Status & ecology of leopard (*Panthera pardus*) in African conservation landscapes

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Abstract

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A thesis submitted by Charlotte E. Searle *in fulfilment of the degree of Doctor of Philosophy in Zoology*

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Although widely considered one of the world's most resilient large carnivores, the leopard (*Panthera pardus*) is severely threatened by habitat fragmentation, prey base declines, and human-induced mortality. In Africa, a relative lack of conservation urgency has resulted in the species' status being poorly understood across much of its remaining range, despite evidence of range contractions and population declines across the continent. In this thesis, I set out to answer some of the most pressing questions facing the long-term persistence of leopard populations in Africa's evolving conservation landscape, using data from two mixed-use landscapes which are likely to represent major strongholds for the species within its remaining African range. In Chapter 3, I find leopard to be widespread across the southern KAZA TFCA, Africa's largest transfrontier conservation area, and show that prey and protection are important predictors of habitat use. I also find that the species is most abundant in areas with high protection and prey availability, whereas trophy hunting appears to have a negative influence on leopard abundance. In Chapter 4, I step back to take a community-level perspective on KAZA wildlife distributions, and show that altered rainfall and rising livestock number are emerging trends that may impact leopard and their prey in this important conservation area. In Chapter 5, I find that leopard density across southern Tanzania's Ruaha-Rungwa landscape is likely to be largely driven by availability of prey, which itself varies with habitat types and anthropogenic impacts. My results show that a hunting area with significant protection investment supports a leopard density comparable to similar habitat in a photographic tourism area, and provide evidence that community-managed WMAs can be highly valuable for wildlife but should be prioritised for monitoring. In Chapter 6, I find evidence that leopard in Ruaha-Rungwa employ fine-scale partitioning mechanisms to facilitate coexistence with both dominant competitors and humans, and that growing anthropogenic pressures may interfere with these adaptations. Taken together, this work provides evidence that leopard are resilient but not immune to human impacts, and that populations may continue to decline across sub-Saharan Africa without major intervention. I use my findings to highlight priorities for leopard conservation in Africa, including securing prey populations, preserving highly-protected areas as refugia within mixed-use landscapes, closely monitoring at-risk populations, and enacting adaptive hunting quotas.

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The second half of this thesis uses data I collected through camera trap surveys in Tanzania's Ruaha-Rungwa landscape – although it goes without saying that this was, in reality, an enormous team effort. I would like to say a heartfelt thank you everybody at the Ruaha Carnivore Project for making me feel so at home during my time in camp in 2018, and for always being willing to lend a hand. A special thank you to Leejiah Dorward and Leandro Abade for your advice; Ana Grau and BenJee Cascio, for your company and support; Mama Bora, Mama Dani, and Esther, for keeping up with my insatiable appetite for maandazi; Rashid Jumbe, for being a fundi extraordinaire; and to King, for always knowing what to do. Asanteni.

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Chapter 2 Literature review

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Chapter 3 Drivers of leopard habitat use and relative abundance in Africa's largest transfrontier conservation area

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In preparation

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In preparation

Chapter 7 Discussion

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CHAPTER 1

Introduction

Introduction

The leopard (*Panthera pardus*) is the most wide-ranging and adaptable of the world's large felids, with populations found in a diverse range of habitats across Africa, Asia, and parts of the Middle East (Hunter, 2015). However, the world's leopards face an uncertain future: like many other large carnivores, the species is severely threatened by habitat fragmentation (Laguardia et al., 2017; Rostro-García et al., 2016), prey base declines (Henschel et al., 2011; Hussain et al., 2018; Wolf & Ripple, 2016), and human-induced mortality (Inskip & Zimmermann, 2009; Oswell, 2010; Parchizadeh & Adibi, 2019; Raza et al., 2012). As a result of these pressures, a number of local extinctions have been documented for leopard (Rasphone et al., 2019; Rostro-García et al., 2016), and the species has been lost from nearly 80% of its former global range (Wolf & Ripple, 2017).

Although classified as one of the least threatened subspecies of leopard, the African leopard (*Panthera pardus pardus*) is nonetheless thought to have lost up to two thirds of its historical range on the continent (48-67%; Jacobson et al., 2016), primarily due to the loss and degradation of natural habitat (Brink & Eva, 2009; Swanepoel et al., 2013) and the decline of many prey species (Craigie et al., 2010). These pressures also cause leopard to come into increasing contact with humans, which can exacerbate conflict, another major threat to the species' survival in Africa (Swanepoel et al., 2015). Although reliable data on trends in leopard status are sorely lacking for sub-Saharan Africa, these combined threats are likely to have caused population declines of at least 30% over the last three generations (Stein et al., 2020). They also show little sign of abating, with economic and population growth, and the associated demand for land, projected to continue across much of sub-Saharan Africa through the 21st century (African Development Bank Group, 2020; UN, 2019), increasing pressure on the continent's remaining wildlife areas (Newmark, 2008; Wittemyer et al., 2008).

Despite this concerning trend, the leopard continues to be widely considered one of the world's most resilient large carnivores, bolstered by evidence of populations successfully persisting in human-dominated and highly-fragmented areas (Athreya et al., 2013; Braczkowski et al., 2018; Kittle et al., 2014; Odden et al., 2014). In Africa, the leopard's reputation of resilience has contributed to a relative

lack of research and conservation urgency for the species (Balme et al., 2014; Jacobson et al., 2016; Stein et al., 2020), particularly compared to other large carnivores like African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), and lion (*Panthera leo*), which are typically considered to be more acutely at-risk (Bauer et al., 2016; Durant et al., 2015; Winterbach et al., 2013; Woodroffe & Sillero-Zubiri, 2020). Because of this, the status and population trends of the African leopard is unknown across much of its remaining range (Jacobson et al., 2016; Stein et al., 2020). Where assessments have been carried out, they have largely been concentrated in areas of lower conservation concern, and many have failed to contribute meaningfully to conservation outcomes (Balme et al., 2014). As a result, although the majority of leopards are believed to occur outside strictly-protected areas across their African range (Hunter et al., 2013), relatively little is actually known about how human pressures impact the species in African conservation landscapes, and how well these populations will be able to persist in the face of rising anthropogenic disturbances (Jacobson et al., 2016). Combined with the species' highly elusive nature, this lack of empirical assessments may be contributing to unseen losses for Africa's remaining leopard populations.

Leopards and other large carnivores require access to large, connected landscapes for populations to thrive (Boitani & Powell, 2012; Crooks et al., 2011). In light of this, there is a growing consensus among conservation experts that, while highly-protected areas remain a vital component of many large carnivore conservation strategies (Karanth & Chellam, 2009), small protected areas alone will not be sufficient to maintain viable populations of large carnivores into the future (Ripple et al., 2014; Swanepoel et al., 2013). A number of complementary strategies have evolved to address this challenge, marking a shift from the current protected area-centric approach to a landscape level approach to conservation, while emphasising the coupling of conservation efforts with development initiatives (Trombulak & Baldwin, 2010). However, as the popularity of these programmes accelerates, there is a pressing need to assess and monitor the impacts these initiatives have on the wildlife populations they contain (Campbell et al., 2002; Witmer, 2005). To understand how best to conserve Africa's leopard populations into the future, we need to expand our research efforts to assess populations across areas under different forms of utilisation and management (Balme et al., 2014), to determine which strategies

can successfully reconcile effective wildlife conservation with both local and national socio-economic development.

In this thesis, I set out to answer some of the most pressing questions facing the long-term persistence of leopard populations in Africa's evolving conservation landscape. Throughout the thesis, I seek to establish just how valid the leopard's reputation of resilience to human impacts is, and how well the species is actually faring across land uses, management strategies, habitats, and levels of anthropogenic impact. I also explore which methods can be used to monitor these wide-ranging and elusive species – particularly against a backdrop of limited funding for conservation and management in many range states. Finally, as African conservation landscapes continue to evolve, I attempt to shed light on which approaches hold promise for securing the continued persistence of the continent's remaining leopard populations. By exploring these questions, this thesis aims to improve our understanding of how leopard can be successfully conserved across the large, multiple-use complexes characteristic of the modern African landscape.

1.1. Thesis outline

This body of work is presented as an integrated thesis. The thesis opens with a general introduction and literature review, followed by four data chapters formatted as independent research articles, before closing with a general discussion. The thesis is followed by six appendices, each comprising a manuscript published, in review, or in preparation, which I have contributed to alongside this DPhil.

My research focuses on two mixed-use landscapes which are likely to represent strongholds for leopard within its remaining global range: the southern Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) across Botswana and Zimbabwe (Chapters 3 & 4), and the Ruaha-Rungwa landscape in southern Tanzania (Chapters 5 & 6).

In Chapter 2, I introduce the challenges of large carnivore conservation in the 21st century, review available literature on methods for monitoring large carnivores, and introduce the study species and study landscapes.

In Chapter 3, I employ data from large-scale spoor surveys to investigate leopard status and habitat use across a mixed-use landscape spanning Botswana and Zimbabwe, in the southern KAZA TFCA. I use occupancy models to estimate the proportion of the landscape used by leopard, and assess how a suite of biotic, anthropogenic, and management variables influence leopard habitat use. I then employ N-mixture models to identify factors influencing relative abundance of the species in the study area. I discuss the implications of my results for leopard conservation in sub-Saharan Africa, and use my findings to highlight conservation priorities for the species across modern conservation landscapes.

In Chapter 4, I employ the same spoor dataset used in Chapter 3 to model multi-species habitat associations across the southern KAZA TFCA. I use the random forest machine learning algorithm to model habitat suitability for 16 mammal species of conservation importance – including six carnivores and ten herbivores – using a multi-scale approach, to identify the scales at which each species responds to different variables. I then combine these species-specific insights to build a multi-species view of the factors determining mammal distribution across southern KAZA, including leopard and their prey, and identify potential future threats to the landscape.

In Chapter 5, I employ data from camera trap surveys I conducted in the mixed-use Ruaha-Rungwa landscape in southern Tanzania in 2018 and 2019. Surveys were carried out in four sites representing a range of habitats and management strategies: a prey-rich, *Acacia-Commiphora* habitat in Ruaha National Park (NP); a miombo woodland habitat in Ruaha NP; the community-managed, *Acacia-Commiphora* MBOMIPA Wildlife Management Area (WMA); and the miombo woodland-dominated Rungwa Game Reserve (GR), a trophy hunting area. I use spatially explicit capture-recapture (SECR) modelling to estimate population density of leopard across the study sites, and discuss the implications of my findings for leopard conservation management across mixed-use landscapes in Tanzania, and in Africa more widely. This study provides one of the first status assessments for leopard in Tanzania, and one of the first in an African miombo habitat.

In Chapter 6, I complement the Ruaha-Rungwa camera trap survey data used in Chapter 5 with concurrent data from camera traps deployed in neighbouring unprotected village land, as part of a

community-engagement programme. Together, I use these data to investigate temporal partitioning and spatiotemporal avoidance and attraction among members of an intact East African large carnivore guild (leopard; lion; spotted hyaena, *Crocuta crocuta*; striped hyaena, *Hyaena hyaena*; African wild dog; and cheetah), and explore how these effects vary across an anthropogenic pressure gradient. In doing so, I identify co-existence mechanisms employed by leopard in Ruaha-Rungwa to minimise intra-guild competition, and shed light on how the species may adjust its behaviour in the presence of heightened human pressures.

In Chapter 7, I synthesise my findings, and discuss the contribution of this thesis to current knowledge on the ecology, monitoring, and conservation management of leopard populations in modern African conservation landscapes.

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CHAPTER 2

Literature review

Literature review

2.1. Large carnivore conservation in the 21st century: Protection beyond parks

The loss of apex predators has been argued to be one of humankind's most significant impacts on nature (Estes et al., 2011). Large carnivores play a key role in regulating ecosystems (Atkins et al., 2019; Ripple et al., 2014; Treves & Karanth, 2003) and can be a valuable asset for the areas in which they are found, bringing economic value at a local and national level through tourism (Lindsey et al., 2007; Okello et al., 2008), and stimulating conservation efforts that can help protect co-occurring species through their role as umbrella species (Roberge & Angelstam, 2004). Beyond the moral implications of condemning species to extinction – a concern which lies at the heart of conservation biology (Soulé, 1985) – the loss of large carnivores can therefore have profound consequences for the structure and function of ecosystems (Estes et al., 2011; Ripple et al., 2014; Ritchie et al., 2012).

The dietary and habitat requirements of large carnivores mean they often occupy large home ranges and persist at naturally low densities (Boitani & Powell, 2012). These traits leave the species particularly susceptible to habitat loss and persecution, as individuals must roam widely across ranges that can extend beyond the borders of protected areas, into lands shaped and occupied by humans (Carter & Linnell, 2016; Ripple et al., 2014). Inside these fragmented landscapes, carnivores are exposed to high levels of mortality (Woodroffe, 2000), often as a result of accidental or intentional killing by humans (Balme, Slotow, et al., 2009; Loveridge et al., 2007). Human impacts also threaten large carnivores indirectly: 25% of the world's large carnivore prey species are classified as threatened on the IUCN Red List, primarily as a result of habitat conversion to agriculture, deforestation, and hunting (Wolf & Ripple, 2016). Reduced prey populations can in turn increase livestock predation by large carnivores, further exacerbating levels of conflict (Khorozyan et al., 2015). Although there are some examples of large carnivore populations successfully persisting in human-dominated areas – such as leopard in Mumbai, India (Braczkowski et al., 2018) and spotted hyaena in northern Ethiopia (Yirga et al., 2015) – such cases are the exception rather than the rule, and the frequency of conflicts between humans and carnivores appears to be on the rise in many areas (Treves & Karanth, 2003; Wittemyer et al., 2008).

Faced by these pressures, many of the world's large carnivores are under threat of extirpation from large parts of their historical habitat. Over three quarters of the world's 31 large carnivore species are known to be in decline, with 17 species occupying less than half of their historical distributions (Ripple et al., 2014). Intact large carnivore guilds, which once occupied 96% of the world's terrestrial area, now cover just 34% of the world's land (Wolf & Ripple, 2017).

Africa holds most of the world's remaining populations of large mammals (Wilson & Mittermeier, 2011), and is home to one of the most functionally diverse guilds of large carnivores (Dalerum et al., 2009). Despite this, the continent has been identified as a hotspot of carnivore decline (Ripple et al., 2014), primarily as a result of habitat loss and degradation (Craigie et al., 2010; Newmark, 2008; Ogutu et al., 2016), direct persecution by humans (Dickman et al., 2014; Ogada et al., 2003; Woodroffe & Frank, 2005), and declining prey numbers (Winterbach et al., 2013; Wolf & Ripple, 2016). Members of the African large carnivore guild are undergoing widespread range contractions – with losses estimated at 94% for lion (*Panthera leo*), 93% for African wild dog (*Lycaon pictus*), 92% for cheetah (*Acinonyx jubatus*), 48-67% for leopard (in Africa; *Panthera pardus*; Jacobson et al., 2016), 27% for brown hyaena (*Parahyaena brunnea*), 24% for spotted hyaena (*Crocuta crocuta*), and 15% for striped hyaena (across its global range; *Hyaena hyaena*; Wolf & Ripple, 2016) – and all but brown hyaena face declining population trends (AbiSaid & Dloniak, 2015; Bauer et al., 2016; Bohm & Höner, 2015; Durant et al., 2015; Stein et al., 2020; Wiesel, 2015; Woodroffe & Sillero-Zubiri, 2020). As a result, four of the seven large carnivore species in Africa are classified as *Threatened* by the IUCN (*Endangered*: African wild dog; *Vulnerable*: lion, leopard, cheetah; Bauer et al., 2016; Durant et al., 2015; Stein et al., 2020; Woodroffe & Sillero-Zubiri, 2020), while striped hyaena and brown hyaena are classified as *Near Threatened* (AbiSaid & Dloniak, 2015; Wiesel, 2015) and spotted hyaena as *Least Concern* (Bohm & Höner, 2015).

Large carnivore range contractions have been shown to be significantly more likely in regions with high rural human population density, cattle density, or cropland (Wolf & Ripple, 2017). These pressures are only set to increase for large carnivores in Africa, driven by a complex combination of social, economic,

and political factors. Human population in sub-Saharan Africa (SSA), which increased approximately six-fold since the start of the 21st century (DeGeorges & Reilly, 2009), is predicted to increase a further 300% by 2100 (UN, 2019). Many African nations are also expected to see continued economic growth as we progress towards the middle of the century, with six economies ranking among the world's ten fastest growers in 2020 (Rwanda, Ethiopia, Côte d'Ivoire, Ghana, Tanzania, and Benin; African Development Bank Group, 2020). Together, economic and population growth across the continent will generate increasing demand for land for the expansion of human settlements and other infrastructure (Tilman et al., 2017). Agricultural demands will also continue to rise: by 2050, food demand for livestock products in SSA will be nearly double what it was in 2010 (van Vuuren et al., 2009), with the total market size of beef (compared to 2005-07; Pica-Ciamarra et al., 2013) and milk consumption (compared to 2000; Herrero et al., 2014) both expected to triple in this period. In addition to demand for food, livestock numbers are likely to be pushed up even further with population growth as a result of the considerable social value placed on livestock ownership in many parts of the region (Thornton, 2010), although this trend may be countered by concurrent urbanisation (Awumbila, 2017). As the intensification of livestock production alone will not be sufficient to meet this increasing demand, these trends will require conversion of land to support the expansion of grasslands for livestock – which is responsible for nearly 60% of land use change in SSA – at the cost of some of the region's remaining wooded savannahs and primary forests (Herrero et al., 2014). All these pressures will be further exacerbated by the impacts of climate change, which is expected to increase temperatures, alter rainfall patterns, and reduce agricultural yields throughout the region (FAO, 2017).

Despite the troubling outlook, efforts to avert an African extinction crisis are underway. In 2017, CMS (Convention on Migratory Species) and CITES (Convention on International Trade in Endangered Species) announced a joint African Carnivores Initiative (ACI; CMS, 2017), intended to provide a shared platform for the implementation of cross-border and trade-related conservation solutions for lion, leopard, cheetah and African wild dog. While this initiative seeks to galvanise international will to save these species, national-level solutions to the large carnivore extinction crisis will depend on developing strategies that facilitate coexistence – that is, the lasting persistence of self-sustaining large carnivore

populations in human-dominated landscapes (Chapron & López-Bao, 2016). Widespread adoption of predator-friendly pastoral and agricultural practices should help to slow large carnivore declines, and can be nurtured through favourable policy and efforts to increase tolerance of predators (Winterbach et al., 2013; Wolf & Ripple, 2017). Stemming the conversion of the region's remaining wild habitats will also be an important step towards securing the future of its large carnivores. As agricultural productivity in SSA is still far below yield potential (Chauvin et al., 2012), intensification of existing croplands and rangelands through the use of modern and novel technologies may go some way to achieving this goal.

However, arguably the most important factor underpinning the future of Africa's large carnivores is the continent's protected area network. Protected areas (PAs) play a key role in safeguarding large carnivores and other species from extinction (Brondizio et al., 2019; Karanth & Chellam, 2009), by providing refugia away from the threats of land conversion and over-exploitation. In doing so, PAs provide areas of higher population abundance which can protect species against detrimental source-sink dynamics (Hansen, 2011), and harbour irreplaceable biodiversity (Le Saout et al., 2013). Approximately 15% of the world's terrestrial area is under some form of protection (UNEP-WCMC & IUCN, 2020), falling short of the goal of 17% by 2020 set out in the Convention of Biodiversity's Aichi Target 11 (CBD, 2010; UNEP-WCMC & IUCN, 2020) – although this target is already being exceeded in some countries, including Zimbabwe (27%; UNEP-WCMC & IUCN, 2020), Botswana (29%; UNEP, 2019a) and Tanzania (38%; UNEP, 2019b). Post-2020 targets are more ambitious still, amounting to as much as 44% protection of the Earth's terrestrial surface (Allan et al., 2019). Levels of protection across different PA categories range widely, from areas wholly set aside for biodiversity to areas where natural resource extraction is permitted (UNEP-WCMC et al., 2018). Over the past century, African countries have established an extensive network of PAs encompassing some of the world's most iconic natural landscapes (Newmark, 2008); the most strictly-protected of these are typically designated as National Parks. However, although the coverage of PAs across the continent has doubled since 1970, many PAs in SSA are becoming increasingly isolated as a result of human pressures (Newmark, 2008).

2.1.1. Achieving large carnivore conservation at scale

The size of PAs has important implications for large carnivores: the smaller the PA in relation to their home range, the greater the proportion of the population that must range beyond its borders and come into potentially lethal contact with humans (Winterbach et al., 2013). This can create population sinks surrounding PA boundaries, and can have major impacts that reverberate throughout populations within PAs (Davidson et al., 2011; Loveridge et al., 2010; Woodroffe & Ginsberg, 1998). These edge effects may be mitigated through conservation efforts that incorporate conflict mitigation strategies, and the development of buffer zones in marginal habitat outside strict PAs (Balme, Slotow, et al., 2010; Winterbach et al., 2013). Such marginal areas can also be highly important for species that are particularly vulnerable to intra-guild competition – such as African wild dog and cheetah – whose avoidance of areas with high densities of dominant competitors can force them into lesser- or non-protected land (Creel, 2001; Durant, 2000).

The issue of scale is particularly important for securing resilient regional populations of large carnivores (Nabe-Nielsen et al., 2010; Rudnick et al., 2012). Failure to maintain connectivity among patches of habitat can impede species' ability to disperse and migrate across wider landscapes, which can lead to increased genetic isolation (Willi et al., 2007), compromised resilience to population bottlenecks (Gilpin, 1987), and reduced opportunities to adapt to a changing climate (Opdam & Wascher, 2004). As such, identifying and maintaining linkages between habitat patches both among and within PAs is recognised as a critical requirement for the effective conservation of large carnivores (Ashrafzadeh et al., 2020; Cushman et al., 2018).

Although it is widely agreed that the continued preservation of highly-protected core areas remains a vital component of large carnivore conservation (Leader-Williams et al., 1990; Lindsey et al., 2018; MacKinnon, 1986; McNeely & Miller, 1982), the considerable costs associated with maintaining strict PAs mean that they are unlikely to be viable at the scale required to overcome edge effects, secure marginal habitats, and maintain connectivity across wider landscapes – particularly with the chronic underfunding already facing Africa's existing PA network (Lindsey et al., 2018, 2014; Packer et al.,

2013). As a result, there is a growing consensus among conservation experts that alternative, landscape-scale conservation models are required to secure viable populations of large carnivores into the future (DeGeorges & Reilly, 2009; Ripple et al., 2014).

Transfrontier conservation areas

Recognition of the need to achieve large carnivore conservation at scale has initiated a shift from the traditional protected area-centric approach toward a landscape-level approach to conservation (Donaldson et al., 2017; Kennedy et al., 2016; Trombulak & Baldwin., 2010). One major example illustrating this shift is the emergence of transfrontier conservation areas (TFCAs).

The importance of policy and governance in preserving wild ecosystems has historically meant that conservation has been restricted to efforts within a country's borders. This approach is at odds with how the world is used by wildlife, and has resulted in a number of otherwise contiguous wild ecosystems and dispersal corridors being severed by political boundaries (Dallimer & Strange, 2015; López-Hoffman et al., 2010). As awareness of this incongruity grew over the last century, the concept of trans-border PAs rose in prominence among bodies like the IUCN, which in 1988 identified more than 70 PAs across 65 countries that straddled national boundaries (Thorsell, 1990).

TFCAs are a model borne from this mismatch between geopolitics and ecology, and were first defined in 1999 by the Southern African Development Community (SADC) as "a component of a large ecological region that straddles the boundaries of two or more countries, encompassing one or more PAs, as well as multiple resource use areas" (SADC, 1999). The SADC is an intergovernmental organisation of 16 southern African states, and is responsible for the oversight of the region's TFCAs. There are currently eighteen such areas in various stages of development across the terrestrial and marine regions overseen by the SADC, covering over 700,000 km^2 (SADC, 1999).

Due to their size, TFCAs have the potential to secure corridors for wildlife that may otherwise be lost to land-use conversion and fragmentation, providing tracts of interconnected land that are critical for wide-ranging and migratory species (Elliot et al., 2014; Naidoo et al., 2016). The SADC also praises

TFCAs as "effective vehicles for fostering regional cooperation and integration, and enhancing socioeconomic development in rural areas through the sustainable use of shared natural and cultural resources" (SADC, 1999). While the success of many tourism destinations within TFCAs pre-dates their establishment, the extra support provided for cross-border tourism and development as part of these schemes augments their potential to generate employment and reduce poverty in areas that are often marginalised (Hanks, 2003). Moreover, the institutional frameworks established for oversight of TFCAs may have value for peace and cooperation efforts (Muboko, 2017). However, TFCAs have also been subject to criticism, including accusations that they represent an undemocratic, centralising and top-down approach to environmental management (Duffy, 2006) that can serve to reinforce controls on the access and use of land by those inhabiting them (Noe, 2010), and that they may function more as "paper parks" than effective vehicles for on-the-ground conservation (Ferreira, 2004).

2.1.2. Overcoming the costs of conservation

In addition to the issue of scale, another major challenge facing Africa's PAs is the question of funding. PAs that do not generate sufficient financial benefits to overcome the local or national opportunity costs of resisting conversion are at risk of downgrading, downsizing, or degazettement (Mascia et al., 2014; Norton-Griffiths et al., 2009). This challenge is particularly acute in developing countries – which are home to many of the world's biodiversity hotspots (Myers et al., 2000) – where areas used by wildlife are often highly enmeshed with those used by marginalised rural populations (UNDP, 2016). In the context of large carnivore conservation, preservation of healthy wildlife populations can also bring considerable additional costs, including the threat of human attack (Kushnir et al., 2010; Packer et al., 2005) and livestock losses (Butler, 2000; Hemson et al., 2009). As such, there is an urgent need to identify land use strategies that can generate sufficient funding to overcome these costs, and enable effective management to limit the loss of both large carnivores and wider biodiversity (Dickman et al., 2019; Lindsey et al., 2018; Sarukhán et al., 2005).

Community-based natural resource management

The preservation of National Parks has been criticised as an example of "fortress conservation" (King, 2010): establishment of these strictly-protected areas can forcibly exclude impoverished populations from natural resources to which they have had traditional access (Adams & Mulligan, 2003), rerouting the economic value of those resources away from these populations, often to centralised governments, while continuing to expect them to bear the burden of coexistence. In many countries, efforts to reconcile the needs of wildlife and local communities have already been initiated, by placing an increased emphasis on decentralised wildlife management policies as a complement to traditional centralised frameworks. Underpinning many such efforts is the concept of community-based natural resource management (CBNRM), a framework for land management based upon the theory that natural resources will be sustainably managed when local communities have ownership of those resources and derive benefits from their use (Magome & Fabricius, 2004). When the concept of CBNRM started to grow in popularity in the late 20th century, it quickly began to filter into land management planning by governments due to its promise as a means of promoting both long-term protection of wildlife and rural economic development. Today, a large number of governments in Africa have integrated large-scale CBNRM programmes into their land management plans.

However, despite its promising premise, CBNRM has been criticised as an idealised approach that is challenging to implement in complex real-world settings (DeGeorges & Reilly, 2009; Garner, 2012), with particular difficulties associated with the distribution of benefits to participating communities. While successful community-based land management initiatives have been documented at sites in Botswana and Kenya (Chisanga, 2016; Measham & Lumbasi, 2013), similar programmes have failed to achieve the anticipated gains in conservation and development elsewhere in Botswana and Kenya, and in Uganda, Zimbabwe, and Zambia (Garner, 2012; Milupi et al., 2017; Wainwright & Wehrmeyer, 1998). In Tanzania, although there is evidence of community-managed Wildlife Management Areas (WMAs) supporting comparable wildlife populations to strongly-protected National Parks (Kiffner et al., 2020), the country's WMAs appear to have achieved mixed success in their engagement of local

communities (Walsh, 2000), and there is no clear evidence of the initiative contributing to widespread poverty reduction (Keane et al., 2020). Reviews of community conservation suggest that, while some initiatives have shown measurable success and others have clearly failed, most examples fall somewhere between these two extremes (Jones, 2015).

Trophy hunting

Tourism is one of the most important industries in Africa, contributing 7.1% of the continent's GDP in 2019 (168.5 billion USD; World Travel & Tourism Council, 2020). Non-consumptive tourism, often termed photographic tourism or ecotourism, is one of the major mechanisms by which funding is generated in African PAs (Lindsey et al., 2017). However, many areas that are critical for the survival of large carnivore populations are not suitable for photographic tourism (Dickman et al., 2019; Lindsey et al., 2007; Winterbach et al., 2015). Large parts of remaining habitat in Africa support relatively low wildlife densities – including less productive habitats like miombo woodlands (Frost, 1996) and many areas critical for connectivity (Jones et al., 2012; Kiffner et al., 2016) – which do not offer the sightings expected by most international tourists. Many of these areas are also very remote, making tourism activities expensive to operate and less competitive against well-established tourist routes offering international flights (such as in Tanzania, where 80% of international tourists visit the northern circuit, despite the wealth of wildlife areas elsewhere in the country; Hunt & Gorenflo, 2019; Mgonja et al., 2015). Wildlife areas can also be infested with tsetse flies, which deliver painful bites and can transmit sleeping sickness (trypanosomiasis; WHO, n.d.; although the presence of this insect is what has actually enabled many areas to resist conversion – it is thought that tsetse eradication would increase cattle density by more than 50 head per km^2 in parts of Tanzania; Swallow, 2000). Moreover, although non-consumptive tourism is often closely aligned with conservation goals at a local scale, it comes with a considerable carbon footprint from the thousands of international flights taken each year by safari-goers (Marzouki et al., 2012).

Trophy hunting is one common alternative to photographic tourism that is used to generate funding from the presence of large mammals. In Africa, colonialists' desire to maintain populations of wild

game for hunting was central to the formation of many National Parks (which were often established alongside forcible eviction of indigenous populations; King, 2010), and hunters are often considered the forebears of modern conservationists (Adams & Mulligan, 2003). Today, hunts of African large carnivores must comply with strict quotas on the number of individuals that may be hunted within a designated area each year – although many quotas lack robust scientific basis, and may be unsustainably high (Lindsey et al., 2013; Trouwborst et al., 2020) – and have to meet a number of other national regulations about when, where, and how hunts can be carried out (e.g. MNRT, 2015). Because tourist hunters are generally more accepting of remote and challenging conditions and often pay substantially higher fees than photographic tourists (Baker, 1997; Lindsey et al., 2007), trophy hunting has been used by conservation managers to attach economic value to many natural habitats unsuitable for photographic tourism (Lindsey et al., 2007), and can do so at a relatively low ecological cost (Dickman et al., 2019; although note that this does not apply to canned hunting, a widely condemned practice that often employs highly unethical practices and secures few conservation benefits for wild populations; IUCN, 2004).

In the absence of viable conservation-oriented land use alternatives, trophy hunting is argued to therefore play an important role in preventing the conversion of valuable habitat to agricultural land (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007). However, the practice can have detrimental long-term impacts on hunted populations if carried out unsustainably or combined with other sources of anthropogenic mortality (Lindsey et al., 2013; Loveridge et al., 2016; Packer et al., 2010; Packer, Kosmala, et al., 2009) – although information on these impacts is lacking even for species which have attracted considerable attention from policymakers (D. W. Macdonald et al., 2017) – and has the potential to distort community structure (Ripple et al., 2016). The trophy hunting industry is also currently fielding global public criticism over the ethics of killing animals for sport (Dickman et al., 2019). As a result, Africa's trophy hunting industry faces an uncertain future, with activities declining in parts of the continent (FZS, 2018; Ministry of Natural Resources and Tourism, 2016). Nevertheless, the industry remains a significant source of funding for Africa's wildlife areas, being the predominant revenue earner for over 1 million km^2 of PAs, and contributing approximately 200 million

USD per year to PAs in Africa (Di Minin et al., 2016; Lindsey et al., 2007). The phasing out of trophy hunting without viable alternative financing or forms of land use already in place therefore risks undermining these resources for protection of vital wildlife habitat (Di Minin et al., 2016; Dickman et al., 2019).

2.1.3. Assessing the impacts of conservation models

In the face of ongoing economic and population growth, the continued protection of Africa's large carnivores and their prey remains precarious. While the majority of wildlife populations in large and well-protected reserves are almost certainly stable (Stoner et al., 2007), many African PAs have failed to mitigate human-induced threats to African large mammal populations (Craigie et al., 2010). At the same time, the African conservation landscape is undergoing widespread changes, including the decline of trophy hunting in parts of the continent (Lindsey et al., 2014) and the growth of landscape-scale and development-linked models like TFCAs and CBNRM (Hackel, 1999; Suich et al., 2009). However, many of these changes are being implemented without sufficient information on the impacts of different conservation models on biodiversity and ecosystem function (Coad et al., 2015; UNEP-WCMC et al., 2018). With Africa's PA network already under-resourced, growing pressures on remaining habitat and rising opportunity costs may also result in decreased support for PAs if their conservation benefits cannot be demonstrated (Coetzee, 2017). As such, there is a pressing need to assess and monitor the extent to which different conservation models, which are underpinned by widely varied cultural and economic factors across the continent, actually fulfil their conservation goals (Coetzee, 2017; Naughton-Treves et al., 2005). Ideally, these efforts should be implemented alongside assessments of long-term social sustainability, to ensure land management plans are also capable of securing their development goals (Sachs et al., 2009; UNEP-WCMC et al., 2018). Information of this kind is an essential component of effective conservation planning, and is particularly critical for large carnivores, whose long-term survival is highly dependent on PA networks and favourable conservation policy (Ripple et al., 2014; Trouwborst, 2015; Winterbach et al., 2013). Only through such empirical

assessments and adaptive policy can we ensure that Africa's land management framework will continue to evolve in a direction that truly benefits wildlife.

2.2. Assessing and monitoring large carnivore populations

Assessing and monitoring the status of large carnivore populations is essential to their conservation (Boitani & Powell, 2012). Effective monitoring allows decision-makers to evaluate the impact of different land uses and management strategies on the health of populations, and can provide the opportunity to intervene and adapt or replace approaches that are not securing their intended benefits before populations suffer too many negative impacts. This is particularly important in areas where extractive activities like trophy hunting are being carried out, as it must be ensured that these activities are carried out sustainably, with no long-term detrimental impacts on populations, to ensure that they are compatible with conservation goals (Bunnefeld et al., 2013; D. W. Macdonald et al., 2017; Selier & Di Minin, 2015). The in-depth understanding of large carnivore populations that can be nurtured through effective monitoring can also feed into longer-term conservation planning, as it enables the potential impacts of different actions to be anticipated before changes are implemented.

There are a number of different aspects of large carnivore ecology and status that should ideally be taken into account when monitoring populations (Boitani & Powell, 2012). Although it may not be possible to monitor all of these in all landscapes – be this due to financial, logistical, or political limitations – decision-makers should strive to develop monitoring programmes that incorporate as many of these different components as possible (Winterbach et al., 2013). In doing so, they will be equipped with the best possible information to be able to enact management plans that can secure the long-term viability of large carnivore populations in a changing world.

2.2.1. Distribution and habitat use

Establishing reliable and accurate population estimates remains a gold standard in large carnivore conservation, and is often cited as an essential component of effective management interventions (Balme, Hunter, et al., 2009). However, the survey efforts required to obtain such estimates can be

prohibitively expensive and time-consuming (Witmer, 2005) – particularly for conservation projects in lower-income countries, which are often equipped with limited funds and small teams (Le Saout et al., 2013; Waldron et al., 2013). Although less robust than measures of density and abundance, simple presence-absence data can be collected rapidly and cost-effectively across large areas (Mackenzie & Royle, 2005). As such, presence-absence data can provide a coarser indicator of status that can be used to monitor the distribution of species at large scales, while providing valuable insights into habitat preferences and tolerance limits.

The ability to accurately model current and potential species distributions has immense value as a tool for conservation: a detailed understanding of current distribution can help decision-makers assess population status (Bahaa-el-din et al., 2015), identify priority areas for conservation (Rodríguez-Soto et al., 2011), and determine levels of connectivity between subpopulations of a species (Kanagaraj et al., 2011). This understanding can also act as a foundation from which to make predictions, which can be used to identify tracts of land with the potential to act as corridors (Cushman et al., 2010) and evaluate changes in landscape connectivity under different climate change and land use scenarios (Cushman et al., 2016).

Occupancy modelling

One method of assessing species distributions is to estimate the proportion of an area occupied by the species of interest (MacKenzie et al., 2006). However, in order for such inferences to be robust, it is essential to account for the fact that detection is not perfect for the vast majority of ecological surveys. This is particularly the case for large carnivores, whose naturally low densities and elusive nature can make them difficult to detect (Boitani & Powell, 2012). Failure to detect a species does not necessarily reflect absence, and failing to account for such "false absences" will lead to underestimates of occupancy (Mackenzie & Royle, 2005). To address this source of bias, Mackenzie et al. (2002) developed the occupancy modelling framework, which uses patterns of detection and non-detection over multiple surveys of a site to estimate detection probabilities (p), and consequently derive unbiased estimates of occupancy (ψ; Mackenzie et al., 2002). The method is based on the closed population

capture-recapture models developed for estimations of abundance (see 2.2.2. Population density) – with sites analogous to individuals – but with the addition of a parameter representing the probability of species presence (MacKenzie et al., 2018).

The proportion of an area occupied by a species is considered a valuable metric for assessing species occurrence, range and distribution, and is accepted as a robust surrogate for abundance in species monitoring efforts (MacKenzie et al., 2006). It is particularly useful as a tool for long-term, large-scale monitoring programmes of rare and elusive species, for which more direct measures of abundance would come at a considerable cost in terms of both time and effort. Moreover, occupancy modelling allows the inclusion of covariates to explain heterogeneity in both occupancy and detection probability, facilitating insights into the factors driving habitat use and selection by a species (MacKenzie et al., 2006) – information that can be highly valuable in informing conservation and management planning. Since their inception, occupancy models have been extended to incorporate modelling of multi-season population dynamics, species interactions, and community-level occupancy (MacKenzie et al., 2018).

While the occupancy modelling framework has been applied to numerous species worldwide, the technique has proven a particularly popular method for assessing status and habitat use patterns of large carnivores, including bobcat (*Lynx rufus*: Clare et al., 2015), cheetah (Andresen et al., 2014), clouded leopard (*Neofelis nebulosa*: Tan et al., 2017), puma (*Puma concolor*: Sollmann et al., 2012), jaguar (*Panthera onca*: Petracca et al., 2013; Sollmann et al., 2012; Zeller et al., 2011), leopard (Ghoddousi et al., 2010; Gubbi et al., 2020; Strampelli et al., 2018a), lion (Everatt et al., 2014; Henschel et al., 2016; Midlane et al., 2014), and tiger (*Panthera tigris*: Karanth et al., 2011; Sunarto et al., 2012).

N-mixture modelling

N-mixture models are a novel extension of occupancy models which use counts of unmarked individuals, rather than simple detection/non-detection data, to estimate site-specific abundance (λ; Royle, 2004). A strict set of assumptions must be met for total abundance to be derived from N-mixture models, and multiple studies have urged against using such models to obtain population estimates (Link et al., 2018; Nakashima, 2020; Rogan et al., 2019). Nevertheless, the N-mixture framework holds

promise as an efficient and cost-effective way to understand the factors affecting species' abundance over large scales, by allowing the effect of covariates on relative abundance to be explored. In doing so, this method can provide a more nuanced view of how a species is faring within different components of a landscape than measures of site use alone (Royle, 2004).

Machine learning to model and predict multi-species distributions

Maintaining healthy plant and animal communities is central to safeguarding functional ecosystems, and is the main motivation underpinning current international biodiversity targets (CBD, 2010). As such, landscape-level wildlife assessments should also strive to incorporate multi-species perspectives, so that this information can be used to inform effective landscape-level conservation and management plans (Zeller et al., 2012).

Identifying habitat preferences for multiple species at a landscape scale is necessarily complex: different species can respond to environmental and biotic variables in complex and divergent ways (Ficetola et al., 2007), and areas of connectivity between subpopulations of one species may not coincide with those of another (Richardson, 2012). As a result, making reliable inferences about multi-species systems over space and time can be extremely challenging (Austin, 2007; Dungan et al., 2002). In recent years, however, machine learning approaches have emerged as a powerful tool to model spatially complex and temporally dynamic systems, as they are able to disentangle complex and non-intuitive interactions from large datasets much more readily than traditional modelling approaches (Evans et al., 2011). One model that is becoming an important part of the ecological toolset is random forest (Breiman, 2001; Cutler et al., 2007; Evans et al., 2011; Rogan et al., 2008), a powerful machine-learning algorithm which has been used in remote sensing (Hengl et al., 2017; Immitzer et al., 2012; Naidoo et al., 2012), restoration ecology (Barnard et al., 2019), habitat suitability and connectivity analyses (Ashrafzadeh et al., 2020; Vanbianchi et al., 2017), and climate change predictions (Ashrafzadeh et al., 2018; Rehfeldt et al., 2006).

In simple terms, random forest models consist of multiple decision trees that operate as an ensemble. Each of these individual decision trees makes a class prediction, and the random forest selects the class

with the most predictions across all its constituent decision trees. The decision trees that make up a random forest are built with random subsets of a complete dataset, selected via a bootstrap aggregation ("bagging") procedure; the remaining "out-of-the-bag" data are then used to evaluate the model. Although the random forest classification algorithm can struggle when sampling is not representative or data are particularly noisy, it is nevertheless considered one of the most accurate learning algorithms available (Yiu, 2019).

2.2.2. Population density

Reliable and accurate population estimates are necessary to monitor population trends, compare species status across different management strategies, land uses and habitat types, and ensure sustainable levels of offtake in hunted populations (Balme, Slotow, et al., 2009; Packer et al., 2010; Strampelli et al., 2018b). Understanding how populations vary across different components of a landscape can also help identify refugia and at-risk populations, including population sinks (Boulanger et al., 2018; Chase Grey et al., 2013; Loveridge et al., 2010). When monitoring wildlife populations, population density – an estimate of population size per unit area – can be a more meaningful metric than simple abundance, as it translates a pure population estimate into something that can be compared directly across sites (Balme, Slotow, et al., 2010; Espinosa et al., 2018) or through time (Harmsen et al., 2017; Satter et al., 2019; provided that comparable methods are used).

Capture-recapture modelling

Capture-recapture models were first developed to overcome the limited information provided by count statistics – the number of animals seen, heard, or caught – obtained by ecologists when surveying animal populations. Such statistics alone are only capable of providing a minimum bound on population size, as the surveys from which they arise only sample an unknown fraction of the population of interest (Nichols, 1992). In the late 19th and early 20th century, a number of ecologists independently reasoned that, by estimating this sampling fraction, it would be possible to derive an estimate of population size from the count statistic (Jackson, 1933; Lincoln, 1930; Petersen, 1896). This thinking gave rise to the Lincoln-Petersen method, the earliest method for estimating population size from marked animals.

From this foundation, subsequent capture-recapture models were developed that account for different sampling frameworks, such as scenarios with more than two sampling occasions. Capture-recapture surveys of this kind result in data summarised using capture histories; rows of 1s and 0s denoting capture and no capture, respectively, for each sampling occasion (Rovero & Zimmermann, 2016). For closed populations, in which neither immigration nor emigration occurs (MacKenzie et al., 2006), these capture histories are modelled in terms of capture probabilities, and can take a number of forms according to the different assumptions that can be made about variation in capture probabilities.

The popularity of capture-recapture methods for the study of animal populations grew dramatically over the 20th century, in step with advances in the technology available for use in such studies, including camera traps (Karanth, 1995), acoustic recording devices (Dawson & Efford, 2009), and DNA sampling methods (Murphy et al., 2016).

Spatially explicit capture-recapture (SECR) modelling

The development of capture-recapture methodologies marked a significant advance in ecological surveying frameworks, particularly for rare and elusive species. However, one major shortfall of classical capture-recapture methods is their failure to explicitly account for spatial characteristics of the ecological system being studied. Specifically, two major problems caused by the spatial distribution of animals was recognised: first, that animals have heterogeneous capture probabilities as a result of the positions of their ranges relative to trap locations; and second, that the translation of measures of abundance into density estimates requires inference about the total area sampled, which will be greater than the area covered by sampling devices (Royle et al., 2014).

Various ad-hoc techniques were developed to deal with these spatial issues. In the earliest applications of capture-recapture to studies of large carnivores, density estimates were calculated by using capture frequency data from photographed animals, identified through their unique pelage markings, to obtain an abundance estimate via the closed capture-recapture statistical framework, before dividing this value by an approximation of the effective sampling area (ESA; Karanth & Nichols, 1998). ESA is typically calculated by adding a boundary strip to the trapping area equal to either half or the full mean maximum

distance moved (MMDM) by captured individuals (Borchers & Efford, 2008). Although widely used, this approach has drawn criticism for its lack of robust theoretical foundation (Efford et al., 2004; Royle et al., 2009), with studies reporting a tendency for half-MMDM buffers to underestimate ESA and thus overestimate density (Soisalo & Cavalcanti, 2006).

Efford et al. (2004) pioneered a solution to this shortfall of traditional capture-recapture with the development of spatially explicit capture-recapture (SECR), an approach which explicitly incorporates information on the spatial distribution of individuals relative to traps. The SECR approach describes the distribution of individuals via a Poisson point process model, with an animal's probability of being captured at any particular trap modelled as a decreasing function of the distance between the centre of the animal's home range and the trap location (Royle et al., 2014). In doing so, this method enables the ESA to be estimated in a statistically rigorous way from the underlying capture-recapture data (Borchers, 2012), and is thus able to directly estimate density.

While Efford et al. (2004)'s method formally described the spatial model for density estimation, it continued to adopt an ad-hoc framework for inference. Subsequent efforts to formalise this component of the analytical framework has resulted in two distinct methods for achieving inference within the SECR framework, one using a more classical, likelihood-based approach (Borchers & Efford, 2008; Efford et al., 2009), and the other adopting a Bayesian framework (Royle et al., 2009; Royle & Young, 2008). While the two methods do not differ significantly in terms of the density estimates they produce, the maximum likelihood approach has the advantage of being computationally faster, and thus advantageous for simpler analyses (Kalle et al., 2011; Noss et al., 2012). In contrast, the Bayesian framework may be more appropriate for studies with small sample sizes, as is typical of rare and elusive species. However, unlike maximum likelihood methods, Bayesian estimates are particularly sensitive to buffer width and augmentation size, and should thus be used with care (Kalle et al., 2011).

Since they were first used to estimate tiger density in India in 1995 (Karanth, 1995), capture-recapture and more recently SECR models have been employed to study populations of most large carnivore species that can be individually identified from their coat markings, including cheetah (Fabiano et al.,

2020; Marnewick et al., 2008), clouded leopard (Borah et al., 2013; Brodie & Giordano, 2012; Sollmann et al., 2014; Wilting et al., 2012), jaguar (Maffei et al., 2004; Silver et al., 2004; Soisalo & Cavalcanti, 2006; Sollmann et al., 2011; Tobler & Powell, 2013), leopard (see S2.1), ocelot (*Leopardus pardalis*: Dillon & Kelly, 2007; Maffei & Noss, 2008; Trolle & Kéry, 2003), snow leopard (*Panthera uncia*: Alexander et al., 2015; Jackson et al., 2006; Sharma et al., 2014), and spotted hyaena (O'Brien & Kinnaird, 2011). The methods have also been applied to less readily-identifiable species by comparing distinguishing features such as scars, ear nicks and subtle differences in colouration, a more challenging and labour-intensive approach that has nonetheless been used to estimate densities for puma (Kelly et al., 2008) and lion (Elliot & Gopalaswamy, 2017).

SECR analysis using camera trap data is a well-established method for estimating population density for marked species, and has been used in a number of locations to assess the status of leopard populations (Jacobson et al., 2016; see S2.1). The main disadvantage of camera trap surveys for density estimation is their relatively high cost: while cameras are continually coming down in price, the area that can be covered in a single survey is limited by the number of cameras that can be purchased and the time available to deploy and check them (Meek & Pittet, 2012; Rovero et al., 2013). Nevertheless, SECR modelling of camera trap data is one of the most widely used methods to estimate density for large carnivores, and can yield accurate estimates of density if cameras are spaced appropriately and cover an area of sufficient size (Balme, Hunter, et al., 2009; Foster & Harmsen, 2012; Tobler & Powell, 2013). Camera trap surveys also bring the added advantage of being able to provide information on population demographics (Anile & Devillard, 2018; Packer, Lichtenfeld, et al., 2009), and can provide a wealth of "bycatch" data on non-target species and human presence, which can be used to monitor wider animal communities (Ahumada et al., 2011; Rovero et al., 2014), human pressures (Ferreguetti et al., 2018; Loveridge et al., 2020), and interspecific associations (Carricondo-Sanchez et al., 2019; Easter et al., 2020). Although camera trapping can be prohibitively expensive and labour-intensive to carry out at a landscape-scale, survey protocols can be employed that target sites within different habitats and land use types that are representative of the wider landscape.

2.2.3. Intra-guild interactions

Finally, comprehensive monitoring programmes should take into account the fact that species do not exist in isolation: large carnivore populations can be strongly impacted by other species, including both prey and sympatric competitors. Interspecific competition can be particularly acute among large carnivores, as they often compete for the same space and resources (Caro & Stoner, 2003), and have an increased likelihood of lethal interactions due to their predatory adaptations (Donadio & Buskirk, 2006). As such, interspecific competition can have a strong influence on large carnivore density and distribution (Winterbach et al., 2013), and can in turn trigger cascading impacts across wider ecological systems (Ritchie & Johnson, 2009). Developing an understanding of competitive interactions among members of the large carnivore guild – and how these may be altered or exacerbated by growing anthropogenic pressures – is therefore highly important for multi-species conservation and management planning.

Many large carnivores make use of partitioning mechanisms to minimise the negative consequences of competition (Linnell & Strand, 2000). While some species may be able to avoid competitors entirely through spatial segregation, this strategy can bear a high fitness cost by limiting access to vital resources (Swanson et al., 2014), and is likely to become increasingly difficult in the face of continued habitat fragmentation (Parsons et al., 2019). As such, finer-scale avoidance – such as fine-scale spatial avoidance (Vanak et al., 2013), temporal avoidance (Hayward & Slotow, 2009), or dietary partitioning (Hayward & Kerley, 2008) – can be valuable strategies for competitors to facilitate coexistence.

There are a variety of ways to investigate competitive interactions among large carnivores, mirroring the variety of ways in which species may respond to competitive pressure. Multi-species occupancy modelling of presence-absence data can be used to explore patterns of co-occurrence and avoidance among different large carnivore species across large areas (Rota et al., 2016), providing a means of investigating spatial segregation and shared habitat preferences (Lombardi et al., 2020; Ramesh, Kalle, & Downs, 2017; Sunarto et al., 2015). Where species co-exist, spatiotemporal data like that collected by camera traps (Balme et al., 2019; Cusack et al., 2017; Sogbohossou et al., 2018) or VHF and GPS

collars (Broekhuis et al., 2013; Dröge et al., 2016; Vanak et al., 2013) can provide information on how dominant competitors influence individual behaviour at finer spatial and temporal scales. In addition, direct observations can shed light on the precise nature of direct competitive interactions – such as killing (Laurenson, 1994) and kleptoparasitism (Balme, Miller, et al., 2017; Cooper, 1991) – and their prevalence within a given population, as well as the behavioural adaptations adopted by large carnivores to minimise such interactions (such as prey caching by leopard; Balme et al., 2017a; Stein et al., 2015).

Interactions among African large carnivores

Africa is home to one of the most functionally diverse guilds of large carnivores (Dalerum et al., 2009), and its members are exposed to a wide range of potential competitive interactions. Competitive dominance within the African large carnivore guild is primarily determined by body size, with the outcome of individual encounters depending on a number of factors including group size (Cooper, 1991; Smith et al., 2008). Lion and spotted hyaena are the dominant carnivores in most protected African ecosystems, acting as one another's main competitors for resources (Périquet et al., 2016) and exhibiting top-down pressure on their smaller-bodied counterparts. For spotted hyaena, kleptoparasitism and direct killing by lion have been shown to contribute to high mortality rates (Trinkel & Kastberger, 2005) and population suppression (Watts & Holekamp, 2008). However, competition between the two species is not asymmetrical, with factors including spotted hyaena clan size (Watts & Holekamp, 2008) and individual behavioural differences (Watts et al., 2010) influencing the outcome of competitive interactions. Despite their high degree of dietary (Hayward, 2006) and temporal (Hayward & Slotow, 2009) overlap, lion and spotted hyaena continue to coexist across much of their range, possibly facilitated by spotted hyaena shifting from active predation to scavenging in areas with a high density of lion relative to spotted hyaena (Périquet et al., 2015).

Lion are known to attack and kill leopard (Balme et al., 2017), which have been shown to move to denser habitats when in close proximity to lion (du Preez et al., 2015) and actively avoid areas where the probability of encountering them is highest (Balme, Pitman, et al., 2017). However, multiple studies have found no evidence of lion suppressing leopard at a population level (Balme, Pitman, et al., 2017;

Miller et al., 2018; Rafiq et al., 2020); this may be facilitated by minor temporal partitioning (Miller et al., 2018) and dietary niche differentiation (du Preez et al., 2017), as well as leopards' ability to cache prey in trees to avoid kleptoparasitism (Stein et al., 2015). Spotted hyaena also typically dominate over leopard (Hayward, 2006), and there is some evidence of temporal partitioning between the two species in Tanzania's Udzungwa Mountains (Havmøller et al., 2020), but the outcome of encounters can depend on the size of the leopard and the number of hyaena in the clan (Bothma & Le Riche, 1984).

Both lion and spotted hyaena are known to kill, steal food from, and display aggression towards cheetah (Hunter et al., 2007; Laurenson, 1994) and African wild dog (Creel & Creel, 1996; van der Meer et al., 2011). Cheetah have been shown to employ fine-scale spatial and temporal avoidance of both dominant species (Broekhuis et al., 2013; Durant, 2000; Swanson et al., 2016), and there is evidence that wild dog avoid using areas with high densities of lion (Dröge et al., 2016; Marneweck et al., 2019) and that lion have contributed to wild dog population declines (Swanson et al., 2014).

Very little is known about intra-guild interactions of striped hyaena, but it is likely that they share a similar competitive status to brown hyaena, below spotted hyaena and lion (Mills, 1984), as both species occupy a similar dietary niche. Primarily scavengers, both species may however benefit from carrion left by sympatric carnivores (Stein et al., 2013).

2.3. The leopard (*Panthera pardus*)

2.3.1. Species description and global status

The leopard is one of the world's most iconic felids. The species has been classified as one of the world's most charismatic animals (Courchamp et al., 2018) and top ambassador species (E. A. Macdonald et al., 2017), and is considered a powerful emblem for many of the countries in which it is found, featuring on the coat of arms of five African nations (Benin, Democratic Republic of the Congo, Gabon, Malawi, and Somalia). Despite being widely considered one of the most adaptable of the world's large carnivores, the leopard is globally classified as *Vulnerable* by the IUCN; this listing marks an upward trend from *Least Concern* in 2002 and *Near Threatened* in 2008, and was upheld in the

species' latest assessment in 2019 (Stein et al., 2020). This status reflects the species' declining trend (Stein et al., 2020), and is a result of evidence that leopard populations have been dramatically reduced worldwide due to habitat fragmentation (Laguardia et al., 2017; Rostro-García et al., 2016), prey base declines (Henschel et al., 2011; Hussain et al., 2018; Wolf & Ripple, 2016), and direct human persecution, including severe levels of conflict (Inskip & Zimmermann, 2009; Kabir et al., 2014; Parchizadeh & Adibi, 2019), illegal wildlife trade (Bergin & Nijman, 2014; Oswell, 2010; Raza et al., 2012), and poorly-managed trophy hunting (Balme, Slotow, et al., 2009; Naude et al., 2020; Packer et al., 2010).

The leopard is the most wide-ranging of the world's felids, with populations found across Africa, Asia, and parts of the Middle East. A highly adaptable species, the leopard has been able to establish itself in a vast range of habitats, tolerating temperatures from -30 °C to 50 °C, and altitudes as high as 5,200 m in the Himalayas (Hunter, 2015). Populations can be found in the desert and semi-desert regions of southern Africa, in the unforgiving aridity of the Arabian Peninsula, along rugged mountain ranges of southwest Asia, and in the snowy mountains of the Russian Far East. The species reaches highest densities in the mesic woodlands, tropical and subtropical forests, and grassland savannahs of its range, where productivity is highest (see S2.1 for a summary of leopard density estimates from camera trap data). The species is unusual among the large carnivores for its relatively high tolerance of human-modified landscapes: with sufficient cover and prey availability, leopards have been known to persist in areas where traditional use of natural resources is permitted (Rostro-García et al., 2018); in agricultural landscapes, including both croplands (Kshettry et al., 2018) and livestock rangelands (Marker & Dickman, 2005; Van Cleave et al., 2018); and even in densely-populated urban environments such as Mumbai (Braczkowski et al., 2018).

A member of the *Felidae*, leopard are one of five extant members of the genus *Panthera*, alongside lion, jaguar, tiger, and snow leopard. Although historically as many as 27 leopard subspecies have been recognised on the basis of geography, morphology and appearance, nine subspecies are currently recognised. At a species level, leopard now occupy 25–37% of their historic range, but there have been

substantial differences in range loss between subspecies: three of the nine recognised subspecies account for 97% of the leopard's extant range (African leopard, *P. p. pardus*; Indian leopard, *P. p. fusca*; Persian leopard, *P. p. saxicolor*), while another three subspecies have each lost as much as 98% of their historic range (Amur leopard, *P. p. orientalis*; Arabian leopard, *P. p. nimr*; North Chinese leopard, *P. p. japonensis*; Jacobson et al., 2016). As such, one subspecies is classified as *Endangered* (Persian leopard; Khorozyan, 2008) and four as *Critically Endangered* (Amur leopard; Jackson & Nowell, 2008; Arabian leopard; Mallon et al., 2008; ; Indochinese leopard, *P. p. delacouri*; Rostro-García et al., 2020; Javan leopard, *P. p. melas*; Ario et al., 2008), with the remaining four subspecies listed as *Vulnerable* (African leopard; Indian leopard; North Chinese leopard; Stein et al., 2020; Sri Lankan leopard, *P. p. kotiya*; Kittle & Watson, 2020).

Leopards are nocturnal, and are generally active from dusk until dawn and at rest for most of the day (Estes, 1991), although in some areas prey activity patterns have brought about diurnal and crepuscular hunting behaviour (Jenny & Zuberbuhler, 2005). Unlike lion and cheetah – the only wild cats to form enduring social groups – leopards lead a largely solitary existence. Adult leopards socialise mainly during mating, and females socialise with offspring before and, to a far lesser extent, after independence. Amicable interactions also occur between males and familiar females and cubs.

Leopards have a polygynous mating system and both sexes are territorial. Adults defend the core of their territory against same-sex conspecifics, with some degree of overlap tolerated in the outer edges of their range. Both sexes mark their territories via scent marks (spraying and cheek-rubbing) and vocal communication (sawing, which can be heard up to 3 km away; Estes, 1991). Male territories often overlap with the smaller ranges of females. Home range size is highly dependent on habitat quality and prey availability, with recorded sizes ranging from 5.6 km^2 for a female in highly-protected Tsavo National Park, Kenya, to 2,750 km^2 for a male in the harsh climate of the southern Kalahari (Hunter, 2015). Consequently, leopards reach their highest densities in highly-productive, well-protected habitats. Upon independence, female cubs will often inherit part of their mother's range, while males

will disperse further to establish their own territory. In the wild, females can live up to 19 years and males up to 14 years (Hunter, 2015).

In step with the diversity of habitat types in which they are found, leopard diet is highly variable across the species' extent. Insects, reptiles, birds and mammals of all sizes are frequently eaten, but medium-sized ungulate prey weighing 10-40 kg are generally preferred where available (Hayward et al., 2006). Although the species is renowned for its dietary plasticity, individual leopard populations usually share a diet dominated by one or two locally abundant species. Leopards are stalk-ambush hunters, with the precise hunting strategy used varying according to prey species. Hunting occurs mostly at night, although opportunistic hunting does take place during the day. Once caught, smaller prey are typically killed with a bite to the back of the skull or neck, while larger prey are usually suffocated with a throat bite. In the presence of competitors, leopards will often cache their larger kills for later consumption by dragging them into dense vegetation or up trees to avoid kleptoparasitism (Balme, Miller, et al., 2017; Stein et al., 2015).

2.3.2. The leopard in Africa

The African leopard is widely but patchily distributed across Central, East and southern Africa, with southern Africa thought to contain the healthiest leopard populations of the species' entire range (Stein et al., 2020). Distribution in West Africa has been dramatically reduced, and the region is now home to only a small number of fragmented populations. In North Africa, where the species was historically found in the northern reaches of Morocco, Algeria and Tunisia, it is thought to either have become extinct or exist only as relict populations. Previously divided into as many as 12 different subspecies, leopard meta-populations on the African continent were consolidated into the present day *P. p. pardus* classification on the basis of mitochondrial and microsatellite analysis at the start of the 21st century (Miththapala et al., 1996; Uphyrkina et al., 2001).

The first in-depth study of African leopard was published in 1993, when Ted Bailey published his seminal book examining the ecology and behaviour of leopard in South Africa's Kruger National Park (Bailey, 1993). In the years that followed, advances in tracking and camera trapping technology enabled

studies of the species' movement patterns (Stander et al., 1997) and saw improved estimation of population densities (e.g. Henschel, 2008). Overall, however, the leopard's reputation as one of the most resilient and adaptable African large carnivores has contributed to a relative lack of research and conservation urgency for the species (Balme et al., 2014; Jacobson et al., 2016; Stein et al., 2020). Leopard research to date in Africa has largely been concentrated in areas of lower conservation concern, such as highly-protected areas reserved for non-consumptive use, and many efforts have failed to contribute meaningfully to conservation outcomes (Balme et al., 2014). As a result, the status and population trends of leopard is unknown across much of its remaining African range (Jacobson et al., 2016). This lack of empirical population assessments may be contributing to unseen losses for Africa's remaining leopard populations.

Nevertheless, the African leopard's adaptability highlights the potential value of a shift from protected area-centric conservation to landscape-level strategies for the species (Athreya et al., 2013). Given their potential to persist across wider mosaic landscapes – in contrast to other species that are more dependent on highly protected, annexed areas of wilderness to survive – leopard are therefore a particularly important species to study across human-defined landscapes, so that effective conservation measures can be integrated to large-scale management plans.

Conservation status

In SSA, the majority of leopards are believed to occur outside of PAs (Hunter et al., 2013). However, despite this reputed ability to persist in human-fragmented landscapes, the African leopard is thought to have lost huge swathes of its former range across the countries in which it remains – with decreases of 45-60% in East Africa and 28-51% in southern Africa (Jacobson et al., 2016). The primary drivers of this decline include the loss and fragmentation of natural habitat (Brink & Eva, 2009; Swanepoel et al., 2013) and the decline of many prey species (Craigie et al., 2010). These pressures also increasingly force leopard to use areas occupied by humans, which can exacerbate human-leopard conflict, another major threat to the species' survival in Africa (Swanepoel et al., 2015). Although reliable data on trends in leopard status are sorely lacking for SSA, these combined threats are likely to have caused population

declines of at least 30% over the last three generations (Stein et al., 2020). As a result, the IUCN Red List currently classifies the African leopard as *Vulnerable*, reflecting the view that the species is considered likely to become endangered unless the circumstances threatening its survival and reproduction improve (Stein et al., 2020).

The US Fish and Wildlife Service (USFWS) defines an *Endangered* species as one in danger of extinction throughout all or a significant portion of its range, while a *Threatened* species is a species deemed likely to become endangered in the foreseeable future throughout all or a significant portion of its range. USFWS lists the leopard as *Endangered* wherever found, except in 18 countries in SSA, where the species is considered *Threatened* (USFWS, n.d.). Although this lower-priority status in parts of Africa has remained unchanged since it was brought into effect in 1982, the classification has been subject to intense debate. In July 2016, The Humane Society of the United States and the Fund for Animals submitted a petition calling on the USFWS to reclassify the leopard as *Endangered* throughout its range (The Humane Society of the United States et al., 2016); this triggered a 90-day period for review of the information presented in the petition (Docket FWS-HQ-ES-2016-0131). The USFWS found the petition to present substantial information indicating that reclassifying the leopard may be warranted, and commenced a review of the status of the species in November 2016, attracting over 16,000 public comments (although this review has yet to lead to any reclassification).

Trophy hunting and trade

The leopard has been listed on Appendix I by CITES – the body responsible for imposing trade controls and setting quotas on the import and export of wildlife specimens – since the classification system's inception, meaning the species is considered to be threatened with extinction. CITES prohibits international trade in specimens of species on Appendix I except when the purpose of the import is not commercial. Despite this, there continues to be a significant global market for international trade of leopard – particularly in the US, which was consistently the biggest importer of leopard trophies from 2000 to 2018 (CITES, 2020b).

As of 2020, nine of the 42 countries in which the African leopard is found allow trophy hunting of the species: Botswana, Central African Republic, Ethiopia, Mozambique, Namibia, South Africa, Tanzania, Zambia and Zimbabwe (CITES, 2020a). Although Kenya, Malawi, and Uganda are permitted to export hunting trophies (CITES, 2020a), these countries have banned trophy hunting. Previous hunting bans in Zambia (2013) and Botswana (except on privately owned game farms; 2014) were lifted in 2016 and 2019, respectively (LaRocco, 2020; Mweetwa et al., 2018). Between 2000 and 2018, the world's largest exporters of leopard trophies were South Africa, Zimbabwe, Namibia, and Tanzania (CITES, 2020b).

South Africa, one of the most popular destinations for overseas trophy hunters (Balme, Hunter, et al., 2010), makes use of an adaptive management framework to adjust quotas annually based on available population data. The country issued a zero quota for leopard in 2016 and 2017, following a report that found the population estimates on which offtake quotas were based to be unreliable, suggesting that hunting levels were unsustainable (Department of Environmental Affairs, 2017a). A precautionary hunting quota was implemented in 2018 following the introduction of a set of standards for management and monitoring of leopard hunts (Department of Environmental Affairs, 2017b). Although a zero quota was again issued in 2019, a quota for 11 leopards was issued for 2020 on the basis of written submissions from stakeholders (Minister of Forestry Fisheries and the Environment, 2020). However, the fact that questions have been raised about South Africa's leopard population estimates, despite the majority of research on the African subspecies being carried out in the country (Balme et al., 2014; Jacobson et al., 2016), raises serious doubts about the sustainability of leopard offtake quotas elsewhere on the continent. Indeed, recent research has highlighted the inadequacy of many current export quotas in meeting the general principles of precaution, sustainable use and adaptive management (Trouwborst et al., 2020). The deficiency of robust population density estimates for leopard in African countries means that most extraction quotas are currently not based on empirical data, which may result in unsustainable offtake and, in turn, have long-lasting detrimental impacts on leopard populations (Naude et al., 2020; Packer et al., 2010).

2.4. Study landscapes

2.4.1. Kavango-Zambezi Transfrontier Conservation Area

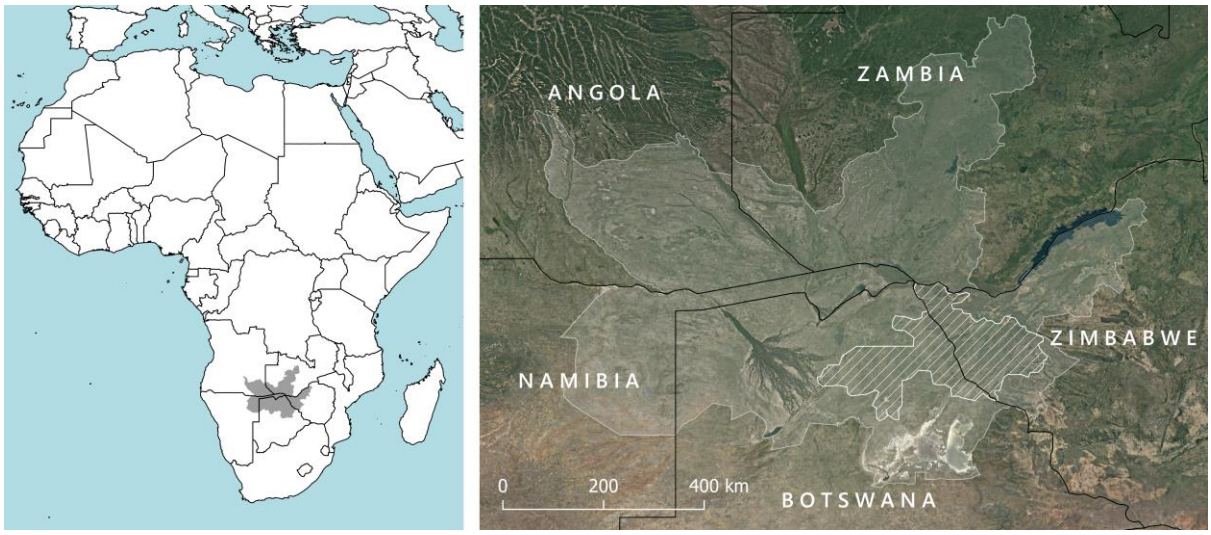

Figure 2.1: Left: location of the KAZA TFCA within southern Africa. Right: location of the spoor survey area within KAZA (see Chapters 3 & 4).

The Kavango-Zambezi (KAZA) Transfrontier Conservation Area (TFCA) in southern Africa was established in 2006, and is named for its location in the Kavango and Zambezi River basins, spanning the region where the borders of Angola, Botswana, Namibia, Zambia and Zimbabwe converge (Fig. 2.1). At approximately 520,000 km^2, KAZA is the world's largest terrestrial TFCA, encompassing 36 National Parks (NPs), as well as a host of Game Reserves (GRs), Forest Reserves, Community Conservancies and Game Management Areas. Due to its vast area, a huge variety of habitats are found within KAZA's extent: at its northernmost reaches are the fertile plains of Zambia's Kafue NP; to the south lies the arid expanse of the Kalahari Desert and, to the east, the patchy woodlands of Hwange NP. At the heart of the TFCA are the swamps of the Chobe-Linyanti river system and the sprawling river networks of the Okavango Delta, one of two world heritage sites found within the TFCA alongside Zimbabwe's Victoria Falls.

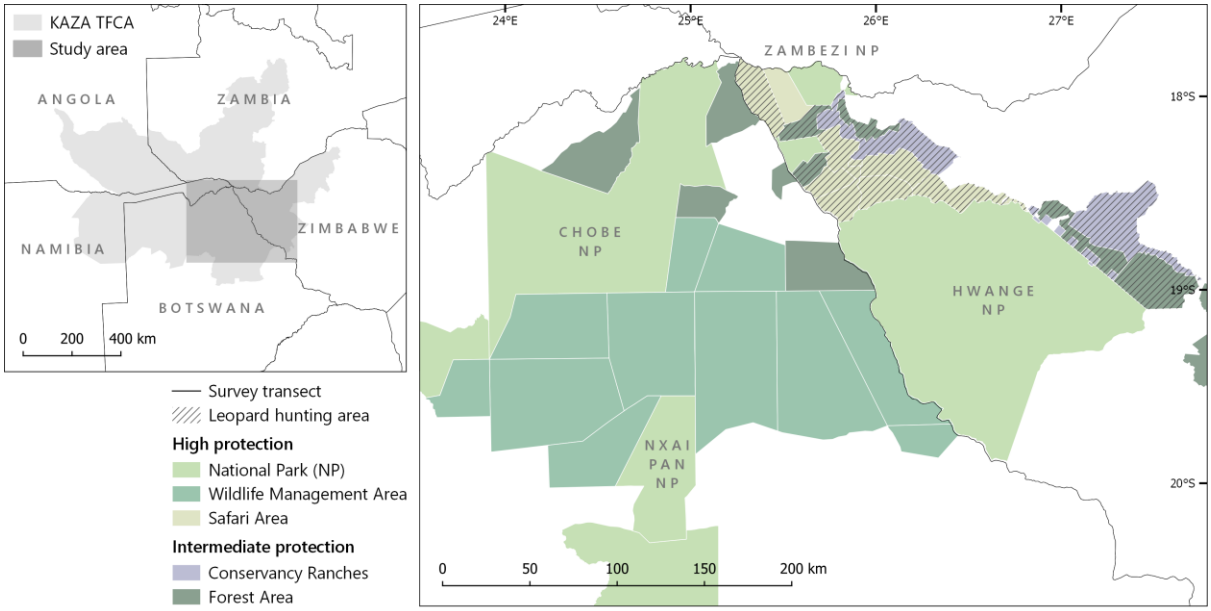

Figure 2.2: Left: the study area within the KAZA TFCA in southern Africa. Right: land use types in the study landscape. PAs are shown only in the study countries (Botswana & Zimbabwe).

The data used in Chapters 3 & 4 were collected within an area of approximately 30,000 km^2 in the southern KAZA TFCA, spanning northeast Botswana and western Zimbabwe (Fig. 2.2). The Zimbabwean portion of the study area is dominated by Hwange NP, the country's largest National Park at approximately 14,650 km^2 (Zimparks, n.d.). Originally occupied by San bushmen, the area was established as royal hunting grounds for the Matebele king Mzilikazi in the early 19th century, before being gazetted as Wankie Game Reserve in 1928 and formally established as an NP two years later (Friends of Hwange Trust, n.d.). The wider study area also includes the Matetsi and Deka Safari Areas to its north, Sikumbi Forest to its east, and Zambezi NP, which lies alongside Victoria Falls at Zimbabwe's northern border with Zambia. Spanning west across the border into Botswana, the study area encompasses a patchwork of former hunting concessions, Kasane, Maikaelelo and Sibuyu Forest Reserves and, at its southernmost reach, Nxai Pan NP.

The study area is generally water-poor. Surface water is available from seasonal waterholes or pans, although only a few continue to hold water into the dry season. Water is artificially pumped to

waterholes scattered across the landscape during the dry season (Valeix et al., 2010), which exist at much higher density in the Zimbabwean part of the study area than in Botswana.

Southern KAZA has an arid steppe climate (Peel et al., 2007). Rainfall is low – with annual averages of around 500 mm, reaching up to 700 mm in the north- and easternmost edges of the study area in Zimbabwe (British Geological Survey, 2018b, 2018a) – and is highly variable from year to year. There is a well-defined dry season from April to October, with maximum temperatures climbing to 35 °C in October, and a wet season from November to March. The climate cools with the arrival of rains, and night time temperatures can drop as low as 6 °C during the coldest months of May, June and July, in part due to the poor heat retention of the Kalahari sands that dominate the region.

The study area sits on a large plateau approximately 1000 m above sea level; topography is relatively flat across much of its extent, but becomes more undulating towards the northeast into the Zambezi River basin. The area is generally nutrient-poor due to its location in the Kalahari basin, although fertility increases towards the north, benefitting from proximity to the Chobe and Zambezi Rivers.

The area is comprised of a mosaic of bushland savannah and woodland, the latter being particularly prominent in Hwange NP to the east, interspersed with patches of grassland. In Hwange NP, the vegetation community is dominated by *Baikiaea plurijuga*, *Colophospermum mopane*, *Combretum spp.*, *Acacia spp.* and *Terminalia sericea*; on the Botswanan side, the dominant communities are sandveld – featuring *Combretum spp.*, *Acacia spp.* and *Terminalia sericea* – and mopane-dominated woodland (European Soil Data Centre (ESDAC), 1991).

The varied landscapes found within its borders contribute to the KAZA TFCA's rich ecosystem and species diversity. The area is home to the largest contiguous population of African elephant (*Loxodonta africana*), with approximately 250,000 individuals, and supports a wide variety of other wildlife, including over 600 bird species (SADC, 2015). Hwange NP alone boasts over 100 species of mammals and nearly 400 species of birds (Zimparks, n.d.). Of over 3,000 plant species found within the TFCA, 100 are endemic to the region (KAZA TFCA, 2016). The region is also an important source of connectivity for wild animal populations: GPS collaring of plains zebra (*Equus quagga*) in Botswana

has revealed the area to be home to the longest terrestrial wildlife migration in Africa (Bartlam-Brooks et al., 2011).

2.4.2. Tanzania's Ruaha-Rungwa landscape

Figure 2.3: Left: location of the Ruaha-Rungwa landscape in Tanzania. Right: close-up location of Ruaha-Rungwa within Tanzania (see Chapters 5 & 6).

The Ruaha-Rungwa landscape is a mixed-use conservation complex in southern Tanzania (Fig. 2.3). Spanning over 45,000 km^2 and encompassing a spectrum of land management structures, Ruaha-Rungwa has been identified as one of the most biologically valuable ecoregions in the world (Olson & Dinerstein, 2002), and is considered a Key Landscape for Conservation by the EU (European Commission, 2016).

At the heart of the landscape lies Ruaha NP, a 20,000 km^2 PA where only photographic tourism is permitted. To the north of the NP over the Mzombe River is a complex of three GRs where trophy hunting is permitted: Rungwa (9,000 km^2), Kizigo (4,000 km^2), and Muhesi (2,200 km^2). Neighbouring the NP along its south-eastern boundary over the Great Ruaha River are two community-managed WMAs, the Idodi-Pawaga MBOMIPA WMA (777 km^2) and Waga WMA, which act as a buffer between Ruaha NP and the surrounding unprotected village land. A number of other, less-strictly

protected areas are also present in the wider landscape, including Open Areas and Game Controlled Areas. As the PAs in the landscape are unfenced, wildlife are able to roam freely between the landscape's PAs and non-protected areas.

Ruaha NP is named for the Great Ruaha River, which runs along part of the NP's south-eastern boundary. Historically a perennial river that flowed year-round, upstream water mismanagement for agricultural projects since the mid-1990s has caused the river to cease to flow during the dry season (Epaphras et al., 2008). This drying out has led to a degradation of the NP's natural ecosystems, and is thought to have had significant impacts on animal numbers and movements in the landscape (Epaphras et al., 2008; Mtahiko et al., 2006). A number of artificial water holes were introduced in 2005 and 2006 to alleviate the water shortage problems (Epaphras et al., 2008).

Climate in Ruaha-Rungwa is arid to semi-arid, with a dry season that occurs from May to October and a wet season from November to April, starting with short rains which become increasingly intense. The area receives an average annual rainfall of 600 mm (Fick & Hijmans, 2017), the majority of which falls between December and April (Mtahiko et al., 2006). Temperature in the landscape does not vary substantially throughout the year, with daytime temperatures ranging from a maximum of around 26 °C in June to highs of up to 35 °C in October and November, and night time minimum temperatures ranging from 13 °C in June to 18 °C in November.

The Rungwa-Ruaha landscape is approximately 1000 m above sea level, although altitude throughout the park ranges from around 700 m to nearly 2,200 m (ESA, 2009). The topography of Ruaha NP is characterised by rolling low hills studded with baobabs and rocky outcrops, and is bisected by a dry escarpment – an offshoot of the Great Rift Valley to the west – from southwest to northeast. Vegetation cover in the landscape is a mosaic of *Acacia-Commiphora* bushland, Central Zambezian miombo *Brachystegia-Jubelnardia* woodland, riverine forest and flood-plain grasslands (Foley et al., 2014).

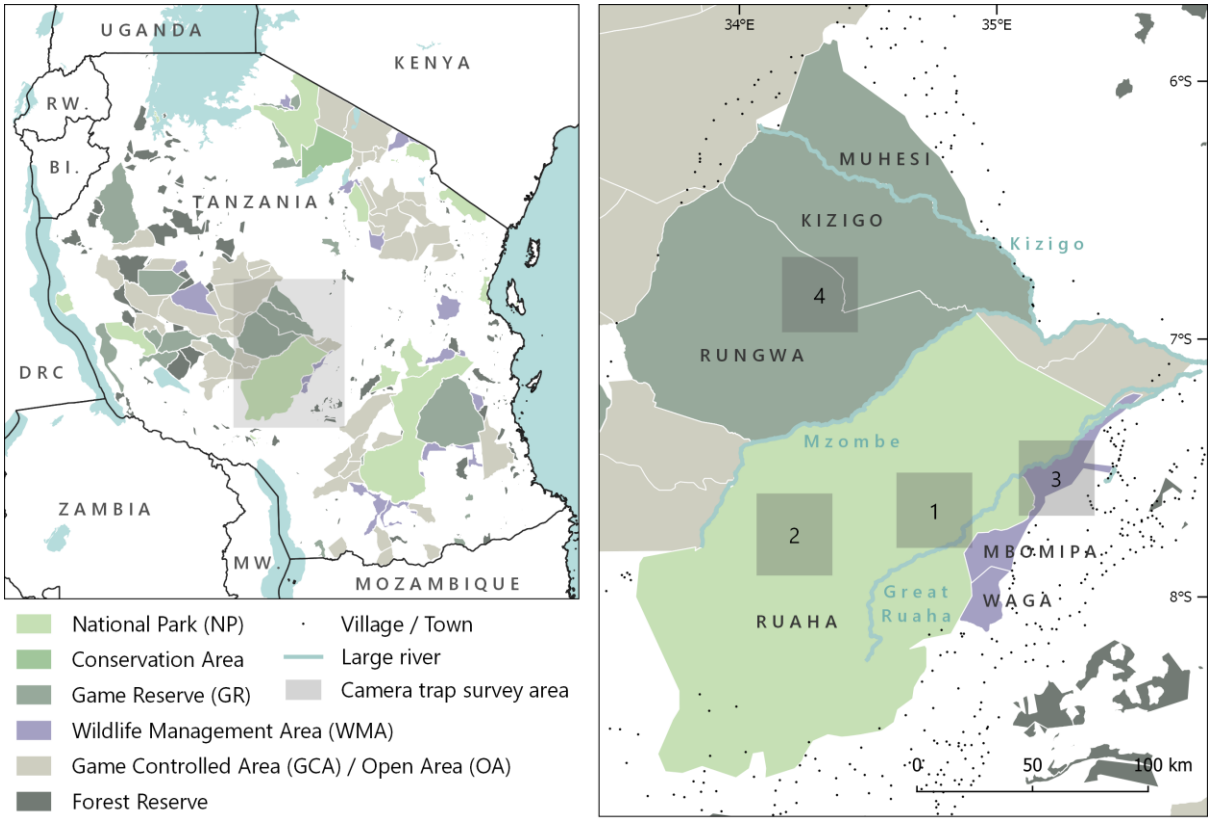

Figure 2.4: Left: Tanzania's PA network; note that changes in status since September 2019 are not shown, with the exception of the upgrading of part of Selous GR to form Nyerere NP. Right: the Ruaha-Rungwa landscape, showing the location of camera trap survey sites in (1) Ruaha NP *Acacia-Commiphora* habitat, (2) Ruaha NP miombo habitat, (3) MBOMIPA WMA *Acacia-Commiphora* habitat, and (4) Rungwa GR miombo habitat (see Chapters 5 & 6). Only villages and towns in close proximity to the PA complex are shown.

Ruaha-Rungwa is recognised by the EU as a Key Landscape for Conservation due to its internationally important wildlife populations, attributed to its unique positioning at the transition zone between eastern and southern African ecoregions (Dickman, 2008). The region is home to over 500 species of birds – half of those found in the whole country – and boasts over 1,700 species of plants (Southern Tanzania Elephant Project, n.d.). The landscape is also home to an intact East African large carnivore guild, supporting globally important populations of lion, leopard, cheetah, African wild dog, spotted hyaena, and striped hyaena, in addition to a number of smaller carnivore species.

The data used in Chapters 5 & 6 (and Appendices 2-5) were collected at sites within Ruaha NP, Rungwa GR, and MBOMIPA WMA, and in unprotected village land to the east of the PA complex (Fig. 2.4).

Ruaha National Park

Ruaha NP historically made up the southern portion of Saba GR, which was established in 1910 by Germany and later renamed Rungwa GR by the British in 1946. Ruaha was elevated to National Park status in 1964, and was expanded in 2008 with the addition of Usangu GR and surrounding wetlands. This expansion made Ruaha the largest National Park in East Africa, a title it held until November 2019, when approximately 30,000 km^2 of Tanzania's Selous GR was upgraded to form Nyerere NP (Kimboy, 2019).

Management of Ruaha NP is overseen by the Tanzania National Parks Authority (TANAPA), and a number of tourist lodges and camps are established both within and outside the park. Due to its remoteness – the park is only accessible by car via dirt road from Iringa, or by plane to two airstrips – Ruaha is advertised to international tourists as a chance to experience untouched wilderness away from the crowds typical of Tanzania's northern circuit (Tanzania Odyssey, n.d.).

Rungwa Game Reserve

Rungwa GR is managed as a single entity alongside Kizigo and Muhesi GRs by the Tanzania Wildlife Management Authority (TAWA; TAWA, n.d.). The three GRs are reserved for trophy hunting, and are sub-divided into hunting blocks that are leased to operators – although some blocks are vacant and not currently hunted (FZS, 2018). The largest of the three, Rungwa GR is divided into six blocks; of these, five were actively hunted during the study period, including the Ikiri block in which data collection was carried out.

MBOMIPA Wildlife Management Area

MBOMIPA WMA is a community-managed PA covering 777 km^2 adjacent to Ruaha NP, along the Great Ruaha River. MBOMIPA was established in 2003 and gazetted in 2007 as part of the Tanzanian Government's Wildlife Management Area initiative to "promote sustainable management of natural resources as a means of enhancing local economic development" (Tanzania Tourist Board, n.d.).

MBOMIPA is an acronym of the project's Swahili name, *Matumizi Bora ya Malihai Idodi na Pawaga* ("sustainable use of wildlife resources in Idodi and Pawaga"; Dickman, 2008).

MBOMIPA is comprised of areas of land carved from villages located in the Idodi and Pawaga administrative wards of Iringa Rural District. While 21 villages are members of the programme, the land itself was contributed by only eight villages; the remaining 13 were included on the grounds that it would incentivise their members to not poach or encroach into the WMA (WWF, 2014). Protection and land-use planning for the WMA falls to the hands of the member villages via an elected board called the Authorised Association. Both photographic tourism and trophy hunting operations are permitted in MBOMIPA, with profits to be shared among member villages (although 35% of revenues must be paid to the government; Trompell, 2019), but neither activity was taking place at the time of study. Due to its position along the border of Ruaha NP, MBOMIPA forms an important buffer zone for wildlife ranging from the core protected area of Ruaha NP towards the village lands that lie to the east.

S2.1 African leopard population density estimates from camera trap data

Table S2.1.1: African leopard population density estimates from camera trap data, with the country and study area, year of data collection, and method used. Study area abbreviations include National Parks (NP) and Game Reserves (GR). Reported densities are the number of individuals per 100 km^2. Methods used include capture-recapture (CR), spatially explicit capture-recapture (SECR), and spatial partial identity model (SPIM). Sources are restricted to peer-reviewed scientific papers and academic theses.

Country	Study Area	Density[1]	Year	Method	Reference
Botswana	Ghanzi commercial farmland	0.3 - 0.6	2009	CR	Kent, 2011
Gabon	Ivindo NP	12.1	2006-2007	CR	Henschel, 2008
Gabon	Rainforest partially inside Ivindo NP	4.6	2006-2007	CR	Henschel, 2008
Gabon	Logging concession rainforest outside Ivindo NP	2.7	2006-2007	CR	Henschel, 2008
Kenya	Mpala Ranch	12.0	2008	SECR	O'Brien & Kinnaird, 2011
Malawi	Kasungu NP	1.9	2016-2018	SPIM	Davis et al., 2020
Malawi	Majete Wildlife Reserve	1.6	2016	SECR	Briers-Louw, 2017
Mozambique	Niassa National Reserve, riparian habitat	9.9 - 12.7	2008-2010	SECR	Jorge, 2012
Mozambique	Niassa National Reserve, miombo woodland habitat	2.2 - 4.3	2008-2010	SECR	Jorge, 2012
Mozambique	Xonghile GR	2.6	2012	SECR	Strampelli et al., 2018
Namibia	Okonjima Nature Reserve	14.5	2015-2016	SECR	Noack et al., 2019
Namibia	Farmland outside Waterberg Plateau Park	3.6	2006	CR	Stein et al., 2011
Namibia	Waterberg Plateau Park	1.0	2006	CR	Stein et al., 2011
Namibia	Commercial farmland east of Namib-Naukluft NP	0.9	2013	CR	Edwards et al., 2015
Namibia	Commercial farmland east of Tsau//Khaeb (Sperrgebiet) NP	0.6	2013	CR	Edwards et al., 2015
Senegal	Niokolo Koba NP	2.1	2013	SECR[2]	Kane, 2014
South Africa	Kruger NP, N'wantesi concession	12.7	2008	CR	Maputla et al., 2013
South Africa	Sabi Sands GR	11.8	2017	SECR	Balme et al., 2019
South Africa	Mkhuze GR	10.8	2008	CR	Balme, Slotow, et al., 2010
South Africa	Soutpansberg Mountains	10.7	2008	SECR	Chase Grey et al., 2013
South Africa	St Lucia Wetland Park, western shores	8.4	2013-2014	SECR	Ramesh, Kalle, Rosenlund, et al., 2017
South Africa	St Lucia Wetland Park, eastern shores	7.4	2013-2014	SECR	Ramesh, Kalle, Rosenlund, et al., 2017
South Africa	Phinda Private GR	7.2	2005	CR	Balme, Slotow, et al., 2010
South Africa	Waterberg Biosphere, commercial farmland	6.6	2009	SECR	Swanepoel et al., 2015

South Africa	Waterberg Biosphere, Lapalala Wilderness	5.4	2009	SECR	Swanepoel et al., 2015
South Africa	Tembe Elephant Reserve	4.8	2013-2014	SECR	Ramesh, Kalle, Rosenlund, et al., 2017
South Africa	Zululand Rhino Reserve	4.8	2009	CR	Chapman & Balme, 2010
South Africa	Waterberg Biosphere, Welgevonden Private GR	4.6	2009	SECR	Swanepoel et al., 2015
South Africa	Soutpansberg Mountains	3.7	2016	SECR	Williams et al., 2017
South Africa	Phinda Private GR	3.4 - 3.7	2012	SECR	Braczkowski et al., 2016
South Africa	Non-protected areas adjoining Phinda & Mkhuze GRs	2.5	2005	CR	Balme, Slotow, et al., 2010
South Africa	Ndumo GR	1.6	2013-2014	SECR	Ramesh, Kalle, Rosenlund, et al., 2017
South Africa	Little Karoo	1.3	2011-2012	SECR	Mann et al., 2020
South Africa	Western Cape, Langberg	1.2	2012	SECR[2]	Devens et al., 2020
South Africa	Cederberg Mountains, fynbos biome	0.7 - 1.0	2004-2007	CR	Martins, 2010
South Africa	Western Cape, Agulhas	0.7	2011-2012	SECR	Devens et al., 2018
South Africa	Western Cape, Garden Route	0.7	2013-2014	SECR[2]	Devens et al., 2020
South Africa	Western Cape, Overberg	0.4	2011-2012	SECR[2]	Devens et al., 2020
South Africa	Eastern Cape, Baviaanskloof	0.2	2011-2012	SECR	Devens et al., 2018
Tanzania	Tarangire NP (wet season)	7.9	2006	CR	Msuha, 2009
Tanzania	Ruaha NP, *Acacia-Commiphora* habitat	6.8	2018	SECR	See Chapter 5
Tanzania	Serengeti NP (wet season)	5.7	2012	SECR	Allen et al., 2020
Tanzania	Serengeti NP (dry season)	5.4	2012	SECR	Allen et al., 2020
Tanzania	MBOMIPA Wildlife Management Area	4.2	2018	SECR	See Chapter 5
Tanzania	Udzungwa Mountains NP & Kilombero Nature Reserve	4.2	2013-2014	SECR	Havmøller et al., 2019
Tanzania	Rungwa GR	3.4	2019	SECR	See Chapter 5
Tanzania	Ruaha NP, miombo woodland habitat	3.2	2018	SECR	See Chapter 5
Zambia	Luambe NP	8.5	2006-2008	CR	Ray, 2011
Zambia	South Luangwa NP	8.5	2012-2014	SECR	Rosenblatt et al., 2016
Zambia	GMA-Chanjuzi	5.1	2006-2008	CR	Ray, 2011
Zambia	Lupande GMA & South Luangwa NP	5.1	2012-2014	SECR	Rosenblatt et al., 2016
Zimbabwe	Bubye Valley Conservancy, Kwalusi	5.4 - 6.1	2012	SECR[2]	du Preez et al., 2014
Zimbabwe	Bubye Valley Conservancy, Mazunga	2.8 - 4.0	2012	SECR[2]	du Preez et al., 2014
Zimbabwe	Mangwe district	1.4	2009-2010	SECR	Grant, 2012

[1] Leopards per 100 km^2

[2] Mean of maximum likelihood and Bayesian estimates

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CHAPTER 3

Drivers of leopard habitat use and relative abundance in Africa's largest transfrontier conservation area

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Title

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Running header

CHAPTER 3: Drivers of leopard habitat use and relative abundance

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Drivers of leopard habitat use and relative abundance in Africa's largest transfrontier conservation area

Abstract

Transfrontier conservation areas (TFCAs) have the potential to provide havens for large carnivores while preserving connectivity across wider mixed-use landscapes. However, information on the status of species in such landscapes is lacking, despite being a prerequisite for effective conservation planning. We contribute information to this gap for leopard (*Panthera pardus*) in Africa, where the species is facing severe range contractions, using data from transect surveys of a 30,000 km^2 area across Botswana and Zimbabwe in the Kavango-Zambezi (KAZA) TFCA. We used occupancy models to assess how biotic, anthropogenic, and management variables influence leopard habitat use, and N-mixture models to identify variables influencing the species' relative abundance. Leopard were detected in 184 out of 413 sampling units of 64 km^2; accounting for imperfect detection resulted in mean detection probability $\bar{\hat{p}}$ = 0.24 (SD = 0.06) and mean probability of site use $\overline{\hat{\Psi}}$ = 0.89 (SD = 0.20). Habitat use was positively influenced by prey availability and high protection. Relative abundance was best predicted by trophy hunting, which had a negative influence, while abundance was positively associated with high protection and availability of steenbok, although the latter result may be an artefact of steenbok range coinciding with areas of lower human impact in the study landscape. Our findings suggest that securing prey populations should be a priority in conservation planning for leopard in Africa, and underline the necessity of preserving highly-protected areas within mixed-use landscapes as strongholds for large carnivores. Our findings also support calls for better assessment of leopard population density in trophy hunting areas, and illustrate the value of N-mixture models to identify factors influencing relative abundance of large carnivores.

3.1. Introduction

Despite being widely considered one of the most adaptable of the world's large felids, the leopard (*Panthera pardus*) is classified as *Vulnerable* by the IUCN (Stein et al., 2020). In Africa, the species is primarily threatened by habitat loss and fragmentation (Di Minin, Slotow, et al., 2016), prey depletion (Wolf & Ripple, 2016), and direct persecution by humans (Inskip & Zimmermann, 2009), which have collectively contributed to the species losing at least 48% of its historical range on the continent (Jacobson et al., 2016).

As apex predators, leopards and other large carnivore populations require large, connected landscapes and viable prey populations to thrive (Crooks et al., 2011). However, the connectivity beyond protected area (PA) borders required by these species is often at odds with the increased demand for land associated with growing and developing human populations (Di Minin, Slotow, et al., 2016). The resulting habitat fragmentation has contributed to substantial range contractions for members of the large carnivore guild across the world (Wolf & Ripple, 2017). In light of this, there is a growing consensus that, while highly-protected areas remain a vital component of many large carnivore conservation strategies (Karanth & Chellam, 2009), small PAs alone will not be sufficient to maintain viable populations of large carnivores into the future (Ripple et al., 2014). A shift from the traditional protected area-centric approach to a landscape-level approach to conservation holds particular promise for leopards in Africa, the majority of which are believed to occur outside strictly-protected areas (Hunter et al., 2013).

In Africa, transfrontier conservation areas (TFCAs) embody this movement, while emphasising the coupling of conservation with development initiatives. Defined as areas spanning international borders and encompassing multiple PAs and land use types, TFCAs are managed as a single contiguous landscape for conservation (SADC, 1999). If effectively managed, TFCAs have the potential to protect large swathes of prime habitat and maintain connectivity within wider mixed-use landscapes, and thus provide havens for leopard within their contracting African range.

Until now, however, there has been relatively little effort to understand how leopards are faring across

these larger conservation areas (Balme et al., 2014; Jacobson et al., 2016), with most research having been restricted to small, highly-protected reserves (but see Balme, Slotow, et al., 2010; Henschel et al., 2011; Strampelli et al., 2018). There is therefore a need to increase knowledge of the species within the context of large, mixed-use landscapes like TFCAs. Understanding how leopards adapt to different components of these modern mosaic landscapes is essential to inform management and conservation planning, evaluate the conservation effectiveness of different land-use types, and ensure the persistence of Africa's leopard populations.

One land-use strategy of particular relevance to the leopard in Africa is trophy hunting, whereby a set quota of individuals may be hunted within a designated area each year. Trophy hunting has been used by conservation managers to attach economic value to wildlife areas by generating revenue for governments and local communities, and thus secure conservation benefits for natural habitats often unsuitable for photographic tourism (Lindsey et al., 2007). In the absence of viable conservation-oriented land use alternatives, trophy hunting is argued to therefore play an important role in preventing their conversion to agricultural land (Di Minin, Leader-Williams, et al., 2016; Dickman et al., 2019). However, the practice can have detrimental long-term impacts on hunted populations if carried out unsustainably or combined with other sources of anthropogenic mortality (Lindsey et al., 2013; Packer et al., 2010). Information on these impacts is lacking even for species which have attracted considerable attention from policymakers (e.g. lion, *Panthera leo;* Macdonald et al., 2017), and these gaps are greater still for leopard. Leopard populations within hunting areas should be assessed and monitored, and their habitat use mechanisms understood, in order to ensure detrimental effects of hunting are avoided, and to inform sustainable and adaptive hunting management plans (Balme, Hunter, et al., 2010).

We employed data from large-scale spoor surveys to investigate leopard status and habitat use across a mixed-use landscape within the southern Kavango-Zambezi (KAZA) TFCA. We used occupancy models to estimate the proportion of this landscape used by leopard, and assess how a suite of biotic, anthropogenic, and management variables influence habitat use for the species. We then employed novel N-mixture models to identify factors influencing relative abundance of leopard within the study

area, and discuss the implications of our findings to highlight conservation priorities for leopard across modern African conservation landscapes.

3.2. Methods

3.2.1. Study area

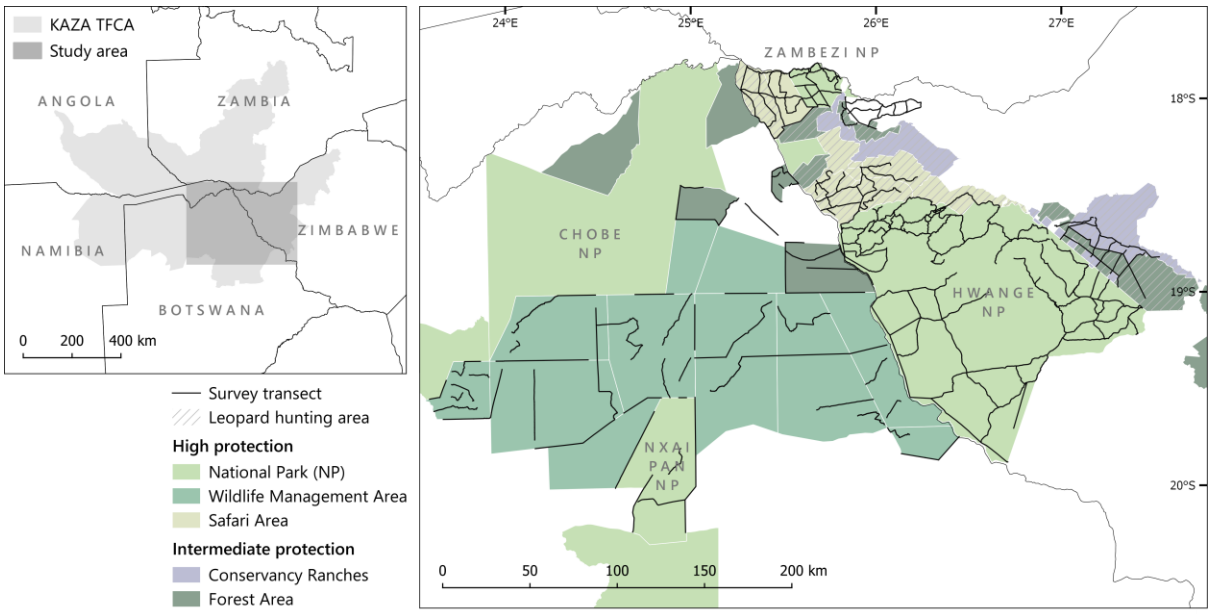


Figure 3.1: Left: the study area within the KAZA TFCA in southern Africa. Right: land use types and locations of survey transects in the study landscape. PAs are shown only in the study countries (Botswana & Zimbabwe). See S3.1 for a description of land use designations in place in the study area. Of the land use designations that permitted trophy hunting of leopard at the time of data collection, Safari Areas are classified as receiving high protection, while Conservancy Ranches and Forest Areas are classified as receiving intermediate protection.

At approximately 520,000 km^2, KAZA is the world's largest terrestrial TFCA, encompassing 36 National Parks (NPs) and a host of other land uses, including unprotected land and communal areas (see S3.1). The study area consists of approximately 30,000 km^2 within the southern part of the TFCA, stretching across northeast Botswana and western Zimbabwe (Fig. 3.1). The area is generally water- and nutrient-poor due to its location in the Kalahari Basin, with an annual rainfall average of 500-700 mm, although there are a large number of artificial waterholes across parts of the landscape. Vegetation is dominated by bushland savannah and woodland, interspersed with patches of grassland. Trophy hunting is permitted in Zimbabwe, and takes place across approximately 14% of the total study area.

Leopard hunts follow an adaptive quota system for offtakes, with only males hunted. Although reinstated in 2019, trophy hunting was suspended in Botswana in 2014; while some data collection for this study was conducted prior to this ban, leopards were not hunted in this period.

3.2.2. Occupancy & N-mixture modelling

Occupancy models use patterns of detection and non-detection over multiple surveys (sampling occasions) of a sampling unit (site) to estimate detection probabilities (p), and consequently derive unbiased estimates of occupancy (ψ; Mackenzie et al., 2002). The occupancy framework allows the inclusion of covariates to explain heterogeneity in both occupancy and detection probability, facilitating insights into factors driving habitat use by species (MacKenzie et al., 2006).

N-mixture models are a novel extension of occupancy models which use counts of unmarked individuals to estimate site-specific abundance (λ; Royle, 2004). While a strict set of assumptions must be met for total abundance to be derived from such models, the N-mixture framework allows the effect of covariates on relative abundance to be explored, which can provide a more nuanced view of how a species is faring within different components of a landscape than measures of site use alone (Royle, 2004).

3.2.3. Data collection

We divided our study area into 8 × 8 km (64 km^2) sites for both occupancy and N-mixture modelling (Fig. 3.2A & 3.2B), a scale we consider appropriate to capture second order selection (Johnson, 1980). As there is free movement of both leopard and their prey species among our sites, we relaxed the closure assumption of occupancy modelling by interpreting our state variable, psi (ψ), as the probability of site use instead of the probability of occupancy (Mackenzie, 2005).

Detection/non-detection data for leopard and other mammal species were collected across the study area from May 2012 to October 2015. Spoor survey transects were carried out by driving a vehicle at a low speed (~10 km/h) along roads, fire-breaks and boundary cutlines (Fig. 3.1), and recording any fresh spoor encountered. As highly-skilled local trackers assisted with spoor detection and identification,

incorrect identification of tracks was highly unlikely. Surveys were started at first light to avoid disturbance and maximise visibility.

Sampling occasions consisted of both spatial replicates and temporal replicates of the same transects. Although the survey effort spanned multiple years, data collection within individual sites was restricted to a single year.

To avoid spatial dependence, we tested for independence by pooling detection/non-detection data into transects of increasing length, with any transect with at least one detection being assigned the value 1. Transects were increased by increments of 2 km until the standard occupancy model without Markovian dependence (Mackenzie et al., 2002) outperformed the model extended to account for Markovian dependence of detections/non-detections (Hines et al., 2010), as per Henschel et al. (2016), using program PRESENCE (Hines, 2006).

3.2.4. Covariate selection

Detection covariate

Detection covariates are factors which are thought to potentially influence the probability of detecting a species given presence in a site (p). For both occupancy and N-mixture modelling, the number of 2 km sections of transect per sampling occasion was modelled as a detection covariate (*effort*) to account for variation in total segment length after pooling to avoid spatial dependence.

Substrate quality was not included as a detection covariate, as it can be considered largely homogenous across the study area due to the prevailing soil type of Kalahari sand and the use of highly-skilled local trackers (Trans-Kalahari Predator Programme (TKPP), unpublished data).

Site use & relative abundance covariates

Site use covariates are factors hypothesised to influence the probability of a site being used by a species (ψ). Candidate variables which are believed to influence leopard spatial use were selected based on prior research wherever possible. The same variables were tested in N-mixture models of relative abundance (λ).

We hypothesised that leopard habitat use and relative abundance would be influenced by five metrics, represented by nine spatial covariates (further information on how covariates were calculated and the rationale behind their inclusion can be found in S3.2):

- Water availability, quantified as the natural log of average pixel distance to nearest water point (name: *ln(water distance)*, hypothesised relationship: negative).

- Prey availability, quantified by developing models of the probability of site use by frequently taken prey species (as per Andresen et al., 2014; Everatt et al., 2014; Strampelli et al., 2018) using the spoor transect dataset, ensuring a measure of availability that accounts for imperfect detection. Probability of site use was modelled for four of the most frequently taken prey species by leopard (Hayward et al., 2006): impala (*Aepyceros melampus*; *impala*, positive), common duiker (*Sylvicapra grimmia*; *duiker*, positive), steenbok (*Raphicerus campestris*; *steenbok*, positive), and common warthog (*Phacochoerus africanus*; *warthog*, positive). Despite being considered an important prey species for leopard (Hayward et al., 2006), our dataset contained insufficient detections of bushbuck (*Tragelaphus scriptus*; n = 20) for probability of site use to be modelled for the species. We hypothesised that habitat use by prey would be influenced by 13 spatial covariates (see S3.3). The mean probability of site use for frequently taken prey was also calculated for each site, producing a variable reflecting general availability of these prey species (*all prey*, positive).

- Human disturbance, quantified as the natural log of average pixel distance to nearest settlement (*ln(settlement distance)*, positive).

- High protection, represented by the proportion of site highly protected (*protection*, positive). Areas classified as being subject to high protection within the study area include National Parks (where only photographic tourism is permitted), Wildlife Management Areas, and Safari Areas (where limited trophy hunting is permitted; see Fig. 3.1 and S3.1).

- Trophy hunting, represented by the proportion of site trophy hunted (*hunting*, negative). At the time of data collection, trophy hunting of leopard was only permitted in the study area within

Zimbabwe's Safari Areas, Conservancy Ranches, and Forest Areas (see Fig. 3.1 and S3.1).

Covariate values for each site were extracted using ArcGIS version 10.5.1 (ESRI, 2016) and QGIS version 2.18.10 (QGIS Development Team, 2017).

3.2.5. Modelling approach

Analysis was conducted in R version 3.6.2 (R Core Team, 2017) using RStudio version 1.2.5033 (RStudio Team, 2020). Single-season, single-species occupancy models (Mackenzie et al., 2002) were produced for each prey species and leopard in package *unmarked* version 0.12-3 (Fiske & Chandler, 2011). All continuous site use covariates were standardised on a z-scale prior to analysis.

Univariate models were ranked based on their Akaike Information Criterion (AIC) scores, corrected for small sample size (AICc; Burnham & Anderson, 2002). Where covariate pairs were correlated by $|r| > 0.7$, the covariate with the highest-ranked univariate model was retained. For leopard, univariate model rankings were employed to determine which prey availability covariate best predicted leopard site use (ψ). We then held a global model consisting of all remaining site use covariates constant, while modelling the covariate hypothesised to affect detection (p), *effort*. The detection model with lowest AICc was then used to rank all possible additive combinations of site use covariates.

A final model set was produced for each prey species and leopard containing all models with ΔAICc < 2, representing models with substantial empirical support (Burnham & Anderson, 2004). Goodness of fit was assessed for the top-ranked and most parameterised models within this model set using the MacKenzie and Bailey goodness of fit test for single-season occupancy models based on Pearson's chi-square (MacKenzie & Bailey, 2004).

The relative importance of covariates was assessed by summing AICc weights of all models in the final model set in which that covariate was present (Burnham & Anderson, 2004). The direction of impact of covariates was represented by the sign of their beta coefficient estimates, and covariates were considered to have a significant impact if the 95% confidence interval of the beta coefficient ($\beta \pm 1.96$ SE) did not span zero. Predicted site use values for each site were extracted via model averaging of the

final model set using package *MuMin* (Bartoń, 2013; note that no inferences were made based on model-averaged coefficients).

N-mixture models (Royle, 2004) were fitted to the leopard data to assess the relative influence of the nine candidate covariates on relative abundance (λ) across sites, following the same procedure as above but with input data comprised of count detections. Goodness of fit was assessed for the top-ranked model and the most parameterised model within the final model set using Sum of Squared Errors, Chi-square, and Freeman-Tukey tests.

3.3. Results

Repeated surveys of 5,055 km of unique transects resulted in a total of 11,665 km driven. We surveyed 474 sites over 286 days, with an average of 10.4 km driven per site.

3.3.1. Prey site use

Results and discussion of prey site use modelling can be found in S3.4. None of the models assessed for goodness of fit indicated lack of fit or overdispersion.

3.3.2. Leopard modelling

For leopard, spatial independence was achieved at 4 km. Sites with only one sampling occasion were excluded from analysis, resulting in 413 sites. 285 leopard detections were obtained in 184 of the 64 km^2 sites, giving a naïve occupancy of 0.45.

The mean probability of site use of the four frequently taken prey species ranked highest among covariates representing prey availability in the occupancy models, while probability of site use for steenbok ranked highest in the N-mixture models (see S3.5). Effort had a significant positive impact on detection probability for both model types, and was retained as the detection covariate for all subsequent model testing.

Three models were retained in the final occupancy model set (Table 3.1A), and seven in the final N-mixture model set (Table 3.1B). None of the models assessed for goodness of fit indicated lack of fit or

overdispersion (see S3.5).

Leopard site use

We estimated a mean detection probability of $\bar{p}$ = 0.24 (SD = 0.06) and a mean probability of site use of $\bar{\bar{\psi}}$ = 0.89 (SD = 0.20) for leopard, which is approximately double the naïve occupancy estimate. Model-averaged estimates suggest a high level of habitat use by leopard across the majority of the study area (Fig. 3.2A).

The best predictors of leopard site use were high protection (summed model weight, Σw = 1.00; Fig. 3.2C) and prey availability (Σw = 1.00; Fig. 3.2D). Both had a positive effect, which was significant for prey availability (Table 3.2A). Site use was also generally negatively associated with distance to settlement (Σw = 0.37), and generally positively associated with distance to water (Σw = 0.19).

Leopard relative abundance

Our estimates of abundance produced using N-mixture models cannot be interpreted as absolute abundance, as individuals whose home range spans multiple sites would be included in the abundance estimate of multiple sites within their home range, and there is growing evidence that N-mixture models do not produce reliable absolute abundance estimates (Link et al., 2018; Nakashima, 2020). Nevertheless, we use these models to make inferences about relative abundance across the study area (Fig. 3.2B).

Overall, leopard abundance was highest across much of the study area in Botswana, and in Zimbabwe's Hwange NP. The best predictors of leopard relative abundance were trophy hunting (Σw = 1.00; Fig. 3.2E) and high protection (Σw = 0.75; Fig. 3.2F). Trophy hunting had a significant negative impact on abundance, while leopard abundance was positively associated with the level of protection, a relationship that was significant in one model (Table 3.2B). Although distance to water (Σw = 0.24), availability of steenbok (Σw = 0.26), and distance to settlement (Σw = 0.21) all appeared in the final model set with consistent relationships to relative abundance, they did not show any robust relationship.

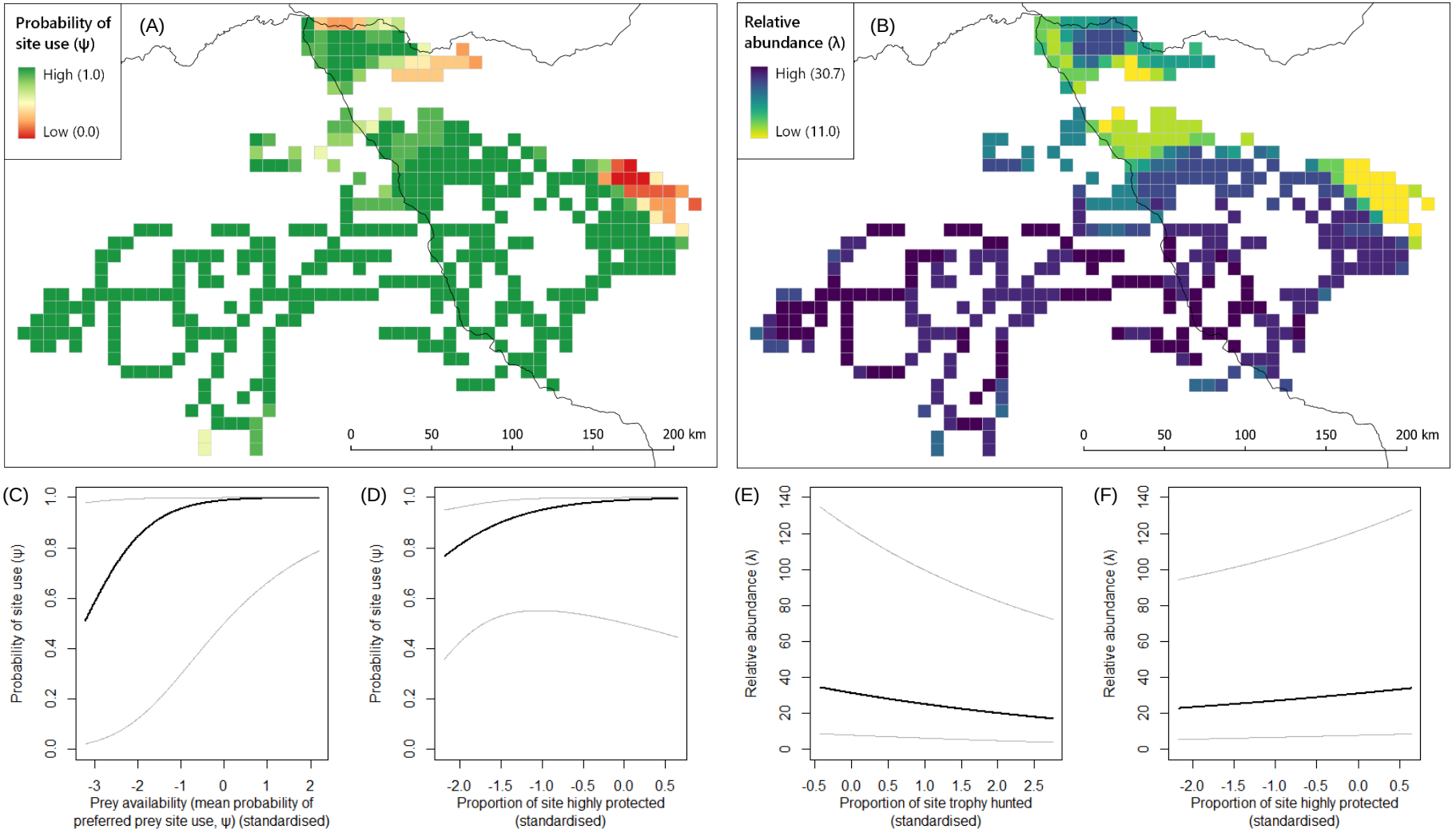


Figure 3.2: Model-averaged estimates of leopard (A) site use ($\hat{\psi}$) and (B) relative abundance ($\hat{\lambda}$) for each site in the southern KAZA TFCA. Estimates (with 95% confidence intervals) of leopard site use given variation in (C) prey availability, and (D) high protection, and relative abundance given variation in (E) trophy hunting, and (F) high protection. Plots were produced using the top-ranked model based on AICc ranking (ψ(all prey + protection),p(effort) and λ(protection + hunting),p(effort)). Each covariate was predicted while holding the other at its mean value.

Table 3.1: Results of multivariate model selection estimating leopard (A) site use (occupancy models) and (B) relative abundance (N-mixture models) in the southern KAZA TFCA.

(A) **Site use (occupancy)**

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	ψ(all prey + protection),p(effort)	5	1060.18	1070.3	0.00	0.43
2	ψ(all prey + ln(settlement distance) + protection),p(effort)	6	1058.41	1070.6	0.29	0.37
3	ψ(ln(water distance) + all prey + protection),p(effort)	6	1059.72	1071.9	1.60	0.19

(B) **Relative abundance (N-mixture)**

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	λ(protection + hunting),p(effort)	6	-676.87	1366.0	0.00	0.24
2	λ(ln(water distance) + protection + hunting),p(effort)	7	-676.31	1366.9	0.94	0.15
3	λ(steenbok + protection + hunting),p(effort)	7	-676.32	1366.9	0.97	0.15
4	λ(hunting),p(effort)	5	-678.47	1367.1	1.14	0.14
5	λ(ln(settlement distance) + protection + hunting),p(effort)	7	-676.58	1367.4	1.48	0.12
6	λ(steenbok + hunting),p(effort)	6	-677.62	1367.4	1.50	0.11
7	λ(ln(water distance) + ln(settlement distance) + protection + hunting),p(effort)	8	-675.74	1367.8	1.88	0.09

All models shown are within ΔAICc < 2 from the top-ranked model.

Table 3.2: Parameter estimates (standard error in parentheses) of the final model set (ΔAICc < 2) for models estimating leopard (A) site use and (B) relative abundance in the southern KAZA TFCA.

(A)	**Site use (occupancy)**	**Intercept ψ**	**β ln(water distance)**	**β all prey**	**β ln(settlement distance)**	**β protection**		**Intercept p**	**β effort**
1	ψ(all prey + protection),p(effort)	4.42 (2.25)		1.36 (0.56)		1.48 (0.99)		-3.25 (0.55)	1.11 (0.28)
2	ψ(all prey + ln(settlement distance) + protection),p(effort)	4.75 (2.00)		1.55 (0.60)	-0.68 (0.61)	1.73 (0.94)		-3.25 (0.55)	1.11 (0.28)
3	ψ(ln(water distance) + all prey + protection),p(effort)	2.79 (1.39)	0.48 (0.45)	1.02 (0.53)		0.92 (0.51)		-3.23 (0.55)	1.14 (0.28)
(B)	**Relative abundance (N-mixture)**	**Intercept ψ**	**β ln(water distance)**	**β steenbok**	**β ln(settlement distance)**	**β protection**	**β hunting**	**Intercept p**	**β effort**
1	λ(protection + hunting),p(effort)	3.18 (0.62)				0.14 (0.08)	-0.22 (0.08)	-6.21 (0.77)	0.90 (0.24)
2	λ(ln(water distance) + protection + hunting),p(effort)	3.17 (0.62)	0.07 (0.07)			0.15 (0.08)	-0.20 (0.08)	-6.22 (0.77)	0.91 (0.24)
3	λ(steenbok + protection + hunting),p(effort)	3.17 (0.62)		0.09 (0.09)		0.13 (0.08)	-0.17 (0.09)	-6.22 (0.77)	0.92 (0.24)
4	λ(hunting),p(effort)	3.19 (0.63)					-0.26 (0.08)	-6.22 (0.78)	0.91 (0.24)
5	λ(ln(settlement distance) + protection + hunting),p(effort)	3.18 (0.61)			-0.06 (0.08)	0.16 (0.09)	-0.24 (0.08)	-6.20 (0.77)	0.90 (0.24)
6	λ(steenbok + hunting),p(effort)	3.18 (0.64)		0.11 (0.08)			-0.20 (0.09)	-6.23 (0.79)	0.92 (0.24)
7	λ(ln(water distance) + ln(settlement distance) + protection + hunting),p(effort)	3.16 (0.62)	0.09 (0.07)		-0.09 (0.08)	0.18 (0.09)	-0.21 (0.08)	-6.20 (0.77)	0.91 (0.24)

Beta coefficients (β) in grey indicate a significant impact on (A) probability of site use or (B) relative abundance in the model shown, as the 95% confidence interval (β ± 1.96 SE) does not span zero.

3.4. Discussion

3.4.1. General importance & impact

The widespread distribution estimated for leopard across the study area indicates that the species is faring relatively well within PAs of the southern KAZA TFCA. This suggests that the KAZA TFCA has been successful in maintaining the continued persistence of the species in this region since its inception, and it will have an important role to play in preserving existing leopard habitat into the future.

Due to their scale, TFCAs have the potential to secure corridors for wildlife that may otherwise be lost to land-use conversion and fragmentation. Such landscape-scale connectivity is of particular value for large carnivores, whose wide-ranging behaviour and vulnerability to conflict mean that a lack of dispersal routes can result in population declines and eventual local extinctions (Winterbach et al., 2013). The mosaic landscapes preserved through TFCAs can be especially important for species that are particularly vulnerable to intra-guild competition – such as the African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) – whose avoidance of areas with high densities of dominant competitors can force them into lesser- or non-protected land (Creel, 2001; Durant, 2000). Large, appropriately-located tracts of interconnected land are also necessary to support migratory species (Naidoo et al., 2016). However, we are unable to make inferences about connectivity from this study, as occupancy modelling is not considered an appropriate proxy for landscape permeability across large scales (Pitman et al., 2017; Zeller et al., 2011), and less than 5% of our total survey effort was conducted in completely unprotected land. We therefore recommend further research to identify important corridors for wildlife populations within KAZA and other TFCAs, with a particular focus on assessments in completely unprotected land surrounding PAs, and collaboration between researchers and land-use planners to ensure their integration into management plans.

Our analysis illustrates that sign-based occupancy modelling can be employed to monitor large carnivore habitat use across vast, mixed-use landscapes such as TFCAs (Thorn et al., 2010). Insights provided by occupancy surveys can therefore be complementary to those obtained from more intensive

survey efforts such as camera trap surveys, which can be used to produce robust population density estimates at finer scales.

This is the first study to employ N-mixture models to investigate relative abundance of leopard, and one of the first to do so for large carnivores (but see Belant et al., 2016). We believe this method holds promise as an efficient and cost-effective way to understand the factors affecting species' abundance over large scales. However, while we did control for spatial autocorrelation in our data, variation in leopard movement patterns across the study landscape may have resulted in artificially high relative abundance estimates in the more arid parts of our study area, where home ranges are likely to be larger (Rogan et al., 2019). Thus, while we show that N-mixture models can provide useful insights through assessments of relative abundance, we echo calls against employing this methodology to obtain population estimates from spoor data (Link et al., 2018; Nakashima, 2020).

3.4.2. Drivers of leopard habitat use & relative abundance

Availability of natural resources

Abundant prey are a key requirement for the survival of large carnivores, and prey base depletion is a major driver of global large carnivore population declines (Wolf & Ripple, 2016). In southern KAZA, leopard habitat use was strongly positively influenced by prey availability, confirming findings elsewhere in Africa (Balme et al., 2019; Burton et al., 2012; Kane, 2014). Our results suggest that it is the general availability of prey of preferred body size, and not of a specific species within this group, that drives leopard habitat use at the scale considered. This is in keeping with the species' generalist feeding behaviour and ability to adapt their diet to a range of prey depending on available resources (Hayward et al., 2006).

In contrast, relative abundance of leopard was better explained by the availability of a single prey species, steenbok. However, this result may be an artefact of steenbok range coinciding with areas of lower human impact in the study landscape, where leopard densities are likely to be higher. Moreover,

an important consideration to note is that our prey availability metrics reflect only presence, so any finer impact of prey abundance on leopard habitat selection and relative abundance will not be captured.

Our results suggest that leopard habitat use increases with distance from water. This finding is likely an artefact of the large number of water points at the northernmost part of our study area, parts of which are not highly protected and are therefore estimated to have a relatively low probability of site use. Nevertheless, this effect was not significant, in line with previous studies of leopard in Asia and elsewhere in Africa (Constant, 2014; Kshettry et al., 2017; Ngoprasert et al., 2007).

High protection

Leopard habitat use was positively associated with high protection, a relationship previously identified in Kenya's Maasai Mara (Madsen & Broekhuis, 2020). We also found a positive association between high protection and leopard relative abundance. The influence of protection may be direct, through the reduced risk of anthropogenic mortality in such areas, or indirect, through the role of protection in supporting higher densities of prey species. The latter mechanism was identified as more important in shaping leopard density in neighbouring Zambia (Rosenblatt et al., 2016). However, these associations were not significant except in a single model, which may be a consequence of insufficient surveys being conducted in completely unprotected areas. Similarly, by grouping areas with a lower level of protection with unprotected areas, we may have failed to capture the importance of these partially-protected areas for leopard. Further conservation-oriented research should be carried out in such areas, as they are thought to contribute substantially to leopard range across Africa (Hunter et al., 2013) and are particularly vulnerable to degazettement (Jones et al., 2018).

Trophy hunting

Trophy hunting did not appear to have an influence on leopard occurrence. Moreover, given the importance of high protection in predicting habitat use by leopard, our results suggest that well-protected hunting areas may represent important areas of habitat for leopard in KAZA. However, results of N-mixture modelling suggest that trophy hunting may exert a top-down effect on this leopard population, even within highly protected hunting areas. The removal of mature individuals from a

population via trophy hunting has been found to negatively impact abundance of hunted carnivore species elsewhere (Lindsey et al., 2013; Packer et al., 2010), and an inverse relationship between abundance and hunting offtake has been observed for lion in the study landscape (Loveridge et al., 2016). Our findings suggest that similar population suppression mechanisms may be occurring in the study area for leopard.

Human disturbance

Habitat use by leopard was generally negatively associated with distance to human settlements. Although this contradicts findings from Angola (Petracca et al., 2019), leopard have been shown to do particularly well near agricultural lands – which often coincide with areas of human settlement – in many other parts of their range (Athreya et al., 2015), a pattern that has been attributed to higher prey availability in such areas (Constant, 2014). However, this result is likely to be an artefact of the large number of human settlements adjacent to the boundary of the highly-productive and relatively well-protected Hwange NP at the south-eastern edge of our study area, where leopard site use and relative abundance were both estimated to be high. This hypothesis is supported by the lack of significance of this relationship and the importance of high protection in our final occupancy and N-mixture models. There is likely to also be a scale-dependency to this relationship, with finer-scale analysis more likely to show avoidance of human settlements by leopard, as found elsewhere (Strampelli et al., 2018).

3.4.3. Conservation recommendations

The wide distribution and habitat tolerance of leopards within PAs in KAZA supports the continued movement towards conservation at the landscape-scale through initiatives such as TFCAs. At the same time, our results highlight the importance of maintaining highly-protected core areas within these mixed-use conservation landscapes, as they provide areas of higher population abundance which can protect species against detrimental source-sink dynamics (Hansen, 2011). We recommend that further similar research be carried out as part of the transition to landscape-scale conservation to understand how other species are faring across different landscape components. TFCA partner countries should

implement joint species-specific action and management plans, alongside landscape-level strategies, to ensure collaboration and uniformity of activities for managing key species across boundaries.

Given the importance of prey availability in shaping leopard habitat use, maintaining sufficient habitat to support prey populations should be a priority for the conservation of African leopard populations. Efforts should also focus on reducing bushmeat poaching of prey species, particularly as this brings the added benefit of reducing accidental snaring, which has severely reduced and even extirpated leopard populations in Asia (Rasphone et al., 2019; Rostro-García et al., 2018) and is a threat to leopard survival in Africa (Swanepoel et al., 2015). These recommendations would benefit all large carnivore species in Africa, where 37% of prey species have decreasing population trends (Wolf & Ripple, 2016).

Our results suggest that trophy hunting can have both positive and negative impacts: well-protected hunting areas can offer valuable habitat for leopard (Di Minin, Leader-Williams, et al., 2016; Dickman et al., 2019; Lindsey et al., 2007), but unsustainably high trophy hunting quotas may contribute to long-term leopard population declines (Loveridge et al., 2016; Packer et al., 2010, 2009). As such, quotas must be informed by robust estimates of population densities in hunting areas of the KAZA TFCA, ideally as part of a long-term monitoring effort with flexible quotas tied to annual population fluctuations (Balme, Hunter, et al., 2010) and combined with meaningful community participation. In recent years, camera trap surveys have been implemented across the study landscape to obtain density estimates for leopard, and findings are being utilised as part of adaptive quota management for leopard trophy hunting in Zimbabwe (ZPWMA, 2018); with the recent reinstatement of trophy hunting in Botswana, similar systems should also be integrated across the border. Given our evidence of trophy hunting influencing leopard abundance, we welcome these actions and recommend similar monitoring frameworks – for leopard and other hunted species – in other trophy hunting areas, to ensure activities are carried out without long-term detrimental effects to populations.

3.5. Acknowledgements

We would like to thank the Governments of Botswana and Zimbabwe for supporting this study, and the respective wildlife authorities for granting the research permits necessary for fieldwork; in Botswana, the Ministry of Environment, Natural Resources Conservation and Tourism (Permit number: EWT 8/36/4 XXIII (15)) and, in Zimbabwe, the Parks and Wildlife Management Authority (Permit numbers: REF:DM/Gen/(T) 23(1)(c)(ii): 12/2012, 08/2013, 51/2014, 10/2015). We thank the field staff of the Hwange Lion Project and TKPP for their assistance with data collection, and the Victoria Falls Wildlife Trust for their support of this project. Funding for the surveys was provided by the Robertson Foundation, the Recanati-Kaplan Foundation, and a Darwin Initiative for Biodiversity Grant DAR17-031 (2009-2012). DPhil scholarship funding for CS is provided by the University of Oxford & Natural Environment Research Council (NERC) Doctoral Training Programme.

3.6. Supplementary material

S3.1 Description of land use designations in the study area

S3.2 Overview and justification of leopard site use and relative abundance covariates

S3.3 Overview and justification of prey site use covariates

S3.4 Prey site use analysis results and discussion

S3.5 Detailed leopard site use and relative abundance analysis results

S3.1 Description of land use designations in the study area

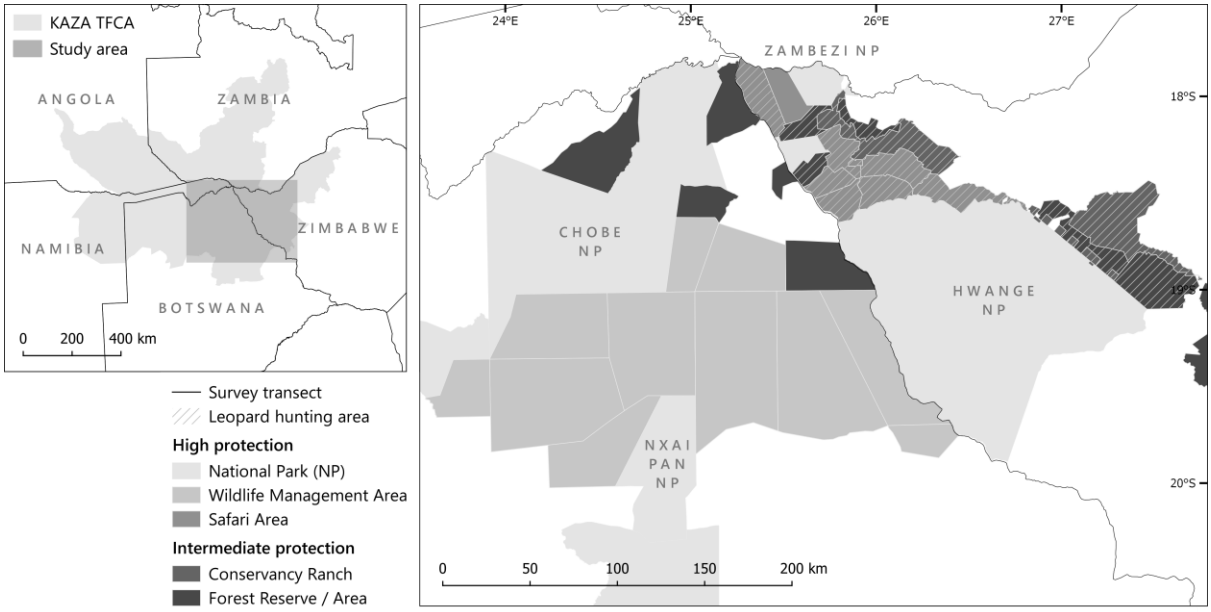


Figure S3.1.1: Left: the study area within the KAZA TFCA. Right: land use types in the study landscape. PAs are shown only in the study countries (Botswana & Zimbabwe).

Land use designations classified as *high protection* in this study:

- **National Park (Botswana & Zimbabwe)**

  PAs managed and run by government authorities – the Department of Wildlife and National Parks in Botswana, and Zimbabwe Parks and Wildlife Management Authority in Zimbabwe – which are preserved for non-consumptive wildlife utilisation (photographic tourism). No hunting is allowed inside National Parks.

- **Wildlife Management Area (Botswana)**

  Gazetted PAs, where wildlife utilization is the primary form of land use. Some Wildlife Management Areas (WMAs) are managed by local communities under the principles of community-based natural resource management (CBNRM). Others are leased out to private concessionaires for either consumptive use (hunting – although leopards were not hunted in Botswana during the data collection period for this study), non-consumptive use (photographic

tourism) or both. WMAs are intended to act as buffer zones around National Parks, provide benefits to local and national economies, and act as models for sustainable development.

- **Safari Area (Zimbabwe)**

  PAs managed by Zimbabwe Parks and Wildlife Management Authority, where the officially designated land-use is consumptive sustainable use of wildlife (usually through trophy hunting). Hunting is managed through an annual quota system and hunting concessions are leased by private hunting operators who market the allocated quota to tourist hunters.

Land use designations classified as *intermediate protection* in this study:

- **Conservancy Ranch (Zimbabwe)**

  Privately owned land, predominantly utilised for wildlife conservation and commercial and subsistence farming. Annual hunting quotas are allocated to individual properties by Zimbabwe Parks and Wildlife Management Authority through an annual stakeholder quota setting process.

- **Forest Reserve (Botswana) / Forest Area (Zimbabwe)**

  In Botswana, Forest Reserves are areas established specifically for the conservation and better regulation of use of forest resources, and are managed by the Department of Forestry and Range Resources.

  In Zimbabwe, Forest Areas are national PAs managed by the Zimbabwe Forestry Commission, primarily for extractive use of forest products (largely indigenous hardwoods in western Zimbabwe). Annual hunting quotas are allocated to Forest Areas, with hunts marketed to tourist hunters either directly by the Forestry Commission or through third party safari hunting operators.

S3.2 Overview and justification of leopard site use and relative abundance covariates

Table S3.2.1: Site covariates hypothesised to affect leopard habitat use and relative abundance across the southern KAZA TFCA.

Covariate	Description	Name	Hypothesised effect on site use	Data source	Justification
Water availability	Natural log of average pixel distance to nearest water point	*ln(water distance)*	-	Water points dataset (TKPP, unpublished data)	Multiple studies have found leopard abundance or habitat use to not be significantly affected by distance to water (Constant, 2014; Kshettry et al., 2017; Ngoprasert et al., 2007) However, the study area is arid, with limited water availability across the landscape. Water may therefore be a limiting factor on leopard habitat use, both directly and through the water-driven distribution of prey.
Prey availability	Duiker site use	*duiker*	+	Spoor dataset	Various studies have shown prey availability to be positively associated with leopard habitat use (Balme et al., 2019; Burton et al., 2012; Kane, 2014; Steinmetz et al., 2013; but see Strampelli et al., 2018) and population density (Boast & Houser, 2012; Marker & Dickman, 2005; Rosenblatt et al., 2016; Stein et al., 2011; but see Balme, Slotow, et al., 2010; Havmøller et al., 2019).
	Impala site use	*impala*	+		
	Steenbok site use	*steenbok*	+		
	Warthog site use	*warthog*	+		
	Mean preferred prey site use	*all prey*	+		
Human disturbance	Natural log of average pixel distance to nearest settlement	*ln(settlement distance)*	+	Settlements dataset (TKPP, unpublished data)	Human disturbance may negatively impact leopards directly (e.g. snaring bycatch) or indirectly (e.g. habitat conversion, poaching of prey species). Multiple studies have shown human disturbance to be one of the strongest predictors of leopard habitat use (Kshettry et al., 2017; Ngoprasert et al., 2007; Petracca et al., 2019; Zakaria & Sanei, 2011).
High protection	Proportion of site highly protected	*protection*	+	Protected areas dataset (TKPP, unpublished data)	Highly-protected areas can provide large carnivores with refugia from human disturbance and habitat fragmentation. Although leopards are widely considered to be highly adaptable species (Stein et al., 2020), multiple studies in Africa have found protection to be positively associated with leopard habitat use (Madsen & Broekhuis, 2018; but see Burton et al., 2012), population density (Balme, Slotow, et al., 2010; Rosenblatt et al., 2016) and survival (Swanepoel, Somers, van Hoven, et al., 2015).
Trophy hunting	Proportion of site with trophy hunting for leopard	*hunting*	-	Protected areas dataset (TKPP, unpublished data)	Leopard populations are demographically sensitive to over-harvesting (Braczkowski et al., 2015), and trophy hunting has been identified as a primary driver of a decline in leopard abundance in Tanzania (Packer et al., 2010).

Covariate calculation

Water availability

In the study region, using distance to rivers as a measure of water availability would fail to account for the fact that many rivers run dry during the dry season. Water was thus included as a covariate via a map of permanent waterbodies, including manmade pumps and perennial rivers.

Water availability was represented by the natural log of distance to water. Distance to water was calculated as the average pixel distance to the nearest dry season water source – a combination of manmade pumped water points and perennial rivers, which were converted into a series of points at 100 m spacing – using the Euclidean Distance Spatial Analyst tool in ArcGIS version 10.5.1 (ESRI, 2016) and Zonal Statistics tool in QGIS version 2.18.10 (QGIS Development Team, 2017). The natural log of this distance was then calculated, to reflect the fact that the impact of a water access point being available should reach an asymptote with the animal's distance from that water (MacKenzie et al., 2018).

Prey availability

As leopards are generalists with a broad spectrum of potential prey species, it would be unfeasible to capture the full suite of potential prey available to leopard in the study area. As such, *prey availability* was quantified by developing models of the probability of site use by the species' most frequently taken prey species (as per Andresen et al., 2014; Everatt et al., 2014; Strampelli et al., 2018) using the spoor transect dataset, ensuring a measure of availability that accounts for imperfect detection and is contemporaneous with our detection/non-detection data for leopard.

Hayward et al.'s 2006 meta-analysis of leopard dietary preferences found the species' top five most frequently taken prey to be impala, followed by common duiker, steenbok, bushbuck, and common warthog. We based our definition of preferred prey on the frequency of predation, as we believe the Jacob's Index of preference used by Hayward et al. (2006) overestimates the importance of rare species in leopard diet. As our dataset contained insufficient detections of bushbuck for the species' occupancy

to be modelled (n = 20), we developed probability of use models for impala, duiker, steenbok and warthog (see S3.3 & S3.4). All four species have been recorded as part of leopard diet in northern Botswana (Stein et al., 2015) and/or Hwange NP, Zimbabwe (Chatikobo, 2017). Finally, a mean probability of site use for the prey species at each site was calculated to produce a variable reflecting general, rather than species-specific, prey availability.

Human disturbance

Proximity to settlements is often used as an easy to derive measure of human disturbance (Maharjan et al., 2017; Ngoprasert et al., 2007) but is likely to be better represented by an asymptotic relationship than a linear relationship. This pattern was recorded in Limpopo NP, Mozambique, where the avoidance of agro-pastoralist settlements by leopards was only observed within 5 km of villages (Strampelli et al., 2018).

Human disturbance was represented by the natural log of distance to settlement. Distance to settlement was calculated as the average pixel distance to the nearest human settlement using the Euclidean Distance Spatial Analyst tool in ArcGIS version 10.5.1 (ESRI, 2016) and Zonal Statistics tool in QGIS version 2.18.10 (QGIS Development Team, 2017), and included as a candidate variable via its natural log to reflect the fact that the impact of a human settlement on leopard habitat use should reach an asymptote with the animal's distance from that settlement.

High protection

For modelling purposes, we grouped PA types into broader categories. The *high protection* variable was therefore determined based on a three level grading of protection across the study area – (1) National Park, Wildlife Management Area, Safari Area; (2) Forest Area or Reserve, Conservancy Ranch; (3) Community Land, State Land, Farming Area – with only the areas with the highest level of protection (category 1) considered. These highly protected areas were assigned a value of 1, and the lesser- and non-protected areas assigned a value of 0. The proportion of area highly protected was then calculated for each cell using the Intersection Geoprocessing tool in QGIS version 2.18.10 (QGIS Development Team, 2017).

Trophy hunting

One land use strategy in place in the Zimbabwean portion of the study area is trophy hunting, which has been shown in certain cases to have an impact on leopard habitat use and relative abundance (Packer et al., 2010).

As there is very limited information available on the leopard quotas in place during this period, the *trophy hunting* variable was based simply on whether trophy hunting of leopard was conducted in a given area or not. Areas where trophy hunting was conducted during the survey period were assigned a value of 1, and areas without trophy hunting assigned a value of 0. The proportion of area hunted was then calculated for each cell using the Intersection Geoprocessing tool in QGIS version 2.18.10 (QGIS Development Team, 2017).

S3.3 Overview and justification of prey site use covariates

Table S3.3.1: Site covariates hypothesised to affect habitat use by the four most frequently taken prey species (duiker, impala, steenbok, warthog) across the southern KAZA TFCA.

Covariate	Description	Code	Hypothesised effect on site use	Data source	Justification
Water availability	Average pixel distance to nearest water point	WDI	-	Water points dataset (TKPP, unpublished data)	Some herbivores, such as impala, are highly water-dependent, and as such can be expected to be positively associated with water availability (Estes, 1991).
	Natural log of average pixel distance to nearest water point	lnWDI	-		
	Average pixel value of water point density raster	WDE	+		
Precipitation	Average monthly precipitation for year surveyed	PR	+	Fick & Hijmans (2017)	Precipitation can be an important factor driving habitat selection by herbivorous species, as it contributes to both vegetation growth and surface water availability (Fang et al., 2005).
Vegetation cover	Vegetation cover (EVI) – Mean	EVI_M	+	Didan (2015)	Vegetation is an important habitat feature for herbivorous prey species due to its importance as a food source, and for the cover it provides for concealment from predators (Estes, 1991).
	Vegetation cover (EVI) – Standard Deviation	EVI_STD	+		
	Leaf area index	LAI	+	Myneni, Knyazikhin, & Park (2015)	
	Canopy cover	VCF	+	Dimiceli et al. (2015)	
Soil nutrients	Soil organic carbon content (g per km at 5 cm depth)	C	+	Hengl, Mendes de Jesus, et al. (2017)	Soil nutrients – including the amount of carbon and nitrogen stored in soil – can have an important influence on plant growth, and thus on food availability for herbivores.
	Total nitrogen by wet oxidation (ppm)	N	+	Hengl, Leenaars, et al. (2017)	
Human disturbance	Average pixel distance to nearest settlement	SDI	+	Settlements dataset (TKPP, unpublished data)	Herbivores can be negatively impacted by humans through both direct (e.g. bushmeat poaching) and indirect (e.g. habitat conversion, competition with livestock) impacts (Ripple et al., 2015), although species vary in their vulnerability to these threats.
	Natural log of average pixel distance to nearest settlement	lnSDI	+		
	Average pixel value of settlement density raster	SDE	-		

Covariate calculation

Water availability

Water availability was represented in the prey models by three covariates: distance to water, the natural log of distance to water, and water density. Distance to water was calculated as the average pixel distance to the nearest water point using the Euclidean Distance Spatial Analyst tool in ArcGIS version 10.5.1 (ESRI, 2016) and Zonal Statistics tool in QGIS version 2.18.10 (QGIS Development Team, 2017). An additional covariate reflecting water availability, water density, was also included in the prey models, to reflect the fact that the number of water points in a given area may influence prey habitat use, in addition to simple proximity having an effect. Water density for each cell was derived as the average pixel value of a density raster, produced via Kernel Density Estimation in the Heatmap Plugin in QGIS version 2.18.10 (QGIS Development Team, 2017).

Precipitation

Average monthly *precipitation* data were obtained from WorldClim (Version 2), at 30 seconds (~1 km) spatial resolution (Fick & Hijmans, 2017). The Cell Statistics tool in ArcGIS version 10.5.1 (ESRI, 2016) was used to calculate the mean monthly precipitation for each year of study (2012-2015 inclusive) across the study area. Each cell was then assigned the average monthly precipitation value for the year in which that cell was surveyed.

Vegetation cover

Four variables reflecting aspects of *vegetation cover* were included as candidate variables for the prey models: vegetation continuous fields (VCF), mean and standard deviation of the Enhanced Vegetation Index (EVI), and the leaf area index (LAI). All vegetation data were accessed via the NASA Earthdata Search application (https://search.earthdata.nasa.gov/).

Vegetation Continuous Fields (VCF) is a measure of canopy cover, representing surface vegetation cover as gradations of three ground cover components: percent tree cover, percent non-tree cover, and percent non-vegetated (bare). VCF values were obtained from the yearly Moderate Resolution Imaging

Spectroradiometer (MODIS)/Terra Vegetation Continuous Fields product (MOD44B), at 250 m spatial resolution (Dimiceli et al., 2015).

The Enhanced Vegetation Index (EVI) is a vegetation index developed to address some of the limitations of the Normalized Difference Vegetation Index (NDVI); namely, to be more sensitive to areas of high biomass, to reduce the influence of atmospheric conditions, and to correct for canopy background signals. The algorithm chooses the best available pixel value from all data collected during the 16 day period. EVI values were obtained from the MODIS/Terra Vegetation Indices product (MOD13Q1), generated every 16 days at 250 m spatial resolution (Didan, 2015). Monthly EVI values were extracted using granules overlapping with the midpoint of each month, with the value for each cell taken from the mean and standard deviation among these monthly values for the year in which that cell was surveyed. We chose to include standard deviation in EVI as well as the mean annual value to account for the potential impact of fluctuations in vegetation on habitat selection by prey.

Leaf Area Index (LAI) is defined as the one-sided green leaf area per unit ground area in broadleaf canopies, and is effectively a measure of how much foliage there is per unit area. LAI values were obtained from the MODIS/Terra & Aqua LAI/FPAR product (MCD15A2H), an 8 day composite dataset with 500 m spatial resolution (Myneni et al., 2015).

Soil nutrients

Two variables representing *soil nutrients* were included in the candidate covariates for preferred prey. Carbon was measured via soil organic carbon content in g per kg at 5 cm depth (ORCDRC_M_sl2) at 250 m spatial resolution, obtained from the International Soil Reference and Information Centre (ISRIC) SoilGrids global gridded soil information interface (Hengl, Mendes de Jesus, et al., 2017). Nitrogen was measured via total nitrogen by wet oxidation (ppm), from ISRIC's soil nutrient maps of sub-Saharan Africa at 250 m spatial resolution (Hengl, Leenaars, et al., 2017).

Human disturbance

Human disturbance was included in the prey models via distance to settlement and the natural log of distance to settlement. Distance to settlement was calculated as the average pixel distance to the nearest human settlement using the Euclidean Distance Spatial Analyst tool in ArcGIS version 10.5.1 (ESRI, 2016) and Zonal Statistics tool in QGIS version 2.18.10 (QGIS Development Team, 2017). An additional covariate reflecting human disturbance, settlement density, was also included in the prey models, to reflect the fact that the number of settlements in a given area may influence prey habitat use, in addition to simple proximity having an effect. Settlement density was estimated as per water density, above.

S3.4 Prey site use analysis results and discussion

Spatial independence was achieved at 2 km for warthog, 4 km for duiker and steenbok, and 6 km for impala. Effort had a significant positive impact on detection probability, and was fixed for all subsequent model testing (Table S3.4.1). The final model set comprised 6 models for duiker, 17 for impala, 9 for steenbok, and 9 for warthog (Tables S3.4.3 & S3.4.4). Model-averaged probabilities of detection and site use for each species and mean prey estimates are shown in Table S3.4.5. None of the models assessed for goodness of fit indicated lack of fit or overdispersion (Table S3.4.6; Fig. S3.4.1).

Table S3.4.1: Model selection procedure for the covariate associated with probability of detection (p) of most frequently taken prey species in the southern KAZA TFCA, *effort*. Models with and without effort were ranked based on AIC scores, with occupancy covariates fixed in both models as the full candidate set for that species. This process was not carried out for warthog as there was no variation in effort in the warthog data.

Species	Model	nPars	AIC	ΔAIC	AIC Wt	cmltv Wt
Duiker	effort	12	845.67	0.00	1.00	1.00
	null	11	865.61	19.94	4.70E-05	1.00
Impala	effort	12	736.58	0.00	1.00	1.00
	null	11	755.41	18.83	8.20E-05	1.00
Steenbok	effort	12	1269.54	0.00	1.00	1.00
	null	11	1299.90	30.35	2.60E-07	1.00

Table S3.4.2: Codes used to refer to prey site covariates in subsequent tables and figures.

Covariate	Description	Code
Water availability	Average pixel distance to nearest water point	WDI
	Natural log of average pixel distance to nearest water point	lnWDI
	Average pixel value of water point density raster	WDE
Precipitation	Average monthly precipitation for year surveyed	PR
Vegetation cover	Vegetation cover (EVI) – mean	EVI_M
	Vegetation cover (EVI) – standard deviation	EVI_STD
	Leaf area index	LAI
	Canopy cover	VCF
Soil nutrients	Soil organic carbon content (g per km at 5 cm depth)	C
	Total nitrogen by wet oxidation (ppm)	N
Human disturbance	Average pixel distance to nearest settlement	SDI
	Natural log of average pixel distance to nearest settlement	lnSDI
	Average pixel value of settlement density raster	SDE

Table S3.4.3: Results of multivariate model selection for occupancy models estimating site use for most frequently taken prey species in the southern KAZA TFCA. All models shown are within ΔAICc < 2 from the top-ranked model, and comprise the final model set for that species.

(A) **Duiker**

Global model call: occu(formula = ~ effort ~ lnWDI + WDE + SDI + SDE + C + EVI_M + EVI_STD + LAI, data = Duiker)

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	ψ(C+EVI_M+EVI_STD+lnWDI+SDE)p(effort)	8	-636.45	1289.2	0.00	0.28
2	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+WDE)p(effort)	9	-635.88	1290.2	0.95	0.17
3	ψ(C+EVI_M+EVI_STD+lnWDI+SDE+WDE)p(effort)	9	-635.89	1290.2	0.97	0.17
4	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE+WDE)p(effort)	10	-634.95	1290.4	1.18	0.16
5	ψ(C+EVI_M+EVI_STD+lnWDI+SDE+SDI)p(effort)	9	-636.34	1291.1	1.87	0.11
6	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE)p(effort)	9	-636.36	1291.1	1.91	0.11

(B) **Impala**

Global model call: occu(formula = ~ effort ~ lnWDI + WDE + SDI + SDE + N + EVI_M + EVI_STD + LAI + VCF, data = Impala)

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	ψ(EVI_M+LAI+lnWDI+N+VCF+WDE)p(effort)	9	-358.37	735.1	0.00	0.09
2	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)	11	-356.29	735.2	0.02	0.09
3	ψ(EVI_M+LAI+lnWDI+N+VCF)p(effort)	8	-359.66	735.6	0.50	0.07
4	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+VCF+WDE)p(effort)	10	-357.59	735.7	0.53	0.07
5	ψ(EVI_M+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)	10	-357.60	735.7	0.54	0.07
6	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF)p(effort)	10	-357.66	735.8	0.65	0.07
7	ψ(lnWDI+N+WDE)p(effort)	6	-361.87	735.9	0.78	0.06
8	ψ(EVI_M+LAI+lnWDI+N+SDI+VCF)p(effort)	9	-358.77	735.9	0.79	0.06
9	ψ(lnWDI+N)p(effort)	5	-362.90	735.9	0.79	0.06
10	ψ(lnWDI+N+VCF+WDE)p(effort)	7	-360.89	736.0	0.88	0.06
11	ψ(LAI+lnWDI+N+VCF)p(effort)	7	-361.12	736.5	1.34	0.05
12	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+VCF)p(effort)	9	-359.05	736.5	1.35	0.05
13	ψ(lnWDI+N+SDI)p(effort)	6	-362.19	736.6	1.42	0.05
14	ψ(LAI+lnWDI+N+VCF+WDE)p(effort)	8	-360.26	736.8	1.69	0.04
15	ψ(lnWDI+N+SDI+VCF+WDE)p(effort)	8	-360.28	736.9	1.73	0.04
16	ψ(lnWDI+N+SDI+WDE)p(effort)	7	-361.33	736.9	1.76	0.04
17	ψ(lnWDI+N+VCF)p(effort)	6	-362.38	736.9	1.81	0.04

(C) **Steenbok**

Global model call: occu(formula = ~ effort ~ lnWDI + WDE + SDI + SDE + PR + EVI_M + EVI_STD + LAI + VCF, data = Steenbok)

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	ψ(LAI+PR+WDE)p(effort)	6	-624.76	1261.7	0.00	0.21
2	ψ(LAI+PR+SDI+WDE)p(effort)	7	-623.82	1261.9	0.17	0.19
3	ψ(EVI_M+LAI+PR+WDE)p(effort)	7	-624.52	1263.3	1.57	0.09
4	ψ(LAI+lnWDI+PR+SDI+WDE)p(effort)	8	-623.50	1263.3	1.60	0.09
5	ψ(EVI_M+LAI+PR+SDI+WDE)p(effort)	8	-623.52	1263.3	1.64	0.09
6	ψ(LAI+lnWDI+PR+WDE)p(effort)	7	-624.59	1263.4	1.72	0.09
7	ψ(LAI+PR+VCF+WDE)p(effort)	7	-624.64	1263.5	1.82	0.08
8	ψ(LAI+PR+SDE+WDE)p(effort)	7	-624.65	1263.5	1.83	0.08
9	ψ(EVI_STD+LAI+PR+WDE)p(effort)	7	-624.66	1263.6	1.85	0.08

(D) **Warthog**

Global model call: occu(formula = ~ 1 ~ lnWDI + WDE + SDI + SDE + PR + EVI_M + EVI_STD + LAI + VCF, data = Warthog)

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	ψ(lnWDI+PR+SDE+VCF)p(.)	6	-874.23	1760.6	0.00	0.20
2	ψ(lnWDI+SDE+VCF)p(.)	5	-875.26	1760.7	0.02	0.19
3	ψ(LAI+lnWDI+PR+SDE+VCF)p(.)	7	-873.81	1761.9	1.23	0.11
4	ψ(lnWDI+SDE+SDI+VCF)p(.)	6	-874.88	1761.9	1.31	0.10
5	ψ(lnWDI+PR+SDE+SDI+VCF)p(.)	7	-874.02	1762.3	1.64	0.09
6	ψ(EVI_STD+lnWDI+SDE+VCF)p(.)	6	-875.07	1762.3	1.69	0.08
7	ψ(lnWDI+PR+VCF)p(.)	5	-876.13	1762.4	1.76	0.08
8	ψ(LAI+lnWDI+SDE+VCF)p(.)	6	-875.12	1762.4	1.78	0.08
9	ψ(lnWDI+SDE+VCF+WDE)p(.)	6	-875.17	1762.5	1.89	0.08

Table S3.4.4: Parameter estimates (standard error in parentheses) of the final occupancy model set for estimating site use for most frequently taken prey species in the southern KAZA TFCA. All models shown are within ΔAICc < 2 from the top-ranked model. Beta coefficients (β) highlighted in grey indicate a significant impact on probability of site use in the model shown, as the 95% confidence interval (β ± 1.96 SE) does not span zero.

(A) **Duiker**		**Intercept (ψ)**	**β (C)**	**β (EVI_M)**	**β (EVI_STD)**	**β (LAI)**	**β (lnWDI)**	**β (SDE)**	**β (SDI)**	**β (WDE)**	**Intercept (p)**	**β (effort)**
1	ψ(C+EVI_M+EVI_STD+lnWDI+SDE)p(effort)	1.26 (0.27)	-0.45 (0.18)	0.42 (0.16)	-0.34 (0.14)		0.64 (0.21)	1.80 (1.28)			-3.14 (0.50)	1.61 (0.26)
2	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+WDE)p(effort)	1.24 (0.27)	-0.39 (0.20)	0.90 (0.41)	-0.32 (0.15)	-0.65 (0.54)	0.68 (0.22)			0.68 (0.51)	-3.18 (0.49)	1.62 (0.26)
3	ψ(C+EVI_M+EVI_STD+lnWDI+SDE+WDE)p(effort)	1.34 (0.30)	-0.50 (0.19)	0.45 (0.17)	-0.38 (0.14)		0.70 (0.22)	1.80 (1.38)		0.18 (0.17)	-3.16 (0.49)	1.61 (0.26)
4	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE+WDE)p(effort)	1.37 (0.31)	-0.45 (0.20)	0.72 (0.30)	-0.34 (0.15)	-0.40 (0.35)	0.72 (0.22)	1.95 (1.61)		0.44 (0.32)	-3.17 (0.49)	1.61 (0.26)
5	ψ(C+EVI_M+EVI_STD+lnWDI+SDE+SDI)p(effort)	1.25 (0.26)	-0.43 (0.18)	0.41 (0.16)	-0.31 (0.15)		0.61 (0.21)	1.84 (1.29)	0.11 (0.23)		-3.14 (0.50)	1.61 (0.26)
6	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE)p(effort)	1.25 (0.27)	-0.42 (0.19)	0.47 (0.21)	-0.32 (0.14)	-0.09 (0.22)	0.63 (0.21)	1.84 (1.30)			-3.14 (0.50)	1.61 (0.26)
	Averaged model	1.29 (0.28)	-0.44 (0.19)	0.56 (0.31)	-0.34 (0.14)	-0.18 (0.37)	0.66 (0.22)	1.52 (1.43)	0.01 (0.08)	0.22 (0.37)	-3.12 (0.49)	1.61 (0.26)

(B) **Impala**		**Intercept (ψ)**	**β (EVI_M)**	**β (EVI_STD)**	**β (LAI)**	**β (lnWDI)**	**β (N)**	**β (SDI)**	**β (VCF)**	**β (WDE)**	**Intercept (p)**	**β (effort)**
1	ψ(EVI_M+LAI+lnWDI+N+VCF+WDE)p(effort)	-0.21 (0.26)	-0.75 (0.44)		1.39 (0.77)	-0.62 (0.19)	0.78 (0.23)		-0.46 (0.21)	0.88 (0.78)	-2.04 (0.57)	0.91 (0.20)
2	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)	-0.22 (0.25)	-1.00 (0.45)	-0.42 (0.33)	1.89 (0.81)	-0.63 (0.20)	0.69 (0.23)	-0.28 (0.18)	-0.50 (0.21)	0.90 (0.79)	-2.04 (0.57)	0.90 (0.20)
3	ψ(EVI_M+LAI+lnWDI+N+VCF)p(effort)	-0.41 (0.18)	-0.60 (0.40)		1.15 (0.70)	-0.72 (0.18)	0.69 (0.22)		-0.41 (0.20)		-2.04 (0.57)	0.92 (0.20)
4	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+VCF+WDE)p(effort)	-0.21 (0.25)	-0.87 (0.44)	-0.30 (0.29)	1.68 (0.80)	-0.63 (0.20)	0.78 (0.23)		-0.48 (0.21)	0.92 (0.79)	-2.04 (0.57)	0.90 (0.20)
5	ψ(EVI_M+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)	-0.22 (0.26)	-0.82 (0.46)		1.49 (0.80)	-0.62 (0.20)	0.71 (0.24)	-0.21 (0.17)	-0.47 (0.21)	0.85 (0.78)	-2.04 (0.57)	0.90 (0.20)
6	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF)p(effort)	-0.42 (0.19)	-0.83 (0.43)	-0.37 (0.31)	1.59 (0.78)	-0.74 (0.19)	0.59 (0.22)	-0.29 (0.18)	-0.44 (0.20)		-2.04 (0.57)	0.91 (0.20)

7	ψ(lnWDI+N+WDE)p(effort)	-0.41 (0.20)				-0.63 (0.18)	0.69 (0.18)			0.63 (0.65)	-2.04 (0.57)	0.91 (0.20)
8	ψ(EVI_M+LAI+lnWDI+N+SDI+VCF)p(effort)	-0.42 (0.19)	-0.67 (0.42)		1.24 (0.73)	-0.72 (0.18)	0.62 (0.22)	-0.22 (0.17)	-0.41 (0.20)		-2.04 (0.57)	0.92 (0.20)
9	ψ(lnWDI+N)p(effort)	-0.53 (0.16)				-0.74 (0.17)	0.61 (0.17)				-2.05 (0.57)	0.93 (0.20)
10	ψ(lnWDI+N+VCF+WDE)p(effort)	-0.40 (0.21)				-0.62 (0.18)	0.79 (0.20)		-0.21 (0.15)	0.69 (0.68)	-2.07 (0.57)	0.92 (0.20)
11	ψ(LAI+lnWDI+N+VCF)p(effort)	-0.52 (0.16)			0.30 (0.21)	-0.66 (0.17)	0.80 (0.20)		-0.31 (0.18)		-2.07 (0.57)	0.94 (0.20)
12	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+VCF)p(effort)	-0.41 (0.18)	-0.70 (0.42)	-0.26 (0.28)	1.39 (0.75)	-0.74 (0.18)	0.68 (0.22)		-0.42 (0.20)		-2.04 (0.57)	0.92 (0.20)
13	ψ(lnWDI+N+SDI)p(effort)	-0.54 (0.16)				-0.72 (0.17)	0.56 (0.17)	-0.19 (0.16)			-2.04 (0.57)	0.93 (0.20)
14	ψ(LAI+lnWDI+N+VCF+WDE)p(effort)	-0.39 (0.21)			0.26 (0.24)	-0.56 (0.19)	0.89 (0.22)		-0.33 (0.19)	0.67 (0.69)	-2.07 (0.57)	0.93 (0.20)
15	ψ(lnWDI+N+SDI+VCF+WDE)p(effort)	-0.42 (0.21)				-0.61 (0.18)	0.74 (0.20)	-0.18 (0.17)	-0.22 (0.15)	0.63 (0.68)	-2.07 (0.57)	0.92 (0.20)
16	ψ(lnWDI+N+SDI+WDE)p(effort)	-0.43 (0.21)				-0.62 (0.18)	0.64 (0.18)	-0.17 (0.16)		0.58 (0.66)	-2.04 (0.57)	0.91 (0.20)
17	ψ(lnWDI+N+VCF)p(effort)	-0.52 (0.16)				-0.74 (0.17)	0.69 (0.19)		-0.14 (0.14)		-2.07 (0.57)	0.94 (0.20)
	Averaged model	-0.37 (0.24)	-0.45 (0.52)	-0.10 (0.23)	0.88 (0.94)	-0.66 (0.19)	0.70 (0.22)	-0.10 (0.16)	-0.31 (0.25)	0.44 (0.68)	-2.05 (0.57)	0.92 (0.20)

(C) **Steenbok**		**Intercept (ψ)**	**β (EVI_M)**	**β (EVI_STD)**	**β (LAI)**	**β (lnWDI)**	**β (PR)**	**β (SDE)**	**β (SDI)**	**β (VCF)**	**β (WDE)**	**Intercept (p)**	**β (effort)**
1	ψ(LAI+PR+WDE)p(effort)	3.13 (0.58)			0.75 (0.20)		-3.30 (0.57)				-1.28 (0.27)	-1.63 (0.37)	1.12 (0.20)
2	ψ(LAI+PR+SDI+WDE)p(effort)	3.00 (0.57)			0.72 (0.20)		-3.02 (0.58)		0.40 (0.29)		-1.19 (0.27)	-1.62 (0.38)	1.12 (0.20)
3	ψ(EVI_M+LAI+PR+WDE)p(effort)	2.97 (0.61)	0.17 (0.26)		0.59 (0.32)		-3.12 (0.62)				-1.20 (0.30)	-1.62 (0.38)	1.12 (0.20)
4	ψ(LAI+lnWDI+PR+SDI+WDE)p(effort)	3.08 (0.61)			0.71 (0.20)	0.18 (0.23)	-2.96 (0.60)		0.45 (0.31)		-1.12 (0.28)	-1.62 (0.38)	1.13 (0.20)
5	ψ(EVI_M+LAI+PR+SDI+WDE)p(effort)	2.82 (0.59)	0.19 (0.25)		0.55 (0.30)		-2.81 (0.62)		0.41 (0.29)		-1.09 (0.29)	-1.61 (0.38)	1.12 (0.20)

6	ψ(LAI+lnWDI+PR+WDE)p(effort)	3.19 (0.61)			0.74 (0.20)	0.13 (0.23)	-3.27 (0.59)				-1.24 (0.28)	-1.63 (0.37)	1.13 (0.20)
7	ψ(LAI+PR+VCF+WDE)p(effort)	3.06 (0.60)			0.79 (0.22)		-3.19 (0.62)			-0.10 (0.20)	-1.27 (0.27)	-1.62 (0.37)	1.12 (0.20)
8	ψ(LAI+PR+SDE+WDE)p(effort)	3.09 (0.58)			0.76 (0.20)		-3.26 (0.57)	-0.12 (0.31)			-1.26 (0.27)	-1.62 (0.37)	1.12 (0.20)
9	ψ(EVI_STD+LAI+PR+WDE)p(effort)	3.11 (0.59)		-0.24 (0.51)	0.81 (0.24)		-3.29 (0.58)				-1.27 (0.27)	-1.62 (0.37)	1.12 (0.20)
	Averaged model	3.05 (0.60)	0.03 (0.13)	-0.02 (0.16)	0.72 (0.24)	0.03 (0.11)	-3.14 (0.61)	-0.01 (0.09)	0.15 (0.27)	-0.01 (0.06)	-1.22 (0.28)	-1.62 (0.37)	1.12 (0.20)

(D) **Warthog**		**Intercept (ψ)**	**β (EVI_STD)**	**β (LAI)**	**β (lnWDI)**	**β (PR)**	**β (SDE)**	**β (SDI)**	**β (VCF)**	**β (WDE)**	**Intercept (p)**
1	ψ(lnWDI+PR+SDE+VCF)p(.)	1.15 (0.46)			-0.82 (0.23)	0.34 (0.24)	5.45 (4.73)		-0.74 (0.19)		-1.14 (0.09)
2	ψ(lnWDI+SDE+VCF)p(.)	1.22 (0.47)			-0.98 (0.21)		5.84 (4.77)		-0.64 (0.17)		-1.15 (0.09)
3	ψ(LAI+lnWDI+PR+SDE+VCF)p(.)	1.12 (0.45)		0.17 (0.19)	-0.78 (0.22)	0.39 (0.24)	5.16 (4.59)		-0.86 (0.24)		-1.14 (0.09)
4	ψ(lnWDI+SDE+SDI+VCF)p(.)	1.33 (0.52)			-1.07 (0.24)		6.71 (5.21)	0.16 (0.19)	-0.67 (0.18)		-1.16 (0.09)
5	ψ(lnWDI+PR+SDE+SDI+VCF)p(.)	1.22 (0.49)			-0.88 (0.26)	0.32 (0.24)	6.04 (5.07)	0.11 (0.18)	-0.74 (0.19)		-1.15 (0.09)
6	ψ(EVI_STD+lnWDI+SDE+VCF)p(.)	1.22 (0.47)	-0.09 (0.15)		-0.98 (0.21)		5.88 (4.80)		-0.63 (0.17)		-1.15 (0.09)
7	ψ(lnWDI+PR+VCF)p(.)	0.73 (0.23)			-0.81 (0.22)	0.38 (0.24)			-0.69 (0.19)		-1.15 (0.09)
8	ψ(LAI+lnWDI+SDE+VCF)p(.)	1.20 (0.47)		0.10 (0.18)	-0.97 (0.21)		5.70 (4.74)		-0.70 (0.21)		-1.15 (0.09)
9	ψ(lnWDI+SDE+VCF+WDE)p(.)	1.21 (0.46)			-1.00 (0.21)		5.88 (4.75)		-0.61 (0.18)	-0.09 (0.20)	-1.15 (0.09)
	Averaged model	1.16 (0.48)	-0.01 (0.05)	0.03 (0.10)	-0.91 (0.24)	0.17 (0.24)	5.32 (4.90)	0.03 (0.10)	-0.70 (0.20)	-0.01 (0.06)	-1.15 (0.09)

Table S3.4.5: Detection information, naïve occupancy, and mean probability of detection & site use estimates (standard deviation in parentheses) for most frequently taken prey species.

Species	Detections	Number of sites in which detected	Naïve occupancy	Mean detection probability $\bar{\hat{p}}$ (SD)	Mean probability of site use $\bar{\hat{\psi}}$ (SD)
Duiker	846	252	0.53	0.45 (0.12)	0.72 (0.21)
Impala	3909	148	0.31	0.55 (0.15)	0.40 (0.25)
Steenbok	1381	306	0.65	0.60 (0.10)	0.76 (0.31)
Warthog	889	206	0.43	0.24 (0.00)	0.65 (0.20)
All prey (mean)	-	-	0.48	0.46 (0.11)	0.63 (0.25)

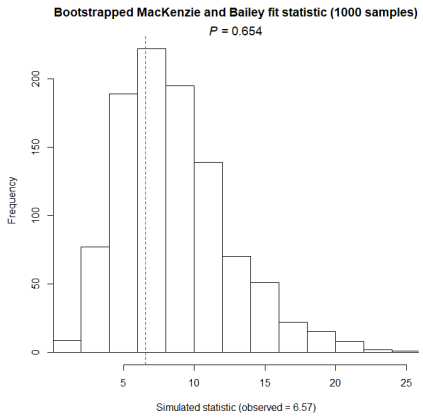
Table S3.4.6: Output of the MacKenzie and Bailey goodness of fit test (1000 bootstraps) for single-season occupancy models of most frequently taken prey species. Outputs are shown for both the highest ranked model (*top*) and the most parameterised model (*parameterised*) within the model-averaged set (ΔAICc < 2).

Species	Model	Model details	X^2 stat	p-value	ĉ
Duiker	top	ψ(C+EVI_M+EVI_STD+lnWDI+SDE)p(effort)	6.57	0.654	0.77
	parameterised	ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE+WDE)p(effort)	6.82	0.638	0.79
Impala	top	ψ(EVI_M+LAI+lnWDI+N+VCF+WDE)p(effort)	0.80	0.721	0.46
	parameterised	ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)	0.93	0.633	0.54
Steenbok	top	ψ(LAI+PR+WDE)p(effort)	9.64	0.324	1.15
	parameterised	ψ(LAI+lnWDI+PR+SDI+WDE)p(effort)	9.63	0.326	1.14
Warthog	top	ψ(lnWDI+PR+SDE+VCF)p(.)	247.36	0.056	1.70
	parameterised	ψ(LAI+lnWDI+PR+SDE+VCF)p(.)	247.01	0.075	1.66

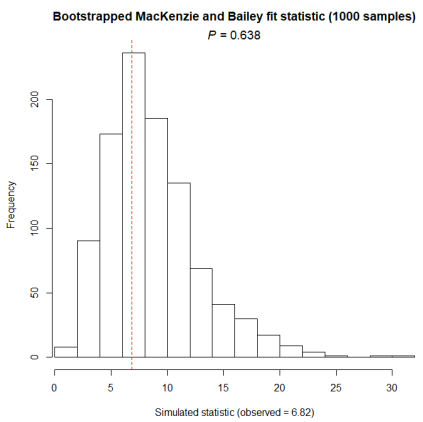
Figure S3.4.1: MacKenzie and Bailey fit statistic plots (1000 bootstraps) assessing goodness of fit of the top-ranked and most parameterised models in the final model set for most frequently taken prey species.

(A) **Duiker**

Top model
ψ(C+EVI_M+EVI_STD+lnWDI+SDE)p(effort)



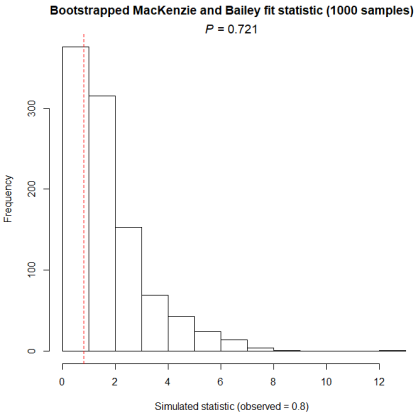
Most parameterised model
ψ(C+EVI_M+EVI_STD+LAI+lnWDI+SDE+WDE)p(effort)



(B) **Impala**

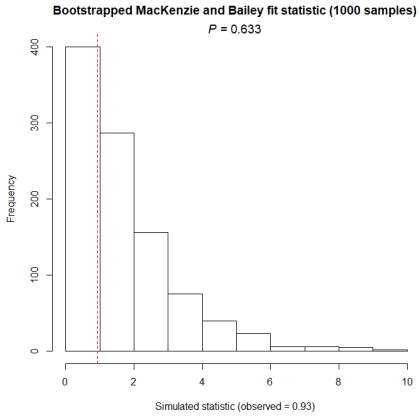
Top model

ψ(EVI_M+LAI+lnWDI+N+VCF+WDE)p(effort)



Most parameterised model

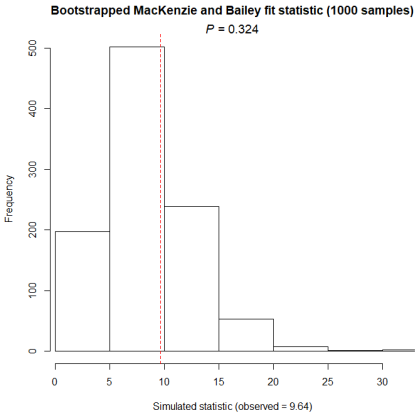
ψ(EVI_M+EVI_STD+LAI+lnWDI+N+SDI+VCF+WDE)p(effort)



(C) **Steenbok**

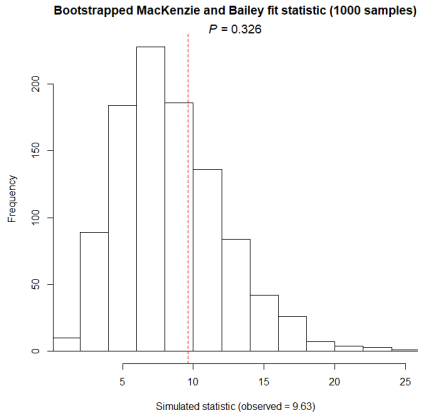
Top model

ψ(LAI+PR+WDE)p(effort)



Most parameterised model

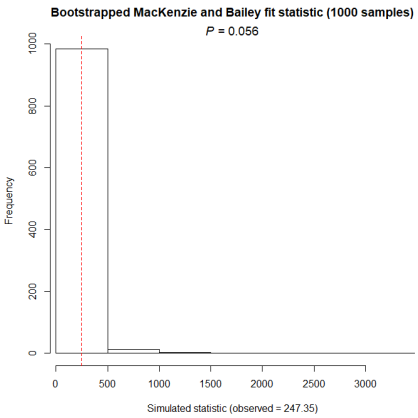
ψ(LAI+lnWDI+PR+SDI+WDE)p(effort)



(D) **Warthog**

Top model

ψ(lnWDI+PR+SDE+VCF)p(.)



Most parameterised model

ψ(LAI+lnWDI+PR+SDE+VCF)p(.)

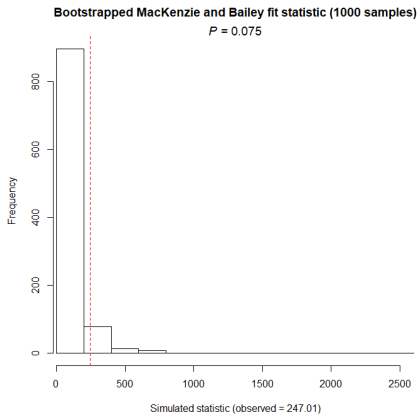


Table S3.4.7: Summed AICc weights and relationship with site use of all site use covariates in the final model set for each most frequently taken prey species.

(A) **Duiker**

Covariate	Summed Weight	Relationship
C	1.00	-
EVI_M	1.00	+
EVI_STD	1.00	-
lnWDI	1.00	+
SDE	0.83	+
WDE	0.50	+
LAI	0.44	-
SDI	0.11	+

(B) **Impala**

Covariate	Summed Weight	Relationship
lnWDI	1.00	-
N	1.00	+
VCF	0.79	-
LAI	0.66	+
EVI_M	0.57	-
WDE	0.56	+
SDI	0.41	-
EVI_STD	0.28	-

(C) **Steenbok**

Covariate	Summed Weight	Relationship
LAI	1.00	+
PR	1.00	-
WDE	1.00	-
SDI	0.37	+
EVI_M	0.18	+
lnWDI	0.18	+
SDE	0.08	-
VCF	0.08	-
EVI_STD	0.08	-

(D) **Warthog**

Covariate	Summed Weight	Relationship
lnWDI	1.00	-
VCF	1.00	-
SDE	0.92	+
PR	0.47	+
SDI	0.19	+
LAI	0.19	+
EVI_STD	0.08	-
WDE	0.08	-

Prey results discussion

Duiker habitat use was found to decrease with increasing soil carbon storage, a counterintuitive finding which may be the result of the species' high adaptability to even relatively unproductive environments (Wilson, 2013). Duiker habitat use was shown to increase with mean annual vegetation and decrease with standard deviation in annual vegetation; together, this indicates that duiker preferentially use areas with thicker vegetation and with less annual fluctuation in vegetation. This aligns with our understanding that the species can live in virtually any habitat that provides sufficient cover for concealment from predators (Estes, 1991). Duiker are not water-dependent, and accordingly habitat use was found to increase with distance to water, suggesting that the species may be specialising in drier areas. Duiker habitat use was also generally associated with higher settlement density, as may be expected for this resilient species which is often found close to human settlements (Foley et al., 2014).

Impala are seldom found more than a few kilometres from water (Foley et al., 2014); in line with this, we found impala habitat use to decrease with increasing distance from water. This is further supported by a general association between impala habitat use and water density. Impala habitat use increased with soil nitrogen content, possibly due to the higher nutritional content available for plant growth. Impala habitat use was also generally associated with higher leaf area index but lower canopy cover, which may relate to the impala's status as an edge species, specialising on intermediary habitats (Estes, 1991).

Steenbok habitat use increased with leaf area index, possibly reflecting the species' preference for areas with a high abundance of leaves (steenbok are browsers, feeding on young shoots and leaves). Steenbok habitat use was negatively associated with both annual precipitation and water density, reflecting the fact that this species is water-independent (Estes, 1991).

Warthog habitat use decreased with distance to water – while warthogs are highly adaptable and able to go long periods without water, some populations have been shown to be dependent on perennial surface water, which may be the case for the population in our study area (Cumming, 2013). Warthog avoid forests and dense vegetation, instead preferring open savannah habitats (Estes, 1991);

accordingly, we found warthog habitat use to decrease with canopy cover. Warthog habitat use was also positively associated with settlement density, possibly as a result of selecting for areas with crops as a food source (warthog have been identified as a problem animal for crop-raiding in neighbouring Zambia; Nyirenda et al., 2011).

S3.5 Detailed leopard site use and relative abundance analysis results

Table S3.5.1: Univariate model ranking for prey availability covariate selection for (A) the simple single-season leopard occupancy model; and (B) the N-mixture model for estimating relative abundance.

(A) **Leopard (Occupancy)**

Variable	nPars	AIC	ΔAIC	AIC Wt	cumltv Wt
all prey	3	1093.20	0.00	0.59	0.59
steenbok	3	1094.29	1.09	0.34	0.93
duiker	3	1098.45	5.25	0.04	0.98
impala	3	1099.70	6.50	0.02	1.00
warthog	3	1105.49	12.29	0.00	1.00

(B) **Leopard (N-mixture)**

Variable	nPars	AIC	ΔAIC	AIC Wt	cumltv Wt
steenbok	4	1386.06	0.00	0.52	0.52
impala	4	1388.01	1.95	0.20	0.72
all prey	4	1388.62	2.56	0.15	0.86
duiker	4	1388.98	2.92	0.12	0.99
warthog	4	1393.32	7.26	0.01	1.00

Table S3.5.2: Model selection procedure for the covariate associated with probability of detection (p) of leopard in the southern KAZA TFCA, *effort*, for (A) the simple single-season leopard occupancy model; and (B) the N-mixture model for estimating relative abundance. Models with and without effort were ranked based on AIC scores, with occupancy covariates fixed in both models as the full candidate set.

Species	Model	nPars	AIC	ΔAIC	AIC Wt	cmltv Wt
(A) Leopard (Occupancy)	Effort	8	1073.87	0.00	1.00	0.98
	Null	7	1081.23	7.36	2.50E-02	1.00
(B) Leopard (N-mixture)	Effort	9	1369.27	0.00	1.00	1.00
	Null	8	1385.23	15.96	3.40E-04	1.00

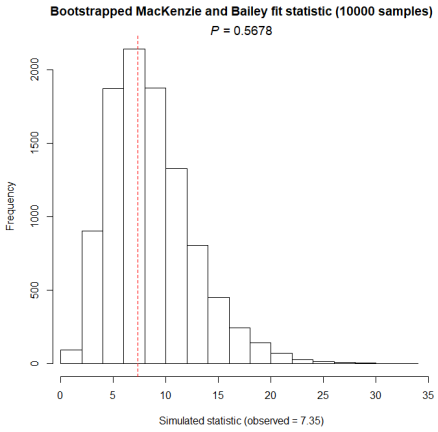
Table S3.5.3: Output of the MacKenzie and Bailey goodness of fit test (10,000 bootstraps) for the simple single-season leopard occupancy model. Outputs are shown for both the highest ranked model (*top*) and the most parameterised model (*parameterised*) within the model-averaged set (ΔAICc < 2).

Species	Model	Model details	X^2 stat	p-value	ĉ
Leopard (Occupancy)	top	ψ(all prey + protection)p(effort)	7.35	0.57	0.85
	parameterised	ψ(all prey + ln(settlement distance) + protection)p(effort)	7.21	0.58	0.84

Figure S3.5.1: MacKenzie and Bailey fit statistic plots (10,000 bootstraps) assessing goodness of fit of the top-ranked and most parameterised models for estimating leopard site use in the final occupancy model set.

Top model

ψ(all prey + protection)p(effort)



Most parameterised model

ψ(all prey + ln(settlement distance) + protection)p(effort)

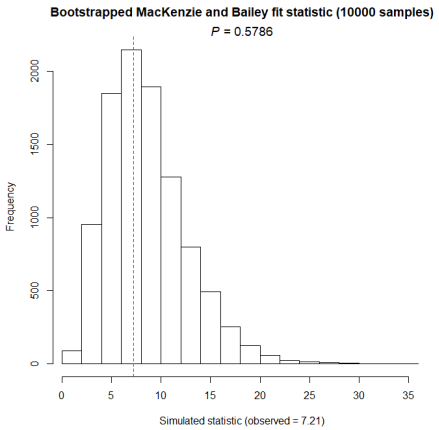


Table S3.5.4: Output of the SSE, Chi-square and Freeman-Tukey goodness of fit tests (10,000 bootstraps) for the N-mixture model for estimating relative abundance. Outputs are shown for both the highest ranked model (*top*) and the most parameterised model (*parameterised*) within the model-averaged set (ΔAICc < 2).

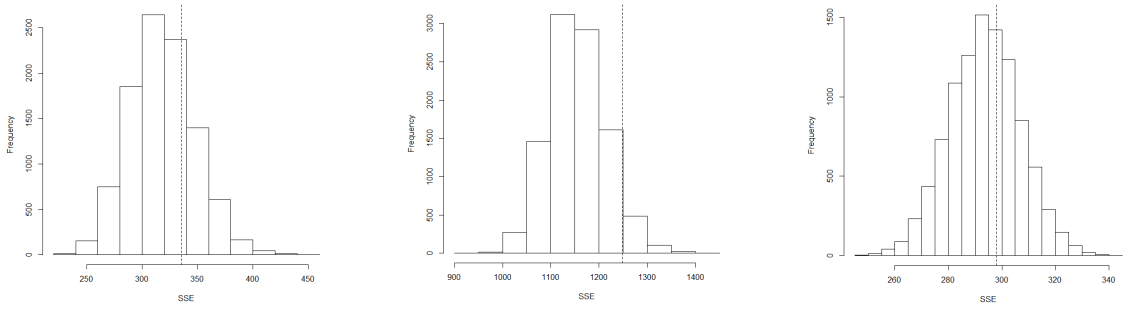
Test	Model	Model details	p-value	ĉ
SSE	top	λ(protection + hunting)p(effort)	0.27	1.06
	parameterised	λ(ln(water distance) + ln(settlement distance) + protection + hunting)p(effort)	0.25	1.06
Chi-square	top	λ(protection + hunting)p(effort)	0.06	1.08
	parameterised	λ(ln(water distance) + ln(settlement distance) + protection + hunting)p(effort)	0.07	1.08
Freeman-Tukey	top	λ(protection + hunting)p(effort)	0.37	1.01
	parameterised	λ(ln(water distance) + ln(settlement distance) + protection + hunting)p(effort)	0.33	1.02

Figure S3.5.2: (i) SSE, (ii) Chi-square, and (iii) Freeman-Tukey fit statistic plots (10,000 bootstraps) assessing goodness of fit of the top-ranked and most parameterised models for estimating leopard relative abundance within the final N-mixture model set.

Top model

λ(protection + hunting)p(effort)

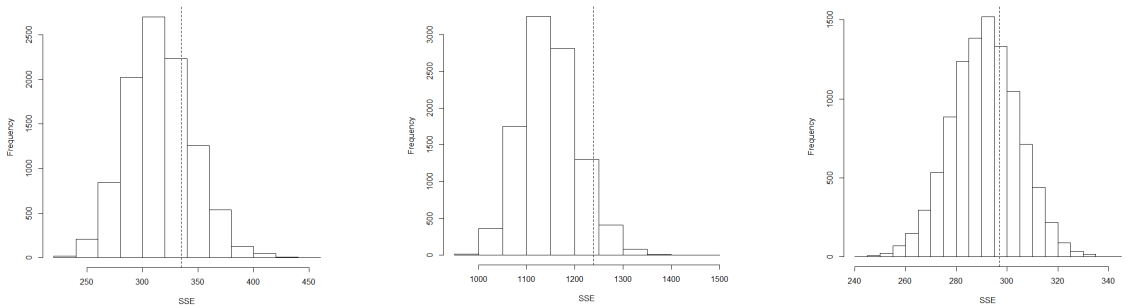
i SSE ii Chi-square iii Freeman-Tukey



Most parameterised model

λ(ln(water distance) + ln(settlement distance) + protection + hunting)p(effort)

i SSE ii Chi-square iii Freeman-Tukey



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CHAPTER 4

Random forest modelling of multi-scale, multi-species habitat associations within Africa's largest transfrontier conservation area

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Title

Random forest modelling of multi-scale, multi-species habitat associations within Africa's largest transfrontier conservation area

Running header

CHAPTER 4: Multi-species random forest modelling

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Random forest modelling of multi-scale, multi-species habitat associations within Africa's largest transfrontier conservation area

Abstract

As landscape-scale conservation models grow in prominence, information on how wildlife communities use multiple-use landscapes is required to inform effective conservation and management planning. We used the random forest machine learning algorithm to investigate scale-dependent habitat associations for 16 mammal species of high conservation importance – including six carnivores and ten herbivores – across the southern KAZA Transfrontier Conservation Area (TFCA) in Botswana and Zimbabwe, using data from large-scale spoor-based transect surveys. Our findings revealed substantial variation in the factors shaping habitat use across species, and illustrate that different species often have divergent responses to the same environmental and anthropogenic factors, and differ in the scales at which they respond to them. For all variables across all species, scale optimisation most often selected our largest scale. Precipitation, soil nutrients, and vegetation appeared to be the most important factors determining mammal distribution across southern KAZA, likely through their associations with food resources for herbivores and, in turn, prey availability for carnivores. Anthropogenic pressures also had an important influence on habitat use, with many species selecting against areas with high cattle density. The variety of relationships with human density indicated that species vary in their tolerance of humans. Although management was not a highly important predictor of habitat use for most species, likely due to non-representative sampling, we found a consistent positive relationship with areas under high protection, and negative relationship with unprotected and less-strictly protected areas. We use our findings to highlight two emerging trends that may impact wildlife populations in the KAZA TFCA: changing rainfall patterns and increasing livestock numbers. This study highlights the importance of adopting a multi-scale, multi-species approach for critical decision-making processes that depend on understanding wildlife distributions and habitat associations.

4.1. Introduction

Protected areas (PAs) play a key role in safeguarding wildlife from the threats of land conversion and over-exploitation (Brondizio et al., 2019; Karanth & Chellam, 2009), and are widely believed to be the most effective means of conserving much of the world's biodiversity (Le Saout et al., 2013; Leader-Williams et al., 1990; MacKinnon, 1986; McNeely & Miller, 1982). However, failing to also maintain connectivity among and within these protected patches of core habitats can lead to the severance of important migratory and dispersal routes (Bartlam-Brooks et al., 2011), increased genetic isolation (Willi et al., 2007), compromised resilience to diseases and population bottlenecks (Gilpin, 1987), and reduced opportunities to shift ranges in response to climate change (Opdam & Wascher, 2004). A lack of intact habitat outside PAs can also exacerbate edge effects around PA boundaries, which can have harmful impacts that reverberate throughout populations (Davidson et al., 2011; Loveridge et al., 2010; Woodroffe & Ginsberg, 1998) and lead to increased human-wildlife conflict (Broekhuis et al., 2017).

As a result, there is a growing consensus that alternative, landscape-scale conservation models are required to secure viable wildlife populations into the future (DeGeorges & Reilly, 2009; Ripple et al., 2014). While critical areas of habitat within individual countries can be secured through coordinated national land management planning, many areas of importance for migratory and dispersing animals do not adhere to political boundaries, and instead straddle multiple countries (Bartoń et al., 2019; Farhadinia et al., 2020; Holdo et al., 2009). In this context, transfrontier conservation areas (TFCAs) provide an institutional framework that can help secure both core habitat and critical linkages.

In step with this shift from localised to landscape-scale conservation, it is critical that we improve our understanding of how wildlife populations use these wider mosaic landscapes, so that this information can be used to inform conservation and management plans (Zeller et al., 2012). In particular, identifying which factors underpin space use by wildlife populations is likely to be a central component of PA, corridor, and buffer zone prioritisation – exercises that will become increasingly necessary in the face of rapid ongoing changes in climate (Collins et al., 2013; Wasserman et al., 2012) and rising

anthropogenic disturbance (Hassan et al., 2005), and the considerable costs associated with maintaining already chronically-underfunded PAs (Lindsey et al., 2018, 2014; Packer et al., 2013).

Maintaining healthy plant and animal communities is critical for safeguarding functional ecosystems, and is the main motivation behind current international biodiversity targets (CBD, 2010). As such, landscape-level wildlife assessments should strive to incorporate multi-species perspectives. Although assessments of habitat use across large landscapes often rely on data from collared or tagged animals (de Knegt et al., 2011; Klaassen & Broekhuis, 2018; Snyman et al., 2018), data of this kind can be difficult and expensive to obtain beyond small sample sizes (Zeller et al., 2018), and typically result in assessments restricted to single species in limited geographic areas. In contrast, presence-only surveys, such as those based on spoor or other sign, can be conducted across large scales rapidly and at relatively low cost, and allow information to be collected simultaneously on multiple species. Presence-only data can therefore be a powerful tool to develop species distribution models and assess habitat associations at the community level (Zeller et al., 2018), which can be used to help decision-makers identify priority areas (Rodríguez-Soto et al., 2011), corridors (Kanagaraj et al., 2011), and threats for multiple species across mixed-use landscapes (Cushman et al., 2013).

Assessments of habitat use should also account for scale, which is widely recognised as a central component of species-environment relationships (Mayor et al., 2009), and is widely recognised as being an important consideration for assessments of habitat use (McGarigal et al., 2016). Failing to account for the relevant scale at which species respond to environmental variables can undermine efforts to disentangle species-habitat relationships, and may result in incorrect inferences being used to guide conservation and management interventions (Everatt et al., 2015). Despite this, many studies investigating habitat use fail to incorporate multiple scales – and of those that do, fewer still make use of scale optimisation procedures to empirically determine the most relevant scale for each covariate of interest (McGarigal et al., 2016).

Identifying factors associated with habitat use for multiple species across multiple scales is a complex task: different species can respond to environmental and biotic variables in unexpected and divergent

ways (Ficetola et al., 2007), and can vary considerably in the scale at which they respond to these factors (Holland et al., 2004). As a result, making reliable inferences over space and time can be challenging for multi-species systems (Austin, 2007; Dungan et al., 2002). In recent years, however, machine learning approaches have emerged as a powerful tool to model spatially complex and temporally dynamic systems, as they are able to disentangle complex and non-intuitive interactions from large datasets much more readily than traditional modelling approaches (Evans et al., 2011). One model that has become an important part of the ecological toolset in the last two decades is the random forest algorithm (Breiman, 2001; Cutler et al., 2007; Evans & Cushman, 2009; Rogan et al., 2008), a powerful machine-learning algorithm which has been used in restoration (Barnard et al., 2019), remote sensing (Hengl, Mendes de Jesus, et al., 2017; Immitzer et al., 2012; Naidoo et al., 2012), deforestation modelling (Cushman et al., 2017), habitat suitability and connectivity analyses (Ashrafzadeh et al., 2020; Vanbianchi et al., 2017), and climate change predictions (Ashrafzadeh et al., 2018; Rather et al., 2020; Rehfeldt et al., 2006).

In this study, we use the random forest machine learning algorithm to investigate scale-dependent habitat associations for 16 mammal species – including six carnivores and ten herbivores – across the southern KAZA TFCA in Botswana and Zimbabwe, using data from large-scale presence-only surveys. Of the 16 study species, six are classified as *Vulnerable* or *Near Threatened* on the IUCN Red List, and nine are thought to have decreasing population trends (IUCN, 2020). We combine these species-specific insights to build a multi-species view of the key drivers of habitat use and potential future trends that may impact wildlife across the study landscape, which forms part of Africa's largest terrestrial TFCA.

4.2. Methods

4.2.1. Study area

The Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) is the world's largest terrestrial TFCA, covering an area of approximately 520,000 km^2 in southern Africa. KAZA spans the boundaries of five countries, encompassing 36 National Parks (NPs) and a host of other land uses, including

community-managed Wildlife Management Areas (WMAs), trophy hunting areas, unprotected land and communal areas (see S3.1 for a description of land use designations in the study area).

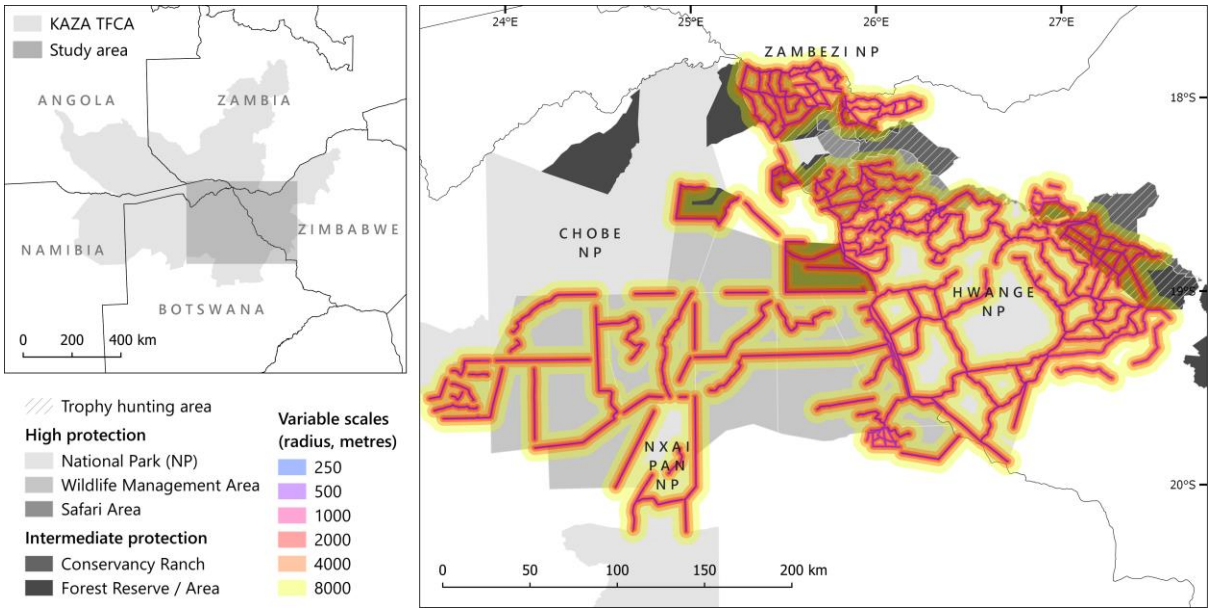


Figure 4.1: Left: the study area within the KAZA TFCA in southern Africa. Right: land use types in the study landscape and multi-scale variable areas surrounding survey transects. PAs are shown only in the study countries (Botswana & Zimbabwe).

Our study area consists of approximately 30,000 km^2 in the southern KAZA TFCA, across Botswana and Zimbabwe (Fig. 4.1). We collected data in Hwange NP & Zambezi NP in Zimbabwe, and Nxai Pan NP in Botswana, as well as areas adjacent to Kazuma Pan NP in Zimbabwe, and Chobe NP & Moremi Game Reserve in Botswana. We also collected data in a number of less-strictly protected WMAs, Safari Areas, Conservancy Ranches, and Forest Areas & Reserves, in addition to unprotected land.

The study area receives an average of 500-700 mm of rainfall per year, and is generally water- and nutrient-poor, although there are a large number of artificial waterholes across parts of the landscape. Vegetation is dominated by bushland savannah and woodland, interspersed with patches of grassland. Trophy hunting took place in Zimbabwe at the time of data collection, across approximately 14% of the total study area.

4.2.2. Data collection

We collected presence data for mammal species across the study area between May 2012 and October 2015. Spoor surveys were carried out by driving transects at a low speed along roads, fire-breaks and boundary cutlines (Fig. 4.1), and recording any fresh spoor (tracks) of all medium and large mammals (see 4.3. Results for a complete list of species ultimately included in the study). As highly-skilled local trackers assisted with spoor detection and identification, incorrect identification of tracks was highly unlikely. Surveys were started at first light to avoid disturbance and maximise visibility.

4.2.3. Data preparation

We divided all transects into 50 m segments. In each segment we noted a presence (1) or absence (0) of each species. Due to large number of absences, we calculated density of the presence locations for each species using a kernel density estimator with 500 m search radius in ArcGIS version 10.6 (ESRI, 2016). As some transects were surveyed multiple times, segments were also assigned a measure of survey effort, represented by the number of times that segment was surveyed.

4.2.4. Multi-scale variables

We selected 15 variables that we hypothesised may influence the distribution of mammals across the study area (Table 4.1). In addition to these, we included longitude and latitude due to the large size of the study area, and survey effort. We employed a multi-scale approach for all variables except latitude, longitude, and effort, to identify the most appropriate scale at which to include each variable in our final models for each species. All raster layers were converted to the same projection, aligned, and resampled to the same extent at 50 m resolution. To test for selection of variables at different scales, we calculated a focal mean at varying circular moving windows of 250, 500, 1000, 2000, 4000, and 8000 m radius in ArcGIS version 10.6 (ESRI, 2016; equating to circles ranging from a minimum area of 0.2 km^2 to a maximum area of 200 km^2; Fig. 4.1). For variables based on point data, we produced multi-scale raster layers using the Point Density tool with a circular radius equal to each scale. The final multi-scale variable values were then extracted by sampling each variable at each scale from the midpoint of all 50

m transect segments. As one of the original aims of this study was to predict connectivity across the study landscape, we did not exclude variables from the same models on the basis of correlations.

4.2.5. Random forest modelling

We fitted random forest models (Breiman, 2001) to the species detection density data using R package *randomForest* (Liaw & Wiener, 2002). For each species of interest, scale optimisation was carried out by running random forest model selection on all variables using the rf.modelSel function in R package *rfUtilities* (Evans & Murphy, 2019). For each variable, we selected the scale with the highest MIR (Model Improvement Ratio; Evans & Murphy, 2019). The model selection process was then repeated with only the scale optimised variables for that species, to produce a final random forest model consisting of the best and most parsimonious combination of variables at their best scales. Model performance was assessed via the percentage of variance explained in the spoor density data.

We investigated the relationship between the final model variables and detection density for each species by producing smoothed splines using the plsmo function in package *Hmisc* (Harrell Jr, 2020). The importance of different variables in the final model for individual species was assessed by ranking MIR values. The importance of variables across all species was assessed by calculating the proportion of species with each variable in its final model, and the average rank (based on MIR) of each variable across all species. The frequency of scales was assessed by calculating the proportion of variables across species at each spatial scale.

Table 4.1: Variables hypothesised to affect distribution of the study species across the southern KAZA TFCA.

Variable		Code	Original resolution	Description	Units	Reference
1	Longitude	X	-	X coordinate (UTM35S) of pixel	-	-
2	Latitude	Y	-	Y coordinate (UTM35S) of pixel	-	-
3	Effort	Effort	-	Number of times segment was surveyed	-	This study
4	Carbon	C	250 m	Soil organic carbon content in g per kg at 5 cm depth (ORCDRC_M_sl2)	dg / kg	Hengl, Mendes de Jesus, et al. (2017)
5	Nitrogen	N	250 m	Soil nutrient maps of sub-Saharan Africa	cg / kg	Hengl, Leenaars, et al. (2017)
6	Vegetation cover (EVI)	EVI	250 m	MODIS/Terra Vegetation Indices (MOD13Q1), averaged from the midpoint of each month within the survey period	EVI	Didan (2015)
7	Leaf area index (LAI)	LAI	500 m	MODIS/Terra+Aqua Leaf Area Index (MCD15A2H), averaged from the midpoint of each month within the survey period	m^2 / m^2	Myneni et al. (2015)
8	Canopy cover (VCF)	VCF	250 m	MODIS/Terra Vegetation Continuous Fields (MOD44B), averaged from each year within the survey period	%	Dimiceli et al. (2015)
9	Precipitation	P	30 s (~1 km)	WorldClim (Version 2), monthly precipitation averaged from each month within the survey period	mm	Fick & Hijmans (2017)
10	Permanent water points	WP	-	Vector layer of permanent water points (pans, manmade pumps)	-	Trans-Kalahari Predator Programme (TKPP), unpublished data
11	Permanent rivers	R	-	Vector layer of major rivers, converted into a series of points at 100 m spacing	-	TKPP, unpublished data
12	Cattle density	CD	5 m (~8 km)	Gridded livestock of the world (GLW3) Global cattle distribution in 2010 (5 minutes of arc)	animals per pixel	Gilbert et al. (2018)
13	Human density	HD	3s (~100 m)	WorldPop 2013 population UN adjusted	population per pixel	Linard et al. (2012)
14	Settlements	S	-	Vector layer of settlements	-	TKPP, unpublished data
15	No protection	NP	-	Rasterised shapefile with value of (1) within all unprotected land, and (0) within PAs	-	TKPP, unpublished data
16	Intermediate protection	IP	-	Rasterised shapefile with value of (1) within Conservancy Ranches, Forest Areas, and Forest Reserves, and (0) elsewhere	-	TKPP, unpublished data
17	High protection	HP	-	Rasterised shapefile with value of (1) within National Parks, Wildlife Management Areas, and Safari Areas, and (0) elsewhere	-	TKPP, unpublished data
18	Trophy hunting	H	-	Rasterised shapefile with value of (1) within areas where trophy hunting was taking place during the study period, and (0) elsewhere	-	TKPP, unpublished data

4.3. Results

We collected species presence data along 4,824 km of transects, most of which were surveyed two times. We divided these transects into 96,474 segments of 50 m for analysis. Restricting the data to medium- and large-bodied mammal species with sufficient detections (> 400) resulted in 16 study species: six carnivores (black-backed jackal, *Canis mesomelas*; caracal, *Caracal caracal* & serval, *Leptailurus serval* [caracal and serval were grouped together due to their highly similar spoor]; leopard, *Panthera pardus*; lion, *Panthera leo*; spotted hyaena, *Crocuta crocuta*; and wildcat; *Felis silvestris*), and ten herbivores (African buffalo, *Syncerus caffer*; African elephant, *Loxodonta africana*; common duiker, *Sylvicapra grimmia*; common warthog, *Phacochoerus africanus*; giraffe, *Giraffa camelopardalis*; greater kudu, *Tragelaphus strepsiceros*; impala, *Aepyceros melampus*; plains zebra, *Equus quagga*; sable antelope, *Hippotragus niger*; and steenbok, *Raphicerus campestris*). Of these species, six are classified as *Vulnerable* or *Near Threatened* on the IUCN Red List (*Vulnerable*: leopard, lion, elephant, giraffe; *Near Threatened*: buffalo, zebra), and nine are thought to have decreasing population trends (leopard, lion, spotted hyaena, wildcat, buffalo, common duiker, warthog, giraffe, zebra; IUCN, 2020).

4.3.1. Scale optimisation

The scale optimisation procedure revealed substantial variation in the scales at which different species responded to variables: the optimal scale varied among species for a given variable, and among variables for a given species (Tables 4.3 & 4.4). For all variables across all species, scale optimisation most often selected our largest scale (8000 m; 84% of scale optimised variables across all species, and 81% of variables in the final models; Tables 4.3 & 4.4), and the second largest scale (4000 m) was the second most frequently selected (9% of scale optimised variables across all species, and 11% of variables in the final models; Tables 4.3 & 4.4).

In the final species models, eight of the 15 multiscale variables appeared at more than one scale (Tables 4.3 & 4.4). The remaining seven multiscale variables were exclusively selected at the largest scale – including variables relating to soil quality (carbon), vegetation (EVI), water availability (rivers),

anthropogenic impact (settlements), and management (no protection, intermediate protection, hunting; Tables 4.3 & 4.4). Interestingly, in contrast to the other protection variables, high protection was most frequently selected at an intermediate scale (4000 m) in the final models (Tables 4.3 & 4.4).

4.3.2. Model performance

Performance of selected models was high across all species, with more than 98% of variance explained for all species (Table 4.2).

4.3.3. Variable importance

Although we did not exclude variables from the same models on the basis of correlations, the relative importance of variables in our models nonetheless provides insights into which factors appear to be most important in predicting species detection densities. Variable pairs correlated by $|r| > 0.70$ (assessed using 250 m values) were carbon-nitrogen (0.70), carbon-precipitation (0.77), EVI-LAI (0.73), and LAI-VCF (0.80).

The total number of variables in the final model for each species ranged from 8 to 18. Variables differed in their importance across species, with some appearing in all final models and others appearing in the final models of only a relatively small number of species (Tables 4.2 & 4.4). Variables that appeared in a high proportion of final models generally also ranked highly (based on MIR) across all species, while variables that appeared in only a small number of final models were generally less important than other variables where they did appear (Table 4.2). The most and least important variables were largely consistent across both carnivores and herbivores, whereas variables of intermediate importance showed more variation between the two species groups (Table 4.4).

Smoothed plsmo splines of all variables in the final model for each species (except longitude, latitude, and effort) are shown in Fig. 4.2, with the five most important variables for each species (based on MIR) shaded in grey.

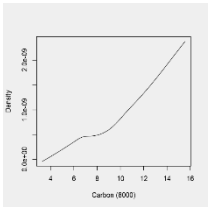
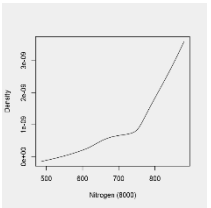
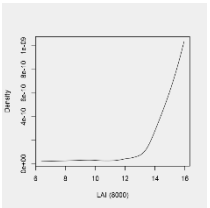
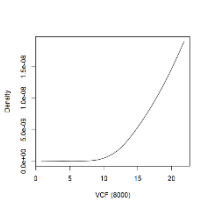
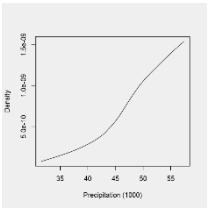
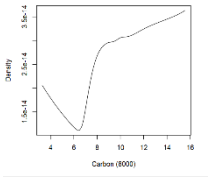
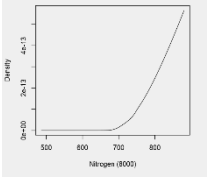
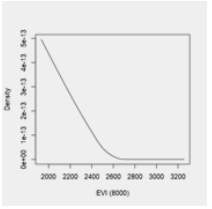
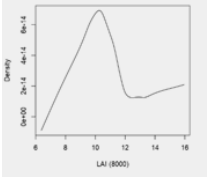
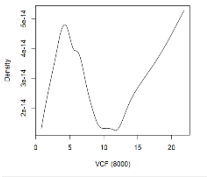
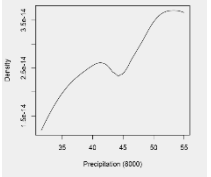
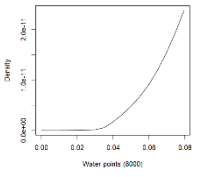
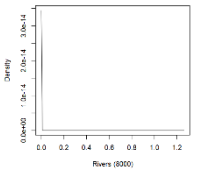
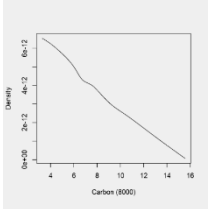
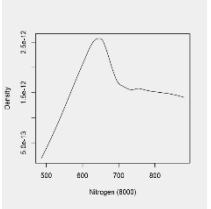
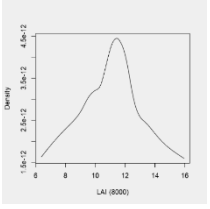
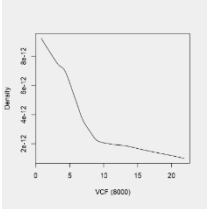
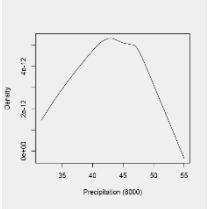
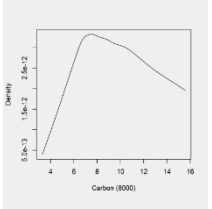
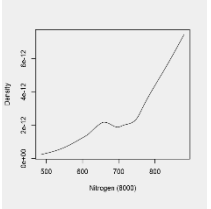
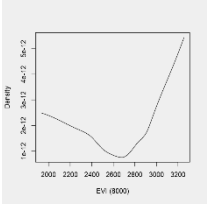
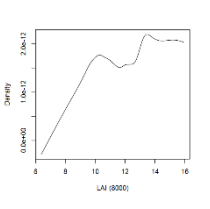
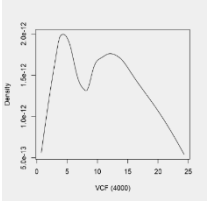
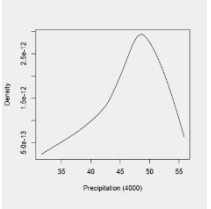
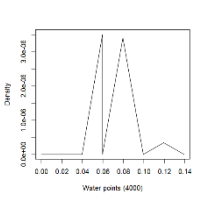
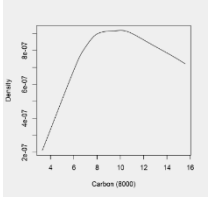
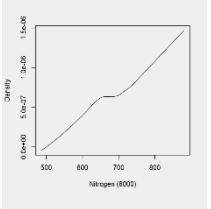
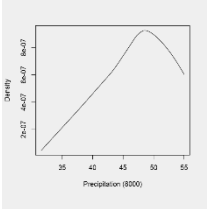
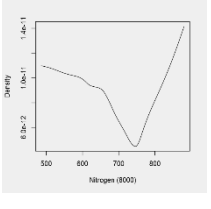
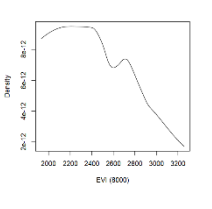
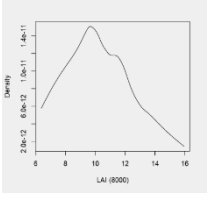
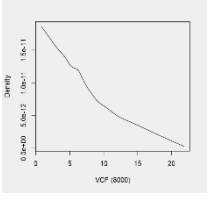
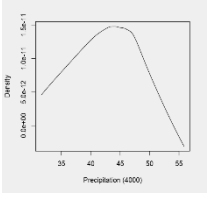
Table 4.2: Percentage of variance explained and importance (MIR, Model Improvement Ratio) of all variables selected for the final random forest model for each species. Cells are coloured according to the MIR of that variable for that species at the optimised scale; variables with higher importance for the species are shaded green, while those with lower importance are shaded yellow. Species have been grouped into carnivores and herbivores. Variables are coded as follows: longitude (X), latitude (Y), carbon (C), nitrogen (N), vegetation cover (EVI), leaf area index (LAI), canopy cover (VCF), precipitation (P), water points (WP), rivers (R), cattle density (CD), human density (HD), settlements (S), no protection (NP), intermediate protection (IP), high protection (HP), and trophy hunting (H).

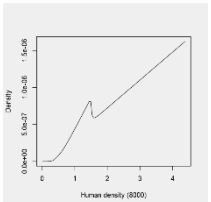
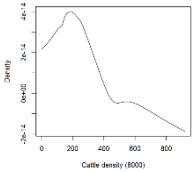
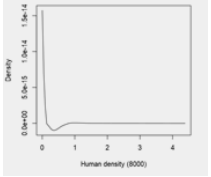
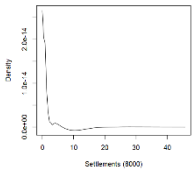
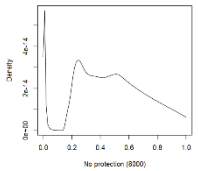
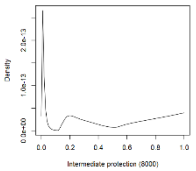
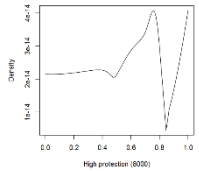
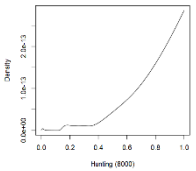
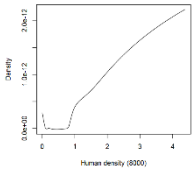
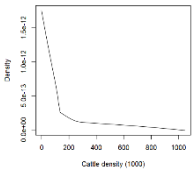
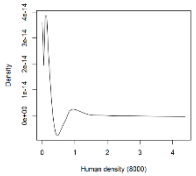
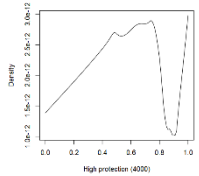
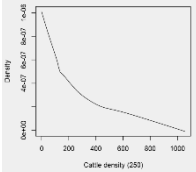
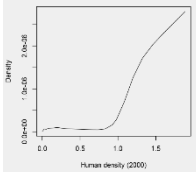
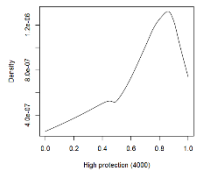
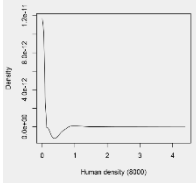
Species	% variance explained	X	Y	Effort	C	N	EVI	LAI	VCF	P	WP	R	CD	HD	S	NP	IP	HP	H
Black-backed jackal	98.51	0.562	0.673		0.507	0.497		0.377	0.377	1.000				0.404					
Caracal & Serval	98.09	0.959	0.949	0.233	0.714	0.998	0.871	0.775	0.742	1.000	0.148	0.007	0.517	0.977	0.072	0.203	0.151	0.277	0.366
Leopard	98.17	0.994	0.827		1.000	0.886		0.791	0.909	0.980				0.734					
Lion	98.02	0.503	0.620	0.183	0.451	0.381	0.376	0.360	0.725	1.000	0.259		0.356	0.374				0.217	
Spotted hyaena	98.46	0.858	0.668		0.762	0.822				0.986			1.000	0.737				0.641	
Wildcat	98.25	0.847	0.742			0.677	0.570	0.583	0.603	1.000				0.639					
African buffalo	98.42	1.000	0.595		0.600		0.532	0.513		0.625			0.547	0.546					
African elephant	99.40	1.000	0.601	0.730	0.729	0.471	0.478	0.407	0.357	0.784	0.540	0.011	0.776	0.437	0.088	0.208	0.152	0.472	0.170
Common duiker	98.89	0.995	0.840	0.605		0.583		0.587		1.000			0.563			0.604			
Common warthog	98.34	0.838	0.765		0.855	0.917	0.906	0.793		1.000			0.825						
Giraffe	98.75	0.875	0.807	0.829	0.629	0.600	0.571	0.555	0.593	1.000	0.304	0.033	0.982	0.654	0.067	0.222	0.196	0.703	0.233
Greater kudu	98.81	0.895	0.689		0.823	0.837				1.000			0.730	0.705				0.606	
Impala	99.03	0.473	0.631	0.187	0.622	0.493	0.345	0.371	0.654	1.000	0.153	0.020	0.306	0.345	0.032	0.111	0.092	0.270	0.169
Plains zebra	98.87	0.519	0.542	0.060	0.566	0.486	0.393	0.419	0.532	1.000	0.431	0.020	0.500	0.364	0.047	0.144	0.095	0.420	0.148
Sable antelope	98.59	0.900	0.849		0.573	0.459	0.460		0.489	1.000				0.506					
Steenbok	98.78	0.043	0.055		0.045	0.093	0.032		0.016	0.092	1.000		0.041			0.027	0.015	0.039	0.033

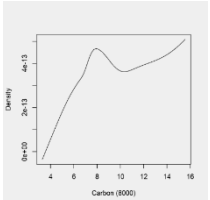
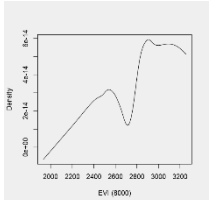
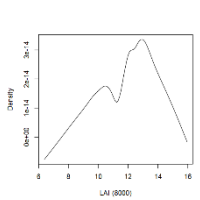
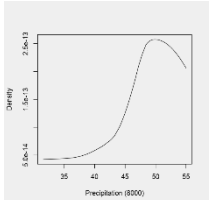
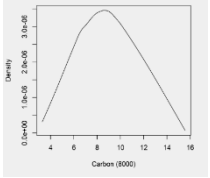
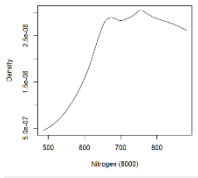
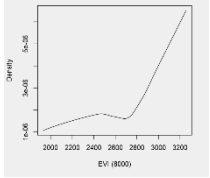
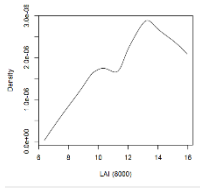
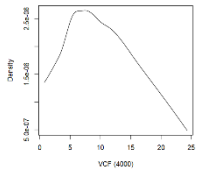
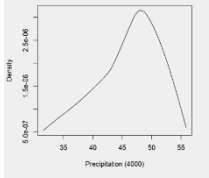
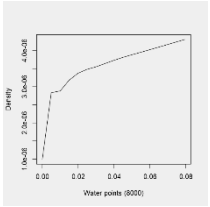
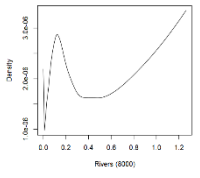
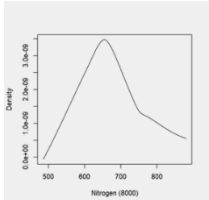
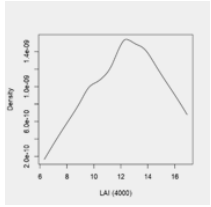
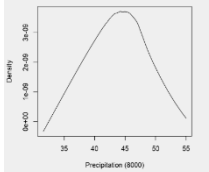
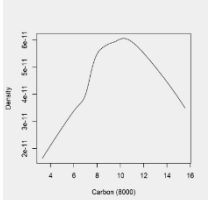
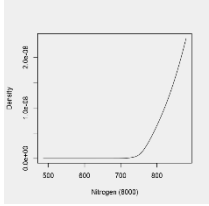
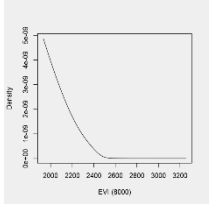
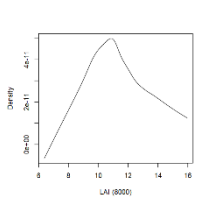
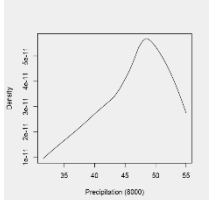
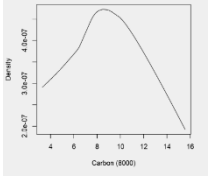
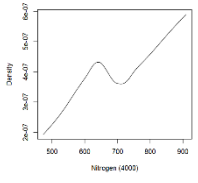
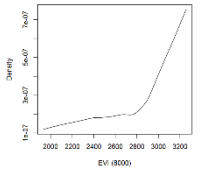
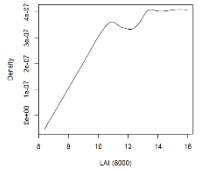
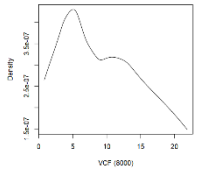
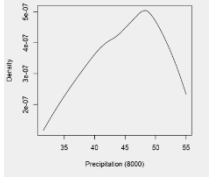
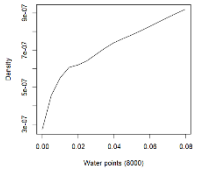
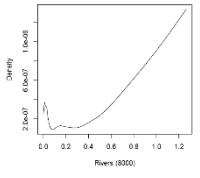
Table 4.3: Percentage of variance explained and optimised scale of all variables selected for the final random forest model for each species. Cells are coloured according to the importance (MIR, Model Improvement Ratio) of that variable for that species at the optimised scale; variables with higher importance for the species are shaded green, while those with lower importance are shaded yellow. Species have been grouped into carnivores and herbivores. Variables are coded as follows: longitude (X), latitude (Y), carbon (C), nitrogen (N), vegetation cover (EVI), leaf area index (LAI), canopy cover (VCF), precipitation (P), water points (WP), rivers (R), cattle density (CD), human density (HD), settlements (S), no protection (NP), intermediate protection (IP), high protection (HP), and trophy hunting (H).

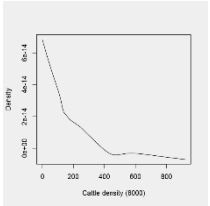
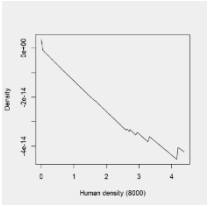
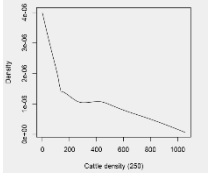
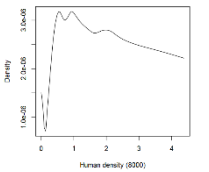
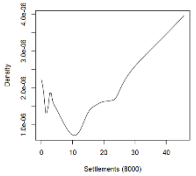
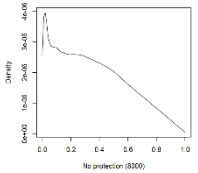
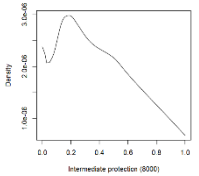
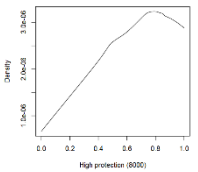
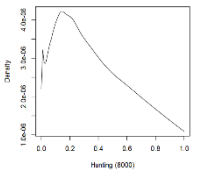
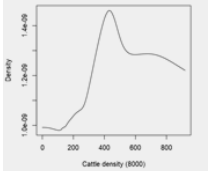
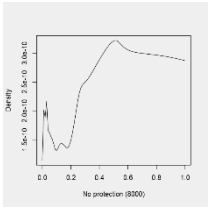
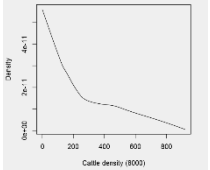
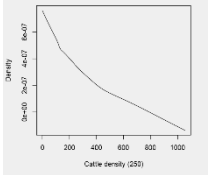
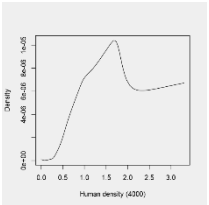
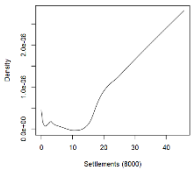
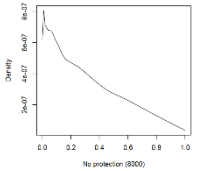
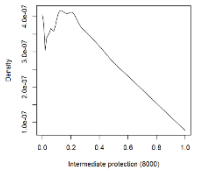
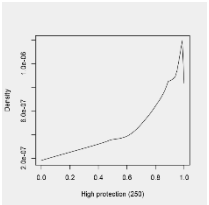
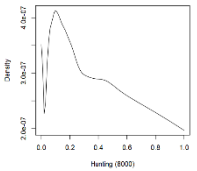
Species	% variance explained	X	Y	Effort	C	N	EVI	LAI	VCF	P	WP	R	CD	HD	S	NP	IP	HP	H
Black-backed jackal	98.51	1	1		8000	8000		8000	8000	1000				8000					
Caracal & Serval	98.09	1	1	1	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000	8000
Leopard	98.17	1	1		8000	8000		8000	8000	8000				8000					
Lion	98.02	1	1	1	8000	8000	8000	8000	4000	4000	4000		1000	8000				4000	
Spotted hyaena	98.46	1	1		8000	8000				8000			250	2000				4000	
Wildcat	98.25	1	1			8000	8000	8000	8000	4000				8000					
African buffalo	98.42	1	1		8000		8000	8000		8000			2000	8000					
African elephant	99.40	1	1	1	8000	8000	8000	8000	4000	4000	8000	8000	250	8000	8000	8000	8000	8000	8000
Common duiker	98.89	1	1	1		8000		4000		8000			8000			8000			
Common warthog	98.34	1	1		8000	8000	8000	8000		8000			8000						
Giraffe	98.75	1	1	1	8000	4000	8000	8000	8000	8000	8000	8000	250	4000	8000	8000	8000	250	8000
Greater kudu	98.81	1	1		8000	8000				8000			8000	8000				4000	
Impala	99.03	1	1	1	8000	8000	8000	8000	4000	2000	8000	8000	8000	8000	8000	8000	8000	4000	8000
Plains zebra	98.87	1	1	1	8000	8000	8000	8000	250	4000	4000	8000	8000	8000	8000	8000	8000	500	8000
Sable antelope	98.59	1	1		8000	8000	8000		8000	250				8000					
Steenbok	98.78	1	1		8000	8000	8000		8000	8000	8000		8000			8000	8000	4000	8000

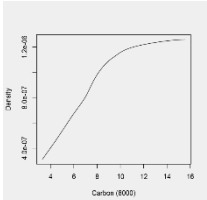
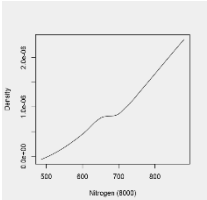
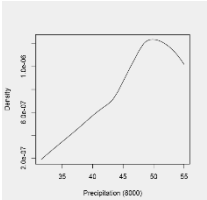
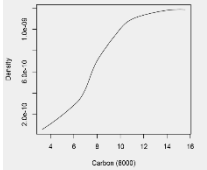
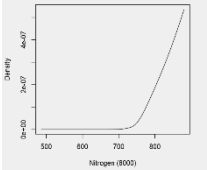
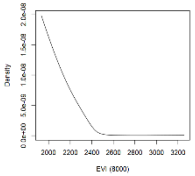
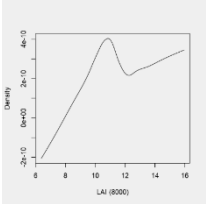
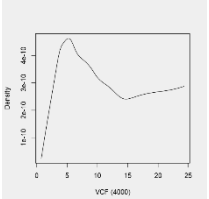
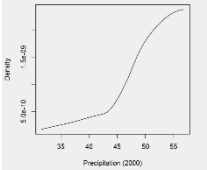
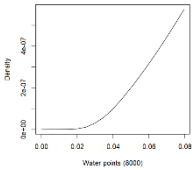
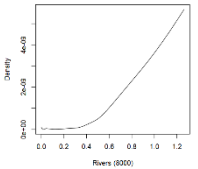
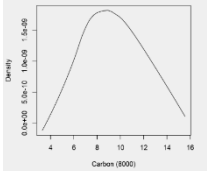
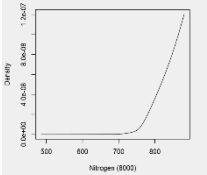
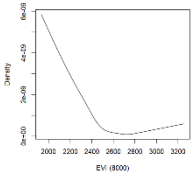
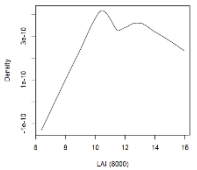
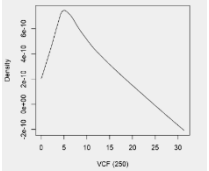
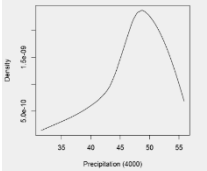
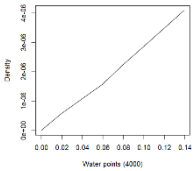
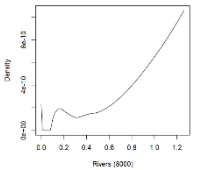
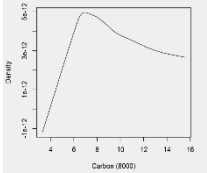
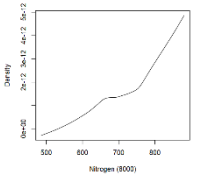
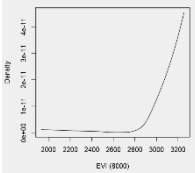
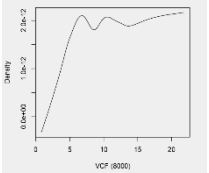
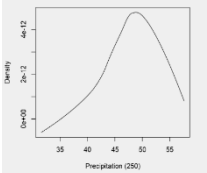
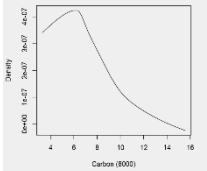
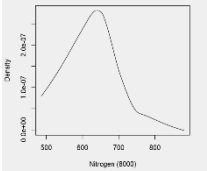
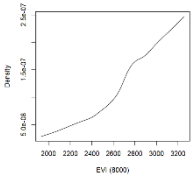
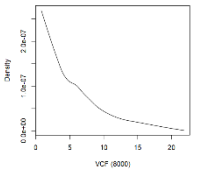
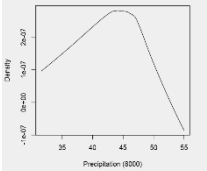
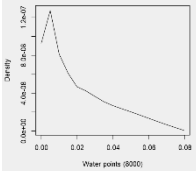
Figure 4.2 (overleaf): Smoothed plsmo splines showing the relationship between the final model variables (x-axis; except longitude, latitude, and effort) and detection density (y-axis) for each species. Variable scales are shown in brackets in the relevant x-axis label; units for each variable can be found in Table 4.1. Plots shaded in grey indicate variables that appear in the five most important variables for that species, based on MIR (Model Improvement Ratio).

Species	Carbon	Nitrogen	EVI	LAI	VCF	Precipitation	Water points	Rivers
Black-backed jackal								
Caracal & Serval								
Leopard								
Lion								
Spotted hyaena								
Wildcat								

Species	Cattle density	Human density	Settlements	No protection	Intermediate protection	High protection	Trophy hunting
Black-backed jackal							
Caracal & Serval							
Leopard							
Lion							
Spotted hyaena							
Wildcat							

Species	Carbon	Nitrogen	EVI	LAI	VCF	Precipitation	Water points	Rivers
African buffalo								
African elephant								
Common duiker								
Common warthog								
Giraffe								

Species	Cattle density	Human density	Settlements	No protection	Intermediate protection	High protection	Trophy hunting
African buffalo							
African elephant							
Common duiker							
Common warthog							
Giraffe							

Species	Carbon	Nitrogen	EVI	LAI	VCF	Precipitation	Water points	Rivers
Greater kudu								
Impala								
Plains zebra								
Sable antelope								
Steenbok								

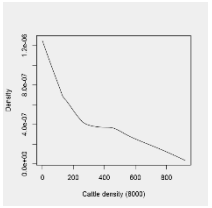
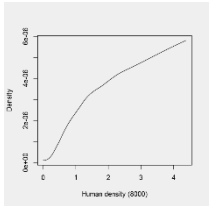
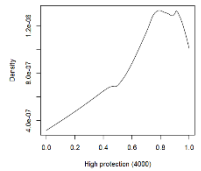
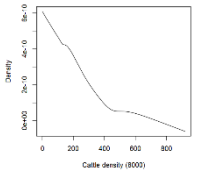
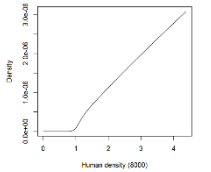
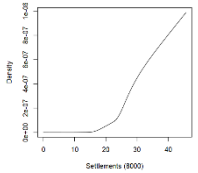
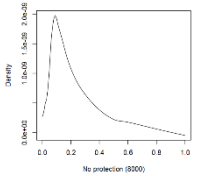
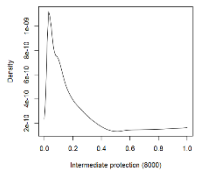
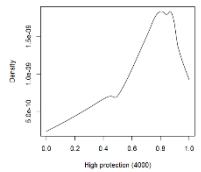
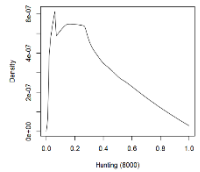
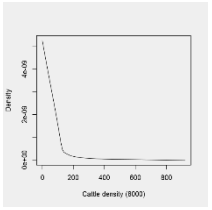
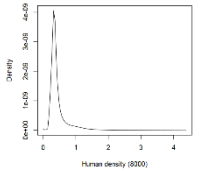
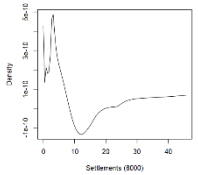
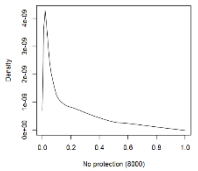
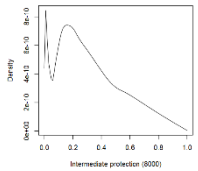
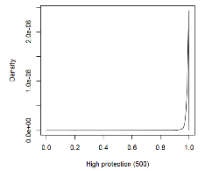
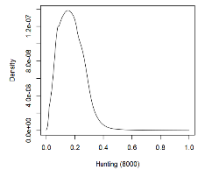
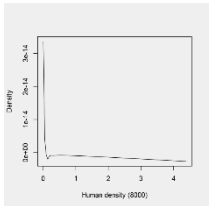
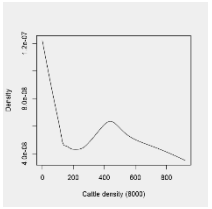
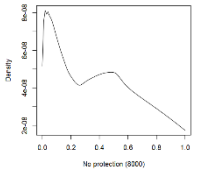
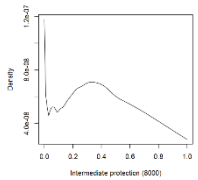
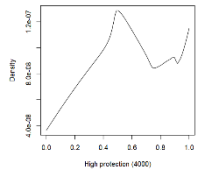
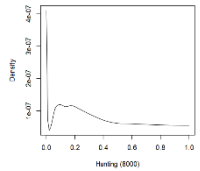
Species	Cattle density	Human density	Settlements	No protection	Intermediate protection	High protection	Trophy hunting
Greater kudu							
Impala							
Plains zebra							
Sable antelope							
Steenbok							

Table 4.4: Variable importance across final random forest models for all species. The number of scales at which each variable was selected during scale optimisation and was included in the final models (out of a possible total of 6) across all species; and the average and most frequent scale at which the variable was selected during scale optimisation and included in the final models. Importance is indicated by the proportion of the 16 study species for which each variable appeared in the final model, separated into carnivores (black-backed jackal, caracal & serval, leopard, lion, spotted hyaena, wildcat) and herbivores (African buffalo, African elephant, common duiker, common warthog, giraffe, greater kudu, impala, plains zebra, sable antelope, steenbok); and the average rank (based on MIR, Model Improvement Ratio) of each variable for each species, from 1 (most important) to 18 (least important). Variables are ordered from those which appeared in the highest proportion of final species models to those which appeared in the lowest proportion of final species models.

		Optimised scale			Scale in final models			% of species with variable in final model			Average rank
Variable	**Code**	**Number**	**Mean**	**Mode**	**Number**	**Mean**	**Mode**	**All**	**Carnivores**	**Herbivores**	
Precipitation	P	5	5703	8000	5	5703	8000	1.00	1.00	1.00	1.4
Longitude (UTM35S)	X	-	-	-	-	-	-	1.00	1.00	1.00	3.2
Latitude (UTM35S)	Y	-	-	-	-	-	-	1.00	1.00	1.00	4.5
Nitrogen	N	2	7750	8000	2	7733	8000	0.94	1.00	0.90	5.5
Carbon	C	1	8000	8000	1	8000	8000	0.88	0.83	0.90	5.1
Human density	HD	3	7375	8000	3	7231	8000	0.81	1.00	0.70	7.8
Cattle density	CD	4	5734	8000	4	4979	8000	0.75	0.50	0.90	7.0
Leaf area index (LAI)	LAI	3	7281	8000	2	7667	8000	0.75	0.83	0.70	9.0
Canopy cover (VCF)	VCF	3	5547	8000	3	6205	8000	0.69	0.83	0.60	8.1
Vegetation cover (EVI)	EVI	1	8000	8000	1	8000	8000	0.69	0.50	0.80	8.4
High protection	HP	5	5109	8000	4	4083	4000	0.56	0.50	0.60	10.3
Water points	WP	2	7250	8000	2	6857	8000	0.44	0.33	0.50	11.8
Effort	E	-	-	-	-	-	-	0.44	0.33	0.50	12.1
No protection	NP	1	8000	8000	1	8000	8000	0.44	0.17	0.60	13.1
Trophy hunting	H	1	8000	8000	1	8000	8000	0.38	0.17	0.50	13.3
Intermediate protection	IP	1	8000	8000	1	8000	8000	0.38	0.17	0.50	15.6
Settlement points	S	1	8000	8000	1	8000	8000	0.31	0.17	0.40	16.9
Rivers	R	3	7375	8000	1	8000	8000	0.31	0.17	0.40	17.9

Longitude and latitude had high importance in our species distribution models, appearing in the final models for all species (average rank: 3.2 and 4.5, respectively; Tables 4.2 & 4.4).

Our results suggest that, alongside location, variables relating to climate, soil quality, and vegetation were the most important factors determining where mammals were found in the study landscape across southern KAZA: precipitation, soil nutrients (carbon and nitrogen), and vegetation indices (VCF, LAI, EVI) all appeared in the final model for more than half of the study species (Table 4.4).

Average monthly precipitation appeared in the final model for all species (average rank: 1.4; Table 4.4), and was the most important variable (MIR > 0.78) for nearly all species considered, except buffalo (0.63) and steenbok (0.09; Table 4.2). For most species this relationship was curvilinear, with detection density increasing with monthly precipitation until a peak at around 50 mm, after which detection decreased with increasing rainfall. This peak occurred at a lower average precipitation for common duiker, leopard, steenbok, and wildcat, possibly suggesting a preference for drier habitats among these species. In contrast, black-backed jackal, caracal & serval, and impala did not show any decline in density at the highest rates of precipitation, suggesting that these species may benefit from particularly high rainfall (Fig. 4.2).

Biogeochemical variables were highly important, with nitrogen appearing in 94% (average rank: 5.5) and carbon in 88% (average rank: 5.1) of final models across all species (Table 4.4). Both variables showed a generally positive relationship with detection density in most of the final models in which they were of high importance, but with detections dropping off after a peak for many species. However, leopard and steenbok showed a negative association with carbon, suggesting a possible preference for less productive habitats by these species (Fig. 4.2).

While precipitation and soil nutrients appeared to be similarly important for herbivores and carnivores, variables relating to vegetation showed some differences between the two groups. LAI and VCF appeared to be more important for carnivores (both appearing in 83% of final models, versus 70% and 60% among herbivores, respectively), and EVI more important for herbivores (80% of final models, versus 50% among carnivores; Table 4.4). Vegetation indices also had less consistent relationships

across different species: LAI generally increased to a peak and then decreased for most species, while EVI and VCF appeared in many final models (Table 4.2), but had highly variable relationships. This variability is likely to be a reflection of the range of habitats and vegetation structures preferred by different species.

Anthropogenic variables appeared to be important for most species in the study area. Both human population density and cattle density showed high importance, each appearing in more than three quarters of final species models (81% for human density and 75% for cattle density; average rank: 7.8 and 7.0, respectively; Table 4.4). Interestingly, human density appeared to be a more important factor influencing habitat use for carnivores than herbivores (appearing in 100% versus 70% of final models), while cattle density was of higher importance for herbivores than carnivores (appearing in 90% versus 50% of final models; Table 4.4).

The relationship between detection density and human density varied substantially between species. Considering only species for which human density was in the top five variables in the final model by MIR, detection density was negatively associated with human density for buffalo, sable antelope, and wildcat, but positively associated for black-backed jackal, giraffe, greater kudu, and spotted hyaena (Fig. 4.2). This suggests that the latter species may be most able to persist in areas of high human density, provided there is sufficient habitat.

Cattle density, in contrast, showed a highly consistent negative relationship with detection density of different species, including buffalo, elephant, caracal & serval, warthog, giraffe, greater kudu, impala, lion, zebra, spotted hyaena, and steenbok. The only species that appeared to be positively associated with cattle density was common duiker (Fig. 4.2).

Management variables – including different levels of protection and whether trophy hunting is carried out in an area – were generally less important than climatic, biogeographic, vegetation, and anthropogenic variables (Tables 4.2 & 4.4). Protection status was much more important for herbivores than carnivores: no protection (MIR < 0.60, average rank: 13.1), intermediate protection (MIR < 0.20, average rank: 15.6), and trophy hunting (MIR < 0.37, average rank: 13.3) all appeared in only 17% of

final carnivore models, versus 60%, 50%, and 50% for herbivores (Tables 4.2 & 4.4). Importantly, however, high protection showed greater importance across all species (average rank: 10.3), appearing in 50% of final carnivore models and 60% of final herbivore models (Table 4.4).

When protection variables did appear in the final model for a species, they exhibited consistent relationships with detection densities: unprotected areas and areas under intermediate protection were negatively associated with detection density, while areas under high protection had a positive association. All three variables relating to protection appeared in the final models for caracal & serval, elephant, giraffe, impala, and zebra, albeit with low to intermediate importance (MIR: 0.02-0.70; Table 4.2).

Trophy hunting, in contrast, had a more variable influence on detections between species, and did not appear to be linked to how heavily different species are hunted: although greater kudu, buffalo, zebra, sable antelope, leopard, elephant and lion have been documented as the seven most hunted species in Zimbabwe (Barnett & Patterson, 2006), of these species, hunting only appeared as a variable in the final models for elephant (MIR: 0.17) and zebra (MIR: 0.15; Table 4.2), showing a negative association with detection density for both species (Fig. 4.2).

The least important variables were settlement points (MIR < 0.09, average rank: 16.9) and rivers (MIR < 0.03, average rank: 17.9; Table 4.2), which each appeared in only 31% of final models (Table 4.4). Although the presence of water points and rivers did not appear to have high importance for most species (MIR < 0.54), both surface water variables appeared together in the final models for caracal & serval, elephant, giraffe, impala, and zebra (Table 4.2). For all of these species, with the exception of caracal & serval, both variables were positively associated with habitat use (Fig. 4.2).

4.4. Discussion

In this study, we used the random forest algorithm to investigate multi-scale, multi-species habitat use across part of Africa's largest transfrontier conservation area. As far as we are aware, this is the first time machine learning has been used to model spoor data in a multi-scale framework. It is also one of

the first studies to assess multi-scale habitat use for such a large and diverse mammal assemblage: our 16 study species range in size from around 5 kg (wildcat; Herbst & Mills, 2010) to more than 5,000 kg (elephant; Laursen & Bekoff, 1978), and feature members of four taxonomic orders (including six carnivorans, eight even-toed ungulates, one odd-toed ungulate, and one proboscidean) and three IUCN Red List categories (ten *Least Concern*, four *Vulnerable*, and two *Near Threatened*; IUCN, 2020).

4.4.1. Factors determining mammal distribution across southern KAZA

This study was based on spoor data collected along roads and cutlines; as such, our inferences about mammal distributions and habitat use relate specifically to the study species' use of these habitat features, and may therefore be more representative of areas used for travel between preferred patches of habitat than broader habitat selection. However, as all variables were most frequently selected at the largest scale in the final models, we believe that our inferences are still likely to be reflective of preferred habitats and areas in which species are able to persist.

The prominence of longitude and latitude in all final species models reflects the importance of geographic variation in species distributions, particularly when assessments are being carried out across a very large area. The clearest example of such geographic variation from this study is impala, which were abundant in Zimbabwe but much more limited across the study area within Botswana, which corresponds to the edge of the species' geographic range (IUCN SSC Antelope Specialist Group, 2016).

Our results suggest that climatic, biogeochemical, and vegetation variables are the most important factors determining mammal distribution across southern KAZA – although it should be noted that their importance may have been slightly amplified by correlations between some of these variables. Average monthly precipitation over the survey period was the most important predictor of habitat use for nearly all species considered. This is an unsurprising finding given the aridity of the study area and its large extent, which enables spatial variation in precipitation to affect the distribution of species in different ways depending on the structure and tolerance of their ecological niches. Precipitation is an important factor affecting nearly all aspects of ecological systems, and is the dominant driver of vegetation structure, density, and biomass. Net primary productivity has been shown to increase significantly with

annual precipitation in the bush and grassland savannahs of southern Africa (Zhu & Southworth, 2013), and droughts often lead to degradation of natural vegetation (Mberego & Gwenzi, 2014).

It is important to note that, by considering only mean precipitation during all months in which surveys were conducted across the study area, this analysis did not take into account seasonal rainfall patterns. These annual fluctuations are known to play an important role in shaping wildlife movement patterns in the study landscape: the longest known mammal migration in Africa has been recorded among zebra moving north from Nxai Pan NP, in the southernmost part of our study area, to dry season habitat on the Chobe River floodplains (Naidoo et al., 2016), and these migratory prey may also be tracked by some predators (Valeix et al., 2009). Similarly, elephant have been found to show seasonal variation in habitat use in part of the study landscape (Roever et al., 2012). As such, modelling how species' distributions vary across different times of year – particularly wet season versus dry season – could reveal valuable insights into how these seasonal dynamics shape species' habitat use across the study landscape, and would be an important component of corridor planning exercises in KAZA.

Soil carbon and nitrogen were also important variables predicting habitat use for many of the study species. Soil carbon and nitrogen stocks are generally higher in more productive ecosystems where litter input into the soil is greater (Wang et al., 2009), and a higher soil nutrient content is associated with greater plant diversity and biomass productivity (Zhou et al., 2011). Mineral content of foods is also an important determinant of the spatial distribution of ungulates (McNaughton, 1988), and rich soils have been estimated to support 20 times more large ungulate biomass than poor soils with low nutrient availability (Fritz & Duncan, 1994). For herbivores, biogeochemical variables are therefore likely to be important predictors of distribution due to their impact on food availability – although the high variation in herbivores' associations with vegetation indices in this study illustrates the divergent habitat preferences that can be found across wider mammal communities. In turn, many African carnivore species are known to make habitat use decisions based on prey availability (Ash et al., 2020; Everatt et al., 2015; Höner et al., 2005; Searle et al., 2020), and carnivore numbers closely scale with prey numbers (Carbone & Gittleman, 2002). As we did not explicitly include information on prey availability in our

carnivore models, it is likely that climatic, biogeochemical, and vegetation variables ranked highly in our carnivore models as they acted as proxies for prey.

Anthropogenic pressures also appeared to have an important direct influence on habitat use by mammals in the southern KAZA TFCA. The majority of species considered in this study showed a strong negative association with cattle density; among the herbivores, this relationship was found not just for grazers (such as buffalo and zebra), which compete directly with cattle for food, but also browsers (such as giraffe and greater kudu). Overgrazing can severely degrade soil nutrients, leaving areas used by cattle with reduced plant biomass and species diversity, and dominated by plant species preferred by livestock (Zhou et al., 2011). As a result, while many ungulates compete directly with livestock for food, even those that do not can be left with little to consume when cattle densities are particularly high. Carnivores may select against areas with a high density of cattle as these areas lack sufficient prey – although livestock can provide an alternative food source to wild prey for carnivores (Winterbach et al., 2013) – but could also be killed or pushed out of these areas by harmful encounters with livestock herders, such as poisonings (Treves & Naughton-Treves, 2005). In line with this, large carnivore range contractions have been shown to be significantly more likely in regions with high cattle density (Wolf & Ripple, 2017).

Human density was also an important predictor of habitat use, but its relationship with detection density varied substantially across species. The negative association with human density found for caracal & serval, lion, wildcat, buffalo, zebra, and sable antelope aligned with our expectations: human population density has been established as a key cause of mammal species becoming threatened with extinction (Karanth et al., 2010; McKee et al., 2013; Parks & Harcourt, 2002), and high rural human population density is a significant predictor of large carnivore range losses (Wolf & Ripple, 2017). In contrast, the positive association with human density observed among black-backed jackal, giraffe, greater kudu, impala, leopard, and spotted hyaena may indicate an ability for these species to persist in areas of higher human density, provided there is sufficient habitat. This finding aligns with previous research for black-backed jackal (Minnie et al., 2016), greater kudu (Riggio et al., 2018), leopard (Balme et al., 2010), and

spotted hyaena (Yirga et al., 2017). However, the relationship between wildlife distributions and human density may partly be confounded in this study by the large number of human settlements adjacent to the boundary of the highly-productive and well-protected Hwange NP, at the south-eastern edge of our study area.

Variables relating to protection status showed consistent relationships across species: habitat use was negatively associated with unprotected and less-strictly protected areas, and positively associated with highly protected areas. Although protection status appeared to be more important for herbivores than carnivores, high protection was similarly important across both groups, highlighting the value of strictly protected areas as refugia for biodiversity (Le Saout et al., 2013). However, as less than 5% of our total survey effort was conducted in completely unprotected land, we are unable to make clear inferences about the importance of protected versus unprotected land in this study. It is likely that wildlife densities are much lower in unprotected areas than PAs across the KAZA landscape, given the role of protection in reducing illegal activities (such as bushmeat poaching; Loveridge et al., 2020), and the well-established link between effective protection and persistence of mammal populations (Karanth et al., 2010), especially large carnivores (Abade et al., 2018; Henschel et al., 2016; Wegge et al., 2009). In light of this, and the mounting pressures on wildlife areas outside PAs across Africa (Newmark, 2008), continued protection of core wildlife areas should remain a priority in the KAZA TFCA.

Trophy hunting was of intermediate importance for most of our study species, and showed greater importance among herbivores than carnivores. The relationship between trophy hunting and habitat use was negative for all herbivores with the variable in their final model. Two of these species – elephant and zebra – are among the most hunted species in Zimbabwe (Barnett & Patterson, 2006), suggesting that hunting activities may be influencing the distribution or density of these species.

Variables relating to permanent surface water showed intermediate importance in our final models for most species, and appeared to be more important for herbivores than carnivores. In particular, surface water availability appeared to be an important factor shaping habitat use for elephant, in line with previous studies of the species (Harris et al., 2008; Shannon et al., 2009), including in the study area

(Valls-Fox et al., 2018). Although we expected water availability to have greater importance in shaping distribution of mammals in the water-limited southern KAZA TFCA, this is likely to be a consequence of the limitations of our water variables: we were not able to incorporate information on how surface water availability may vary over the course of different seasons, and the water source information is believed to contain some errors with regards to the number, location and activity status of artificial bore holes. Nevertheless, most species with variables representing permanent surface water in the final model showed a positive relationship with these variables, as expected.

4.4.2. Importance of a multi-scale, multi-species approach

We identified a number of spatial scales at which species respond to different variables, and at which different species responded to the same variables, in line with previous multi-scale habitat use studies (Ashrafzadeh et al., 2020; Grand et al., 2004; Khosravi et al., 2019). This highlights the importance of adopting a multi-scale approach for species distribution modelling, as it can reveal divergent patterns of decision-making both among and within species.

Our results suggest that the 16 studied mammals in southern KAZA generally make habitat use decisions at relatively broad scales – possibly at even broader scales than those considered in this study, as our maximum scale (a radius of 8000 m, equating to an area of approximately 200 km^2) was most frequently selected as the most representative scale for all variables across all species. This is consistent with previous studies that have found that mammals with large home ranges respond to habitat variables at broader spatial scales, a pattern that appears commonly among carnivores (Cushman & Wasserman, 2018; Hearn et al., 2018; Khosravi et al., 2019; Macdonald et al., 2019; Rather et al., 2020) and has also been observed in herbivores (Zweifel-Schielly et al., 2009).

We also illustrate that different species can have divergent responses to the same variables (McGarigal et al., 2016), underscoring the importance of adopting a multi-species approach for critical decision-making processes that depend on understanding wildlife distributions and habitat associations, such as PA expansion & prioritisation and corridor planning (Macdonald et al., 2020; Penjor et al., 2020). Basing decisions on only a small number of species, and not considering species-specific spatial extents

of habitat components or anthropogenic effects, can fail to emphasise the importance of different habitat types and conditions for the wider mammal community (Anderson et al., 2016; Gandiwa, 2013; Smit et al., 2007). Integrating multi-species, multi-scale thinking into these processes should help decision-makers to prioritise areas of habitat that maximise value for as many species as possible (Cushman et al., 2013; Le Saout et al., 2013). Efforts of this kind are likely to be key to preserving biodiversity in the face of ongoing loss of the world's remaining natural habitat (Hoekstra et al., 2005), and the chronic lack of funding for conservation and management (Lindsey et al., 2018). To date, very few assessments of multi-species ecology have been carried out in sub-Saharan Africa at the scale achieved in this study – both in terms of spatial scale (but see Brennan et al., 2020, also in KAZA) and number of species.

4.4.3. Potential future trends in the southern KAZA TFCA

The critical importance of precipitation in predicting the distributions of all species highlights the significant impacts that altered rainfall patterns could have on wildlife distributions in water-limited areas like KAZA. Rainfall is predicted to decrease across southern Africa under multiple climate change scenarios (Solomon et al., 2007), with significant drying (~10-20%) projected over parts of Botswana (Meehl et al., 2007; Moise & Hudson, 2008). Our models suggest that these changes could have substantial impacts on wildlife distributions across the KAZA TFCA, with potential implications for the landscape's long-distance ungulate migration (Naidoo et al., 2016). As such, management authorities in KAZA must work to ensure the area's current PA network will remain fit for purpose under anticipated changes in rainfall patterns, through modelling exercises and adaptive management.

The clear negative impact of cattle density on mammals in the study area hints at another concerning trend for KAZA's wildlife populations. Livestock numbers across sub-Saharan Africa are expected to increase substantially in the coming years: food demand for livestock products in the region is expected to be nearly double what it was in 2010 by 2050 (van Vuuren et al., 2009), with both the market size of beef (compared to 2005-07; Pica-Ciamarra et al., 2013) and milk consumption (compared to 2000; Herrero et al., 2014) projected to triple. Not only will the intensification of livestock production required to meet this demand increase the direct competition faced by wild herbivores and contribute to habitat

degradation, but it is also likely to require conversion of habitat to support grassland expansion for grazing – a process responsible for nearly 60% of land use change in sub-Saharan Africa (Herrero et al., 2014).

In light of these projections, efforts must be made to ensure protection is enforced across KAZA's PA network, to prevent encroachment by livestock and illegal grazing in strictly protected areas, and safeguard the landscape's remaining natural habitat. This is particularly pressing given that cattle are known to enter Hwange NP, one of the best-protected parts of the study landscape, in the rainy season (Valls-Fox et al., 2018) – which may partly explain why cattle density was more important than protection in predicting habitat use for many species in this study. At the same time, management authorities should strive to enact directives that promote the coexistence of wildlife and livestock, such as through controlled grazing and other sustainable pastoral practices, which have been shown to regenerate vegetation in overgrazed areas (Western et al., 2020; Zhou et al., 2011). Initiatives of this kind are likely to be particularly important in large conservation landscapes like the KAZA TFCA which encompass mosaics of protected and communal land (Valls-Fox et al., 2018), and will be a critical component of efforts to align conservation with human development.

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CHAPTER 5

Leopard population density across habitats and management strategies in Tanzania's Ruaha-Rungwa landscape

Title

Leopard population density across habitats and management strategies in southern Tanzania's Ruaha-Rungwa landscape

Running header

CHAPTER 5: Leopard density across habitats and management strategies

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Leopard population density across habitats and management strategies in southern Tanzania's Ruaha-Rungwa landscape

Abstract

Although widely considered one of the most resilient African large carnivores, the status of leopard (*Panthera pardus*) is unknown across much of its remaining African range. We provide the first comparison of leopard population density within different components of a mixed-use landscape in Tanzania, via spatially explicit capture-recapture (SECR) modelling of data from camera trap surveys conducted in the Ruaha-Rungwa landscape in 2018 and 2019. Population density was highest in highly-productive Acacia-Commiphora habitat in the core tourist area of Ruaha National Park (6.81 ± 1.24 leopards per 100 km^2). The next highest density (4.23 ± 1.02 per 100 km^2) was estimated in similar habitat in a neighbouring community-managed area (MBOMIPA WMA). Lowest densities were estimated in miombo (*Brachystegia-Jubelnardia*) woodland habitat, both in a trophy hunting area (Rungwa Game Reserve; 3.36 ± 1.09 per 100 km^2) and inside the National Park (3.23 ± 1.25 per 100 km^2). Population density was highly correlated with prey abundance, suggesting that variation in leopard density may be primarily driven by availability of prey, which likely varies with habitat types and anthropogenic impacts. Anthropogenic mortality may also have a direct influence on leopard in more impacted areas, but further research is required to investigate this. Our findings show that a hunting area with significant protection investment supports a leopard density comparable to similar habitat in a photographic tourism area. We also provide evidence that community-managed areas have the potential to effectively conserve large carnivore populations at relatively high densities, but may be vulnerable to edge effects.

5.1. Introduction

Despite being considered the least threatened subspecies of leopard (*Panthera pardus*; Stein et al., 2020), the African leopard (*Panthera pardus pardus*) has nonetheless lost up to two thirds of its historical range (48-67%; Jacobson et al., 2016). The primary drivers of this decline include the loss and fragmentation of natural habitat (Brink & Eva, 2009) and the decline of many prey species (Craigie et al., 2010). These pressures also increasingly force leopard to use areas occupied by people, which can exacerbate human-leopard conflict, another major threat to the species' survival in Africa (Swanepoel et al., 2015). Although reliable data on trends in leopard status are sorely lacking for sub-Saharan Africa, these combined threats are likely to have caused population declines of at least 30% over the last three generations (Stein et al., 2020).

Nevertheless, the leopard's reputation as one of the most resilient and adaptable African large carnivores has contributed to a relative lack of research and conservation urgency for the species (Balme et al., 2014; Jacobson et al., 2016; Stein et al., 2020). Leopard research to date in Africa has largely been concentrated in areas of lower conservation concern, such as highly protected areas reserved for non-consumptive use, and many efforts have failed to contribute meaningfully to conservation outcomes (Balme et al., 2014). As a result, the status and population trends of leopard across much of its remaining African range is unknown (Jacobson et al., 2016). This lack of empirical population assessments may be contributing to unseen losses for Africa's remaining leopard populations, particularly outside core protected areas (Durant et al., 2016).

Meaningful assessments of a species' status often involve the estimation of population densities or abundances, and are a key requirement to monitor population trends, assess habitat requirements, and select and evaluate appropriate management and conservation strategies (Boitani & Powell, 2012). In particular, estimates of population density allow for comparisons between sites and can be used as a tool to monitor population trends. Spatially explicit capture-recapture (SECR) analysis using camera trap data is a well-established method for estimating population density for marked species (Rovero &

Zimmermann, 2016), and is one of the most widely-used and robust methods to assess the status of leopard populations (Jacobson et al., 2016).

Information on leopards in Tanzania is "particularly poor" (Packer, Lichtenfeld, et al., 2009), despite the country being thought to contain approximately 10% of extant African leopard range (Stein et al., 2020). Although several camera trap surveys have been carried out in Tanzania as part of the Tanzania Mammal Atlas Project (Lobora et al., 2008), only three sets of leopard population density estimates have been published for the country, with only two of these employing comparatively statistically-robust methods (Allen et al., 2020; Crosmary et al., 2018; Havmøller et al., 2019).

Tanzania has the largest proportion of land under formal protection of any African country (approximately 48.2%; Riggio et al., 2019), but only around a third of the country's PAs are designated as National Parks (NPs) or Conservation Areas, where photographic tourism is the only permitted revenue-generating activity (Riggio et al., 2019). In contrast, around two thirds of Tanzania's PAs are set aside for trophy hunting, with other forms of extractive use permitted alongside this in all except the most strictly-protected hunting areas, Game Reserves (GRs). However, as a result of a lack of population estimates, trophy hunting quotas for leopard in the country are currently largely based on unpublished status assessments (MNRT, 2018). Although trophy hunting has been shown to have the potential to foster conservation of wildlife, particularly large carnivores, with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007), it can have strong detrimental impacts on large carnivore populations if carried out unsustainably (Lindsey et al., 2013; Naude et al., 2020; Packer, Kosmala, et al., 2009). Thus, there is a pressing need to assess hunted leopard populations to ensure that quotas are sustainable (Packer et al., 2010; MNRT, 2018).

In addition, the status of many of the country's hunting areas has been in flux in recent years: while six GRs have been upgraded to NP status since 2018 (including two thirds of Selous GR being upgraded to create Nyerere NP, the largest National Park in East Africa; Kimboy, 2019), a number of lesser-protected areas have been degazetted during this same period (Kideghesho, 2019). Revenue from trophy hunting has also declined in recent years, and there is uncertainty over the long-term economic

sustainability of this industry in sub-Saharan Africa (Lindsey et al., 2014). Information on leopard population density is therefore also required to provide insights into the potential impacts these changes may have on the country's leopard populations, and feed into PA prioritisation exercises.

Finally, in recent years, a growing proportion of the country has been gazetted for community-management as Wildlife Management Areas (WMAs), with 38 existing and planned WMAs set to cover 7% of the country (Keane, 2015). Based on the principles of community-based natural resource management (CBNRM), WMAs are formed from parcels of land set aside for conservation by member villages, and are designed to empower local communities by giving them greater authority over the management of natural resources (WWF, 2014). Communities benefit from participation in WMAs by receiving a share of revenues generated by any wildlife-based enterprises established on the land (normally photographic or trophy hunting tourism; WWF, 2014). However, despite their promise as a means of promoting both long-term protection of wildlife and rural economic development (WWF, 2014), few studies have set out to scientifically assess how effective the WMA initiative has been in meeting its conservation goals (but see Lee, 2018; Lee & Bond, 2018; Kiffner et al., 2020), with a particular research gap across southern Tanzania.

Against this changing conservation landscape, and given Tanzania's potential importance as a stronghold for leopard in sub-Saharan Africa, there is a pressing need to understand the status of the country's leopard populations within the different forms of land use, management strategies, and habitats that make up its PA network. To contribute research to this knowledge gap, we carried out SECR modelling of camera trap data at four sites in the Ruaha-Rungwa landscape in southern Tanzania, including two within different habitats in a National Park, one within an actively-hunted Game Reserve, and one in a community-managed WMA. We expected leopard density to be highest in the National Park and lower in the community-managed area, despite its comparable habitat, as a result of edge effects (Abade et al., 2018; Balme et al., 2010). We expected lower densities in the miombo woodland sites within the National Park and trophy hunting area due to lower habitat productivity (Frost, 1996), possibly with lower densities in the hunting area as a result of hunting offtake (Packer et al., 2010).

Together, our findings provide the first comparison of leopard status across different habitats and land management strategies within a mixed-use landscape in Tanzania, and have important implications for conservation management.

5.2. Methods

5.2.1. Study area

The study area is situated within the Ruaha-Rungwa landscape, a ~45,000 km^2 mixed-use PA complex in southern Tanzania (Fig. 5.1), which is recognised by the EU as a Key Landscape for Conservation due to its internationally important wildlife populations (European Commission, 2016).

Ruaha-Rungwa encompasses a spectrum of land management strategies. At its heart lies Ruaha NP, the second largest NP in East Africa at over 20,000 km^2, where only photographic tourism is permitted. To the north of the NP are Rungwa, Kizigo, and Muhesi Game Reserves, where trophy hunting is permitted. Neighbouring the park to its east over the Great Ruaha River are two community-managed WMAs, the Idodi-Pawaga MBOMIPA WMA and Waga WMA, which act as a buffer between Ruaha NP and the surrounding unprotected village lands. Although both photographic tourism and trophy hunting are permitted in these WMAs, neither activity was taking place at the time of study. A number of other, less-strictly protected areas are also present in the wider landscape. As the PAs in the landscape are unfenced, wildlife often move between these areas and neighbouring non-PAs.

Climate in Ruaha-Rungwa is arid to semi-arid, with average annual rainfall of 600 mm (Fick & Hijmans, 2017), the majority of which falls during a single wet season from December to April (Mtahiko et al., 2006). Vegetation cover in the landscape is a mosaic of Southern *Acacia-Commiphora* bushlands and Central Zambezian miombo (*Brachystegia-Jubelnardia*) woodlands, riverine forests, and flood-plain grasslands.

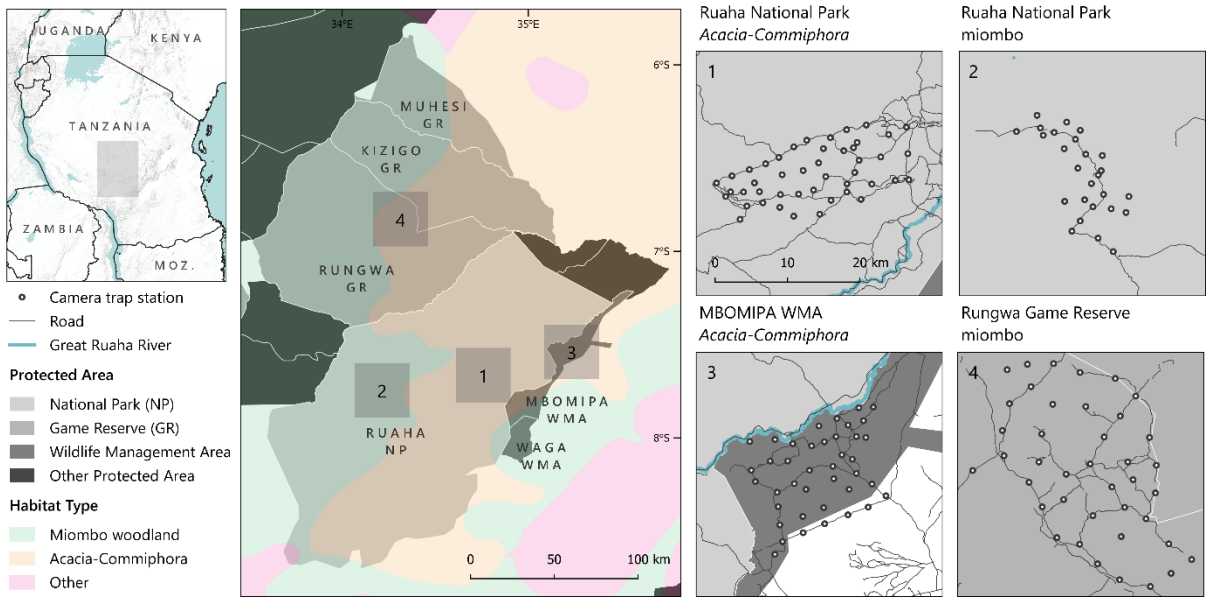


Figure 5.1: Top left: Location of the Ruaha-Rungwa landscape within Tanzania. Centre: the different land use types in place in the study landscape and the location of camera trap survey areas. Right: detail of camera trap grids in (1) Ruaha NP *Acacia-Commiphora* habitat, (2) Ruaha NP miombo woodland habitat, (3) the community-managed MBOMIPA WMA (*Acacia-Commiphora* habitat), and (4) Rungwa GR (a trophy hunting area; miombo woodland habitat). Hunting is permitted in Game Reserves and Wildlife Management Areas, but was only carried out in Game Reserves at the time of the study. Note that the survey site in Rungwa GR is dominated by miombo woodland, but lies at the transition zone with *Acacia-Commiphora* habitat; this is not accurately reflected in the figure due to minor discrepancies in the habitats shapefile.

5.2.2. Camera trap surveys

We estimated population density using data from camera trap surveys at four sites in the Ruaha-Rungwa landscape, each representing a different habitat and management strategy (Fig. 5.1):

- The strongly-protected and highly productive core tourist area of Ruaha NP, which is dominated by *Acacia-Commiphora* bushland and open grassland habitat. This site is located near the Great Ruaha River, which exhibits very high herbivore densities as one of the few dry season water sources in the landscape (TAWIRI, 2019).
- The miombo woodland in western Ruaha NP, which receives less on-the-ground protection than the core tourist area of the NP due to its remoteness and lower tourist traffic.

- The community-managed MBOMIPA WMA, a less-strongly protected area of *Acacia-Commiphora* habitat, located in a highly productive area near the Great Ruaha River but directly adjacent to unprotected village land. This area received a relatively high level of foot patrols in 2018 after several years of absence of law enforcement effort (STEP, 2019).
- The Ikiri hunting block of Rungwa GR, an area under strong protection where trophy hunting is permitted and was taking place at the time of data collection. The survey site is dominated by miombo woodland.

Camera set up

We conducted surveys during the dry seasons of 2018 and 2019, using various models of motion-activated camera (Cuddeback Professional Color Model 1347 & X-Change Color Model 1279, Non Typical Inc., Wisconsin, USA; HC500 HyperFire, Reconyx, Wisconsin, USA). The majority of cameras used xenon white flash, to improve the clarity of markings in photos for individual identification. All but one station used paired cameras to maximise the probability of photographing both flanks of animals passing through the station. Cameras were mounted in protective cases and secured with binding wire to prevent damage and loss to both animals and humans. In particularly high-risk areas, cases were further secured with padlocks and camouflaged to reduce the risk of theft.

Survey design

We spaced camera stations according to the smallest hypothesised female home range size, to ensure that all individuals in each survey area had a non-zero probability of capture (Noss et al., 2013; Rovero & Zimmermann, 2016). As we did not have *a priori* information on leopard home range sizes in the study area, we set camera spacing conservatively based on female home range data from similar ecosystems elsewhere in Africa (e.g. 25 km^2 in nearby Piti GR, Tanzania; Caso, 2002). At the same time, we sought to ensure the total area covered by each survey grid exceeded hypothesised average male home range (e.g. 136 km^2 in Piti GR; Caso, 2002), as this is recommended for robust density estimation (Noss et al., 2013; Tobler & Powell, 2013). Average spacing between stations varied between sites due to logistical factors.

We set stations along roads whenever possible, prioritising junctions, to maximise captures of large carnivores, and off-road stations were added along major game trails to avoid gaps in the grid. Cameras were mounted on trees along roads and game trails at a height of 30-40 cm, and checked every 1-4 weeks. Each grid was surveyed for 2-3 months, to ensure sufficient captures without violating the assumption of population closure (Tobler & Powell, 2013).

Survey grids

Forty-five stations (all but one paired; 89 cameras) were deployed over an area of 223 km^2 (average spacing 1.96 km) in the core tourist area of Ruaha NP, for 83 days between June and September 2018.

Twenty-six stations (all paired; 52 cameras) were deployed in the miombo woodland of Ruaha NP, covering an area of 152 km^2 (average spacing 1.88 km), for 90 days between August and November 2018.

Forty stations (all paired; 80 cameras) were deployed across 270 km^2 (average spacing 2.08 km) in MBOMIPA WMA, for 70 days between September and November 2018.

Forty stations (all paired; 80 cameras) were deployed over an area of 555 km^2 (average spacing 3.46 km) in the Ikiri block of Rungwa GR, for 90 days between July and October 2019.

Detailed summary information for the four survey grids can be found in Table 5.1.

5.2.3. Density estimation

We estimated population density of leopard (defined as the number of adult individuals per 100 km^2) at each site via maximum likelihood SECR analysis (Efford, 2011), using package *secr* version 3.2.1 (Efford, 2019a) in R version 3.6.2 (R Core Team, 2017) and RStudio version 1.2.5033 (RStudio Team, 2020).

Following data collection, individual leopards were identified from camera trap photos via visual inspection of their unique pelage patterns and sexed based on visible external genitalia (Tobler & Powell, 2013), with IDs verified by a second observer; photos in which individuals could not be

confidently identified were excluded from analysis. Data inputs for each grid consisted of a capture history detailing the location and sampling occasion of captures for each individual, using the flank with the greatest number of captures for each grid, and the trap layout, containing information on the location and activity of each camera station. Sampling occasions were defined as a 24 hour period running from midday to midday, as recommended for nocturnal species (Rovero & Zimmermann, 2016). See S5.1 for additional details on the SECR modelling process.

5.2.4. Model selection

We included station location (on- or off-road) as a covariate hypothesised to influence capture probability (g0), to account for the fact that capture probabilities are likely to be higher at stations located on roads (which are often used preferentially by large carnivores; McKenzie et al., 2012) than on trails. We included sex as a covariate hypothesised to influence both capture probability (g0) and the movement parameter (σ), as large felids are known to exhibit sex-specific traits in their ranging behaviours (Tobler & Powell, 2013). Sex was modelled as a covariate by fitting a hybrid mixture model, which allows the inclusion of individuals of unknown sex by applying a random effect to individuals in this category (Efford, 2019b).

We fitted eight models to estimate population density and test the influence of camera location and sex on model parameters (see S5.2). Models were ranked based on their Akaike Information Criterion score, corrected for small sample size (AICc). Where more than one model had substantial empirical support (ΔAICc < 2; Burnham & Anderson, 2004), we used model averaging to determine the final population density and parameter estimates for that grid. The width of the buffer around each trapping grid was increased until density estimates stabilised, to ensure that individuals whose home range centre was located outside the buffer had a negligible chance of being detected (Efford, 2020).

5.2.5. Precision of estimates

To assess the precision of our population density estimates, we calculated the half relative confidence interval width (HRCIW) for each grid, using the equation: $HRCIW = \frac{0.5 \times (UCL - LCL)}{Density} \times 100$, where

UCL and LCL are the upper and lower 95% confidence limits of the density estimate for that grid, respectively (Dröge et al., 2020). HRCIW provides a measure of the magnitude of population change that an estimate has a reasonable probability of detecting.

5.2.6. Prey relative abundance

We calculated the relative abundance index (RAI) of leopard prey species from the camera trap data from each survey, to provide a measure of prey availability in each study site. We classified 13 mammal species as prey based on known dietary preferences of leopard (Hayward et al., 2006; full details can be found in S5.3). We calculated RAI for each species by multiplying the number of capture events for that species in each grid by 100, and dividing this by the number of trap nights for that grid (Rovero & Zimmermann, 2016). Capture events were defined as captures taking place more than 30 minutes after the previous capture of that species at the same station. We then summed the RAI of each prey species for each survey, to produce a measure of overall prey relative abundance across the different study sites. As we were unable to directly test the effect of prey RAI on leopard density (as this would require RAI values to be extrapolated beyond our station locations; Efford, 2020), we carried out a correlation test between the leopard density estimates and prey RAI for each survey site.

5.3. Results

5.3.1. Survey effort

Across the four study sites, a total sampling effort of 11,668 camera trap nights across 151 stations yielded 925 images of leopard, 95.2% of which were suitable for individual identification (Table 5.1). Counting only the flank with the greatest number of captures for each grid resulted in a total of 362 unique capture events, from which 90 individuals were identified. 73.0% of identified individuals were recaptured at more than one station in the Ruaha NP *Acacia-Commiphora* grid, versus 66.7% in the Ruaha NP miombo grid, 50.0% in the MBOMIPA WMA grid, and 26.3% in the Rungwa GR grid.

Sex was confidently assigned to 83.8% of individuals identified in the Ruaha NP *Acacia-Commiphora* grid (15 female, 16 male, 6 unknown), 83.3% of individuals in the Ruaha NP miombo grid (7 female,

3 male, 2 unknown), 77.3% of individuals in the MBOMIPA WMA grid (8 female, 9 male, 5 unknown), and only 47.4% of individuals in the Rungwa GR grid (4 female, 5 male, 10 unknown). The lower rates of recapture and sex identification in the Rungwa GR grid were likely a result of wider spacing between stations in this survey. None of the identified individuals were captured across more than one survey site.

5.3.2. Population density

We estimated density based on left flank captures for the Ruaha NP *Acacia-Commiphora*, MBOMIPA WMA, and Rungwa GR grids, and from right flank captures for the Ruaha NP miombo grid. Buffer width stabilised at 12 km for the Ruaha NP *Acacia-Commiphora* grid, 14 km for the MBOMIPA WMA grid, 16 km for the Rungwa GR grid, and 30 km for the Ruaha NP miombo grid.

The top-ranked model of population density was secr.road.sex.s (g0 varies with station location; σ varies with sex) for the Ruaha NP *Acacia-Commiphora* grid, and secr.sex.s (σ varies with sex) for the Ruaha NP miombo grid, in each case being the only model with substantial support. For both MBOMIPA WMA and Rungwa GR grids, there were two models of density with substantial support (ΔAICc < 2): secr.road.sex.s and secr.sex.s in MBOMIPA WMA, and secr.0 (null model) and secr.sex.s in Rungwa GR. Results of model ranking for all sites can be found in S5.2. Sex therefore had a significant impact on leopard movement across all four sites, with males moving greater distances than females, while capture probabilities were higher at stations on roads than those on trails in the two *Acacia-Commiphora* sites.

We estimated the highest population density in the Ruaha NP *Acacia-Commiphora* grid, at 6.81 ± 1.24 leopards per 100 km^2. The next highest density of 4.23 ± 1.02 individuals per 100 km^2 was estimated for the *Acacia-Commiphora* MBOMIPA WMA grid, followed by 3.36 ± 1.09 per 100 km^2 in the miombo-dominated Ikiri block of Rungwa GR, and 3.23 ± 1.25 per 100 km^2 in the miombo of Ruaha NP (Table 5.2; Fig. 5.2).

A HRCIW of 50% or lower indicates that a density estimate has a reasonable probability of detecting a critical population decline of 50%, thus meeting the IUCN A2 criterion to classify a leopard population as *Endangered* if that decline takes place within 10 years or 3 generations (whichever is longer; IUCN, 2019; Dröge et al., 2020). The density estimates from the Ruaha NP *Acacia-Commiphora* grid (HRCIW = 36.1%) and MBOMIPA WMA (48.3%) were sufficiently precise to fall below this threshold, but the estimates from miombo woodland in Rungwa GR (65.6%) and Ruaha NP (80.2%) were not (Table 5.2).

5.3.3. Prey relative abundance

We estimated an overall prey RAI of 104.8 in the Ruaha NP *Acacia-Commiphora* grid, 73.7 in the *Acacia-Commiphora* MBOMIPA WMA grid, 43.5 in the miombo woodland of Rungwa GR, and 41.2 in the Ruaha NP miombo woodland grid (Table 5.1). RAI and capture information for individual prey species can be found in S5.3. A Pearson's product-moment correlation test between the leopard density estimates and prey RAI showed that these values are highly positively correlated across our four sites ($r(2) = .97$, $p = .031$). We do, however, acknowledge the limitations of this test, as it is based on a very small number of data points, and does not incorporate information on the error in our density estimates.

Table 5.1: Summary information for the four survey grids in Ruaha-Rungwa.

	Ruaha NP *Acacia-Commiphora*	**Ruaha NP** miombo woodland	**MBOMIPA WMA** *Acacia-Commiphora*	**Rungwa GR** miombo woodland
Study site details				
PA name	Ruaha	Ruaha	MBOMIPA	Rungwa
PA designation	National Park	National Park	WMA	Game Reserve
Management authority	TANAPA[1]	TANAPA[1]	Member villages[2]	TAWA[3]
Trophy hunting permitted	No	No	Yes	Yes
Trophy hunting carried out at the time of study	No	No	No	Yes
Camera trap survey details				
Survey period	19 Jun - 10 Sep 2018	5 Aug - 3 Nov 2018	19 Sep - 28 Nov 2018	3 Jul - 12 Oct 2019
Survey duration (nights)	83	90	70	90
Stations	45	26	40	40
Trap nights	3,601	2,187	2,689	3,395
Average spacing	1.96 km	1.88 km	2.08 km	3.46 km
Survey area[4]	223 km^2	152 km^2	270 km^2	555 km^2
Leopard capture details				
Buffer width	12 km	30 km	14 km	16 km
Flank with most captures	Left	Right	Left	Left
Individuals recorded[5]	37	12	22	19
Female	15	7	8	4
Male	16	3	9	5
Sex unknown	6	2	5	10
Capture events[5]	201	44	85	32
Recapture rate[5,6]	73.0%	66.7%	50.0%	26.3%
Summed prey relative abundance index (RAI)	104.8	41.2	73.7	43.5

[1] Tanzania National Parks Authority

[2] The WMA is managed by an elected board called the "Authorised Association", comprised of representatives from the 21 member villages located in the Idodi and Pawaga administrative wards of Iringa Rural District

[3] Tanzania Wildlife Management Authority

[4] Area of the minimum convex polygon around all stations (does not include buffer)

[5] Based on the flank with most captures for each grid

[6] Percentage of identified individuals recaptured at more than one station during the survey period

Table 5.2: Leopard population density and parameter estimates for the four survey sites. Estimates taken from models with substantial empirical support (ΔAICc < 2); where more than one model had substantial support, model averaging was used to obtain averaged estimates.

Parameter	Estimate	Ruaha NP[1] *Acacia-Commiphora*	Ruaha NP[2] miombo	MBOMIPA WMA[3] *Acacia-Commiphora*	Rungwa GR[4] miombo
$g0$[5]	Mean ± SE		0.015 ± 0.006		0.007 ± 0.003
	95% CI		0.007 – 0.033		0.003 – 0.015
$g0_{on\text{-}road}$[5]	Mean ± SE	0.035 ± 0.004		0.022 ± 0.004	
	95% CI	0.028 – 0.044		0.015 – 0.032	
$g0_{off\text{-}road}$[5]	Mean ± SE	0.003 ± 0.002		0.013 ± 0.005	
	95% CI	0.001 – 0.011		0.006 – 0.029	
σ_{female}[6]	Mean ± SE	1532 ± 109	1964 ± 377	1865 ± 190	2321 ± 594
	95% CI	1333 – 1761	1352 – 2852	1529 – 2276	1416 – 3804
σ_{male}[6]	Mean ± SE	3211 ± 215	12964 ± 3663	3521 ± 482	2868 ± 537
	95% CI	2816 – 3661	7530 – 22318	2696 – 4599	1992 – 4128
Density[7]	Mean ± SE	**6.81 ± 1.24**	**3.23 ± 1.25**	**4.23 ± 1.02**	**3.36 ± 1.09**
	95% CI	4.78 – 9.70	1.55 – 6.73	2.65 – 6.74	1.82 – 6.23
HRCIW (%)[8]		36.1	80.2	48.3	65.6

[1] Parameter estimates from only model with strong support (ΔAICc < 2); secr.road.sex.s

[2] Parameter estimates from only model with strong support; secr.sex.s

[3] Averaged parameter estimates from models with strong support; secr.road.sex.s and secr.sex.s

[4] Averaged parameter estimates from models with strong support; secr.0 and secr.sex.s

[5] g0 = capture probability at home range centre

[6] σ = distance parameter related to home range size

[7] Population density defined as the number of individuals per 100 km^2

[8] HRCIW = half relative confidence interval width; a measure of the magnitude of population change that could be confidently detected

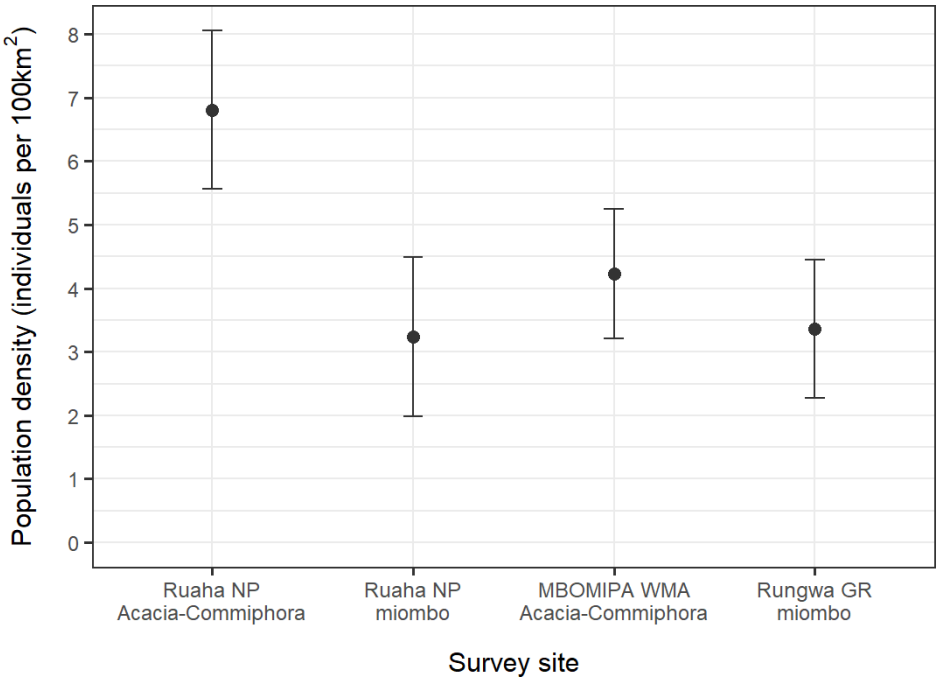


Figure 5.2: Leopard population density estimates for the four survey sites, with error bars showing the standard error (SE) for each estimate.

5.4. Discussion

This study provides evidence of a globally-important leopard population in the Ruaha-Rungwa landscape of southern Tanzania. In line with our expectations, we estimated a high population density for leopard in the riverine core tourist area of Ruaha NP, a slightly lower density in the neighbouring MBOMIPA WMA, and lowest densities in the miombo woodlands of Rungwa GR and Ruaha NP. These are some of the first such estimates for the country (but see Allen et al., 2020; Havmøller et al., 2019), including one of the first robust estimates of leopard population density in a trophy hunting area in Tanzania. This study also provides some of the first insights into leopard ecology in a miombo woodland habitat (but see Davis et al., 2020; Jorge, 2012), which represent an important component of the species' range in Africa (~18% of extant range; Olson et al., 2001; Stein et al., 2020).

The density estimates for the core tourist area of Ruaha NP and MBOMIPA WMA are sufficiently precise to detect a critical population decline per IUCN guidelines, suggesting that future surveys at the same sites could provide valuable information on population dynamics through open capture-recapture

analysis (Karanth et al., 2006). In contrast, neither density estimate from the miombo woodland sites met this threshold, indicating that caution should be exercised when using these estimates as a baseline for population monitoring. However, future surveys at the same sites could nonetheless provide valuable information on mortality by allowing the comparison of individuals captured across years.

Our estimates of leopard population density are comparable to densities estimated using SECR methods elsewhere in Africa, which range from 0.76 leopards per 100 km^2 in South Africa's Little Karoo (Mann, 2014) to 14.51 per 100 km^2 in Namibia's fenced Okonjima Nature Reserve (Noack et al., 2019). Looking specifically to Tanzania, our estimates are consistent with the range of leopard densities estimated using comparable methods in the Udzungwa Mountains (2-8 per 100 km^2; Havmøller et al., 2019), while our estimate for the core tourist area of Ruaha NP is higher than the dry season density estimated in the similarly highly-protected Serengeti NP (5.41 per 100 km^2; Allen et al., 2020). The densities we estimated in miombo woodland are comparable to densities estimated in the Eastern miombo woodland of Niassa National Reserve, Mozambique (2.18-4.31 per 100 km^2; Jorge, 2012), and are higher than the mean density estimated in the human-impacted Central Zambezian miombo woodland of Kasungu NP, Malawi (1.9 per 100 km^2; Davis et al., 2020).

5.4.1. Possible drivers of variation in density

Although it was not possible to formally test for the effect of prey on leopard density, the strong correlation between prey availability and leopard density estimates across our four study sites suggests that prey may be a key driver of variation in leopard density within the study landscape. This aligns with studies elsewhere in Africa that have found prey abundance to be an important predictor of leopard population density (Boast & Houser, 2012; Marker & Dickman, 2005; Rosenblatt et al., 2016; Stein et al., 2011).

The high population density estimated in the *Acacia-Commiphora* core tourist area of Ruaha NP, which also had the highest leopard prey RAI of our study sites, is likely to be a result of this area's strong protection and location near the highly-productive Great Ruaha River, which supports the highest dry season ungulate biomass across the landscape (TAWIRI, 2019).

Despite having similar highly-productive habitat to the core tourist area of Ruaha NP, we found the community-managed MBOMIPA WMA to support a lower density of leopard in the area surveyed. This may be linked to the lower abundance of prey in this site, as indicated by our RAI estimates. The lower availability of prey in this area may itself be a result of edge effects acting on prey populations (Balme et al., 2010): habitat is highly degraded in unprotected lands beyond the WMA's south-eastern boundary (Abade et al., 2018), and prey species in this area are likely to face higher levels of anthropogenic impact than those in our other study sites. Evidence for this is provided by the fact that nine illegal incursions (two picturing captured bushmeat) were photographed in the community-managed area during the survey period, versus two in Rungwa GR, one in the Ruaha NP miombo, and none in the core tourist area of Ruaha NP.

In addition to potential edge effects impacting prey populations, there may also be edge effects acting directly on leopard in this part of the landscape. Bushmeat poaching has been shown to directly contribute to leopard mortality when individuals get caught in snares (Swanepoel et al., 2015), including in the study landscape (Ruaha Carnivore Project, unpublished data), and high levels of human-leopard conflict and anthropogenic mortality are reported in the area (Abade et al., 2018; Dickman et al., 2014).

While we were unable to disentangle the relative importance of bottom-up (prey availability) and top-down (anthropogenic mortality) processes in shaping leopard density in this study, future surveys of the same sites would help answer this question by allowing density and survival rates to be compared between MBOMIPA WMA and the core area of Ruaha NP (per Balme et al., 2010; Rosenblatt et al., 2016). Regardless of the exact mechanism by which human encroachment around the community-managed area impacts density, our results are consistent with other studies across Africa which have found negative relationships between leopard population density and human encroachment around PAs (Balme et al., 2010; Havmøller et al., 2019; Henschel et al., 2011; Marker & Dickman, 2005; Rosenblatt et al., 2016).

Whereas the lower recapture rate in Rungwa GR was likely a result of the wider spacing between stations in this grid, the lower recapture rate in MBOMIPA WMA – where stations were spaced more

comparably to the grid in the Ruaha NP *Acacia-Commiphora* habitat – could result from the area supporting a greater proportion of transient individuals, such as dispersing sub-adults, than the core area of Ruaha NP (Braczkowski et al., 2015). If mortality risk is heightened in the area as a result of edge effects, this could indicate that the community-managed area is acting as a population sink.

The lower leopard population density estimated in both miombo woodland sites is probably a result of the lower abundance of prey supported by miombo woodlands, due to naturally low soil productivity of this habitat (Frost, 1996). This is supported by our prey RAI estimates – which were very similar across the two miombo sites, and lower than those in *Acacia-Commiphora* habitat – and mirrors findings from miombo woodlands in northern Mozambique (Jorge, 2012). However, comparisons between density estimates for these sites should be made with caution, given their relatively low precision.

Although population densities of a species may be expected to be lower in areas with particularly high densities of dominant competitors, multiple studies have found no evidence of lion suppressing leopard at a population level (Balme, Pitman, et al., 2017; Miller et al., 2018; Rafiq et al., 2020). In the study landscape, we found population densities of leopard, lion, and spotted hyaena to be highly correlated across our systematic survey sites (leopard-lion: 0.97; leopard-hyaena: 0.94; lion-hyaena: 0.88; see S5.4 and Appendices 3 & 4), suggesting that the abundance of dominant competitors at each site may not have a significant effect on leopard densities. This may be a result of leopard employing fine-scale avoidance mechanisms (see Chapter 6) and adaptive behaviours such as prey-caching (Balme, Miller, et al., 2017; Stein et al., 2015) to minimise antagonistic interactions and facilitate coexistence, in order to secure access to limited shared resources.

5.4.2. Trophy hunting areas and sustainable quotas

Our study provides the first published spatially explicit population density estimate for a trophy-hunted leopard population in Tanzania. Such robust estimates of population densities are particularly important in trophy hunting areas, to form the basis of sustainable hunting quotas (Strampelli et al., 2018). Although wildlife authorities in Tanzania strive to base leopard hunting quotas on robust, empirical

population data, they are currently limited by the lack of information available for the country's leopard populations (TAWIRI, 2009; MNRT, 2018).

At present, leopard quotas in Tanzania are based on a national population estimate extrapolated from average densities of 7.9 per 100 km^2 for NPs and 4.5 per 100 km^2 for GRs, largely derived from unpublished camera trap studies (MNRT, 2018). While Tanzania's Ministry of Natural Resources & Tourism (MNRT) administer block-specific hunting quotas, the lack of density estimates for the majority of Tanzania's hunting areas means that these often cannot be based on information specific to the population of interest. The figures currently employed are higher than our estimated population densities for Ruaha NP and Rungwa GR, respectively, which are each the second largest PA of their type in Tanzania. Although the average estimate used for WMAs is, at 2.3 per 100 km^2, lower than our estimate for MBOMIPA WMA, this figure also applies to GCAs, where human settlement and livestock grazing are unrestricted and leopard densities are therefore likely to be lower. Our density estimate from MBOMIPA WMA was also from the best protected and most productive part of a WMA which forms a boundary along a major river, so is likely to support higher wildlife densities than many other WMAs across the country. As a result, we encourage our estimates to be employed alongside existing population estimates from elsewhere in the country to inform conservation policy.

Although there is evidence of some large carnivore populations existing below carrying capacity in trophy hunting areas (Balme et al., 2009, 2010; Loveridge, Valeix, Chapron, et al., 2016; Packer et al., 2010), our results suggest that the Ikiri block of Rungwa GR supports a leopard population comparable to that in similar habitat in an adjacent photographic tourism area in Ruaha NP. Our findings are likely a result of the substantial management investment received in the Ikiri block over the last four years, particularly in the form of frequent ground and law enforcement patrols, investment in roads and infrastructure, and ranger training support (STEP, 2019). We therefore caution against extrapolating these findings to other areas, and instead encourage additional block-specific surveys, especially in hunting blocks not receiving comparable levels of protection investment or those that border unprotected village land.

5.4.3. Insights into effectiveness of community-management in Tanzania

We provide evidence that MBOMIPA WMA is an important area of habitat for leopard and its prey species in the Ruaha-Rungwa landscape, acting as a buffer zone between Ruaha NP and the surrounding unprotected village lands, where intense human activities and human-induced mortality are a key limiting factor to leopard distribution (Abade et al., 2018). The WMA is particularly important for wildlife in the wider landscape as it lies along the Great Ruaha River, thus protecting one of the few sources of dry season surface water in the landscape. However, this area may be acting as an attractive sink, drawing wildlife from the adjoining area of strong protection and good habitat to an area with higher mortality risk (Loveridge, Valeix, Elliot, et al., 2016). Nevertheless, our results suggest that WMAs have the potential to effectively conserve large carnivore populations at relatively high densities.

Like MBOMIPA, many of Tanzania's WMAs and other forms of lesser-protected areas are positioned along the boundaries of strongly-protected areas (WWF, 2014). As such, these areas not only play an important role on a local scale, insulating highly-protected areas from illegal activities and other anthropogenic impacts, but may also act as stepping-stones linking multiple strongly-protected areas on a national scale. These areas are therefore critical to many of the country's potential wildlife corridors (Riggio & Caro, 2017). However, despite their potential to contribute to conservation goals, the country's WMAs appear to have achieved mixed success in their engagement of local communities (Walsh, 2000), and there is no clear evidence of the initiative contributing to widespread poverty reduction (Keane et al., 2020). Challenges of this kind – which are also faced by similar initiatives elsewhere on the continent – may limit the efficacy of community management as a long-term conservation tool if left unaddressed.

5.4.4. Conservation recommendations

The level of variation in our density estimates illustrates the importance of surveying different components of a landscape, and not extrapolating density estimates from a single study site (Foster & Harmsen, 2012). This is particularly important as there is a general bias in density studies towards

selecting survey sites in areas thought to support higher densities of the target species (Suryawanshi et al., 2019). We therefore recommend that future studies of leopard in Ruaha-Rungwa complement our findings by assessing population status in the landscape's more marginal zones, such as vacant or less-protected hunting blocks, less productive areas, and completely unprotected land, to provide a more complete view of leopard status across the landscape.

Given the apparent importance of prey abundance in shaping leopard population density, our findings support recommendations that securing prey populations should be a priority for the conservation of African leopard populations (Rosenblatt et al., 2016; Searle et al., 2020). Conservation efforts aimed at reducing bushmeat poaching and other human impacts in areas adjacent to unprotected land should not only benefit prey populations, but also help mitigate direct threats to leopard occupying these areas.

We recommend that our results be employed to inform sustainable use management in the Ikiri block of Rungwa GR. We also encourage the research and hunting communities to collaborate on similar monitoring efforts for hunting areas elsewhere in Africa, to equip policymakers with the information required to set sustainable levels of offtake. If carried out sustainably, trophy hunting has the potential to foster conservation of wildlife with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007). We therefore recommend the continued implementation of regulations that have been shown to improve sustainability of trophy hunting and reduce long-term risk of extinction of hunted leopard populations, such as minimum age and size requirements for hunted individuals (Balme et al., 2012; Braczkowski et al., 2015). Given that trophy hunting areas comprise a significant portion of leopard range in Tanzania (MNRT, 2018) and a number of other African range states (Stein et al., 2020), and law enforcement in many hunting areas is funded primarily through hunting revenues (MNRT, 2018), proposals to phase out trophy hunting must be supported with viable alternative financing or forms of land use, so as not to risk undermining resources for the protection of vital habitat for the species (Di Minin et al., 2016; Dickman et al., 2019).

Finally, given the potentially important role of many WMAs in maintaining healthy ecosystems across Tanzania, as well as their potential contributions to local development, we suggest that support for

community-managed areas be considered a national and international conservation priority, with particular efforts made to empower participating communities and secure the initiative's intended development benefits. We also recommend the implementation of long-term wildlife monitoring in WMAs like MBOMIPA, which are adjacent to highly-protected areas, to assess trends in wildlife populations and monitor edge effects. MBOMIPA WMA in particular should be prioritised for additional investment and support, to safeguard its position as a critical buffer for the globally-important wildlife populations of Ruaha-Rungwa.

5.5. Acknowledgements

Fieldwork for this research was carried out under permits 2018-368-NA-2018-107, 2019-96-ER-97-20 and 2019-424-NA-2018-184, granted by the Tanzania Commission for Science and Technology (COSTECH) and Tanzania Wildlife Research Institute (TAWIRI). We would like to thank the Government of Tanzania, TAWIRI, Tanzania National Parks Authority (TANAPA), Tanzania Wildlife Management Authority (TAWA), and Idodi-Pawaga MBOMIPA WMA for their support of this research. We also thank the field staff of the Southern Tanzania Elephant Program (STEP) and Ruaha Carnivore Project (RCP) for their assistance with data collection, and WMA Village Game Scouts, TANAPA Rangers, TAWA Game Scouts, and Tanzania Big Game Safaris for their assistance during fieldwork. Scholarship funding for CS is provided by the University of Oxford NERC Environmental Research DTP. AD was funded by a Recanati-Kaplan Fellowship. Additional funding was provided for this research by grants from National Geographic Society Early Career Grants (EC-348C-18), Cleveland Metroparks Zoo Africa Seed Grants, Chicago Zoological Society Chicago Board of Trade (CBOT) Endangered Species Fund, and Pittsburgh Zoo & PPG Aquarium Conservation & Sustainability Fund.

5.6. Supplementary material

S5.1 Additional details on the SECR modelling process

S5.2 Results of model ranking

S5.3 Preferred prey relative abundance indices (RAI)

S5.4 Ruaha-Rungwa large carnivore population density estimates

S5.1 Additional details on the SECR modelling process

As camera traps do not physically capture animals, we classed stations as proximity detectors, which act independently of one another. Detection probability was modelled using a half-normal detection function, which describes the probability of capture (P) of individual i at trap j as a decreasing function with distance (d) from that individual's home range centre: $Pij = g0 \exp(-dij^2/2\sigma^2)$, where g0 is the capture probability at the home range centre, and σ is a distance parameter related to home range size (Efford, 2004).

In line with previous studies (Royle et al., 2009), we fitted a Bernoulli encounter model; under this model, an individual can only be captured at most once at a single station on any sampling occasion (as multiple visits to a single station on the same night are unlikely to be independent), but can be captured at more than one station within a single sampling occasion. The width of the buffer around each trapping grid was increased until density estimates stabilised, to ensure that individuals whose home range centre was located outside the buffer had a negligible chance of being detected (Efford, 2020).

S5.2 Results of model ranking

Table S5.2.1: Model ranking of leopard density models for the four survey sites in Ruaha-Rungwa, based on AIC corrected for small sample size, AICc. Rows shaded grey indicate models with substantial empirical support (ΔAICc < 2 from the top-ranked model).

Model[1]	nPar	LogLik	AICc	ΔAICc	AICc Wt
Ruaha NP – *Acacia-Commiphora*					
secr.road.sex.s	6	-1135.938	2286.675	0.000	0.8084
secr.road.sex	7	-1135.846	2289.554	2.879	0.1916
secr.sex.s	5	-1150.683	2313.302	26.627	0.0000
secr.sex	6	-1150.639	2316.078	29.403	0.0000
secr.road.sex.g	6	-1155.316	2325.433	38.758	0.0000
secr.road	5	-1160.210	2332.355	45.680	0.0000
secr.sex.g	5	-1171.889	2355.713	69.038	0.0000
secr.0	4	-1176.064	2361.378	74.703	0.0000
Ruaha NP – miombo					
secr.sex.s	5	-284.223	588.446	0.000	0.9574
secr.road.sex.s	6	-283.375	595.551	7.105	0.0274
secr.sex	6	-283.965	596.730	8.284	0.0152
secr.0	4	-293.380	600.475	12.029	0.0000
secr.road	5	-292.787	605.574	17.128	0.0000
secr.sex.g	5	-293.129	606.258	17.812	0.0000
secr.road.sex	7	-283.044	608.088	19.642	0.0000
secr.road.sex.g	6	-292.361	613.522	25.076	0.0000
MBOMIPA WMA – *Acacia-Commiphora*					
secr.road.sex.s	6	-522.214	1062.029	0.000	0.5937
secr.sex.s	5	-524.877	1063.503	1.474	0.2841
secr.road.sex	7	-522.065	1066.129	4.100	0.0764
secr.sex	6	-524.779	1067.157	5.128	0.0457
secr.road	5	-530.902	1075.553	13.524	0.0000
secr.road.sex.g	6	-529.338	1076.276	14.247	0.0000
secr.sex.g	5	-532.613	1078.976	16.947	0.0000
secr.0	4	-534.380	1079.114	17.085	0.0000
Rungwa GR – miombo					
secr.0	4	-218.094	447.046	0.000	0.4176
secr.sex.s	5	-216.491	447.597	0.551	0.3171
secr.sex	6	-215.575	450.150	3.104	0.0885
secr.sex.g	5	-218.094	450.804	3.758	0.0638
secr.road	5	-218.094	450.804	3.758	0.0638
secr.road.sex.s	6	-216.489	451.979	4.933	0.0355
secr.road.sex.g	6	-218.094	455.189	8.143	0.0071
secr.road.sex	7	-215.570	455.323	8.277	0.0067

[1] secr.0 = null model
secr.sex = σ and g0 vary with sex
secr.sex.s = σ varies with sex
secr.sex,g = g0 varies with sex
secr.road = g0 varies with station location (on- or off-road)
secr.road.sex = g0 varies with station location and sex; σ varies with sex
secr.road.sex.s = g0 varies with station location; σ varies with sex
secr.road.sex,g = g0 varies with station location and sex

S5.3 Preferred prey relative abundance indices (RAI)

Relative species abundance is a component of biodiversity, and refers to how common or rare a species is relative to other species in a defined community (O'Brien, 2011). The relative abundance index (RAI) of all leopard preferred prey species was calculated from the 2018 and 2019 CT data to provide a measure of prey availability for each study site. Mammal species were classified as preferred prey based on the preferred prey body size range and known dietary preferences of leopard (Hayward et al., 2006).

RAI was calculated by multiplying the number of capture events for a given species in each grid by 100, and dividing this by the number of trap nights for that grid (Rovero & Zimmermann, 2016). Capture events were defined as captures taking place more than 30 minutes after the previous capture of that species at the same station.

While RAI is limited by its inability to account for imperfect and variable detection (particularly as our camera locations were optimised for captures of carnivores, and were thus not optimised for ungulates; Sollmann et al., 2013), these issues are somewhat mitigated by the fact that we are comparing similar species across grids of similar design.

Table S5.3.1: Relative abundance indices (RAI) for leopard preferred prey species in Ruaha-Rungwa, based on data from the 2018 and 2019 camera trap surveys.

		Relative Abundance Index (RAI)			
Common name	**Latin name**	**Ruaha NP** *Acacia-Commiphora*	**Ruaha NP** miombo	**MBOMIPA WMA** *Acacia-Commiphora*	**Rungwa GR** miombo
African savanna hare	*Lepus victoriae*	1.5	4.8	0.0	0.0
Bushbuck	*Tragelaphus scriptus*	1.7	2.4	1.3	0.1
Bushpig	*Potamochoerus larvatus*	0.0	0.2	0.3	0.1
Common duiker	*Sylvicapra grimmia*	1.8	8.6	7.0	25.1
Common warthog	*Phacochoerus africanus*	8.2	18.8	2.9	8.3
Impala	*Aepyceros melampus*	77.3	0.2	46.8	0.8
Kirk's dik-dik	*Madoqua kirkii*	12.7	0.4	4.8	5.3
Klipspringer	*Oreotragus oreotragus*	0.0	0.0	0.0	0.0
Lesser kudu	*Tragelaphus imberbis*	1.6	0.0	10.4	0.0
Natal red duiker	*Cephalophus natalensis*	0.0	0.0	0.3	0.0
Oribi	*Ourebia ourebi*	0.0	1.7	0.0	2.3
Sharpe's grysbok	*Raphicerus sharpei*	0.0	2.9	0.0	0.3
Southern reedbuck	*Redunca arundinum*	0.0	1.1	0.0	1.2
	Total	104.8	41.2	73.7	43.5

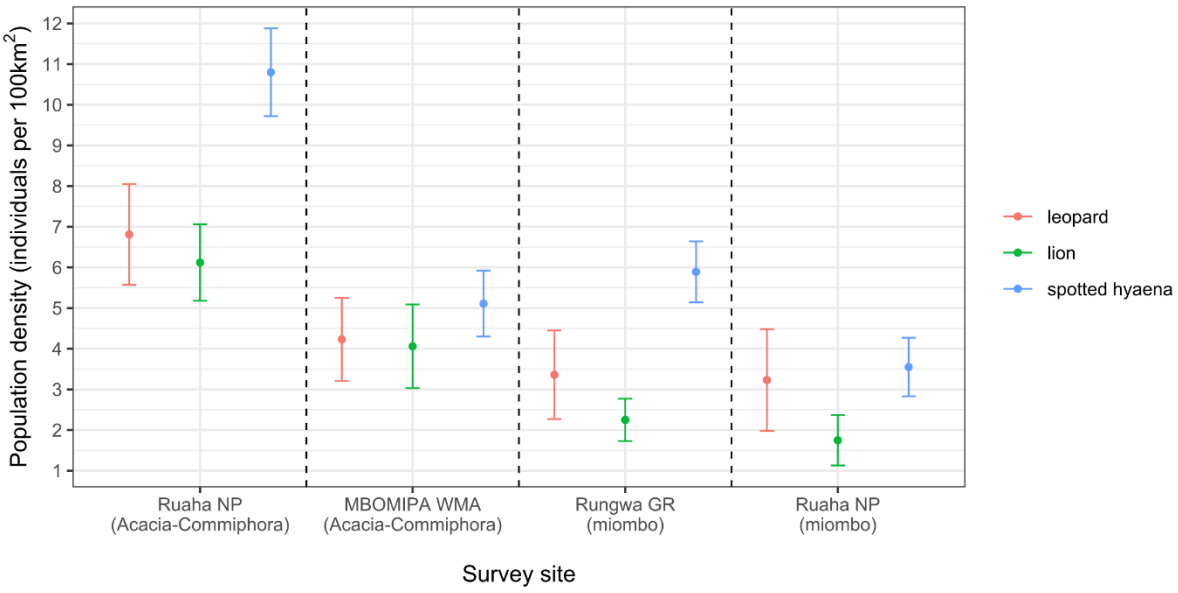
S5.4 Ruaha-Rungwa large carnivore population density estimates

Table S5.4.1: Population density estimates for leopard, lion (see Appendix 3), spotted hyaena (see Appendix 4), and striped hyaena (see Appendix 5). Estimates were produced via spatially explicit capture-recapture (SECR) modelling of data from the systematic camera trap surveys in Ruaha NP, MBOMIPA WMA, and Rungwa GR.

	Population density[1]			
Survey site	**Leopard**	**Lion**	**Spotted hyaena**	**Striped hyaena**
Ruaha NP *Acacia-Commiphora*	6.81 ± 1.24	6.12 ± 0.94	10.8 ± 1.08	N/A
Ruaha NP miombo woodland	3.23 ± 1.25	1.75 ± 0.62	3.55 ± 0.72	N/A
MBOMIPA WMA *Acacia-Commiphora*	4.23 ± 1.02	4.06 ± 1.03	5.11 ± 0.81	1.36 ± 0.50
Rungwa GR miombo woodland	3.36 ± 1.09	2.25 ± 0.52	5.89 ± 0.75	N/A

[1] Individuals per 100 km^2

Figure S5.4.1: Plot of leopard, lion, and spotted hyaena population density estimates across the four survey sites in Ruaha-Rungwa (see Appendices 3 & 4).



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CHAPTER 6

Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape

Title

Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape

Running header

CHAPTER 6: Large carnivore coexistence in a human-impacted landscape

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Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape

Abstract

Africa is home to some of the world's most functionally diverse guilds of large carnivores. However, they are increasingly under threat from anthropogenic pressures that may exacerbate already intense intra-guild competition. Understanding the coexistence mechanisms employed by these species in human-impacted landscapes could help shed light on some of the more subtle ways in which humans may impact wildlife populations, and inform multi-species conservation planning. We used camera trap data from Tanzania's Ruaha-Rungwa landscape to explore temporal and spatiotemporal associations between members of an intact East African large carnivore guild, and determine how these varied across gradients of anthropogenic impact and protection. All large carnivores except African wild dog exhibited predominantly nocturnal road-travel behaviour. Leopard appeared to employ minor temporal avoidance of lion in all sites except those where human impacts were highest, suggesting that leopard may have been freed up from avoidance of lion in areas where the dominant competitor was less abundant, or that the need for leopard to avoid humans outweighed the need to avoid sympatric competitors. Lion appeared to modify their activity patterns to avoid humans in the most impacted areas. We also found evidence of avoidance and attraction among large carnivores: lion and spotted hyaena followed leopard; leopard avoided lion; spotted hyaena followed lion; and lion avoided spotted hyaena. Our findings suggest that large carnivores in Ruaha-Rungwa employ fine-scale partitioning mechanisms to facilitate coexistence with both sympatric species and humans, and that growing human pressures may interfere with these behaviours.

6.1. Introduction

Competitive interactions have important fitness consequences for individuals and populations (Linnell & Strand, 2000), and can trigger cascading impacts across wider ecological systems (Ritchie & Johnson, 2009). Competition can be particularly acute among large carnivores, as they often compete for the same space and resources (Caro & Stoner, 2003) and have an increased likelihood of lethal interactions due to their predatory adaptations (Donadio & Buskirk, 2006). As a result, interspecific competition can have a strong influence on the distribution, density, and habitat use of large carnivore populations, and thus has important implications for their conservation and management (Winterbach et al., 2013).

Intra-guild competition among large carnivores can be indirect, through species needing to access limited shared resources (exploitative competition), or direct, in the form of harassment, kleptoparasitism, or killing (interference competition). Many large carnivores make use of partitioning mechanisms to minimise the negative consequences of this competition (Linnell & Strand, 2000). However, while some species may be able to avoid competitors entirely through spatial segregation, this strategy can bear a high fitness cost by limiting access to vital resources (Swanson et al., 2014). As such, finer-scale avoidance – such as fine-scale spatial avoidance (Vanak et al., 2013), temporal avoidance (Hayward & Slotow, 2009), or dietary partitioning (Hayward & Kerley, 2008) – can be a valuable strategy for subordinate competitors to facilitate coexistence.

Africa is home to the most functionally diverse guild of large carnivores (Dalerum et al., 2009), and its members are therefore exposed to a wide range of potential competitive interactions. Competitive dominance within the African large carnivore guild is primarily determined by body size, with the outcome of individual encounters depending on a number of factors, including group size (Cooper, 1991; Smith et al., 2008). Lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) are the dominant carnivores in most African ecosystems, acting as one another's main competitors for resources (Périquet et al., 2016) and exhibiting top-down pressure on their smaller-bodied competitors. Kleptoparasitism and direct killing by lions have been shown to contribute to high mortality rates (Trinkel & Kastberger, 2005) and population suppression (Watts & Holekamp, 2008) for spotted hyaena. However,

competition between the two species is not asymmetrical, with factors including spotted hyaena clan size (Watts & Holekamp, 2008) and individual behavioural differences (Watts et al., 2010) influencing the outcome of competitive interactions. Lion are known to attack and kill leopard (*Panthera pardus*; Balme et al., 2017), which have been shown to move to denser habitats when in close proximity to lion (du Preez et al., 2015) and actively avoid areas where the probability of encountering the dominant competitor is highest (Balme, Pitman, et al., 2017). However, multiple studies have found no evidence of lion suppressing leopard at a population level (Balme, Pitman, et al., 2017; Miller et al., 2018; Rafiq et al., 2020), and it has been theorised that the species may be forced to share space in more anthropogenically impacted areas (Strampelli et al., 2018). Spotted hyaena also typically dominate over leopard (Hayward, 2006), and there is evidence of temporal partitioning between the two species (Havmøller et al., 2020). Both lion and spotted hyaena are also known to kill, steal food from, and display aggression towards cheetah (*Acinonyx jubatus;* Hunter et al., 2007; Laurenson, 1994) and African wild dog (*Lycaon pictus*; Creel & Creel, 1996; van der Meer et al., 2011). Very little is known about intra-guild interactions of striped hyaena (*Hyaena hyaena*), but it is likely that they share a similar competitive status to brown hyaena (*Parahyaena brunnea*), below spotted hyaena and lion (Mills, 1984).

Regardless of their competitive status, all of Africa's large carnivores are increasingly under threat from habitat fragmentation, conflict with humans, and declining prey populations (Ripple et al., 2014). As a result, members of the African large carnivore guild have been extirpated from large parts of their former range, with range contractions estimated at 94% for lion, 93% for African wild dog, 92% for cheetah, 48-67% for leopard (Jacobson et al., 2016), 27% for brown hyaena, 24% for spotted hyaena, and 15% for striped hyaena (Wolf & Ripple, 2016). In addition to directly impacting survival, anthropogenic pressures are likely to exacerbate already intense intra-guild competition among these species. Habitat fragmentation has been shown to lead to higher levels of spatial overlap among large carnivores (Parsons et al., 2019), limiting options for spatial avoidance. The threat of human-induced mortality can also trigger large carnivores to partition their activities to avoid direct encounters with humans (Oriol-Cotterill et al., 2015), which may interfere with temporal avoidance of competitors. In

addition, declining prey populations may force an increase in dietary overlap among large carnivores (Creel et al., 2018) – which would increase exploitative competition and potential antagonistic interactions – or force subordinates to shift their diet toward livestock (Harihar et al., 2011), which can intensify conflict with humans.

Given the ongoing decline of Africa's large carnivores, there is an urgent need to understand how coexistence mechanisms employed by these species vary across modern, human-shaped landscapes, and how they may be affected by anthropogenic impacts. Such knowledge is key to better understand species responses to these novel landscapes, and help inform multi-species and landscape-scale conservation planning. In this study, we used camera trap data from across Tanzania's Ruaha-Rungwa landscape to explore temporal and spatiotemporal associations between members of an intact East African large carnivore guild, including lion, leopard, spotted hyaena, striped hyaena, African wild dog and cheetah. We used activity overlap analysis to explore temporal partitioning among species across habitats, land use types, and gradients of anthropogenic impact, and temporal spacing analysis to investigate spatiotemporal associations between species with sufficient capture data (lion, leopard, and spotted hyaena). By incorporating data from two habitat types within a National Park, a trophy hunting area (Game Reserve), a community-managed area (Wildlife Management Area), and village land, we explore how intra-guild associations between large carnivores vary across a mixed-use, human-impacted area typical of modern African conservation landscapes.

6.2. Methods

6.2.1. Study area

The Ruaha-Rungwa landscape is a mixed-use landscape of over 45,000 km^2 located in southern Tanzania. The complex is comprised of an unfenced network of protected areas (PAs) and unprotected land, including Ruaha National Park (NP; allocated for non-consumptive tourism); Rungwa, Kizigo, and Muhesi Game Reserves (GRs; consumptive use through trophy hunting tourism); community-managed MBOMIPA and Waga Wildlife Management Areas (WMAs; consumptive and non-consumptive use); and a number of other less-strictly protected areas (Game Controlled Areas and Open

Areas). The landscape is home to a complete East African large carnivore guild (Wolf & Ripple, 2017), including the continent's southernmost population of striped hyaena (Foley et al., 2014).

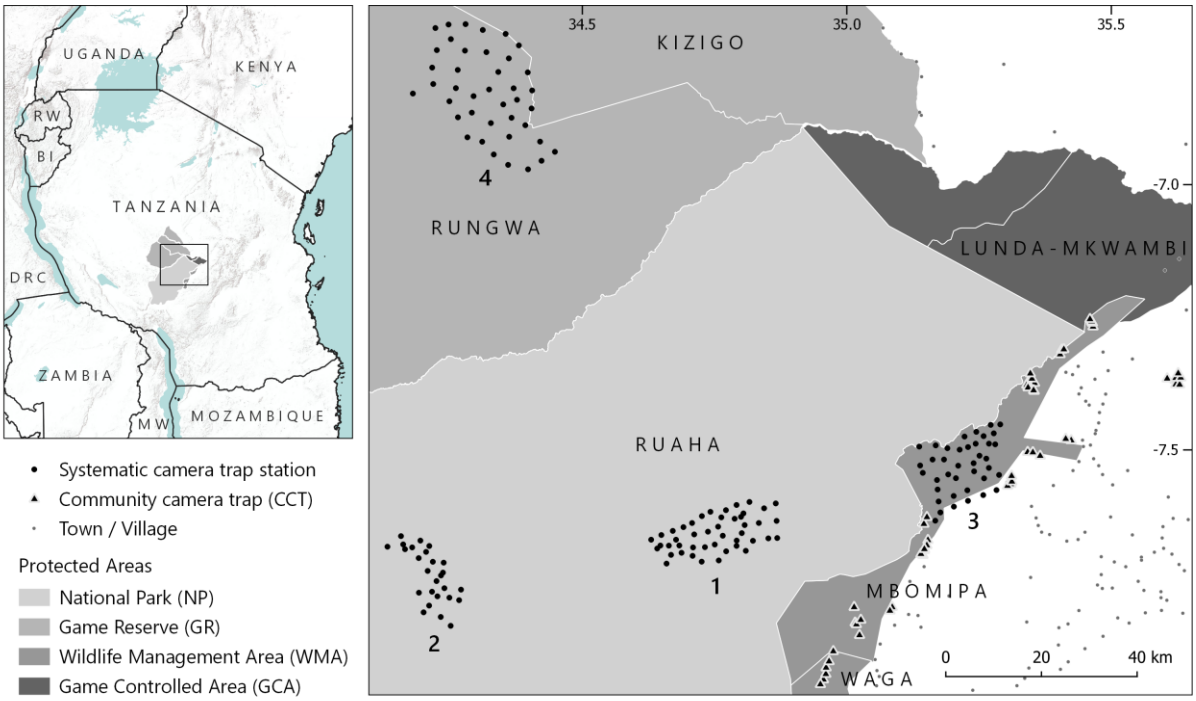


Figure 6.1: Left: the location of the Ruaha-Rungwa landscape within Tanzania. Right: detail of the four systematic camera trap grids, comprising a total of 151 camera pairs, and the 56 unpaired cameras deployed in village land as part of a community camera-trapping (CCT) programme. Systematic camera trap grids were located in (1) Ruaha NP *Acacia-Commiphora* habitat, (2) Ruaha NP miombo habitat, (3) MBOMIPA WMA *Acacia-Commiphora* habitat, and (4) Rungwa GR miombo habitat.

6.2.2. Data collection

Systematic camera trap surveys

We used data from camera trap surveys at four sites in the Ruaha-Rungwa landscape. Systematic camera trap grids were deployed in an *Acacia-Commiphora* site in Ruaha NP (45 stations, average spacing 1.96 km), in the miombo woodland of western Ruaha NP (26 stations, average spacing 1.88 km), and in an *Acacia-Commiphora* site within MBOMIPA WMA (40 stations, average spacing 2.08 km) during the 2018 dry season; and in the miombo woodland-dominated Ikiri block of Rungwa GR (40 stations,

average spacing 3.46 km) in the 2019 dry season (Fig. 6.1; see Chapter 5 and S5.1 for detailed information on the four survey grids).

The systematic surveys used various models of motion-activated camera (Cuddeback Professional Color Model 1347 & X-Change Color Model 1279, Non Typical Inc., Wisconsin, USA; HC500 HyperFire, Reconyx, Wisconsin, USA). The majority of cameras used xenon white flash, to improve the clarity of markings in photos for individual identification. All but one station used paired cameras, to maximise the probability of photographing both flanks of animals passing through the station. Cameras were mounted in protective cases and secured with binding wire to prevent damage and loss to both animals and humans.

We set stations along roads or major game trails, prioritising junctions, to maximise captures of large carnivores. Cameras were mounted on trees at a height of 30-40 cm, and deployed for a total of 2-3 months (see S5.1).

Of the four systematic survey sites, the site in MBOMIPA WMA was the most anthropogenically impacted. Although the area was receiving a relatively high level of anti-poaching patrols at the time of data collection, after several years of absence of law enforcement effort (STEP, 2019), it was nevertheless the site most strongly affected by illegal human impacts (including poaching, charcoal production, and livestock encroachment), as a result of its location directly adjacent to unprotected land and the lack of tourism activities taking place in the WMA at the time of study.

Community camera traps

Data from village land were obtained from 56 camera traps deployed non-systematically as part of the Ruaha Carnivore Project's community camera-trapping programme (Ruaha Carnivore Project, 2019). To facilitate comparisons with the systematic camera trap grids, the data employed were restricted to the 2018 and 2019 dry seasons (June to November inclusive; Fig. 6.1). See S6.1 for detailed information on the location and activity of community camera traps.

Community camera traps were deployed on land belonging to 16 villages within the Iringa region. Cameras were placed opportunistically to maximise captures of large carnivores and other wildlife, mostly along trails or water points, and were comprised of both xenon and infrared flash cameras (Cuddeback Professional Color Model 1347, Non Typical Inc., Wisconsin, USA; HC500 HyperFire, Reconyx, Wisconsin, USA; Scout Guard, HCO Outdoor Products, Georgia, USA).

As sunrise and sunset times do not vary significantly during the dry season in the study area, we did not standardise observations to account for this variation (Vazquez et al., 2019).

6.2.3. Analyses

We used camera trap data to investigate activity patterns (defined as the active period) of the six large carnivore species found in Ruaha-Rungwa: leopard, lion, spotted hyaena, striped hyaena, African wild dog, and cheetah. We assessed activity pattern overlap between these species to identify potential temporal partitioning mechanisms (Meredith & Ridout, 2020b; Ridout & Linkie, 2009), and investigated temporal spacing between detections of different species at stations where they co-occurred, to shed light on spatiotemporal avoidance and attraction among large carnivores in the landscape (Cusack et al., 2017).

As our camera traps were placed predominantly along roads and major trails, it is important to note that the activity we discuss in this study relates specifically to the times at which the study species travel along these habitat features.

Activity overlap

We determined activity patterns for each species, and estimated the coefficient of overlap (Δ) between each large carnivore species pair at each of our five sites and between different sites for the same species, using the package *overlap* (Meredith & Ridout, 2020b) in R version 3.6.2 (R Core Team, 2017) and RStudio version 1.3.959 (RStudio Team, 2020). All community camera traps in village land were grouped and treated as a single site for this analysis.

To avoid pseudoreplication, captures recorded within 30 minutes of the previous capture of the same species at the same station were excluded from analysis, with the earliest capture retained, unless the animals captured could be confidently distinguished as different individuals (Linkie & Ridout, 2011). Individuals were identified based on unique coat patterns (see Chapter 5 and Appendix 4), and other distinguishing features, such as manes, scars, and whisker spots (see Appendix 3). Where possible, sex was assigned to photographed lion and leopard so that differences in activity patterns of males and females could be investigated for these species.

The overlap estimator for each species pair was selected based on the sample size of the species with the fewest captures at that grid, as recommended based on simulations (Meredith & Ridout, 2020a; Ridout & Linkie, 2009): the Δ_1 estimator was used if the species with the smallest number of captures at that site had fewer than 75 observations; otherwise, the Δ_4 estimator was used (Table 6.1).

We estimated confidence intervals for each coefficient of overlap via smoothed bootstrapping with 10,000 resamples (Meredith & Ridout, 2020a). Confidence intervals with an upper limit > 1 were corrected on a logistic scale and back-transformed.

We used the function compareCkern in package *activity* (Rowcliffe, 2019) to test whether activity patterns were significantly different for the same species across different sites; for different species at the same site; and between males and females of the same species at the same site (for lion and leopard only).

Spatiotemporal avoidance and attraction

We used a temporal spacing analysis developed by Cusack et al. (2017) to investigate whether large carnivores exhibited intra-guild spatiotemporal avoidance or attraction at stations where they co-occurred. Input data consisted of all captures of leopard, lion, and spotted hyaena across all grids combined, as we did not obtain sufficient captures to analyse avoidance and attraction at each site separately. Insufficient captures of striped hyaena, African wild dog, and cheetah were obtained for this analysis, and these species were therefore excluded.

For each species pair, we investigated whether one species (species B) was more or less likely than expected to be detected in the 12 hours before and after a capture of the other species (species A), divided into one-hour units.

For all camera stations where the two species co-occurred, we calculated the minimum time before and after each capture of species A to capture species B at the same camera station. Captures of species A were excluded from analysis if they were followed or preceded more closely by another capture of the same species than by a capture of species B. Recorded minimum times were then aggregated into one-hour bins, limited to 12 hours before or after the reference capture.

We randomised detection times of species B 1000 times to obtain an expected detection distribution, by selecting a date at random from the survey period of that camera station and sampling a time from the observed activity pattern probability density function for that species. These expected detection probabilities were then compared to the observed detection probabilities via a standard permutation test, to test whether the observed detection probabilities were more or less than expected if the temporal spacing between detections of species A and species B at a camera station was random. We applied a Bonferroni correction to estimated p-values to account for multiple tests.

6.3. Results

6.3.1. Survey effort

Data from 151 systematically-deployed paired camera stations and 56 non-systematic unpaired camera stations yielded a total of 2,969 unique captures of spotted hyaena, 860 of lion, 563 of leopard, 222 of African wild dog, 102 of striped hyaena, and 22 of cheetah (Table 6.1). Leopard, lion, spotted hyaena, African wild dog, and cheetah were captured across all systematic grids and in village land, while striped hyaena were only captured in MBOMIPA WMA and village land. Maps of large carnivore capture events can be found in S6.2.

6.3.2. Activity overlap

Intra-specific differences between sites

All large carnivores in our study area, with the exception of African wild dog, exhibited predominantly nocturnal activity.

Leopard activity in the *Acacia-Commiphora* of Ruaha NP and in Rungwa GR followed a bimodal pattern, with an evening peak around 21:00-22:00 and an early morning peak around 04:00-05:00 (Fig. 6.2A). In the miombo woodland of Ruaha NP the species exhibited only an evening peak, and then a gradual drop off in activity. In the more human-impacted areas (MBOMIPA WMA and village land), the peak of leopard activity was shifted towards the hours after midnight (02:00-03:00). Leopard activity was significantly different ($p < .05$) between both sites in Ruaha NP and the site in MBOMIPA WMA, and between both sites in Ruaha NP and village land, and highly significantly different ($p < .001$) between the *Acacia-Commiphora* site of Ruaha NP and village land (Table 6.2). There was no significant difference between the activity of male and female leopard in any of the study sites, although note that sex identification was limited in village land as a result of camera positioning, making effective investigation of sex differences difficult in this site (Table 6.3).

Lion were most active in the very early morning (around 02:00-04:00) in all sites except village land, where they exhibited an earlier peak of activity just after midnight (Fig. 6.2B). Lion activity was significantly different in the miombo woodland of Ruaha NP compared to all other sites (Table 6.2); however, this is likely a result of a pride of three females regularly resting in front of one of the cameras by a water source during the day, which also gave rise to a higher level of daytime activity recorded in this site. Lion activity was also significantly different between MBOMIPA WMA and the *Acacia-Commiphora* area of Ruaha NP, Rungwa GR, and village land, and between Rungwa GR and village land. There was a significant difference in activity patterns of male and female lions in MBOMIPA WMA, where female lions were most active later in the morning than males (Table 6.3).

Spotted hyaena exhibited a very consistent drop-off and pick-up in activity around sunrise and sunset (07:00 and 19:00), respectively (Fig. 6.2C). Activity was fairly consistent throughout the night-time hours in both sites within Ruaha NP, while in Rungwa GR, MBOMIPA WMA, and village land there was a peak in activity in the early morning, between 03:00 and 05:00, which was most pronounced in village land. Spotted hyaena activity was significantly different between all sites except the two different habitats in Ruaha NP; this difference was highly significant for both habitats in Ruaha NP versus both MBOMIPA WMA and village land, but not Rungwa GR (Table 6.2).

Striped hyaena exhibited a bimodal activity pattern in village land, with peaks at around 22:00 and 04:00 (Fig. 6.2D). In MBOMIPA WMA, the species exhibited a significantly different activity pattern, with activity instead concentrated around midnight (Table 6.2).

African wild dog showed a consistent peak in activity around sunrise, although this effect is likely to have been amplified by pack behaviour (Fig. 6.2E). Insufficient captures of African wild dog were obtained in Rungwa GR to assess activity in this site. African wild dog activity patterns were significantly different between all sites where comparisons were possible (Table 6.2).

For all sites combined, cheetah activity peaked in the evening, at around 22:00 (Fig. 6.2F). There were insufficient captures of cheetah to investigate differences in activity patterns between sites or temporal overlap with other species.

Inter-specific differences within sites

Activity patterns of leopard and lion were highly significantly different within both habitat types in Ruaha NP and significantly different in Rungwa GR – where lion consistently exhibited more morning activity than leopard, and leopard more evening activity than lion – but did not differ significantly in MBOMIPA WMA or village land (Table 6.3).

Leopard and spotted hyaena exhibited significantly different activity patterns in both Ruaha NP sites, where spotted hyaena were more active than leopard in the early hours of the morning, and were more

strictly nocturnal. They also exhibited highly significantly different activity in village land, where spotted hyaena were more crepuscular than leopard (Table 6.3).

Spotted hyaena appeared to be more active in the evenings than lion, and activity patterns of the two species were significantly different everywhere except MBOMIPA WMA (this difference was highly significant in all sites except village land; Table 6.3).

Striped hyaena activity was significantly different from lion across both grids where striped hyaena were recorded (MBOMIPA WMA and village land; Table 6.3), while leopard and striped hyaena activity were significantly different in village land (Table 6.3). Striped hyaena and spotted hyaena activity did not differ significantly (Table 6.3).

African wild dog exhibited significantly different activity patterns from all other large carnivores for all sites where comparisons were possible (Table 6.3).

Plots of within- and between-species activity overlap can be found in S6.3.

6.3.3. Spatiotemporal avoidance and attraction

Leopard were significantly more likely to be captured than expected in the hour before a lion capture at the same station (Fig. 6.3A), and lion were more likely to be captured than expected in the hour after a leopard capture (Fig. 6.3B; although the latter result was not significant). A similar pattern was also found when detection probabilities were estimated for units of 30 minutes, instead of one hour (see Fig. S6.4A in S6.4). These results suggest that lion may be following leopard, or that leopard may be vacating areas due to lion moving in.

We also found evidence of leopard avoiding lion, as lion were significantly less likely to be captured than expected in the hour before a leopard capture (Fig. 6.3B). Although not significant, leopard were also less likely to be captured than expected in the hour after a lion capture (Fig. 6.3A).

We found evidence of lion avoiding spotted hyaena, with lion being significantly less likely to be captured than expected on nights when spotted hyaena were captured (Fig. 6.3D). Spotted hyaena were

also more likely to be captured than expected two or three hours after a lion capture (Fig. 6.3C; although not significantly), suggesting that they may be following lion.

Finally, our results suggest that spotted hyaena may be following leopard, as leopard were significantly more likely to be captured than expected in the hour before a spotted hyaena capture (Fig. 6.3E; a pattern also found with a time unit of 30 minutes; see Fig. S6.4A in S6.4). Although we found no evidence of leopard avoiding hyaena at the one hour time unit, spotted hyaena were significantly less likely to be captured than expected in the six hours before a leopard capture (see Fig. S6.4C in S6.4).

Table 6.1: Number of large carnivore capture events at each survey site. For lion and leopard, the number of capture events featuring males (M), females (F), individuals of unknown sex (Unk), and all captures combined (All) are shown. We define capture events as photographic captures taken at least 30 minutes from the previous capture of that species at that camera (for unpaired cameras) or station (for paired cameras), unless the animal photographed could be confidently distinguished as a new individual.

	Leopard				**Lion**							
	M	**F**	**Unk**	**All**	**M**	**F**	**Unk**	**All**	**Spotted hyaena**	**Striped hyaena**	**African wild dog**	**Cheetah**
Ruaha NP *Acacia-Commiphora*	141	90	22	253	227	239	22	488	1525	0	71	8
Ruaha NP miombo woodland	24	21	17	62	22	63	7	92	327	0	36	2
MBOMIPA WMA *Acacia-Commiphora*	48	40	12	100	39	43	1	83	427	54	51	6
Rungwa GR miombo woodland	14	17	19	50	60	49	1	110	337	0	5	3
Village land (community camera traps)	34	11	53	98	38	32	17	87	353	48	59	3
Total	261	179	123	563	386	426	48	860	2969	102	222	22

Table 6.2: Coefficients of overlap (Δ) for each large carnivore species between the different survey sites. Confidence intervals (shown in parentheses) were estimated via smoothed bootstrapping with 10,000 resamples; confidence intervals with an upper limit > 1 were corrected on a logistic scale and back-transformed. Overlap analysis was only carried out for survey site interactions where the sample size of the site with fewest captures was > 30 (see Table 6.1). Cells highlighted in light green indicate significant differences ($p < .05$) in activity between the two sites, while cells highlighted in dark green indicate highly significant differences ($p < .001$).

Site A	Site B	Leopard	Lion	Spotted hyaena	Striped hyaena	African wild dog
Ruaha NP *Acacia-Commiphora*	Ruaha NP miombo woodland	0.83 (0.74 – 0.90)	0.70 (0.61 – 0.78)	0.93 (0.89 – 0.96)	-	0.63 (0.50 – 0.74)
Ruaha NP *Acacia-Commiphora*	MBOMIPA WMA *Acacia-Commiphora*	0.81 (0.71 – 0.89)	0.79 (0.70 – 0.87)	0.86 (0.81 – 0.90)	-	0.74 (0.63 – 0.84)
Ruaha NP *Acacia-Commiphora*	Rungwa GR miombo woodland	0.89 (0.80 – 0.95)	0.88 (0.81 – 0.93)	0.91 (0.86 – 0.96)	-	-
Ruaha NP *Acacia-Commiphora*	Village land (community camera traps)	0.75 (0.65 – 0.83)	0.85 (0.76 – 0.92)	0.87 (0.82 – 0.91)	-	0.66 (0.52 – 0.78)
Ruaha NP miombo woodland	MBOMIPA WMA *Acacia-Commiphora*	0.73 (0.61 – 0.85)	0.63 (0.53 – 0.74)	0.86 (0.80 – 0.91)	-	0.58 (0.44 – 0.71)
Ruaha NP miombo woodland	Rungwa GR miombo woodland	0.81 (0.68 – 0.92)	0.70 (0.60 – 0.79)	0.89 (0.84 – 0.94)	-	-
Ruaha NP miombo woodland	Village land (community camera traps)	0.76 (0.63 – 0.88)	0.74 (0.64 – 0.84)	0.86 (0.80 – 0.92)	-	0.67 (0.54 – 0.79)
MBOMIPA WMA *Acacia-Commiphora*	Rungwa GR miombo woodland	0.84 (0.72 – 0.93)	0.76 (0.65 – 0.85)	0.90 (0.85 – 0.94)	-	-
MBOMIPA WMA *Acacia-Commiphora*	Village land (community camera traps)	0.84 (0.74 – 0.93)	0.80 (0.68 – 0.90)	0.88 (0.82 – 0.93)	0.79 (0.65 – 0.90)	0.72 (0.58 – 0.83)
Rungwa GR miombo woodland	Village land (community camera traps)	0.80 (0.69 – 0.91)	0.78 (0.67 – 0.88)	0.90 (0.85 – 0.94)	-	-

Table 6.3: Coefficients of overlap (Δ) for all large carnivore species pairs at each survey site. Confidence intervals (shown in parentheses) were estimated via smoothed bootstrapping with 10,000 resamples; confidence intervals with an upper limit > 1 were corrected on a logistic scale and back-transformed. Overlap analysis was only carried out for species interactions where the sample size of the species with fewest captures was > 30 (see Table 6.1). Cells highlighted in light green indicate significant differences ($p < .05$) in activity between the two species, while cells highlighted in dark green indicate highly significant differences ($p < .001$).

Survey location	Leopard Lion	Leopard Spotted hyaena	Leopard Striped hyaena	Leopard African wild dog	Lion Spotted hyaena	Lion Striped hyaena
Ruaha NP *Acacia-Commiphora*	0.82 (0.75 – 0.88)	0.89 (0.84 – 0.93)	-	0.69 (0.58 – 0.78)	0.82 (0.77 – 0.86)	-
Ruaha NP miombo woodland	0.68 (0.56 – 0.79)	0.81 (0.70 – 0.90)	-	0.53 (0.36 – 0.69)	0.66 (0.58 – 0.74)	-
MBOMIPA WMA *Acacia-Commiphora*	0.86 (0.76 – 0.94)	0.91 (0.84 – 0.97)	0.81 (0.68 – 0.91)	0.57 (0.44 – 0.69)	0.91 (0.83 – 0.97)	0.77 (0.63 – 0.89)
Rungwa GR miombo woodland	0.78 (0.66 – 0.90)	0.88 (0.79 – 0.95)	-	-	0.81 (0.72 – 0.88)	-
Village land (community camera traps)	0.85 (0.75 – 0.94)	0.78 (0.69 – 0.86)	0.74 (0.61 – 0.86)	0.39 (0.28 – 0.51)	0.81 (0.73 – 0.88)	0.77 (0.64 – 0.88)

Survey location	Lion African wild dog	Spotted hyaena Striped hyaena	Spotted hyaena African wild dog	Striped hyaena African wild dog	Leopard (M) Leopard (F)	Lion (M) Lion (F)
Ruaha NP *Acacia-Commiphora*	0.78 (0.67 – 0.87)	-	0.66 (0.56 – 0.76)	-	0.82 (0.72 – 0.91)	0.90 (0.85 – 0.95)
Ruaha NP miombo woodland	0.55 (0.40 – 0.69)	-	0.57 (0.43 – 0.72)	-	0.87 (0.69 – 0.99)	0.63 (0.47 – 0.78)
MBOMIPA WMA *Acacia-Commiphora*	0.55 (0.42 – 0.68)	0.84 (0.73 – 0.93)	0.55 (0.43 – 0.66)	0.48 (0.35 – 0.61)	0.87 (0.75 – 0.97)	0.79 (0.63 – 0.92)
Rungwa GR miombo woodland	-	-	-	-	-	0.83 (0.70 – 0.93)
Village land (community camera traps)	0.48 (0.36 – 0.61)	0.83 (0.72 – 0.92)	0.49 (0.37 – 0.59)	0.44 (0.30 – 0.57)	-	0.77 (0.62 – 0.90)

Figure 6.2: Kernel density function plots of large carnivore activity in Ruaha-Rungwa, centred on midnight (00:00). Plotted using package *overlap* (Meredith & Ridout, 2020b). Kernel density functions were fitted to all unique capture events of (A) leopard, (B) lion, (C) spotted hyaena, (D) striped hyaena, (E) African wild dog, and (F) cheetah, using camera trap data from four systematic camera trap grids, and from cameras deployed non-systematically in village land. Striped hyaena were only recorded in MBOMIPA WMA and village land (community camera traps), while insufficient captures of wild dog were obtained in Rungwa GR (n = 5) for activity to be modelled in this site. Due to a low number of overall captures (n = 22), cheetah activity is only plotted for all sites combined.

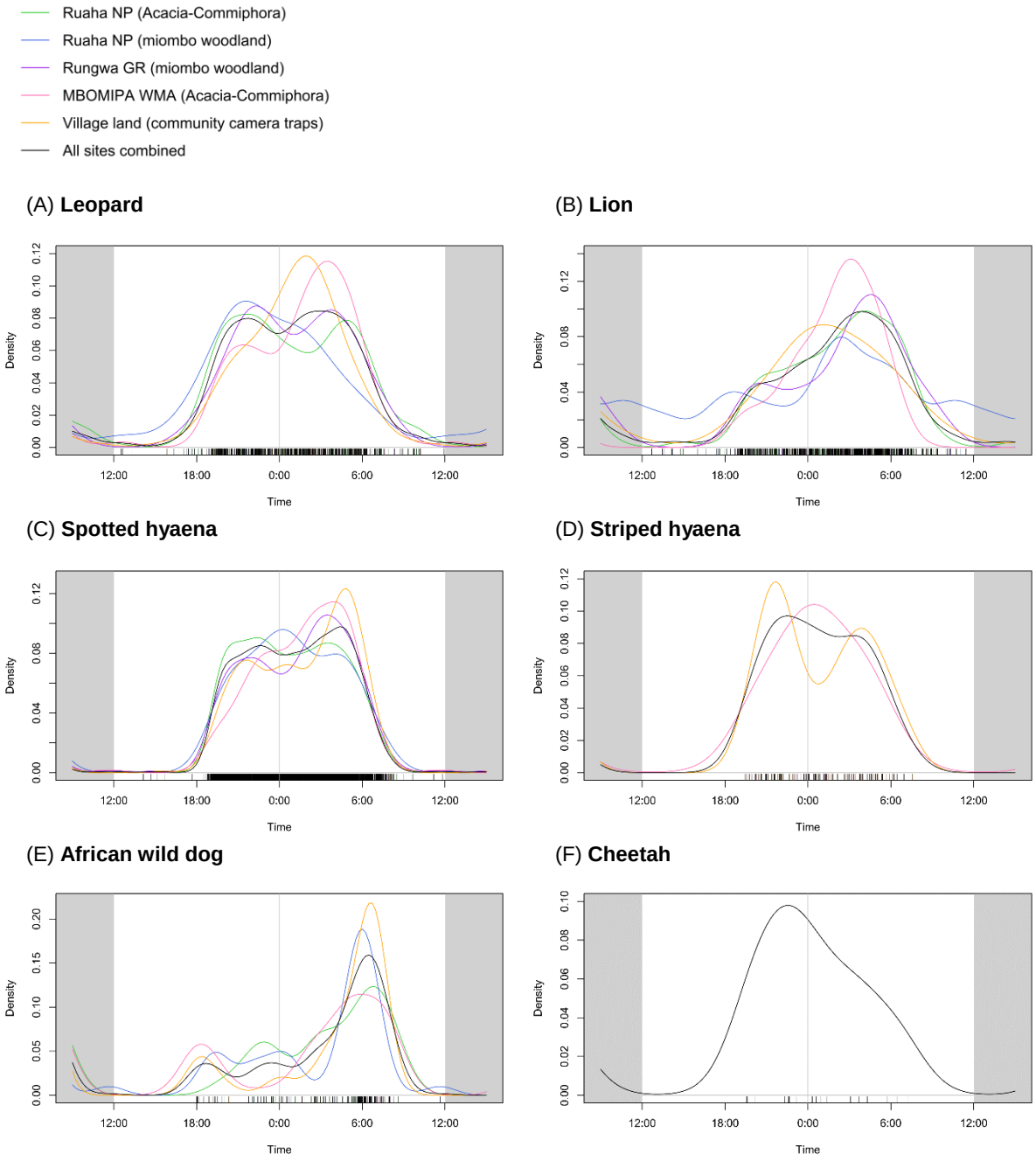
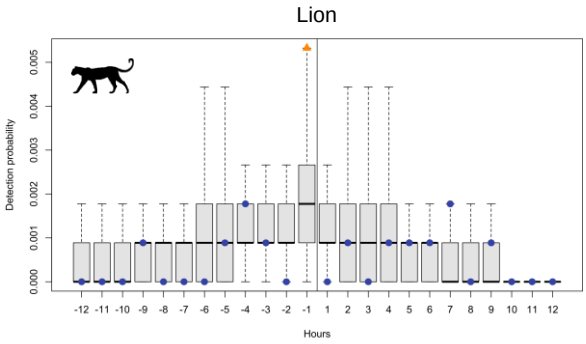
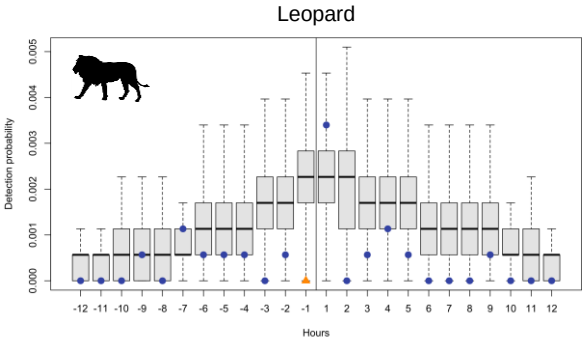


Figure 6.3: Detection probability of species B (shown via silhouettes) in the 12 hours before and after a capture of species A (at hour 0) at the same station, divided into one-hour units. Boxplots show the expected probability of detecting species B in each hour before and after capture of species A if there were no relationship between detections of species A and species B, while points indicate the observed detection probability of species B for each hour before and after capture of species A. Expected detection probabilities were derived by randomly sampling 1000 times from the observed activity pattern probability density function for that species. Observed detection probabilities that differ significantly ($p < 0.05$) from the expected probability of detection are shown with orange triangles; those that do not differ significantly are shown with blue dots.

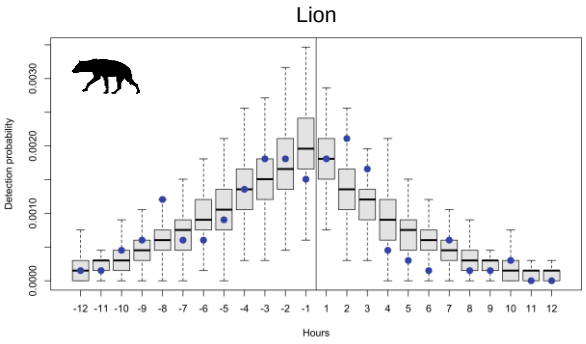
(A) **Species A: lion, Species B: leopard**



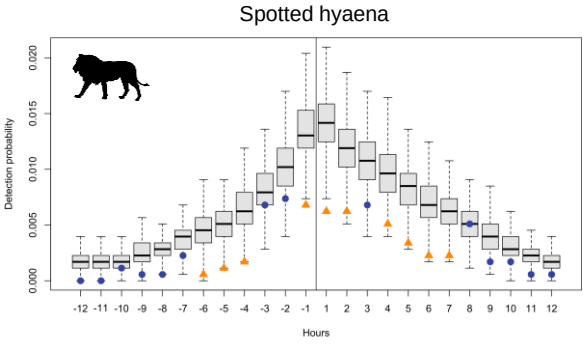
(B) **Species A: leopard, Species B: lion**



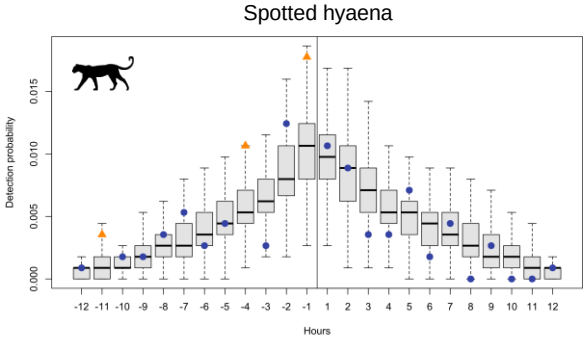
(C) **Species A: lion, Species B: spotted hyaena**



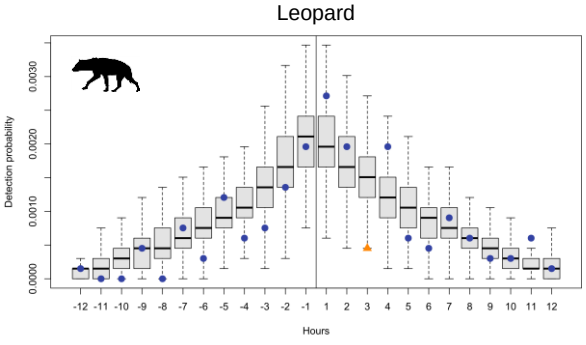
(D) **Species A: spotted hyaena, Species B: lion**



(E) **Species A: spotted hyaena, Species B: leopard**



(F) **Species A: leopard, Species B: spotted hyaena**



6.4. Discussion

We employed camera trap data to reveal insights into interactive processes between large carnivores in the mixed-use Ruaha-Rungwa conservation landscape in Tanzania. We compared activity patterns – specifically, movement along roads and trails – across different habitats and land use types, and found evidence of temporal partitioning by large carnivores with intra-guild competitors. We also found evidence of significant avoidance and attraction behaviours between leopard, lion, and spotted hyaena.

6.4.1. Activity patterns and species overlap

We found no evidence of sex differences in leopard activity patterns, in contrast to a study in Tanzania's Udzungwa Mountains (Havmøller et al., 2020). We did, however, find evidence of intra-specific differences in activity among leopard between our study sites, with the species' peak of activity occurring deeper into the night-time hours in the more human-impacted sites.

Leopard and lion activity differed significantly in Ruaha NP and Rungwa GR. Supported by our findings that lion followed leopard and leopard avoided lion, this suggests that leopard may employ minor temporal partitioning to avoid the dominant competitor in this landscape. However, the shift of leopard activity towards the early morning in more human-impacted sites resulted in a greater activity overlap with lion. This may be a result of the need to avoid humans outweighing the need to avoid dominant competitors in areas where human activity is higher, as suggested elsewhere (Strampelli et al., 2018). Leopards have been shown to partition temporally from humans (Odden et al., 2014; Van Cleave et al., 2018) and avoid bushmeat poachers (Henschel et al., 2011), and 47% of humans within the WMA illegally that were captured by the systematic camera traps were photographed between the hours of 18:00 and 00:00, versus 13% between 00:00 and 06:00 (this study). A similar trade-off has been observed in African wild dog, where temporal avoidance of humans left packs more vulnerable to competition from lion and spotted hyaena (Rasmussen & Macdonald, 2012).

However, this pattern may also, at least in part, reflect leopard being freed up from avoidance of the dominant competitor in areas with fewer lions. Although lion population density was higher in

MBOMIPA WMA (4.06 ± 1.03 per 100 km^2) than the miombo woodland of Rungwa GR (2.25 ± 0.52 per 100 km^2) and Ruaha NP (1.75 ± 0.62 per 100 km^2; see S5.4 and Appendix 3), there appears to be a strong density gradient within the WMA, with 93% of lion detections in this site occurring within 5 km of the Great Ruaha River, further from the boundary with unprotected village land (see Fig. S6.2.1B in S6.2). It is also highly probable that lion persist at very low densities in unprotected village land, as a result of widespread habitat conversion and degradation, low prey availability, and high anthropogenic mortality (Abade et al., 2019). In these areas, lion densities may therefore be sufficiently low that leopard no longer need to adjust their activity patterns to avoid harmful interactions with lion – particularly as this would increase their exposure to humans – and can instead rely more heavily on reactive avoidance strategies (Vanak et al., 2013).

The significant difference between leopard and spotted hyaena activity in the site with highest spotted hyaena density (Ruaha NP *Acacia-Commiphora*: 10.8 ± 1.08 per 100 km^2; see S5.4 and Appendix 4) may indicate some temporal partitioning by leopard to avoid competitive interactions with spotted hyaena, as observed elsewhere in Tanzania (Havmøller et al., 2020). This is supported by our finding that spotted hyaena appear to follow leopard where the two species co-occur, a pattern which has also been observed in South Africa (Balme et al., 2019).

Most lion activity was concentrated in the early hours of the morning except in village land, where they exhibited an earlier peak of activity around midnight. This predominantly nocturnal activity is consistent with numerous studies of the species elsewhere in Africa (Hayward & Slotow, 2009). The activity shift observed in village land likely reflects avoidance of humans – either through lion modifying their overall activity patterns, or reducing their use of roads at times when humans are more likely to be encountered along them. Such avoidance of human-dominated areas by lion during the day has also been observed in Kenya (Oriol-Cotterill et al., 2015). Although we did not find evidence of partitioning with humans by lion in the WMA grid, we would expect any human avoidance to be less noticeable in this site than in village land, both because the majority of lions in this grid were recorded in the best-protected area along the Great Ruaha River (see Fig. S6.2.1B in S6.2), and because illegal

human incursions in the WMA took place mostly before midnight, and so did not coincide with the consistent peak of lion activity we observed within PAs.

Spotted hyaena activity was significantly different in Ruaha NP versus the more human-impacted sites of MBOMIPA WMA and village land, where the species exhibited a more pronounced peak in activity in the hours before sunrise. This may be a result of individuals in unprotected or more encroached areas having to travel extensively along roads – and thus pass in front of the camera traps – to return to safe areas where they can hide during the day before sunrise, when human activity increases substantially. Similar avoidance of humans has been observed among spotted hyaena in livestock grazing areas, where they have been shown to shift toward more strictly nocturnal activity (Boydston et al., 2003) and travel faster and farther (Green & Holekamp, 2019).

Although we obtained a low number of detections of cheetah, our data suggest that the species may exhibit predominantly nocturnal activity in Ruaha-Rungwa. This contrasts with a number of studies that have found the species to be largely diurnal or crepuscular (Dröge et al., 2016; Hayward & Slotow, 2009; Swanson et al., 2016). However, research in Namibia has found cheetah to show increased nocturnal activity as ambient temperatures increase (Hetem et al., 2019), and a study in Botswana's Okavango Delta revealed an unexpectedly high rate of nocturnal activity for the species, with higher rates of night-time activity on nights with more moonlight (Cozzi et al., 2012). Although we did not account for moon phase in this study, our findings nonetheless add to a growing body of evidence that cheetah may be more nocturnal than previously thought.

For all species, it is important to note that the apparent differences in activity revealed by our camera trap data may in fact reflect differences in the times at which species travel along roads between the study sites, rather than differences in overall activity. Species may still be active when off-road – for example, wild dog in northern Botswana have been shown to select roads when travelling, but ignore roads when running at high speeds or resting (Abrahms et al., 2016). However, this may nevertheless reflect behavioural adaptations to avoid competition, as species may shift their movement away from roads to avoid intra-guild competitors or humans. This is a particular possibility for cheetah, as there is

evidence that the species can detect lion presence and adjust their behaviour to avoid lion spatially, but may not need to do so in areas with denser vegetation (Broekhuis et al., 2013).

6.4.2. Spatiotemporal avoidance and attraction

The results of our temporal spacing analysis suggest that leopard employ fine-scale avoidance of lion in areas where they co-occur in Ruaha-Rungwa. Lion are known to attack and kill leopard (Balme, Pitman, et al., 2017), steal kills from the smaller-bodied felid (Balme, Miller, et al., 2017), and impact cub survival and recruitment rates in leopard populations (du Preez, 2014). However, multiple studies have found leopard to not spatially segregate from lion over larger areas (Balme, Pitman, et al., 2017; Miller et al., 2018; Rafiq et al., 2020). In our study landscape, this is likely a result of the species' shared habitat preferences (Abade et al., 2014): large-scale avoidance of lion would prevent leopard from accessing many vital resources, particularly in human-impacted areas where resources are more limited, and this may pose a fitness cost to leopard that outweighs the benefits of complete avoidance of the dominant competitor (Strampelli et al., 2018). Instead, by prioritising resource acquisition and responding reactively to the presence of lion through fine-scale behavioural adaptations, leopard are able to minimise the risk of antagonistic encounters while maintaining access to preferred habitats (Broekhuis et al., 2013).

In addition to the fine-scale temporal avoidance observed here, a number of additional coexistence mechanisms have been observed in other leopard populations, including fine-scale spatial avoidance in the presence of lion (du Preez et al., 2015; Vanak et al., 2013), avoiding areas where the probability of encountering lion is highest (Balme, Pitman, et al., 2017), minor temporal partitioning (Miller et al., 2018), dietary niche differentiation (du Preez et al., 2017), and prey caching to avoid kleptoparasitism (Balme, Miller, et al., 2017; Stein et al., 2015). Thus, although this study provides evidence of fine-scale spatiotemporal avoidance and possible minor temporal partitioning, it is likely that leopard in Ruaha-Rungwa also make use of other adaptations that could not be identified by this study.

We also found evidence that spotted hyaena follow leopard in Ruaha-Rungwa. This mirrors the results of a similar study in South Africa (Balme et al., 2019), and is likely to be a behaviour employed by

spotted hyaena to increase kleptoparasitism and scavenging opportunities. Kleptoparasitism by spotted hyaena is often mainly targeted at leopard (Vanak et al., 2013), and previous research has found spotted hyaena to be responsible for 50% of kleptoparasitism suffered by the species (Balme, Miller, et al., 2017). High rates of kleptoparasitism are associated with reduced reproductive success among female leopards (Balme, Miller, et al., 2017); the loss of prey to competitors, and particularly to spotted hyaena, therefore represents a threat to leopard fitness. Nevertheless, as spotted hyaena are ubiquitous across the Ruaha-Rungwa landscape (see Appendix 1), it is likely to be impossible for leopard to fully spatially segregate from them at coarse scales, even in unprotected areas (Balme et al., 2019). As a result, behavioural adaptations like those employed to avoid lion may be necessary for leopard to also avoid competitive interactions with spotted hyaena, and thus minimise the fitness consequences of coexistence.

Our findings suggest that spotted hyaena also actively follow lion, and that lion avoid spotted hyaena in Ruaha-Rungwa. This could reflect spotted hyaena being more reliant on scavenging than active predation in the study area – a shift that has been observed in areas of high lion density (Périquet, Valeix, et al., 2015) – and following lion to maximise their chances of being able to take over a kill once it has been abandoned (Kissui & Packer, 2004). The corresponding avoidance shown by lion may suggest attempts by lion to minimise these antagonistic interactions. However, this apparent avoidance could also be reflective of periods of high spotted hyaena activity along roads coinciding with lion activity being focused off-road, which may occur when lion are on a kill.

Interestingly, we did not find evidence of reciprocal following behaviour by lion toward spotted hyaena, despite both species being known to steal kills from one another (Périquet, Fritz, et al., 2015). Lion and spotted hyaena have been found to actively track one another in Serengeti NP (Swanson et al., 2016), and in a previous temporal spacing study in the *Acacia-Commiphora* area of Ruaha NP (Cusack et al., 2017). However, the previous study in Ruaha NP only found evidence of reciprocal following between the two species in the first of the two dry seasons studied. Although is important to note that the inclusion of data from other parts of the Ruaha-Rungwa landscape in this study may have obscured any

reciprocal following within individual sites, we obtained more than 50% of both lion and spotted hyaena captures in the *Acacia-Commiphora* of Ruaha NP (Table 6.1); as such, it is likely that we would have picked up on any evidence of lion following spotted hyaena in this site if this were still taking place. Comparing our findings to this previous research therefore illustrates the variability of intra-guild interactions, and suggests that there may have been a shift from reciprocal to one-sided following behaviour between lion and spotted hyaena between 2013 and 2018. A change of this kind could be indicative of an increased ratio of spotted hyaena to lion in Ruaha-Rungwa – as a result of an increase in spotted hyaena population or a declining lion population, or a combination of the two – or of the sex ratio of lion in the study area becoming more female-weighted, both of which confer a higher competitive status to spotted hyaena (Cooper, 1991; Watts & Holekamp, 2008). Evidence of lion ceasing to follow spotted hyaena may also point to changes in diet, as mutual attraction between the species can indicate mutual attraction to shared prey (Swanson et al., 2016). Such changes may be linked to the ongoing drying of the once-perennial Great Ruaha River due to upstream water mismanagement, which has resulted in a considerable loss of dry season habitat (Coppolillo et al., 2003; Epaphras et al., 2008), and warrant further investigation into the impacts of this ecological shift on Ruaha-Rungwa's wildlife populations.

It should be noted that our inferences about the direction of intra-guild interactions were informed by existing knowledge of associations between different large carnivore species (Cusack et al., 2017), and we acknowledge that camera trap data can only provide limited insights into complex competitive interactions – particularly as these are not limited to roads, and often take place over very short timescales. In Ruaha-Rungwa, movement data from GPS or VHF collars would be a valuable tool to investigate the fine-scale coexistence mechanisms being used by large carnivores (Vanak et al., 2013), and provide a clearer picture of how individuals may be modifying their movements to avoid humans (Odden et al., 2014; Oriol-Cotterill et al., 2015; Van Cleave et al., 2018).

6.4.3. Conservation implications

Despite the evidence we found of spatiotemporal avoidance among members of Ruaha-Rungwa's large carnivore guild, population densities of leopard, lion, and spotted hyaena were nonetheless highly correlated across our systematic survey sites (leopard-lion: 0.97; leopard-hyaena: 0.94; lion-hyaena: 0.88; see S5.4), and there is no evidence of large scale avoidance between the three species in this landscape (Strampelli et al., in prep). Our results therefore highlight the importance of the observed fine-scale avoidance mechanisms employed by large carnivores to minimise the negative impacts of intra-guild competition, and secure access to limited shared resources, as well as to avoid competition with humans (Chapron & López-Bao, 2016).

However, these adaptations are likely to become both increasingly important and more difficult for species to employ as the availability of intact habitat and prey continue to decline as a result of anthropogenic pressures (Powers & Jetz, 2019; Wolf & Ripple, 2016), and large carnivores are forced into smaller, more fragmented areas (Wolf & Ripple, 2017). In this context, information on how species modify their behaviour to co-exist with one another and with humans, as provided in this study, can inform conservation management plans in increasingly human-modified landscapes, and help secure Africa's large carnivore diversity. In particular, efforts should be made to prioritise multi-species conservation efforts; maintain heterogeneity in prey species, habitats, and habitat features; and minimise activities which would interfere with known coexistence mechanisms during critical periods of activity for species.

6.5. Acknowledgements

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6.6. Supplementary material

S6.1 Location and activity of community camera traps

S6.2 Maps of large carnivore capture events

S6.3 Plots of within- and between-species activity overlap

S6.4 Full temporal spacing analysis results

S6.1 Location and activity of community camera traps

Table S6.1.1: Location and activity of the 56 community camera traps, deployed in village land to the east of Ruaha NP and MBOMIPA WMA.

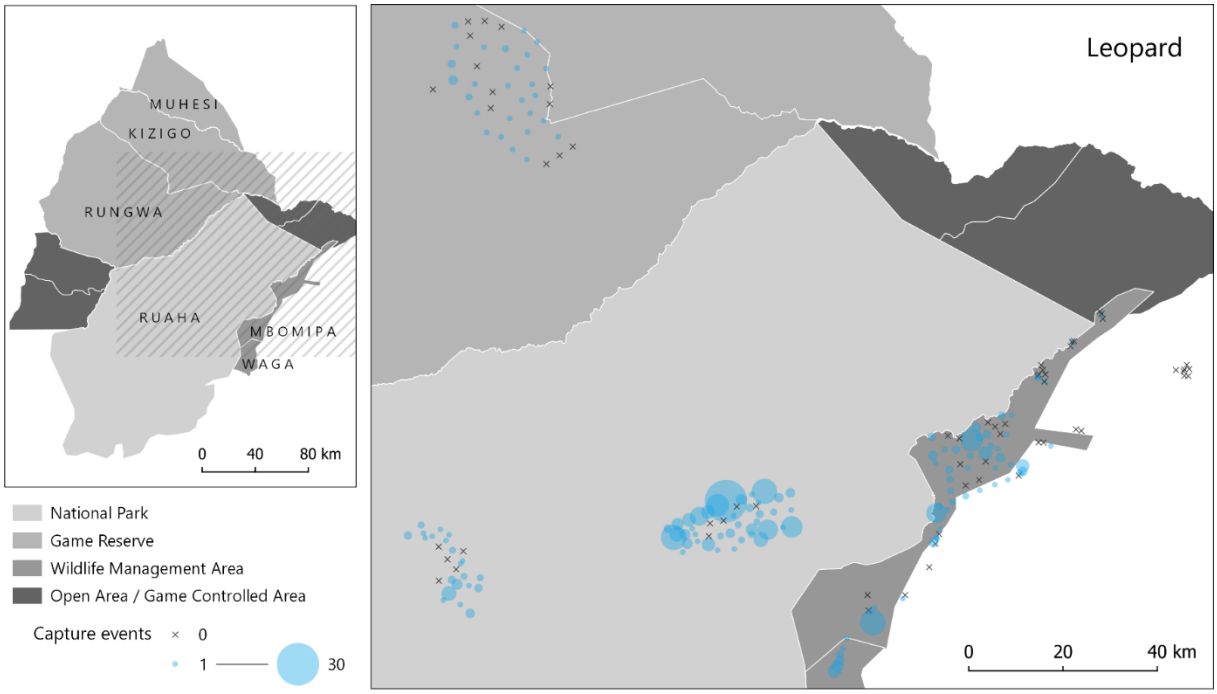
						2018						2019					
Village	**Camera**	**Longitude**	**Latitude**	**Large carnivores detected**	**Camera make**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**
Idodi	CCT-17-02	35.15034	-7.64235	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	0
Idodi	CCT-17-08	35.15601	-7.62953	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	0
Idodi	CCT-18-01	35.15811	-7.67280	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	0
Idodi	RCP-106--	35.15607	-7.68267	N	HCO Scout Guard	1	1	1	0	0	0	0	0	0	0	0	0
Isele	CCT-17-05	35.35852	-7.37561	Y	Reconyx	1	1	1	1	1	1	0	0	0	0	0	0
Isele	CCT-17-09	35.34554	-7.37561	Y	Reconyx	1	1	1	1	1	0	0	0	0	0	0	0
Isele	CCT-17-24	35.34396	-7.37921	N	HCO Scout Guard	1	0	0	0	0	0	0	0	0	0	0	0
Isele	CCT-17-37	35.34396	-7.37921	Y	HCO Scout Guard	0	1	1	1	1	1	0	0	0	0	0	0
Isele	CCT-18-21	35.35356	-7.36744	N	Cuddeback	0	0	0	0	0	0	0	0	0	0	1	0
Isele	CCT-18-22	35.35040	-7.35769	N	Cuddeback	0	0	0	0	0	0	0	0	0	0	1	0
Kinyika	CCT-17-16	35.40663	-7.32134	Y	Reconyx	1	1	0	1	0	0	0	0	0	0	0	0
Kinyika	CCT-17-38	35.40953	-7.31277	Y	HCO Scout Guard	0	1	1	1	1	1	1	1	0	0	0	0
Kinyika	CCT-18-10	35.40957	-7.31277	N	Cuddeback	0	0	0	0	0	1	0	0	0	0	0	0
Kinyika	CCT-18-23	35.41363	-7.31180	N	Cuddeback	0	0	0	0	0	0	0	0	0	0	1	0
Kitisi	CCT-17-27	35.15161	-7.69181	Y	HCO Scout Guard	1	1	1	1	1	1	1	1	0	0	0	0
Kitisi	CCT-17-34	35.14868	-7.70122	Y	HCO Scout Guard	1	1	0	0	0	0	0	0	0	0	0	0
Kitisi	CCT-18-11	35.14508	-7.69897	Y	Cuddeback	0	0	0	0	0	0	1	1	1	1	1	0
Kitisi	CCT-18-18	35.15145	-7.68975	Y	Cuddeback	0	0	0	0	0	0	1	1	1	1	1	0
Kitisi	CCT-18-26	35.15145	-7.68975	Y	Cuddeback	0	0	0	0	0	0	0	0	0	0	1	0
Kisilwa	CCT-18-01	34.96141	-7.93679	Y	Cuddeback	0	0	0	1	1	1	1	1	1	1	1	1
Kisilwa	CCT-18-02	34.95568	-7.94571	Y	Cuddeback	0	0	0	1	1	1	1	1	1	1	1	1
Kisilwa	CCT-18-04	34.96589	-7.92630	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	1
Kisanga	CCT-17-10	35.46862	-7.26873	Y	Reconyx	1	1	1	1	1	1	0	0	0	0	0	0
Kisanga	CCT-17-25	35.46744	-7.26157	Y	HCO Scout Guard	1	1	1	1	1	1	1	1	1	1	1	1
Kisanga	CCT-18-11	35.46591	-7.25899	Y	HCO Scout Guard	0	0	0	1	0	0	0	0	0	0	0	0
Kisanga	CCT-18-12	35.46274	-7.25460	N	Cuddeback	0	0	0	0	0	0	1	1	1	0	0	0
Luganga	CCT-18-08	35.42846	-7.48337	Y	Cuddeback	0	0	0	1	1	1	1	1	1	1	1	1

Luganga	CCT-18-14	35.41808	-7.48063	N	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	1
Mafuluto	CCT-17-12	35.34613	-7.50591	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	1
Mafuluto	CCT-17-29	35.35599	-7.50629	Y	HCO Scout Guard	1	1	1	1	1	1	0	0	0	0	0	0
Mafuluto	CCT-17-36	35.36992	-7.51287	Y	HCO Scout Guard	0	0	0	1	1	1	0	0	0	0	0	0
Magombwe	CCT-17-17	35.35799	-7.39066	Y	Reconyx	1	1	1	1	1	1	0	1	1	1	1	1
Magombwe	CCT-17-28	35.34626	-7.38422	Y	HCO Scout Guard	1	1	1	1	1	1	1	1	1	1	1	0
Magombwe	CCT-18-15	35.35676	-7.38935	N	HCO Scout Guard	0	0	0	1	1	1	0	0	0	0	0	0
Mahuninga	CCT-17-18	34.96635	-7.91420	Y	HCO Scout Guard	1	1	1	0	0	0	0	0	0	0	0	0
Mahuninga	CCT-17-19	34.97984	-7.88327	Y	HCO Scout Guard	1	1	1	0	0	0	0	0	0	0	0	0
Mahuninga	CCT-18-03	34.97188	-7.90242	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	1
Makifu	CCT-17-11	35.02943	-7.85269	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	0
Makifu	CCT-17-32	35.02088	-7.82928	Y	HCO Scout Guard	1	1	1	1	1	1	1	1	1	1	1	0
Makifu	CCT-18-02	35.02336	-7.83232	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	0
Malinzanga	CCT-17-01	35.31456	-7.56639	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	1
Malinzanga	CCT-17-36	35.30836	-7.56968	N	HCO Scout Guard	1	1	1	0	0	0	0	0	0	0	0	0
Malinzanga	CCT-18-08	35.31647	-7.56163	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	0
Malinzanga	RCP-NEW-3	35.31595	-7.55106	Y	HCO Scout Guard	1	1	1	1	1	1	1	1	1	1	1	1
Mapogoro	CCT-18-07	35.09116	-7.79963	Y	HCO Scout Guard	0	0	0	1	1	1	1	1	1	1	1	1
Mapogoro	CCT-18-09	35.08677	-7.80631	Y	Cuddeback	0	0	0	0	0	1	0	0	0	0	0	0
Mboliboli	CCT-18-05	35.62420	-7.36832	N	Cuddeback	0	0	0	1	1	1	1	1	1	1	1	1
Mboliboli	CCT-18-06	35.62579	-7.37670	N	Cuddeback	0	0	0	0	1	0	0	0	0	0	0	0
Mboliboli	CCT-18-13	35.63313	-7.37713	N	HCO Scout Guard	0	0	0	0	1	1	1	0	0	0	0	0
Mboliboli	CCT-18-25	35.60953	-7.36586	N	Cuddeback	0	0	0	0	0	0	0	0	0	0	1	1
Mbugani	CCT-18-03	35.62559	-7.36450	N	Cuddeback	0	0	0	1	1	1	1	1	1	0	0	1
Mbugani	CCT-18-04	35.63512	-7.36379	N	Cuddeback	0	0	0	1	1	1	1	1	1	0	1	1
Mbugani	CCT-18-12	35.63026	-7.35585	N	HCO Scout Guard	0	0	0	1	1	1	1	1	1	0	1	1
Tungamalenga	CCT-17-14	35.01892	-7.79996	Y	Reconyx	1	1	1	1	1	1	1	1	1	1	1	1
Tungamalenga	CCT-17-35	35.03171	-7.82388	Y	HCO Scout Guard	1	1	1	1	1	1	0	0	0	0	0	0
Tungamalenga	CCT-18-16	35.01892	-7.79996	N	Cuddeback	0	0	0	0	0	0	1	1	1	0	0	0

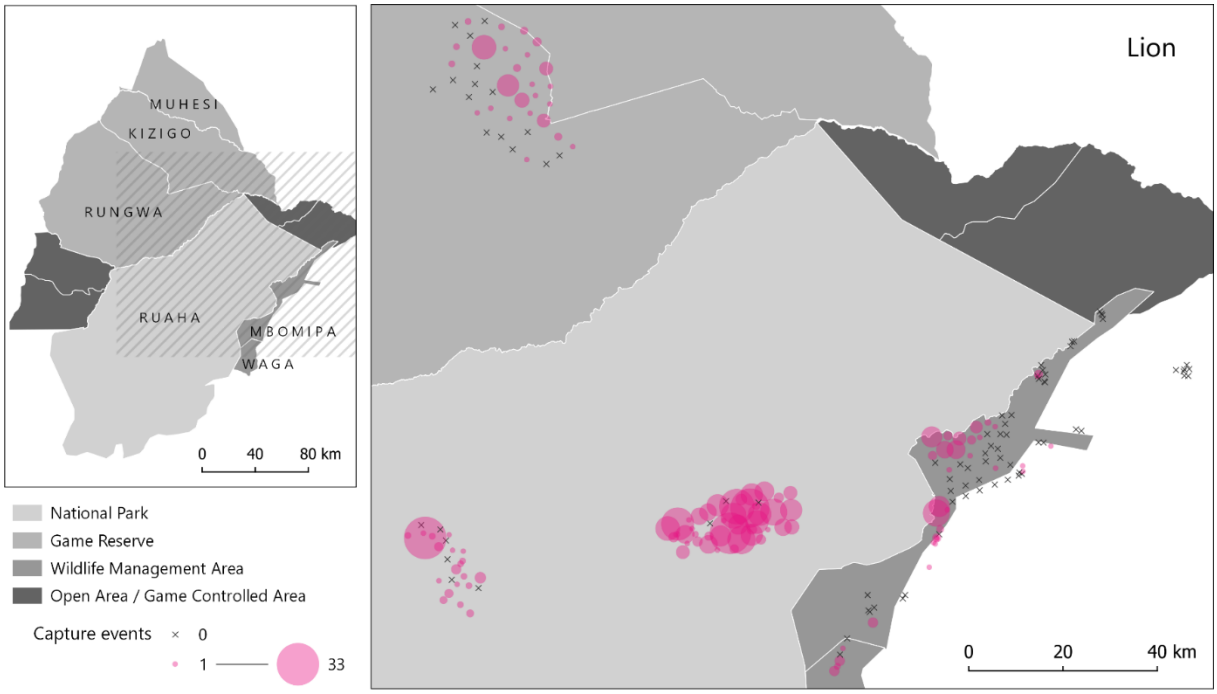
S6.2 Maps of large carnivore capture events

Figure S6.2.1: The number of unique large carnivore capture events at each camera station. Captures were considered unique if they occurred more than 30 minutes after the previous capture of the same species at the same station, unless the animals captured could be confidently distinguished as different individuals. Circles are scaled according to the number of captures at that station; note that a unique scale is used for each species, dependent on the maximum number of captures at a single station for that species.

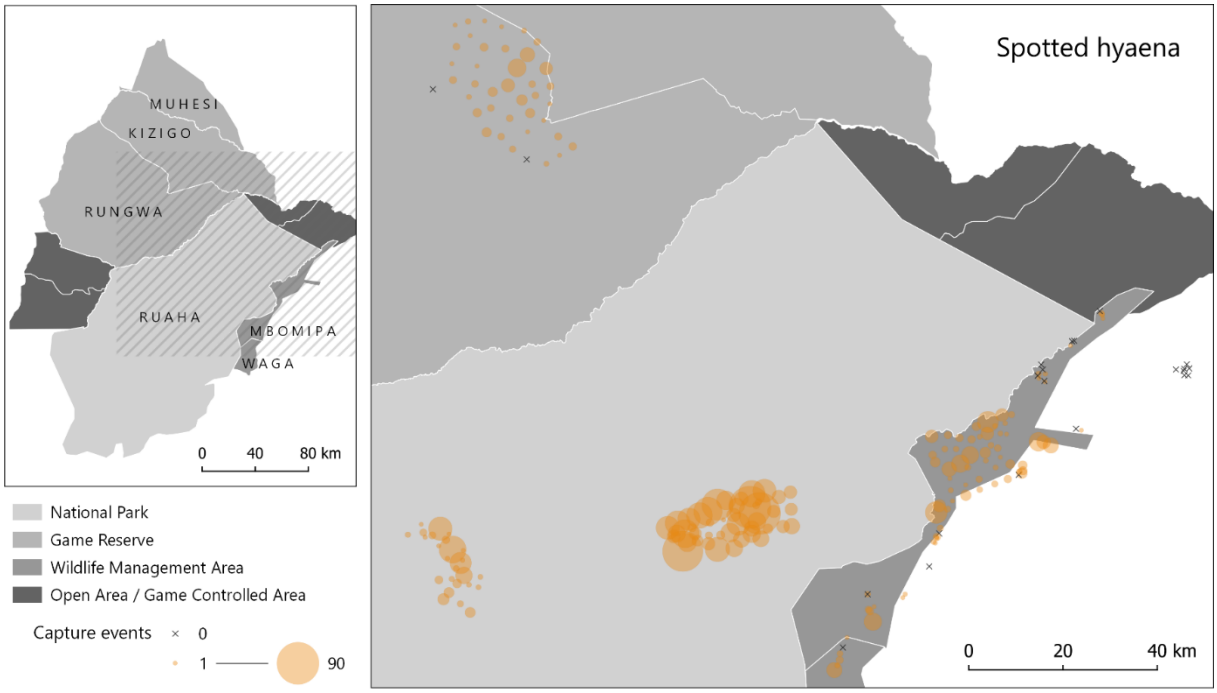
(A) **Leopard**



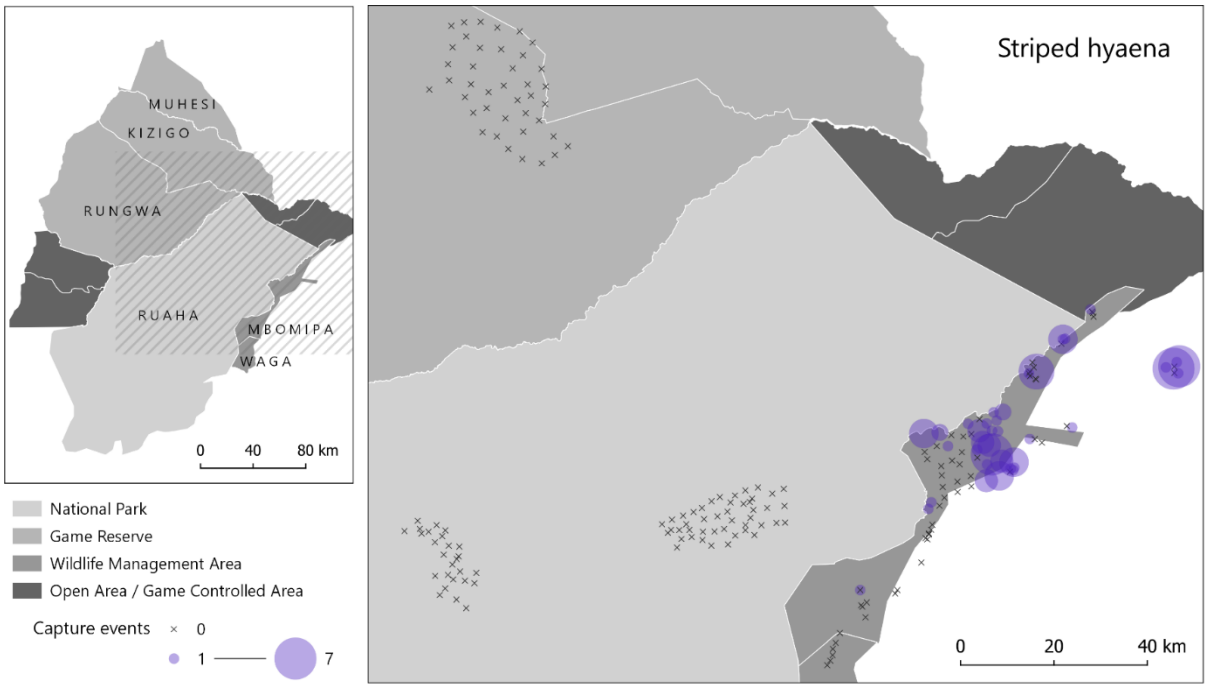
(B) **Lion**



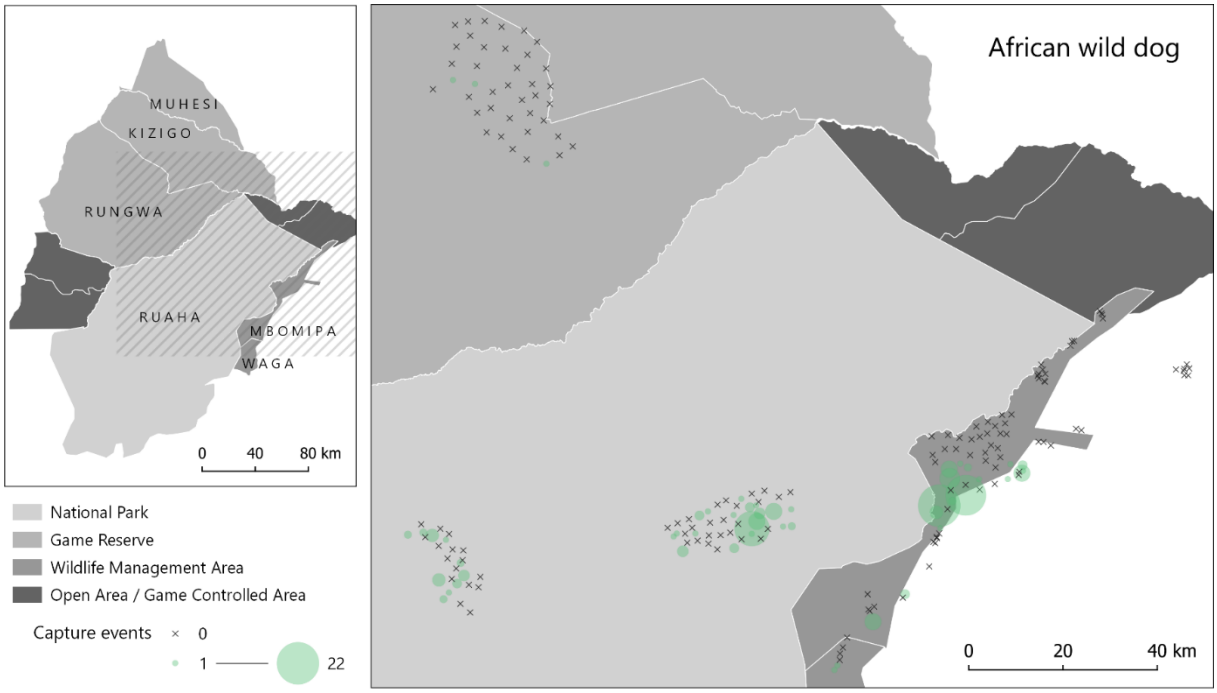
(C) **Spotted hyaena**



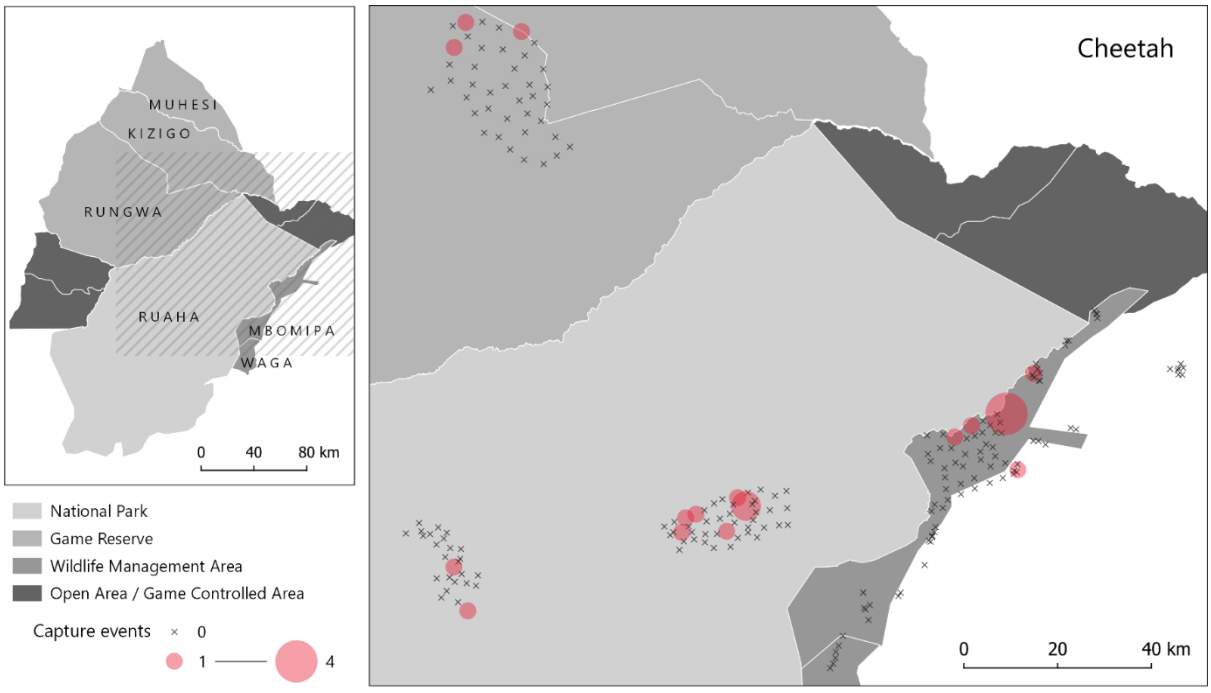
(D) **Striped hyaena**



(E) **African wild dog**



(F) **Cheetah**

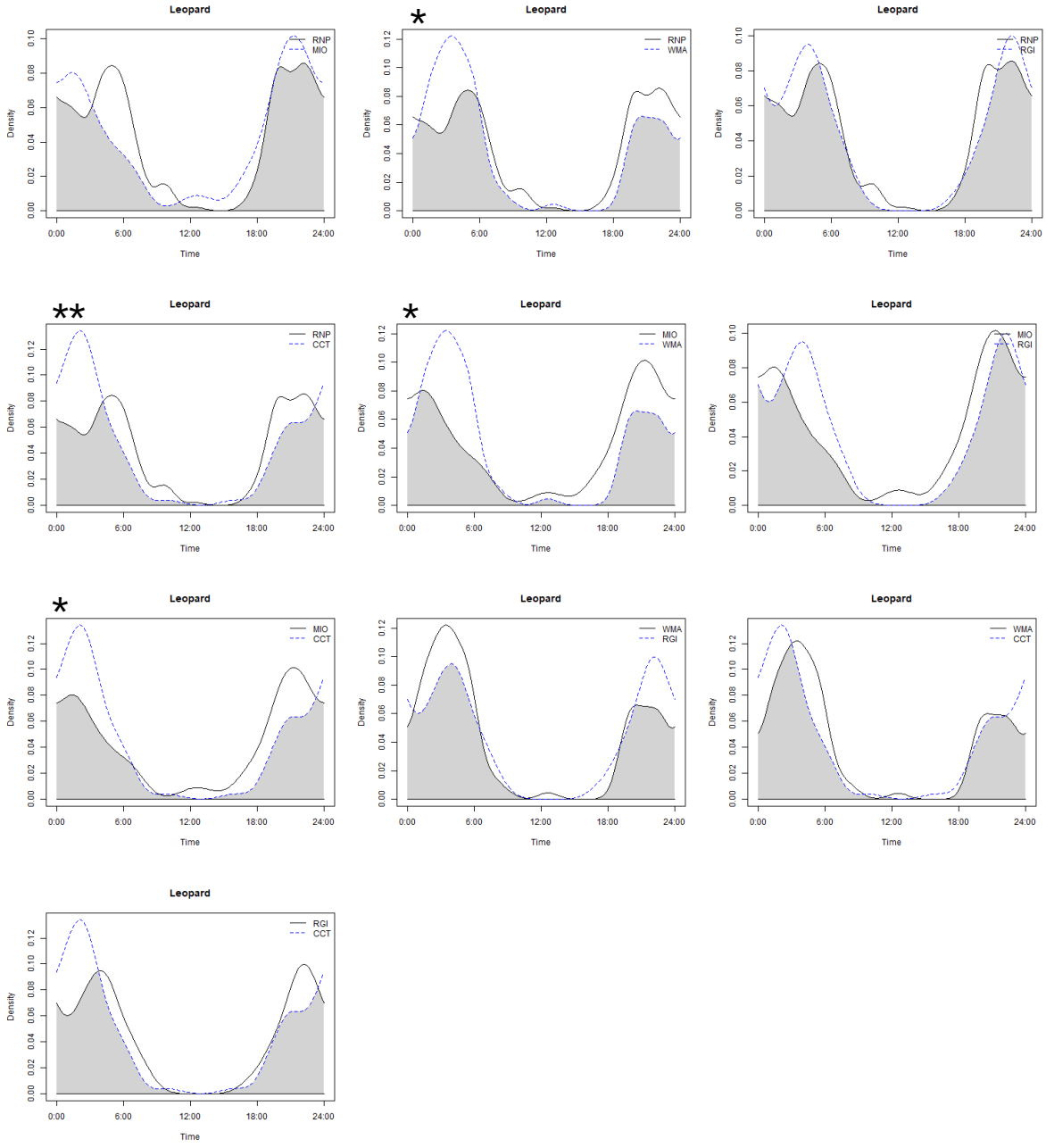


S6.3 Plots of within- and between-species activity overlap

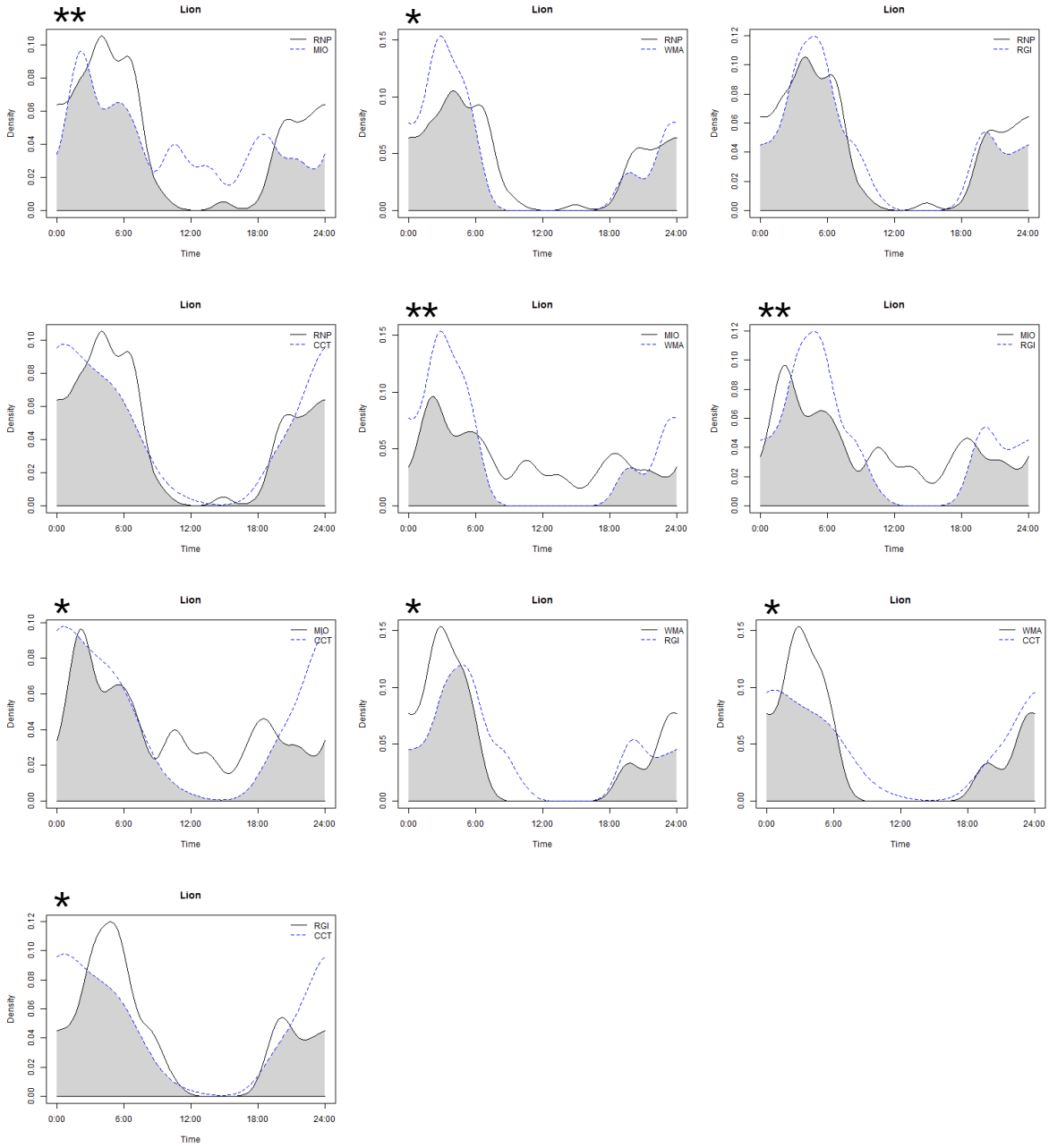
Within-species overlap

Figure S6.3.1: Activity pattern overlap for each large carnivore species between the different survey sites, produced by fitting a kernel density function to the capture data for each species. Areas shaded in grey correspond to the coefficient of overlap (Δ) for the species between the two sites of interest. Each study site is represented by a three letter code: RNP = Ruaha NP *Acacia-Commiphora*, MIO = Ruaha NP miombo woodland, WMA = MBOMIPA WMA *Acacia-Commiphora*, RGI = Rungwa GR miombo woodland, CCT = unprotected village land (community camera-trapping programme). Activity patterns marked with a single asterisk are significantly different (*; $p < .05$), and those marked with two asterisks are highly significantly different (**; $p < .001$).

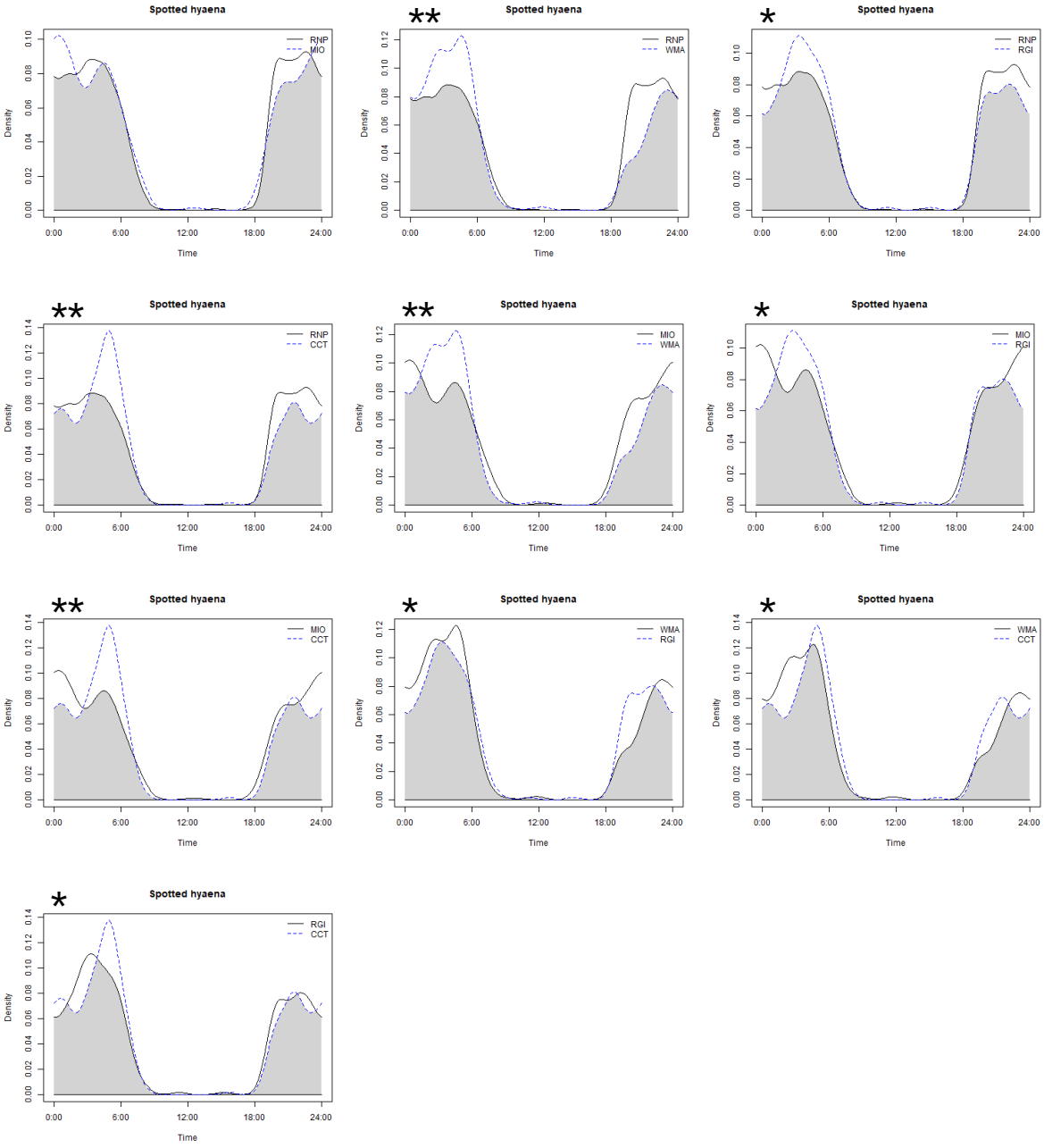
(A) **Leopard**



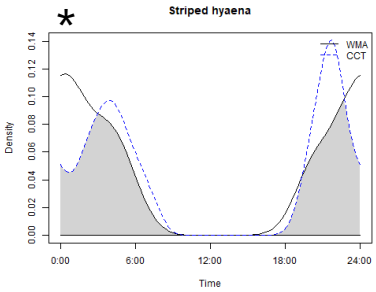
(B) **Lion**


**
Lion
RNP
MIO
Density
Time
0:00
6:00
12:00
18:00
24:00
*
Lion
RNP
WMA
Lion
RNP
RGI
Lion
RNP
CCT
**
Lion
MIO
WMA
**
Lion
MIO
RGI
*
Lion
MIO
CCT
*
Lion
WMA
RGI
*
Lion
WMA
CCT
*
Lion
RGI
CCT

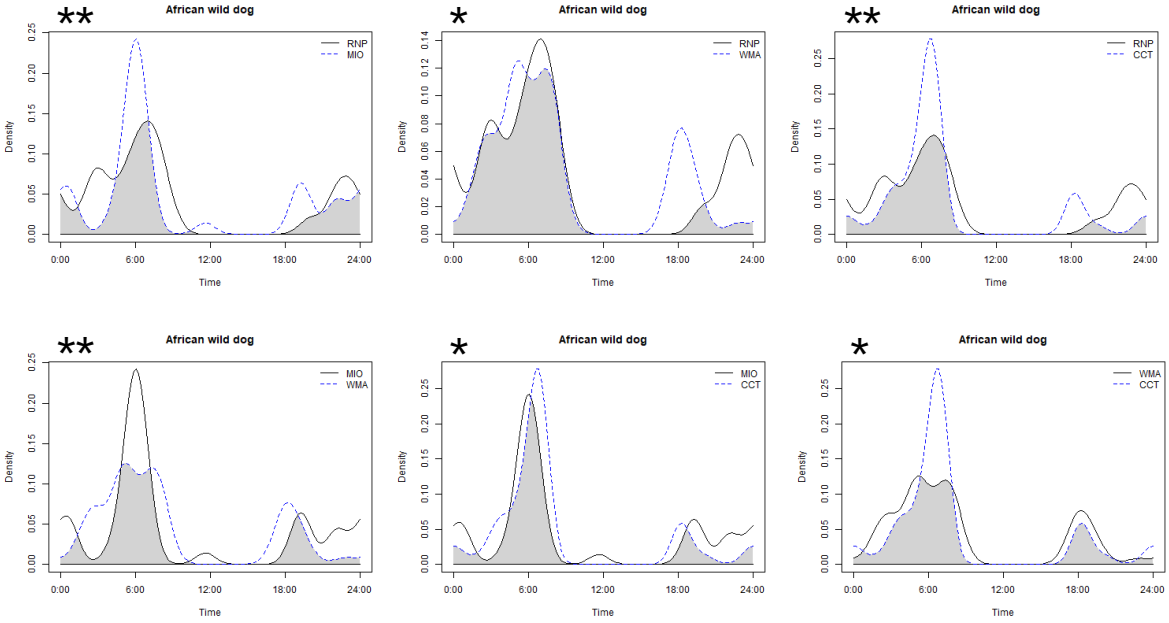
(C) **Spotted hyaena**



(D) **Striped hyaena**



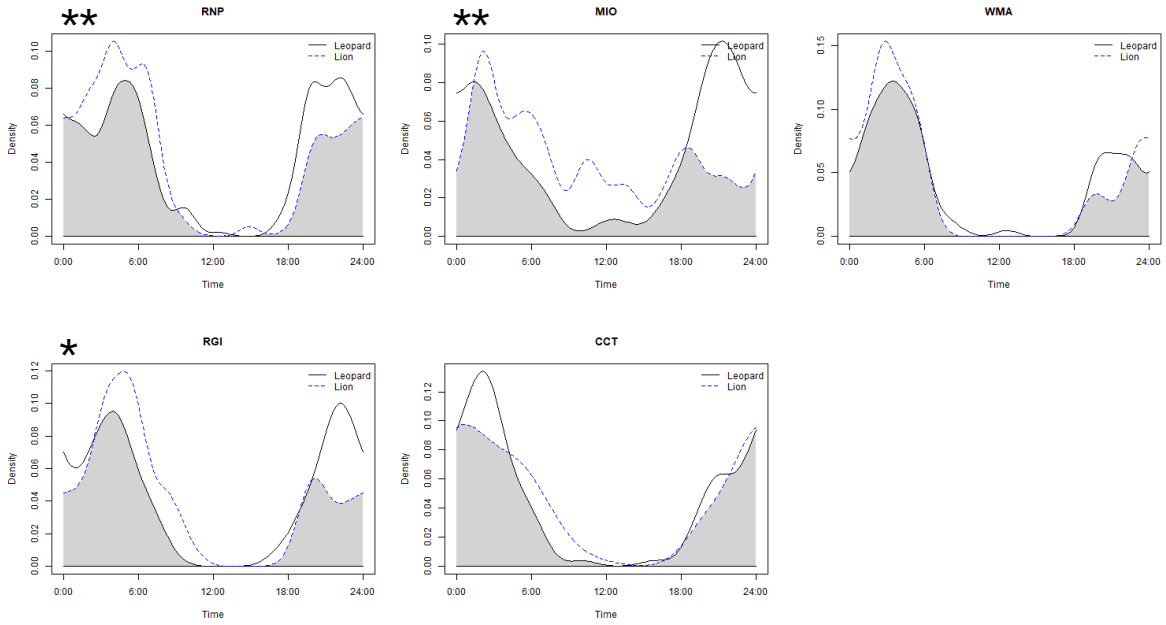
(E) **African wild dog**



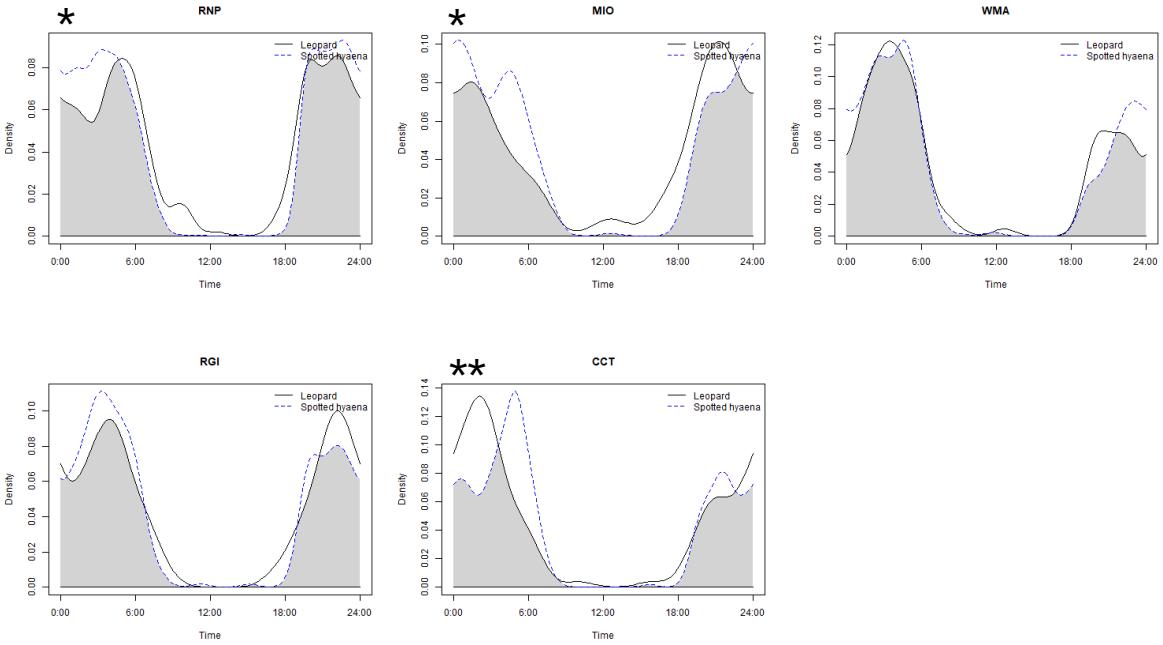
Between species overlap

Figure S6.3.2: Activity pattern overlap for each large carnivore species or sex pair (for lion and leopard only) across the five survey sites and using data from all sites combined, produced by fitting a kernel density function to the capture data for each species. Areas shaded in grey correspond to the coefficient of overlap (Δ) for that species pair. Each study site is represented by a three letter code: RNP = Ruaha NP *Acacia-Commiphora*, MIO = Ruaha NP miombo woodland, WMA = MBOMIPA WMA *Acacia-Commiphora*, RGI = Rungwa GR miombo woodland, CCT = unprotected village land (community camera-trapping programme). Activity patterns marked with a single asterisk are significantly different (*; p < .05), and those marked with two asterisks are highly significantly different (**; p < .001).

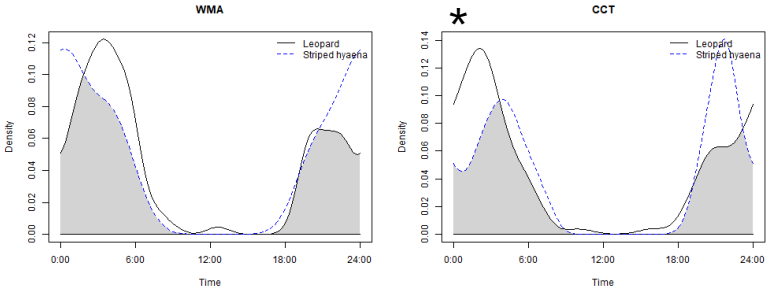
(A) **Leopard – Lion**



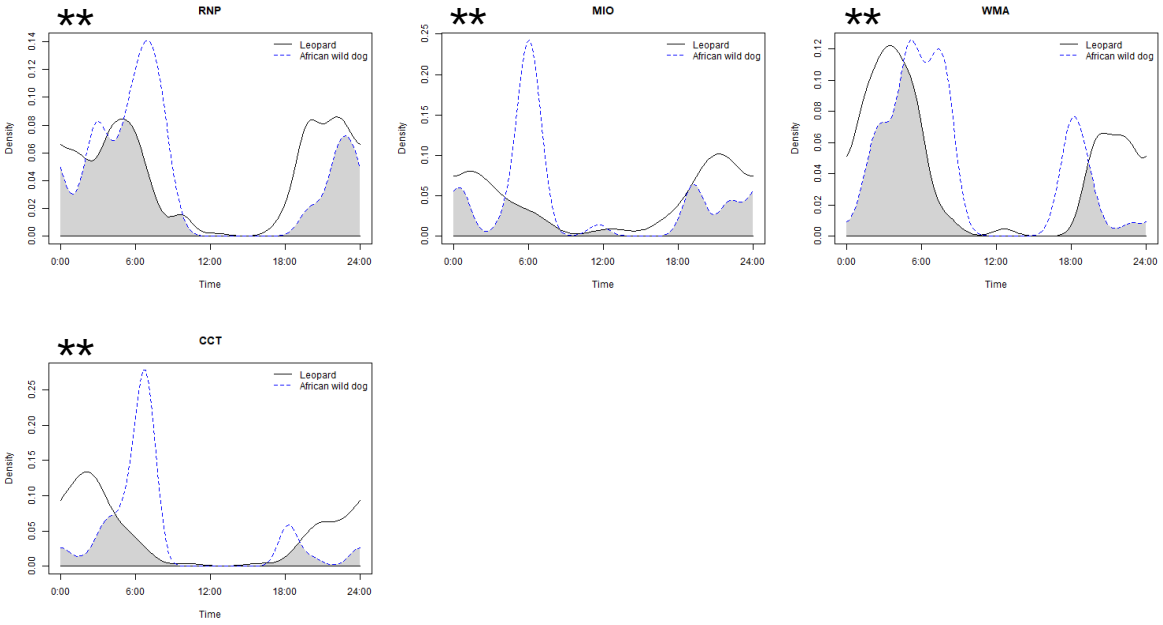
(B) **Leopard – Spotted hyaena**



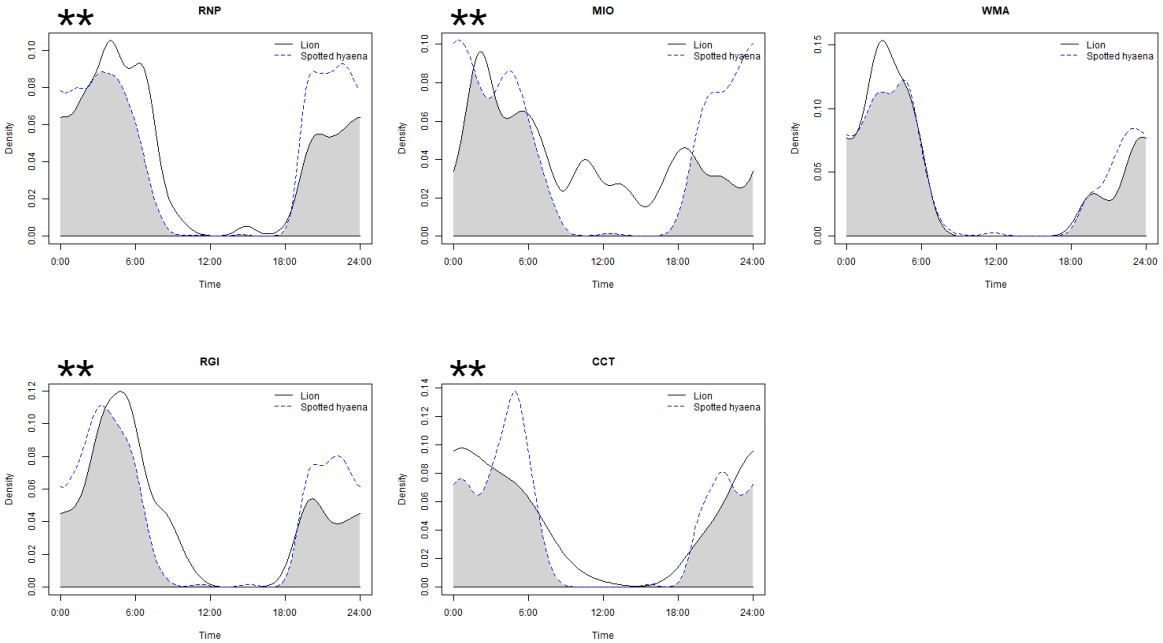
(C) **Leopard – Striped hyaena**



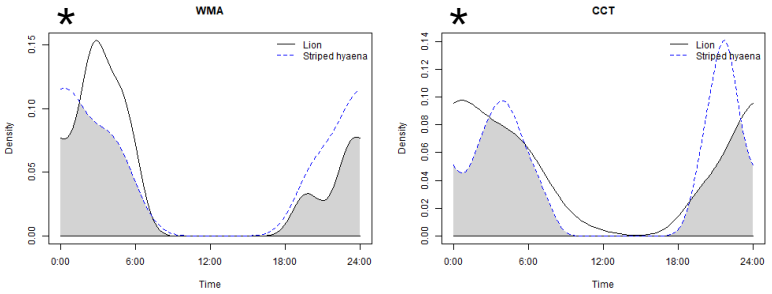
(D) **Leopard – African wild dog**



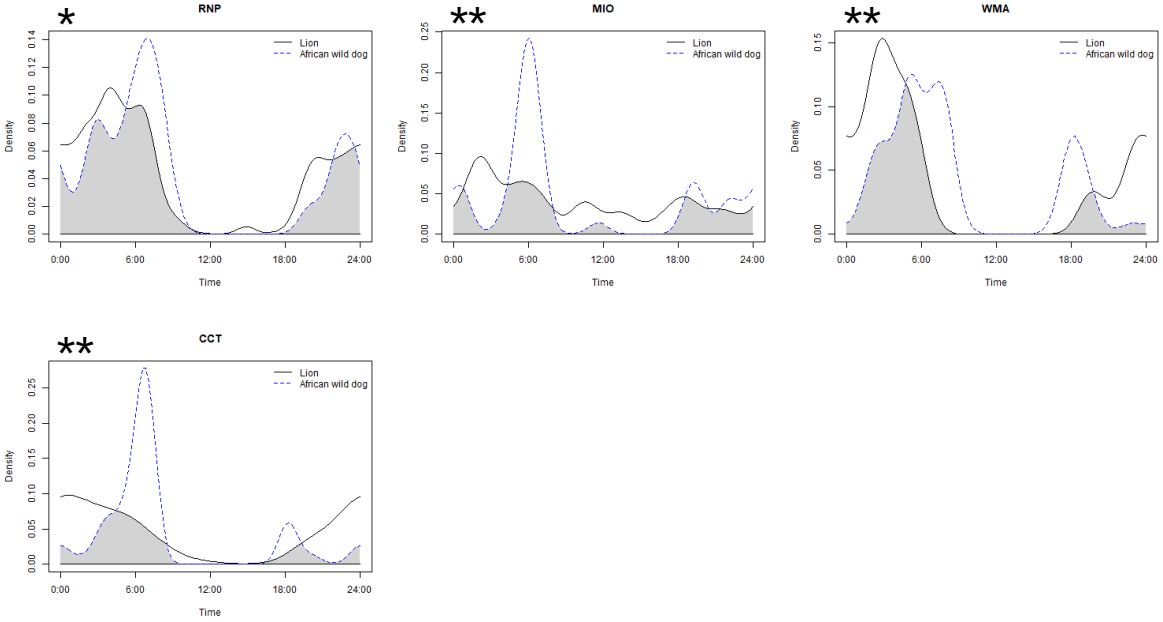
(E) **Lion – Spotted hyaena**



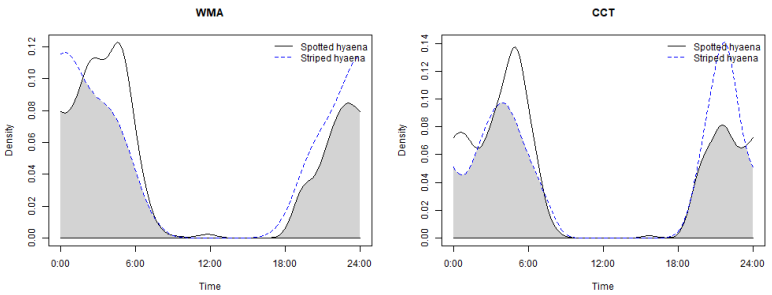
(F) **Lion – Striped hyaena**



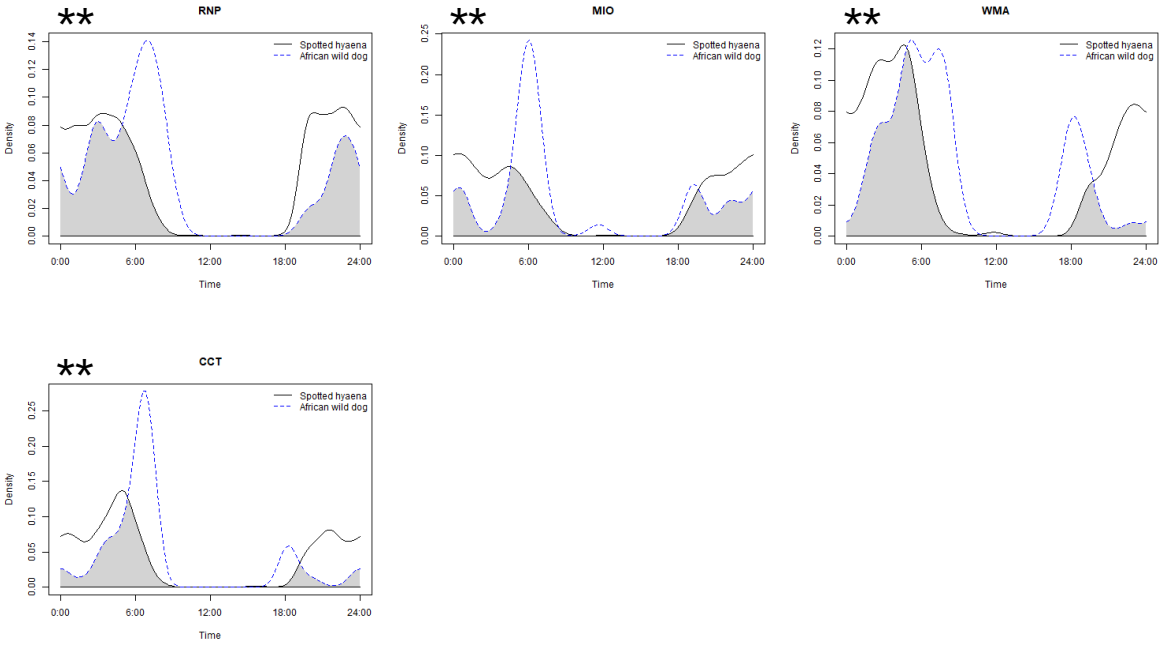
(G) **Lion – African wild dog**



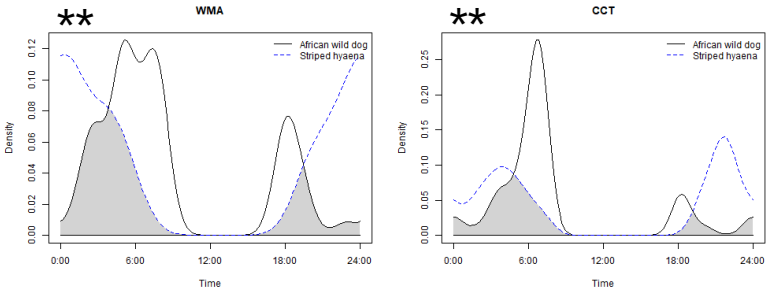
(H) **Spotted hyaena – Striped hyaena**



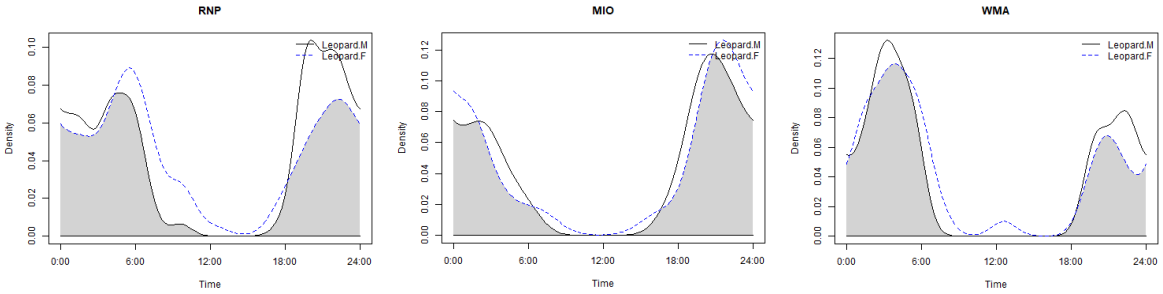
(I) **Spotted hyaena – African wild dog**



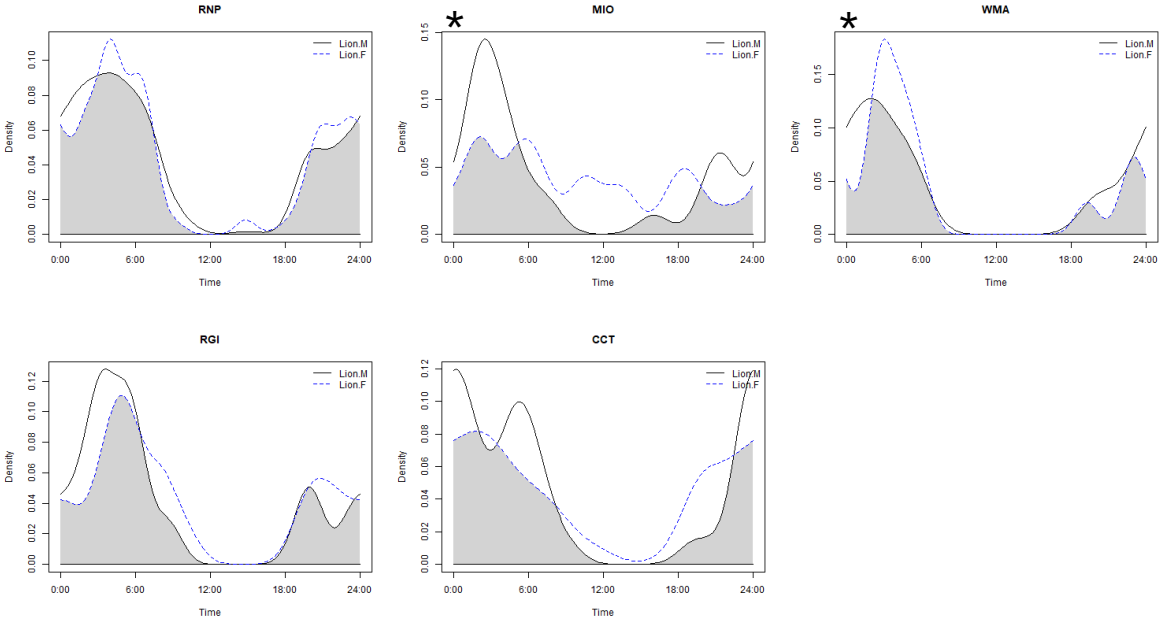
(J) **Striped hyaena – African wild dog**



(K) **Leopard (M) – Leopard (F)**



(L) **Lion (M) – Lion (F)**

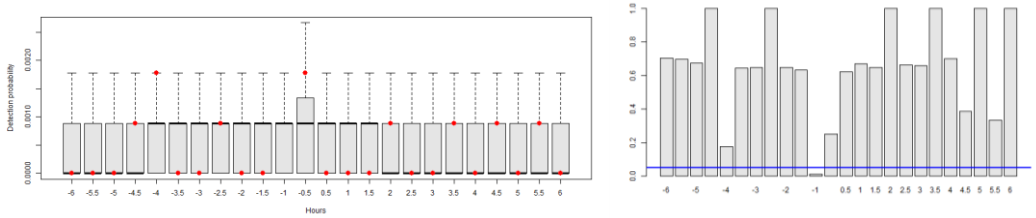


S6.4 Full temporal spacing analysis results

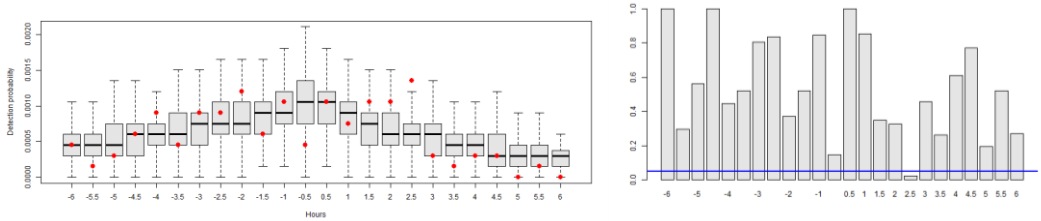
Figure S6.4.1 (overleaf): Full temporal spacing analysis results. Left-hand plots show the detection probability of species B before and after a capture of species A (at hour 0) at the same station. Boxplots show the expected probability of detecting species B in each time unit before and after capture of species A if there were no relationship between detections of species A and species B, while dots indicate the observed detection probability of species B for each time unit before and after capture of species A. Expected detection probabilities were derived by randomly sampling 1000 times from the observed activity pattern probability density function for that species. Right-hand plots show p-values for each time unit; bars below the blue line indicate time units where the observed probability of detecting species B differed significantly from the expected probability of detection ($p < .05$).

(A) **6 hours before and after capture, in units of 30 minutes**

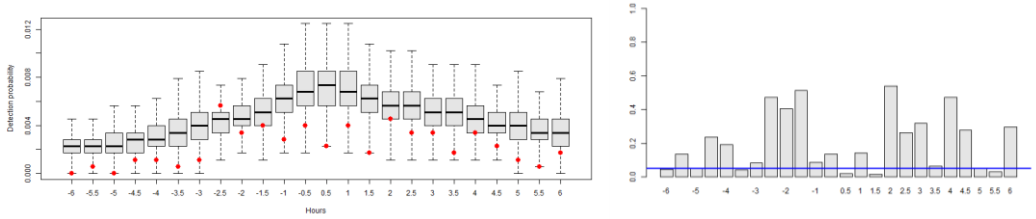
Species A: lion, Species B: leopard



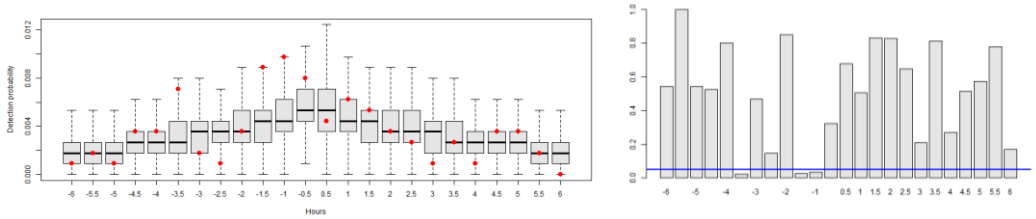
Species A: lion, Species B: spotted hyaena



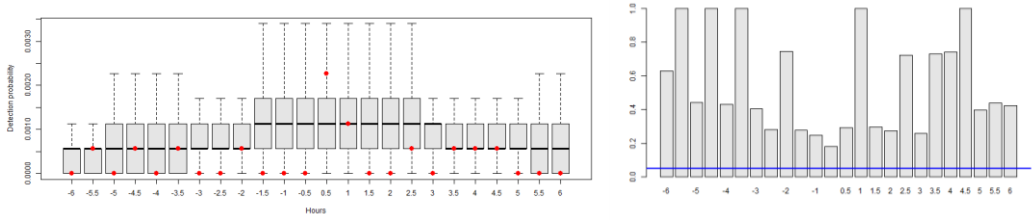
Species A: spotted hyaena, Species B: lion



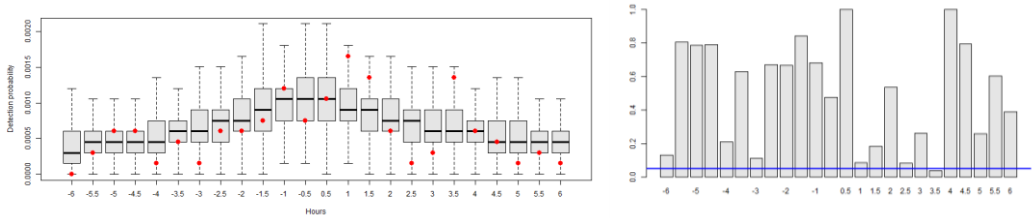
Species A: spotted hyaena, Species B: leopard



Species A: leopard, Species B: lion

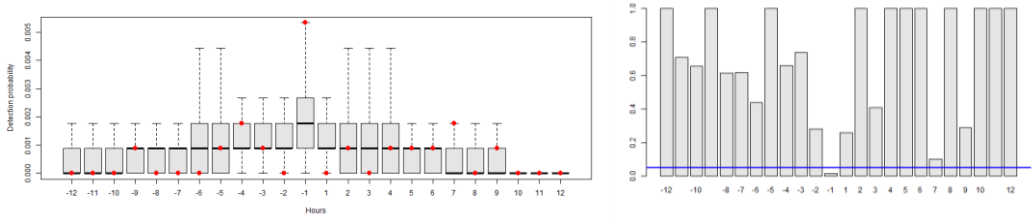


Species A: leopard, Species B: spotted hyaena

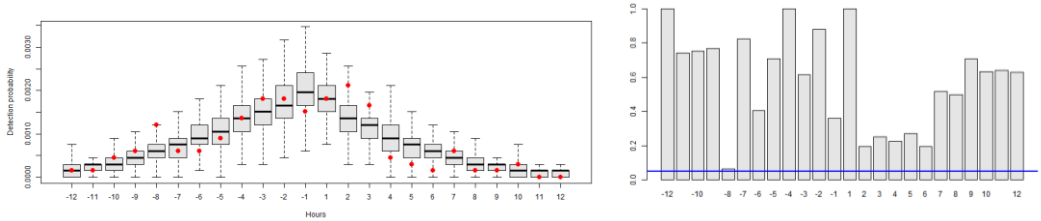


(B) **12 hours before and after capture, in units of 1 hour**

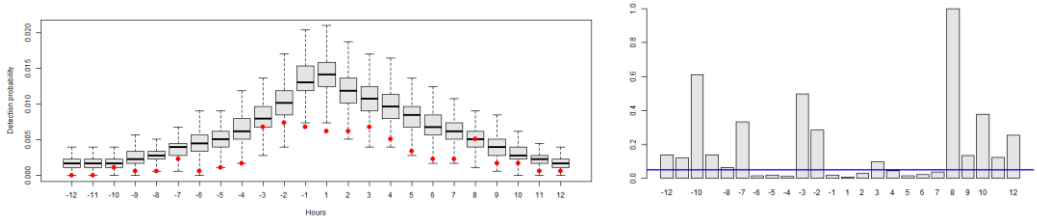
Species A: lion, Species B: leopard



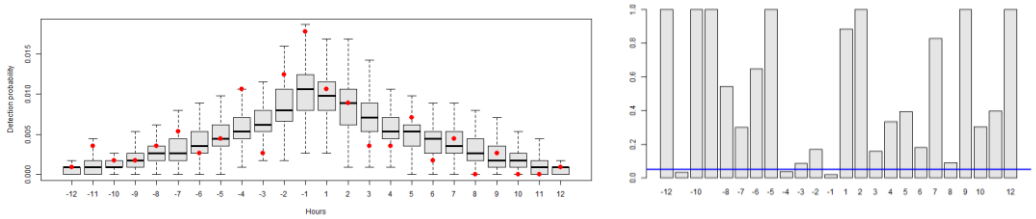
Species A: lion, Species B: spotted hyaena



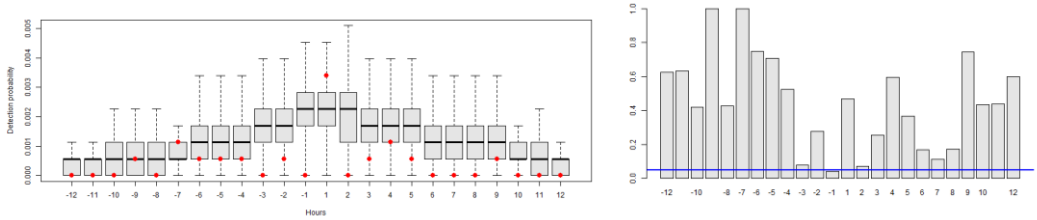
Species A: spotted hyaena, Species B: lion



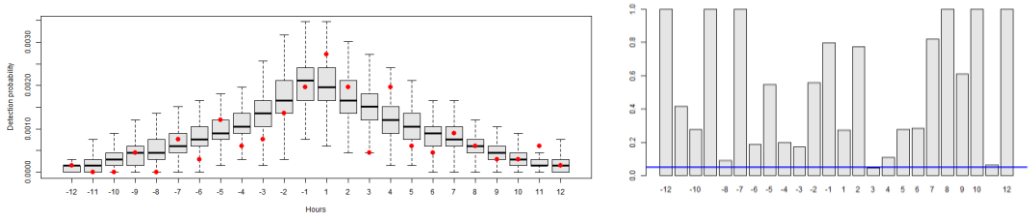
Species A: spotted hyaena, Species B: leopard



Species A: leopard, Species B: lion

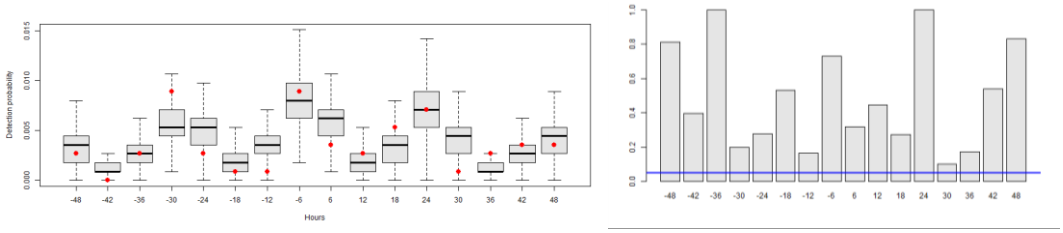


Species A: leopard, Species B: spotted hyaena

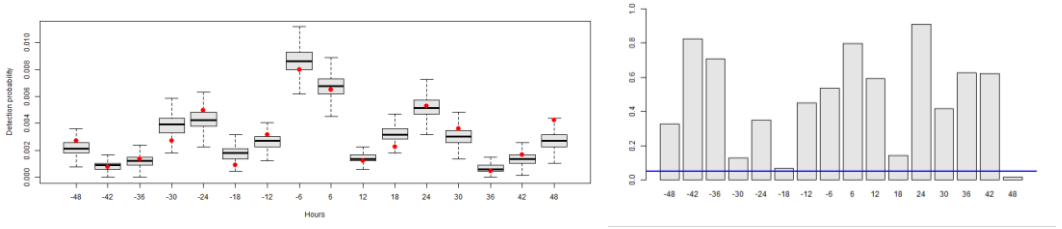


(C) **48 hours before and after capture, in units of 6 hours**

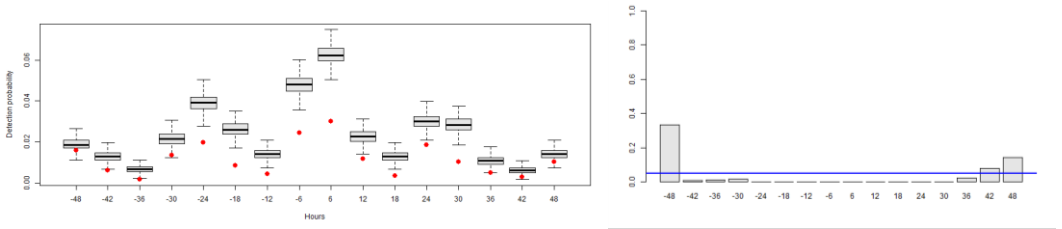
Species A: lion, Species B: leopard



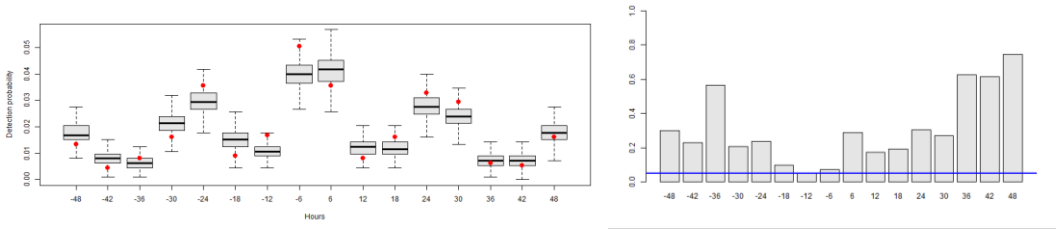
Species A: lion, Species B: spotted hyaena



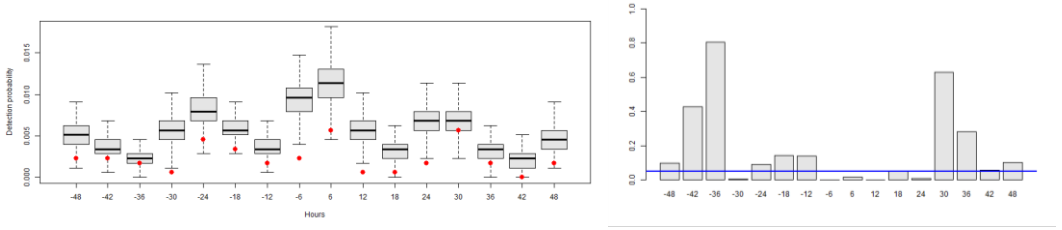
Species A: spotted hyaena, Species B: lion



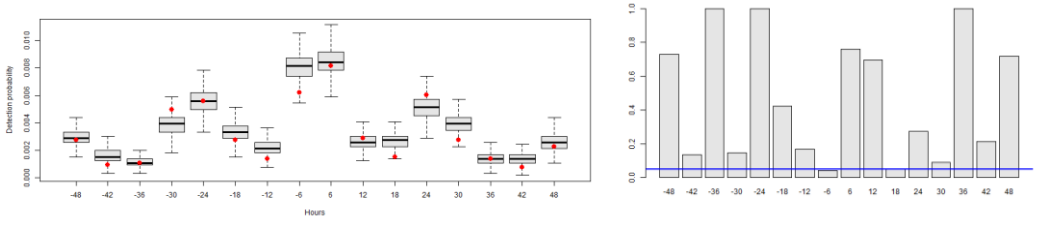
Species A: spotted hyaena, Species B: leopard



Species A: leopard, Species B: lion



Species A: leopard, Species B: spotted hyaena



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CHAPTER 7

Discussion

Discussion

7.1. Assessing and monitoring leopard populations

In the face of ongoing range losses and population declines among large carnivores (Ripple et al., 2014; Wolf & Ripple, 2017) and the underfunding of many PAs (Lindsey et al., 2018, 2014; Packer et al., 2013), there is a pressing need to understand how different conservation models can be used to effectively secure large carnivore populations while aligning with development goals (Coetzee, 2017; Naughton-Treves et al., 2005). A critical part of this process is the assessment and monitoring of large carnivore populations. However, successfully integrating monitoring into management plans is not just a question of which methods can deliver the best and most detailed insights, but also which can do so while being feasible for PA management to enact, ideally as part of a long-term monitoring framework integrated into adaptive management.

This thesis presents a multi-faceted example of how large carnivore status can be assessed in modern, mixed-use landscapes. The work presented makes use of two prominent large carnivore survey methods: spoor surveys (Chapters 3 & 4), which can be rapidly implemented across large areas at relatively low cost (Henschel et al., 2016; Thorn et al., 2010) to develop a landscape-level understanding of species distribution, habitat use drivers, and potential threats; and camera trap surveys (Chapters 5 & 6), which can be used to tease out population dynamics and behaviours in greater detail within representative areas of a wider landscape. While this thesis does not present an exhaustive example of the ways in which data collected through these survey methods can be used, it explores some of the most well-established uses of such data (occupancy modelling of spoor data, Chapter 3; SECR modelling of camera trap data, Chapter 5), as well as presenting examples of more novel applications (N-mixture modelling of spoor data, Chapter 3; machine learning modelling of spoor data, Chapter 4; spatiotemporal interactions from camera trap data, Chapter 6). Together, these survey methods can form a powerful toolkit capable of delivering complementary status insights for both single species (Chapters 3 & 5) and wider communities (Chapters 4 & 6) across mixed-use conservation landscapes. Importantly, these methods can be used to simultaneously collect data on multiple species across different scales in

a way that can be relatively cost- and time-efficient, and show great promise as methods that can be integrated into long-term monitoring by PA management authorities, whose resources are typically stretched thin. Finding ways to formally integrate the two methods (Dey et al., 2017) is a promising frontier for future research.

In recent decades, single-species assessments have fallen out of favour in conservation research (Roberge & Angelstam, 2004; Simberloff, 1998), giving way to an increased focus on community- and ecosystem-oriented assessments (Egoh et al., 2007). This reflects an increasing appreciation of the complex and highly variable nature of associations between sympatric species (Green & Sadedin, 2005), and the importance of maintaining ecosystem function (Harvey et al., 2017). However, making this transition without continuing some level of species-specificity can result in assessments that fall short in delivering actionable conservation recommendations where specific species are of particular interest. Large carnivores fall firmly into this category: not only do these species' range and dietary requirements leave them particularly vulnerable to habitat loss and conflict with humans (Ripple et al., 2014; Winterbach et al., 2013), but they can also be an important generator of funding for conservation, both through their value as flagship species for fundraising campaigns (Verissimo et al., 2011) and their ability to attract fee-paying tourists to ecotourism and hunting areas (Stein et al., 2010; van der Meer et al., 2016). This is exemplified by the leopard, which has been singled out as one of the world's most charismatic animals (Courchamp et al., 2018) and top ambassador species (Macdonald et al., 2017). As such, conservation efforts targeting leopard may be able to attract funding that benefits the large number of other species that co-occur alongside them, not just in Africa but across the species' extensive global range.

In light of this, monitoring programmes should continue to pursue single-species studies of priority species like leopard, but nest these within a multi-species perspective (Lindenmayer et al., 2007), to deliver complementary insights that reflect the many factors critical to populations' survival. This thesis illustrates how such an approach can be employed, by presenting assessments of leopard status alone

(Chapter 5), with the explicit incorporation of data on prey (Chapter 3) and competitors (Chapter 6), and as part of the wider mammal community (Chapter 4).

The divergent findings of my two habitat use analyses using the same dataset in Chapters 3 & 4 demonstrate how community-level assessments can provide insights that contrast to those revealed by assessments of individual species. For leopard, these differences were likely a result of the explicit incorporation of information on prey in Chapter 3, rather than prey being represented by environmental proxies – which are also linked to an area's protection status, and thus may have overshadowed the importance of other variables – in Chapter 4. Accounting for imperfect detection, as I was able to do in Chapter 3, may also be a factor underlying these differences for the highly-elusive leopard. Nevertheless, the multi-species perspective employed in Chapter 4 enabled me to identify additional emerging threats facing leopard and their prey in the KAZA landscape, which were not revealed by my species-specific analysis. My findings therefore underline the complementarity of single- and multi-species assessments.

7.2. The African leopard: How resilient really?

The leopard has a longstanding reputation as one of the most resilient and adaptable African large carnivores (Hunter et al., 2013), despite the species' status being poorly understood across much of its remaining range (Balme et al., 2014; Jacobson et al., 2016; Stein et al., 2020). One of the major themes I explored throughout this thesis is just how valid this reputation actually is, by investigating how well leopard are faring across different land uses, management types, and habitats in two major African conservation landscapes.

My findings suggest that this reputation is at least partly deserved: leopard are capable of remaining widespread across multiple-use landscapes (Chapter 3), and are able to persist in unprotected areas (Chapter 6) – including areas with higher human density (Chapter 4) – less-strictly protected areas (Chapters 3, 4 & 5), and strictly protected areas with consumptive use (Chapters 3, 4 & 5). This aligns with previous research in Africa and Asia which has found that, although low human disturbance is often one of the best predictors of leopard habitat use (Kshettry et al., 2017; Ngoprasert et al., 2007;

Zakaria & Sanei, 2011) and the species has been extirpated from some particularly heavily-impacted areas (Rasphone et al., 2019; Rostro-García et al., 2016), populations are able to successfully persist in areas with intermediate human impacts (Athreya et al., 2015; Burton et al., 2012; Constant, 2014; Maharjan et al., 2017; Strampelli et al., 2018). The species' highly elusive nature and dietary plasticity are likely to play an important part in this resilience, as leopard are particularly adept at fine-scale avoidance of both competitors (Chapter 6; Balme et al., 2017; du Preez et al., 2015; Miller et al., 2018; Stein et al., 2015) and humans (Chapter 6; Henschel et al., 2011; Odden et al., 2014; Strampelli et al., 2018; Van Cleave et al., 2018), and are able to adapt their diet to a range of prey depending on available resources (du Preez et al., 2017; Hayward et al., 2006).

However, being resilient to impacts does not mean a species is immune to them: while leopard populations may be able to persist in spite of pressures, these pressures can still have long-term consequences for individual and population fitness. In Chapters 3 & 5, I show that the density of leopard populations can be negatively affected by both direct and indirect human impacts – a pattern that has been observed not just outside PAs but also within them, through edge effects and illegal activities that penetrate PA boundaries, as well as legal extraction activities within PAs (Abade et al., 2018; Balme et al., 2010; Havmøller et al., 2019; Henschel et al., 2011; Marker & Dickman, 2005; Rosenblatt et al., 2016; Williams et al., 2017). These local declines can compromise the long-term resilience of populations, exposing them to detrimental population sinks (Dias, 1996; Loveridge et al., 2007) and demographic shifts that may eventually lead to local extinctions (Loveridge et al., 2016; Naude et al., 2020).

In Chapters 3 & 5, I highlight impacts on prey availability – itself one of the most important predictors of leopard persistence (Chapter 3; Abade et al., 2018; Burton et al., 2012; Constant, 2014; Kane, 2014; Steinmetz et al., 2013) and abundance (Chapter 5; Boast and Houser, 2012; Marker and Dickman, 2005; Rosenblatt et al., 2016; Stein et al., 2011) – as one of the most important mechanisms by which humans impact leopard populations. Large carnivore numbers are strongly correlated with prey abundance (Carbone & Gittleman, 2002), and prey numbers are themselves tightly linked to habitat conversion and

other human impacts (Wolf & Ripple, 2016). With these pressures showing no signs of abating across Africa as we progress through the 21st century (Tilman et al., 2017), it seems likely that leopard numbers will continue to decline throughout the continent without major intervention (Stein et al., 2020). These losses are likely to be further exacerbated by the effects of ongoing climate change (FAO, 2017), which could have significant impacts on the distribution and movement patterns of prey (Chapter 4).

The additional direct impacts of humans on leopards, which include retaliatory killings in response to predation on livestock (although in Africa the species is targeted to a far lesser degree than lion and spotted hyaena; Kissui, 2008), accidental bycatch in snares, and poisoning (which, like snaring, may be targeted at other species but can cause indiscriminate harm; Naderi et al., 2018; Rostro-García et al., 2016; Swanepoel et al., 2015; Zafar-ul Islam et al., 2018), is likely to further endanger populations already suffering the effects of a depleted prey base in heavily impacted areas. This is a particular threat in areas where the loss of wild prey forces an increased reliance on livestock, which can in turn worsen human-leopard conflict (Harihar et al., 2011; Inskip & Zimmermann, 2009). What's more, I show in Chapter 6 that human pressures may interfere with some of the coexistence mechanisms employed by leopard to minimise harmful interactions with competitors. Human impacts may therefore exacerbate already intense levels of intra-guild competition for leopard in areas where they must compete with other species for increasingly limited resources, and must be taken into account in conservation planning.

7.3. Conserving leopard in modern African conservation landscapes

Armed with the knowledge that leopard are vulnerable to anthropogenic impacts both within and outside PAs, the findings presented in this thesis have important implications for different conservation models in place across sub-Saharan Africa.

Throughout the thesis, I provide evidence that PAs are of critical importance for leopard populations. However, as I argue above, leopard can still suffer the effects of anthropogenic pressure within PA boundaries, and it is well established that poor management can undermine the conservation gains offered by PAs (Coetzee, 2017; Lindsey et al., 2017; Watson et al., 2014). As a result, it is imperative

that areas already under protection continue to be managed effectively, and that adequate funding and support is provided to management authorities to ensure effective law enforcement within these areas (Adams et al., 2019; Bruner et al., 2004; Lindsey et al., 2018).

In Chapter 3 I found that, even where mixed-use landscapes are managed from a landscape-scale perspective, highly protected areas remain a strong predictor of habitat use by leopard. As such, to secure leopard populations at these scales, there is a clear need to focus on either promoting large-scale persistence outside PAs – which can be extremely difficult to achieve, particularly with the substantial pressure to convert remaining natural habitat across sub-Saharan Africa – or, more realistically, prioritising key corridors for protection to maintain functional connectivity between areas of core habitat. While landscape-scale management frameworks like TFCAs do not in and of themselves ensure persistence of wildlife outside PAs, they do provide the institutional framework necessary to establish and maintain linkages between populations, which are vital for dispersal, migration, and long-term persistence. TFCAs provide the means to secure these areas when they span country boundaries; where critical linkages lie within a single country, national conservation and land management planning must provide the equivalent tools (Arts et al., 2017).

In Chapters 3 & 5, I show that community-managed wildlife areas can hold significant value for leopard and other species. By their very nature – encompassing areas of habitat that are highly enmeshed with areas of human settlement, often neighbouring more strictly-protected areas – community-managed wildlife areas typically face greater anthropogenic pressures than strict PAs like National Parks, and can struggle to raise sufficient funding for conservation due to lower wildlife densities and a lack of capacity to establish revenue-generating activities (Measham & Lumbasi, 2013). However, these same traits are what make such areas so critical for effective conservation at scale: community-managed areas are often a key component of connectivity between strict PAs (Riggio & Caro, 2017), and can play an important role in buffering core populations from severe impacts (Denninger Snyder et al., 2019).

By remaining in the hands of communities, community-managed wildlife areas have the potential to deliver local benefits that outweigh the often substantial opportunity costs of not converting land or

otherwise exploiting natural resources, instead providing a framework for sustainable use (Magome & Fabricius, 2004). However, many community-managed wildlife areas in sub-Saharan Africa continue to fall short in realising these benefits. In Tanzania, WMAs have achieved mixed success in their engagement of local communities (Walsh, 2000), and do not appear to have contributed to widespread poverty reduction (Keane et al., 2020). To ensure the continued existence of these important wildlife areas, support for community-managed areas must therefore remain a national and international conservation priority, with increased efforts made to empower member communities and secure the intended development benefits. Monitoring of wildlife populations is also particularly important in these areas, which are at risk of acting as population sinks if negative impacts on species remain high.

In Chapters 3 & 5 I contribute to evidence that, while trophy hunting can have a top-down impact on hunted leopard populations (Packer et al., 2010), it can also secure vital habitat for the species that may otherwise be lost through degradation or conversion to agriculture (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007). Crucially, this value is only realised when hunting activities are effectively and sustainably managed, and investments are made into habitat and wildlife protection activities (IUCN, 2016; Lindsey et al., 2007). To balance top-down pressure on leopard populations in favour of their long-term conservation, trophy hunting must be closely monitored and adaptively managed to ensure offtake quotas remain at a level that will not have detrimental long-term impacts (Creel et al., 2016; Loveridge et al., 2007; Naude et al., 2020). Other forms of human impacts in trophy hunting areas must also be closely monitored, to ensure that density suppression in hunted populations is not compounded by other pressures (Loveridge et al., 2020).

The importance of diversified conservation models has been thrown into sharp relief by the COVID-19 pandemic and its devastating impacts on international tourism, which forms the backbone of many large carnivore conservation strategies in sub-Saharan Africa (Lindsey et al., 2020). At the outset of the pandemic, it was projected that revenue collected by the institutions responsible for PA management in Tanzania would shrink substantially, with losses predicted at 82% for TANAPA, which oversees National Parks (reserved for photographic tourism), and 62% for TAWA, which oversees Game

Reserves and other areas primarily reserved for hunting (Kolumbia, 2020). Although this suggests that the country's trophy hunting industry may have weathered the international travel restrictions of 2020 slightly better than the photographic tourism industry – likely as a result of differences in their business models, with trophy hunting typically bringing in smaller volumes of tourists paying higher fees per person (Ministry of Natural Resources and Tourism, 2016) – both industries have undoubtedly been severely impacted by the precipitous drop in international travel in 2020, which will in turn have had profound impacts on the livelihoods of millions of people (Christie et al., 2014). The pursuit of alternative mechanisms for funding and managing wildlife resources – such as payment for ecosystem services, private philanthropy, and debt for nature swaps (Crossman et al., 2011; Pringle, 2017; Venter et al., 2009) – should therefore be seen as a priority to build long-term resilience into conservation models, and ensure the continued protection of Africa's remaining natural habitats.

7.4. Limitations and future directions

Although this thesis sheds light on multiple aspects of leopard status across mixed-use African landscapes, all of the assessments presented (Chapters 3, 4, 5 & 6) are snapshots of species status at a single point in time. Future research efforts in the study landscapes should seek to replicate these studies over longer periods, so that the data collected can be used to understand long-term and seasonal trends in leopard distribution (Chapter 3) and density (Chapter 5). Information of this kind is central to conservation planning, and is a particularly important requirement for core habitat and corridor prioritisation exercises. Ideally, multi-year assessments should be carried out in the study landscapes as part of long-term monitoring programmes overseen by the relevant management authorities, to fully integrate monitoring into management planning and allow for an adaptive management approach to conservation.

For instance, SECR analysis of data from repeated camera trap surveys at the same sites in Ruaha-Rungwa (Chapter 5) would provide critical information on rates of mortality in the studied populations. This would help identify whether any parts of the landscape are acting as population sinks, and therefore having knock-on effects on the stability of the core leopard population in the complex. This is a

particularly important possibility to investigate in MBOMIPA WMA, due to the area's critical positioning along the Great Ruaha River and its vulnerability to human impacts, but should also be prioritised in Rungwa GR and other hunting areas to enable adaptive quota-setting and sustainable offtake (IUCN, 2016). Long-term monitoring would also help establish what impacts the progressive drying of the Great Ruaha River may be having on the ecosystem's leopard population. If a declining trend is identified even in the best-protected part of the landscape (and particularly if similar trends are identified for other species), this could provide an impetus for authorities to take further action to safeguard this critical water source for the wildlife populations that rely upon it.

Throughout this thesis, I emphasise the importance of assessing species status at the landscape scale, and incorporating information from as many different components of a landscape as possible into these assessments. While I do go some way to achieving this goal, there would be considerable value in expanding the scope of the assessments presented to cover wider and more varied areas. In the KAZA TFCA (Chapters 3 & 4), conducting spoor surveys not just in the southern part of the landscape but across the whole TFCA, and including more unprotected areas, would enable leopard distribution and multi-species connectivity to be modelled for a vast, contiguous area spanning five countries. This would hold significant value for corridor planning within the landscape. In Ruaha-Rungwa (Chapters 5 & 6), carrying out camera trap surveys at more sites – including less productive areas, such as the dry escarpment within Ruaha NP; less strictly-protected components of the landscape, such as Game Controlled Areas and Open Areas; and completely unprotected areas – would help develop a more comprehensive assessment of leopard status, population drivers, and threats across the landscape. Although a number of factors would make implementing surveys in these areas challenging, including lack of accessibility and risk of camera theft, this information would provide a more nuanced understanding of how to improve the long-term viability of leopard in this critical stronghold.

While the spoor and camera trap surveys presented in this thesis represent valuable sources of information on leopard and sympatric species, there are some aspects of leopard status and ecology that could not be investigated with these data. In Chapter 6, for example, it was not possible to determine

the exact underlying mechanisms of avoidance and attraction among large carnivores in Ruaha-Rungwa from the camera trap dataset, and my inferences about the direction of intra-guild interactions were informed by existing knowledge of associations between different large carnivore species (Cusack et al., 2017). As such, I recommend more in-depth research into competitive interactions and dietary overlap between leopard and other large carnivores in Ruaha-Rungwa and elsewhere, to disentangle the precise coexistence mechanisms employed by the species, and how these may be impacted by heightening human pressure.

Movement data from GPS or VHF collars would be particularly complementary to the data employed in this thesis, as they would reveal additional insights into leopard ecology and behaviour beyond those I was able to explore here. Collar data can be a powerful tool to gain insights into dispersal and connectivity (Elliot et al., 2014; Zeller et al., 2018), and could be used in the KAZA TFCA to explore linkages between leopard subpopulations across PA and country boundaries (see Brennan et al., 2020 for an example with other species). Moreover, movement data from KAZA could be used to investigate the potential consequences of climate change projections and management changes on the landscape's leopards (Ashrafzadeh et al., 2018; Rather et al., 2020). Collar data could also be used to investigate the fine-scale coexistence mechanisms being used by leopard to reduce harmful encounters with other large carnivores in more detail than was possible from camera trap data alone (Chapter 6; Vanak et al., 2013), in addition to providing a clearer picture of how the species' movement patterns vary across mixed-use and human-impacted landscapes, and how individuals may be modifying their movements to avoid humans (Odden et al., 2014; Oriol-Cotterill et al., 2015; Van Cleave et al., 2018). Investigating possible spatial responses would be particularly interesting given the evidence of temporal avoidance of humans in the landscape (Chapter 6).

Finally, given my conclusion that leopard are resilient but not immune to human impacts, there is a clear need to delve deeper into how leopard populations are able to persist in impacted areas, and what their thresholds of tolerance are to different pressures. Human-induced mortality is one area that would particularly benefit from further research: while it is known that illegal hunting, snaring, and poisoning

have an impact on African leopard populations (Balme et al., 2009; Stein et al., 2020; Swanepoel et al., 2015), their impacts can be very difficult to quantify given the species' highly elusive nature, and the fact that these activities typically take place in remote or unprotected areas away from oversight (Liberg et al., 2012; Ogada, 2014). Similarly, although unprotected land is currently thought to make up a considerable part of the species' African range (Swanepoel et al., 2013), continuing to assume that leopard can withstand human impacts in these areas without clear evidence of this could contribute to unseen losses, and have potentially devastating consequences for the species. Because of this, there is a pressing need for more research into leopard inhabiting completely unprotected areas – which was achieved to a limited extent in this thesis (Chapters 3, 4, & 6) – to help find ways to preserve these acutely vulnerable populations, and minimise population-endangering edge effects (Woodroffe & Ginsberg, 1998).

7.5. Conclusion

This thesis contributes to our understanding of how leopard are faring in the mixed-use conservation landscapes characteristic of modern day Africa. By shedding light on the status of populations in two of the species' remaining continental strongholds (Chapters 3 & 5), as well as their drivers (Chapters 3, 4 & 5) and threats (Chapters 3, 4, 5 & 6), I hope that the findings of this research will make a meaningful contribution to conservation and management planning for the globally important leopard populations of the KAZA TFCA and Ruaha-Rungwa, as well as populations elsewhere in the species' African range.

Pursuing novel and conservation-focused research will be essential to conserve Africa's remaining leopard populations. In this thesis, I have attempted to provide a case study in how such research may be achieved, by making use of new and emerging tools to investigate leopard status and ecology across two human-impacted landscapes. My assessment of leopard habitat use and relative abundance in KAZA (Chapter 3) represents the first use of N-mixture models to study leopard, in addition to being one of the first studies to model African leopard habitat use over such a large scale. My investigation of multi-scale, multi-species habitat selection in KAZA (Chapter 4) is the first time machine learning has been used to model spoor data in a multi-scale framework, and one of the first studies of multi-scale

habitat use for such a large and diverse mammal assemblage. My analysis of leopard population density in Ruaha-Rungwa (Chapter 5) provides some of the first such estimates for the country, including one of the first estimates in a Tanzanian trophy hunting area, and in a miombo woodland habitat, which represent an important component of the species' range in Africa (Olson et al., 2001; Stein et al., 2020). Finally, my investigation of interspecific interactions in Ruaha-Rungwa (Chapter 6) is one of the first studies of how coexistence mechanisms among large carnivores may be modified by the presence of humans.

Looking to the future, it is clear that securing the continued persistence of Africa's large carnivore populations will be an uphill battle, and will require the needs of the continent's remaining wilderness areas to be balanced with the needs of its human populations. With this shared goal in mind, researchers, governments, land managers, and other stakeholders must work together to develop future-proof monitoring programmes and conservation mechanisms, that secure benefits not just for Africa's iconic large carnivores, but for the rights and livelihoods of communities that live alongside them.

7.6. References

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APPENDIX 1

Multi-scale habitat use of an intact large carnivore guild and their prey in a modern mixed-use African landscape

Paolo Strampelli, Philipp Henschel, Charlotte E. Searle, David W. Macdonald, Amy J. Dickman

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Understanding habitat use of large carnivores and their prey in modern, human-impacted landscapes is essential to ensure their long-term conservation. Few quantitative assessments, however, adopt an integrated approach that can capture the complex and diverging habitat requirements of complete carnivore guilds, with most focusing on single species and scales. Here, we attempt such an investigation by modelling habitat use of an intact East African large carnivore guild, their prey, and illegal human activity across the 50,000 km^2 Ruaha-Rungwa landscape in Tanzania. We employed occupancy modelling to investigate space use at two biologically meaningful scales, and determine the relative impact of biotic, anthropogenic, and management variables on habitat use across land-use types and anthropogenic impact gradients. Habitat conversion to agriculture and prey availability, not legal protection, were the major limiting factors for large carnivores at a landscape scale, highlighting the importance of intact habitat outside protected areas for wide-ranging species. Lion appear particularly vulnerable to human disturbances, with evidence of top-down limitation even within the best-protected areas of the landscape. Conversely, African wild dog were limited by habitat features within protected areas, appearing to avoid areas of high sympatric predator density, while also exhibiting the lowest tolerance to habitat conversion. Spotted hyaena and leopard were the most adaptable large carnivores, although results reveal persistence thresholds lower than expected. There was no evidence of large carnivore occurrence being impacted by whether an area was used for photographic or trophy hunting tourism, with on-the-ground law enforcement being more important. All species fared better in actively managed hunting areas than in vacant hunting areas, and we identify a novel threat to Tanzania's conservation areas in the form of decreased management investments associated with the abandonment of trophy hunting areas. Finally, our findings also reveal the importance of drier and less-productive habitats, typically less prioritised for conservation, for both large carnivore and prey species.

APPENDIX 2

Insights into the status and distribution of cheetah (*Acinonyx jubatus*) in an under-studied potential stronghold in southern Tanzania

Paolo Strampelli, Charlotte E. Searle, Josephine Smit, Ana Grau, Philipp Henschel, Alex L. Lobora, Nicholas Mitchell, David W. Macdonald, Amy J. Dickman

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Research on the African cheetah (*Acinonyx jubatus*) exhibits strong geographical biases, with most studies taking place within a few, well-studied populations. Here, we provide the first insights into the population status and distribution of a globally important cheetah population, in the 50,000 km^2 Ruaha-Rungwa landscape in southern Tanzania. We employed data from four methods (systematic camera trap surveys, sign surveys, community camera trapping, and direct observations by ecotourism guides) to improve our knowledge of this under-studied population. Our findings indicate that cheetah are widespread across the landscape, although they appear to exist at relatively low population densities, likely primarily due to biotic factors. Our surveys revealed an extension of confirmed geographical range of the species, and we provide some of the first evidence that miombo woodlands, which are not typically associated with the species, may be an important habitat for cheetah across its eastern African range. We employ these findings to identify research priorities for the species elsewhere in the region. Community camera trapping in village lands revealed that cheetah are using these unprotected areas, although rarely. Finally, we show that collaborations with tourism operators can be employed to monitor cheetah populations within this landscape, although we also identify potential limitations of this method. Overall, our results provide some of the first insights into this globally important cheetah population and have implications for conservation of the species both in southern Tanzania and elsewhere across its African range.

APPENDIX 3

Spatially explicit density estimates from a globally important African lion population in southern Tanzania: Implications for applied conservation

Paolo Strampelli, Charlotte E. Searle, Josephine Smit, Philipp Henschel, Dennis Ikanda, David W. Macdonald, Amy J. Dickman. In preparation.

Accurate and precise estimates of population status are required to inform conservation management and evaluate policy interventions. Although the lion (*Panthera leo*) is a charismatic species receiving increased conservation attention, robust status estimates are lacking for most of its populations, in part due to the lack of standardised methodologies. This is especially relevant to Tanzania, home to Africa's greatest number of lions, including many located within trophy hunting areas, but where population estimates are lacking. We employed systematic camera trap surveys, combined with spatially explicit capture-recapture (SECR) modelling, to estimate lion population density at four sites in different land management and habitat types in Tanzania's Ruaha-Rungwa conservation landscape, a global lion stronghold for which no empirical estimates of status are available. We provide the first spatially explicit density estimates for a lion population in Tanzania, including the first for a trophy hunting area. Our findings indicate that lions currently exist at highest densities in the strongly-protected and prey-rich core area of Ruaha National Park (6.12 ± SE 0.94 per 100 km^2), and at a relatively high density (4.06 ± SE 1.03 per 100 km^2) in a community-managed area of similar riparian-grassland habitat. Results also reveal that miombo woodlands in both photographic tourism and trophy hunting areas appear able to sustain intermediate densities of lion (1.75 ± SE 0.62 per 100 km^2 and 2.25 ± SE 0.52 per 100 km^2, respectively), providing one of the first insights into lion population status in this important habitat in Tanzania. Double-blind identification by two independent investigators revealed low inter-observer variation in photo identification (92% agreement), indicating that the methodology can be reliably applied to lion. We suggest that the method employed can be an important tool to aid the monitoring of lion populations, and show that it is applicable across a range of habitats and land use types. Finally, we discuss implications of our findings for the study area and for broader lion conservation management.

APPENDIX 4

Population density of spotted hyaena across habitats and management strategies in a mixed-use landscape in Tanzania

Charlotte E. Searle, Josephine Smit, Paolo Strampelli, Lameck Mkuburo, David W. Macdonald, Andrew J. Loveridge, Amy J. Dickman. In preparation.

Although the spotted hyaena (*Crocuta crocuta*) is widely believed to be resilient to human impacts, populations of the species are nonetheless thought be undergoing population declines both outside and within protected areas due to ongoing habitat loss and persecution. However, only a handful of spatially explicit population density estimates are available for the species across Africa, despite the importance of this information for monitoring population trends. In this study, we provide the first set of spatially explicit population density estimates for spotted hyaena in Tanzania, via spatially explicit capture-recapture (SECR) modelling of data from camera trap surveys conducted in 2018 and 2019 in the Ruaha-Rungwa landscape. Population density was highest in highly-productive *Acacia-Commiphora* habitat in the core tourist area of Ruaha National Park (NP; 10.8 ± 1.08 spotted hyaena per 100 km^2). We estimated the next highest density (5.89 ± 0.75 per 100 km^2) in a trophy hunting area, in the miombo (*Brachystegia-Jubelnardia*) woodland-dominated Ikiri block within Rungwa Game Reserve. We estimated a slightly lower density (5.11 ± 0.81 per 100 km^2) in relatively human-impacted MBOMIPA Wildlife Management Area (WMA), despite the site being similar *Acacia-Commiphora* habitat to the site with highest density. We estimated the lowest density (3.55 ± 0.72 per 100 km^2) in the miombo woodland of western Ruaha NP. Our results suggest that spotted hyaena may be less resilient to human pressures than widely thought, and we identify well-protected hunting areas as a stronghold for the species in Tanzania, alongside NPs. We also found evidence of injuries to spotted hyaena in the WMA as a result of bushmeat snaring, highlighting possible edge effects in the landscape.

APPENDIX 5

Density responses of lesser-studied carnivores to habitat and management strategies in southern Tanzania's Ruaha-Rungwa landscape

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Compared to emblematic large carnivores, less charismatic or smaller carnivore species often receive little conservation attention, despite facing increasing anthropogenic pressure, and their status being poorly understood across much of their range. We employed systematic camera trapping and spatially explicit capture-recapture modelling to estimate variation in population density of serval, striped hyaena and aardwolf across the mixed-use Ruaha-Rungwa landscape in southern Tanzania. Three sites were selected as representative of different habitat types, management strategies, and levels of anthropogenic pressure: Ruaha National Park's core tourist area, dominated by *Acacia-Commiphora* bushlands and thickets; the Park's miombo woodland; and the neighbouring community-run MBOMIPA Wildlife Management Area, also covered in *Acacia-Commiphora*. Our results show that the Park's miombo woodlands supported a higher serval density than the core tourist area and Wildlife Management Area, with 5.56 [Standard Error = ±2.45], 3.45 [±1.04] and 2.08 [±0.74] individuals per 100 km^2, respectively. This variation is likely driven by precipitation, the abundance of apex predators, and the level of anthropogenic pressure. Striped hyaena were detected only in the Wildlife Management Area and at low density (1.36 [±0.5] individuals per 100 km^2), potentially due to the location of the surveyed sites at the edge of the species' global range, high densities of sympatric competitors and anthropogenic edge effects. Finally, aardwolf were captured in both the Park's core tourist area and the Wildlife Management Area, with a higher density in the Wildlife Management Area (13.25 [±2.48] versus 9.19 [±1.66] individuals per 100 km^2), possibly as a result of lower intra-guild predation and late fire outbreaks in the area surveyed. By shedding light on three understudied African carnivore species, this study highlights the importance of miombo woodland conservation and community-managed conservation, as well as the value of camera trap data to improve ecological knowledge of lesser-studied carnivores.

APPENDIX 6

Innovative solutions are required to halt the degradation of Africa's protected areas and achieve global conservation targets

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Submitted to *One Earth* (in review)

Protected areas (PAs) play an invaluable role in biodiversity conservation, but incur significant management and opportunity costs at both local and national levels. Across Africa, eco-tourism and trophy hunting are currently the most prevalent economic instruments employed to underwrite these costs. However, there is a substantial funding shortfall across Africa's PAs. This has been exacerbated by recent reductions in trophy hunting, as well as rapidly increasing opportunity costs driven by wide-scale socio-economic change. To understand these impacts, we analysed data from Tanzania, which has set aside more land as PAs (>40%) than any other African country, and assessed the effectiveness of different PA types at preventing forest loss between 2000 and 2018. We found that 67.5% of Tanzania's PAs are at least partly dependent on revenue from trophy hunting, and that hunting areas currently protect considerable geographical range of 18 threatened large mammals, with a median coverage of 47% of species range in the country. However, by 2018, 51% of PAs with hunting had been vacated by operators, leading to decreased management investments and losses in conservation revenue. On average, PAs suffered 3.23% forest loss (an index of habitat degradation), compared to 6.85% outside. Forest losses were significantly higher, and increasing rapidly, in vacated hunting blocks. Given the volatility of international tourism (demonstrated by the effects of COVID-19), continuing pressure on trophy hunting, and growing socio-economic demands, we highlight the need for alternative mechanisms to safeguard biodiversity and achieve global conservation goals. Furthermore, urgent additional investment is needed to ensure the viability of existing PAs to effectively deliver positive outcomes for conservation and development.