0.001	0.98

Table A5.2. Estimates of difference in activity between years for spotted hyaena in Kasungu National Park, Malawi. Bootstrapped activity patterns, with 10,000 smoothed bootstrap samples, were compared using Wald statistic (*W*) on a chi-square distriubtion with one degree of freedom in order to test for significance (*P*) at the 5% level.

Species Interaction	**Difference**	**SE**	***W***	***P***
Spotted hyaena 2016 – Spotted hyaena 2017	0.08	0.06	1.91	0.16
Spotted hyaena 2016 – Spotted hyaena 2018	0.06	0.05	1.40	0.24
Spotted hyaena 2017 – Spotted hyaena 2018	-0.01	0.05	0.06	0.80

Appendix VI

Table A6. Summary of Hermans-Rasson uniformity test to assess if a random activity pattern was exhibited over a circadian cycle for leopard (both sexes and individual) and spotted hyaena in Kasungu National Park, Malawi. The number of samples (N) is presented, alongside the Hermans-Rasson test statistic (T) and the p-value (P), where a p-value below 0.05 shows activity patterns were significantly different from a random distribution. The number of iterations was set to 10,000 samples for all tests.

Species	N	T	P
Leopard (both sexes)	273	545.7	< 0.001
Leopard (♂)	77	149.8	< 0.001
Leopard (♀)	170	343.1	< 0.001
Spotted hyaena	385	737.8	< 0.001