Status and spatial ecology of a large carnivore guild in a heterogeneous, multiple-use landscape: Implications for conservation in modern African settings

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ABSTRACT

Status and spatial ecology of a large carnivore guild in a heterogeneous, multiple-use landscape: Implications for conservation in modern African settings

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Understanding the ecology of large carnivores in increasingly complex, multi-use conservation landscapes is crucial for their effective conservation in 21st century Africa, as is determining which management strategies can reconcile conservation with economic growth and human development. Reliable population monitoring techniques are essential to achieve both these goals. This thesis aims to address key knowledge gaps in the above themes, through a study of an intact large carnivore guild in Tanzania's Ruaha-Rungwa landscape. First, I apply occupancy modelling to sign-based data to investigate the distribution and habitat use of large carnivores, their prey, and human activity across the complex, at multiple spatial scales (Chapter 3). I show that species are limited by anthropogenic, management, and biotic factors, revealing the importance of integrated research and conservation planning for large carnivore management. I also identify a novel threat to Tanzania's biodiversity, in the form of increased habitat degradation associated with trophy hunting block abandonment. To investigate interspecific interactions within the large carnivore guild, I then apply conditional co-occupancy models to the same dataset, again for multiple species and at multiple scales (Chapter 4). I find that African wild dog (*Lycaon pictus)* avoid lion (*Panthera leo*) at both coarser and finer spatial scales, with effects being strongest in disturbed areas. Findings indicate that interspecific pressures can have a strong influence on the habitat use of large carnivores in multi-use landscapes, and must be appreciated in conservation planning. To then complement these insights with finer-scale metrics, I apply spatially explicit capture-recapture (SECR) models to camera trap data to investigate the effects of habitat and land management strategies on lion population density (Chapter 5). Lion exist at highest

densities in well-protected, prey-rich environments, including in community-managed areas, and at intermediate densities in miombo woodlands and in trophy hunting areas. I show that the method employed has the potential to be an important tool for lion population management. In Chapter 6, I use a range of data to provide insights into the status of Ruaha-Rungwa's cheetah (*Acinonyx jubatus*) population. Findings reveal an extension of known geographical range for the species, and provide some of the first evidence that miombo woodlands may be important for cheetah across its eastern African range. I also show that collaborations with tourism operators hold potential for cheetah population monitoring, and I identify regional research priorities for the species. Finally, I contextualise my findings by reviewing two decades of peer-reviewed African large carnivore population assessments, and identifying trends, biases, and opportunities in research (Chapter 7). I find that studies are biased towards southern and eastern Africa, particularly South Africa and Kenya, and that population assessments are significantly positively biased towards lion, and significantly negatively biased against striped hyaena (*Hyaena hyaena*). Most populations are understudied, and opportunities exist for research on most species and in most countries, and for increased inclusion of local authors and capacity building in range countries. Overall, the collective findings of this thesis highlight the necessity for increasingly integrated and synthetic research, as heterogeneity and complexity of conservation systems increases, and for an increased appreciation of the effects of anthropogenic impacts on large carnivores, even within protected areas. They also show that conserving large carnivore guilds will require robust population monitoring, and, more broadly, a shift towards more inclusive approaches to conservation that can secure wildlife without sacrificing human well-being and socio-economic development.

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The survey team, on the first day of two seasons of spoor transects.
From left to right: Stivin 'King' Pangamwene, myself, and Hamis Dongo

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CHAPTER 8 Ruaha-Rungwa's large carnivore assemblage: Conservation status, threats, and future research priorities

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CHAPTER 9 General Discussion & Conclusion

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CONTENTS

Abstract ii

Acknowledgments iv

Funding vii

Author Contributions viii

Contents x

Chapter 1: Introduction 1

1.1. Large carnivore conservation research in 21st century Africa 2

1.2. Thesis outline & structure 6

Chapter 2: Literature Review 9

2.1. Eastern Africa's large carnivore guild 10

2.2. Large carnivore assessments for conservation management 37

2.3. Study area: the Ruaha-Rungwa landscape 44

2.4. Appendices 60

Chapter 3: Multi-scale habitat use of an intact large carnivore guild and their prey in a modern mixed-use African landscape 83

3.1. Introduction 86

3.2. Methods 89

3.3. Results 107

3.4. Discussion 127

3.5. Acknowledgements 149

3.6. Appendices 150

3.7. References 199

Chapter 4: Spatial co-occurrence patterns of sympatric large carnivores in a multi-use African system 211

4.1. Introduction 214

4.2. Methods 218

4.3. Results 226

4.4. Discussion 234
4.5. Acknowledgements 242
4.6. Appendices 243
4.7. References 246

Chapter 5: Spatially explicit density estimates from a globally important lion population in southern Tanzania: Implications for monitoring and conservation management 255

5.1. Introduction 258
5.2. Methods 261
5.3. Results 266
5.4. Discussion 271
5.5. Acknowledgements 281
5.6. Appendices 282
5.7. References 289

Chapter 6: Insights into the status and distribution of cheetah (*Acinonyx jubatus*) in an understudied potential stronghold in southern Tanzania 298

6.1. Introduction 301
6.2. Methods 303
6.3. Results 306
6.4. Discussion 308
6.5. Acknowledgements 313
6.6. Appendices 314
6.7. References 322

Chapter 7: Trends and biases in African large carnivore population assessments: Identifying priorities and opportunities from two decades of research 326

7.1. Introduction 329
7.2. Methods 331
7.3. Results 337
7.4. Discussion 350
7.5. Appendices 361
7.6. References 391

Chapter 8: Ruaha-Rungwa's large carnivores: Conservation status, threats, and future research priorities **398**

8.1. Introduction 399

8.2. Threats & recommendations, takeaways, and future research 406

8.3. Conclusion 416

8.4. References 417

Chapter 9: General Discussion & Conclusion **425**

9.1. Introduction 426

9.2. Contribution to knowledge 427

9.3. Broader relevance & implications of findings 430

9.4. Limitations 441

9.5. Conclusion 442

References **444**

Appendix I: Leopard population density across habitats and management strategies in southern Tanzania's Ruaha-Rungwa landscape 479

Appendix II: Density responses of lesser-studied carnivores to habitat and management strategies in southern Tanzania's Ruaha-Rungwa landscape 480

Appendix III: Innovative solutions are required to halt the degradation of Africa's protected areas and achieve global conservation targets 481

CHAPTER 1

Introduction



1.1. LARGE CARNIVORE CONSERVATION RESEARCH IN 21ST CENTURY AFRICA

Large carnivores are some of the world's most charismatic species, and play important ecological regulatory roles in their communities (Beschta & Ripple, 2009; Ritchie et al., 2012). They are, however, naturally rare and vulnerable to local extinction (Carbone & Gittleman, 2016; Cardillo et al., 2004), and their loss can induce fundamental changes in community structure and functioning (Atkins et al., 2019; Estes et al., 2011; Ripple et al., 2014) and reduce ecosystem resilience (Martinez del Rio et al., 2001; Worm & Duffy, 2003). Understanding large carnivore ecological dynamics, and ensuring their effective conservation, is therefore essential for preserving intact ecosystems (Cardillo et al., 2004; Di Minin, Slotow, et al., 2016; Marshall et al., 2016).

In its infancy, the ecological study of large African carnivores took place within well-protected conservation areas, where species could be studied with negligible anthropogenic disturbance (e.g. lion, *Panthera leo*, Schaller, 1972; cheetah, *Acinonyx jubatus*, Schaller, 1968; leopard, *Panthera pardus*, Bailey, 1993; spotted hyaena, *Crocuta crocuta*, Kruuk, 1972). Similarly, their conservation was historically associated with the concept of protected areas (PAs) as islands of wilderness, kept as separate as possible from human interference ('fortress conservation'; Adams, 2013; Wilson & Primack, 2019). However, while core areas with minimal human impact remain critical to the survival of many populations (Balme et al., 2010; Bauer et al., 2015; Pacifici et al., 2020), there is a growing consensus that approaches focusing only on strict PAs underplay the complex socio-economic and political realities involved in conservation (Wilshusen et al., 2002; Winterbach et al., 2013), and that these alone will not be sufficient to maintain viable populations of large carnivores (Athreya et al., 2013; Swanepoel et al., 2013; Woodroffe & Ginsberg, 1998).

Indeed, due to a rapidly expanding regional human population, coupled with an associated increase in demand for land and in global consumptive needs (Oakleaf et al., 2015; Riggio et al., 2020), large African carnivores have experienced significant range contractions and population declines in recent decades (Ripple et al., 2014; Wolf & Ripple, 2017). Few populations are now completely isolated from human disturbances; instead, the majority are forced to inhabit areas experiencing a range of

anthropogenic impacts and interactions, including habitat conversion to agriculture, competition for space with livestock, prey base depletion, and direct mortality due to human-carnivore conflict, accidental and targeted poaching, and trophy hunting (Bauer et al., 2016; Bohm & Höner, 2015; Durant et al., 2015; Stein et al., 2020; Woodroffe & Sillero-Zubiri, 2020). Consequently, there is an urgent need to understand large African carnivore ecology in the context of these modern, multiple-use landscapes (Balme et al., 2014; Klaassen & Broekhuis, 2018; Oriol-Cotterill et al., 2015). Human presence can affect large carnivores in a number of ways (Petracca et al., 2019; Suraci et al., 2019), and disentangling the relationship of large carnivores with human disturbances, and identifying the thresholds of their anthropogenic tolerances, in addition to their biotic preferences, will be critical to guide their conservation in increasingly heterogeneous, anthropogenically shaped landscapes (Athreya et al., 2013; Everatt, Moore, et al., 2019; Qi et al., 2020).

Such an understanding is particularly required if, rather than focusing on individual species, we are to implement landscape-scale approaches (Trombulak & Baldwin, 2010) that can ensure the persistence of some of the world's last remaining intact carnivore guilds. In eastern Africa, complete large carnivore assemblages include the lion, the leopard, the cheetah, the African wild dog (*Lycaon pictus*), the spotted hyaena, and the striped hyaena (*Hyaena hyaena*); however, intact guilds are increasingly rare. The conservation of those that remain is a priority (Woodroffe & Ginsberg, 2005), and will require an in-depth understanding not only of the ecological requirements of each species, but also of how they influence one another's, and how the responses to anthropogenic threats of one may affect the persistence of another (Balme et al., 2017; Swanson et al., 2014). Indeed, a critical question for conservation management is whether, once environmental and anthropogenic factors are accounted for, species interactions still influence distribution or habitat use (Brodie et al., 2017; Bullock et al., 2000).

In addition, reliable assessments of population status will be critical to guide the management and ultimately the successful conservation of large carnivores in modern landscapes (Campbell et al., 2002; Hoekstra et al., 2002). In particular, recently there has been growing concern for, and resources invested in, the conservation of lion populations (Macdonald et al., 2016). Although arguably the most charismatic felid on the continent (Macdonald et al., 2015), robust population estimates are lacking

across the species' range (Elliot & Gopalaswamy, 2016), precluding informed conservation decision making and the implementation of adaptive management frameworks (Braczkowski et al., 2020). Moreover, most of the few estimates available are from populations in well-protected photographic tourism areas (e.g. National Parks); in Tanzania, however, the country with the greatest amount of lion range on the continent (Bauer et al., 2016), the majority are located within trophy hunting and other multiple-use areas (MNRT, 2016). Lion population assessments from these areas are therefore urgently needed, as are efforts to understand how status varies with habitats, anthropogenic pressure gradients, and competing land management strategies (Kane et al., 2015; Mills, 1991). To help achieve this, novel solutions are required that can facilitate the surveying and monitoring of lion populations (Elliot & Gopalaswamy, 2016). Similarly, there is also evidence that biodiversity monitoring and research in general is under-represented in Africa (Di Marco et al., 2017; Martin et al., 2012; Stocks et al., 2008; Velasco et al., 2015), and that conservation research does not always occur where it is most required (Velasco et al., 2015; Wilson et al., 2016). Identifying such biases is also crucial, to re-align efforts where needed and monitor progress made (Di Marco et al., 2017; Donaldson et al., 2016).

Finally, it is increasingly clear that for conservation solutions to be effective in the long-term, objectives must be aligned with both local and national economic development agendas (Buscher & Fletcher, 2020; Pringle, 2017), and respect access to natural resources by local communities (Oldekop et al., 2016). As a result, there is a need to determine which conservation models can successfully protect biodiversity while also improving local livelihoods (Balmford & Whitten, 2003; Coetzee, 2017; Naughton-Treves et al., 2005). This issue is again particularly timely in Tanzania, which is home to some of Africa's last remaining vast and intact conservation landscapes, but where rapid population growth and associated demand for land is placing increasing pressure on these wild areas (Lobora et al., 2017; Riggio et al., 2019). In this context, trophy hunting has been argued to have the potential to benefit the conservation of large carnivores and of wider landscapes as a whole, by bringing in strong economic incentives by creating tangible value for wildlife (Di Minin, Leader-Williams, et al., 2016; Lindsey et al., 2006, 2007, 2012). If poorly managed or combined with other sources of anthropogenic mortality, however, it can negatively impact populations, at times to such an extent that they are no

longer viable in the long term (Creel et al., 2016; Loveridge et al., 2007; Packer et al., 2010). In Tanzania, where hunting areas cover approximately one third of the country and comprise the majority of protected land (MNRT, 2016; Riggio et al., 2019), obtaining a better understanding of the landscape-scale effects of trophy hunting – and the extent to which this can be a successful tool for the conservation of large carnivore habitat – is therefore particularly urgently required (Brink et al., 2012).

In this thesis, I aim to help address the above knowledge gaps by improving our understanding of large carnivore ecology and conservation in modern, human-shaped African conservation systems. Following a literature review (Chapter 2), most research questions are addressed through a series of landscape-scale investigations of the spatial and population ecology of a complete large carnivore guild in the Ruaha-Rungwa conservation landscape, in south-central Tanzania (Chapters 3-6). The study area is a 50,000 km^2 mosaic of multiple-use protected and non-protected areas, which are under a range of management strategies, exhibit varying levels of legal and on-the-ground protection, and experience most of the anthropogenic threats faced by large carnivores in modern Africa. Furthermore, although home to a complete eastern African large carnivore guild, including what are believed to be globally important populations of most species, the area has received very little research attention to date. The complex is therefore an ideal setting in which to study large carnivores in a multiple-use, human-shaped conservation systems representative of much of their contemporary African range. Following this set of studies, I place my findings in a wider context through a review of twenty years of large carnivore population assessments in Africa (Chapter 7). This thesis is then completed by two concluding chapters; in the first (Chapter 8), I bring together findings from Chapters 3 – 6 to synthesise insights on Ruaha-Rungwa's large carnivores, and develop management and research recommendations for the landscape. Finally, I follow this with a general discussion and conclusion (Chapter 9), which ends this thesis.

1.2. THESIS OUTLINE & STRUCTURE

Following the format of an integrated thesis, this dissertation begins with an introduction (Chapter 1) and literature review (Chapter 2), followed by five data chapters presented as a collection of manuscripts (Chapters 3 – 7), and ends with a summary chapter (Chapter 8) and a general discussion and conclusion (Chapter 9). Data chapters are formatted as journal articles, each with its own appendices and list of references (as for Chapter 8). Chapters 1 (Introduction), 2 (Literature Review), and 9 (General Discussion & Conclusion) have instead a joint list of references, found at the end of the thesis. Finally, I have included as appendices three additional in-review journal papers on which I am a co-author and worked on alongside this thesis, and that I believe complement well this study.

In **Chapter 2** I introduce the study species, with a particular focus on their spatial ecology and habitat use. I also outline the concepts and challenges underpinning large African carnivore conservation in the 21st century, particularly in Tanzania, and introduce the study area and its different components.

In **Chapter 3** I aim to improve our knowledge of large carnivores in modern, multiple-use African landscapes, through a study of the distribution and habitat use of Ruaha-Rungwa's large carnivore guild. Occupancy modelling is applied to 2,789 km of spoor-based survey data, collected over two years, to model multi-scale habitat use of lion, leopard, cheetah, African wild dog, and spotted hyaena, as well as of their prey and illegal human activity. I assess the relative impact of a suite of biotic, anthropogenic, and management factors on each species, and determine how this varies across gradients of human disturbance and competing land management strategies.

As interspecific interactions between sympatric large carnivores can also play an important a role in shaping their habitat use, in **Chapter 4** I complement findings of the previous study by applying co-occurrence occupancy models to the same dataset. I investigate co-occurrence patterns between large carnivores in Ruaha-Rungwa, and assess the role of interspecific competition in habitat use, once again at multiple spatial scales. Particular emphasis is placed on the impact of lion on shaping both landscape and finer scale habitat use of African wild dog.

In **Chapter 5**, I apply spatially explicit capture-recapture (SECR) models to data from systematic camera trap surveys to estimate lion population density at four sites in Ruaha-Rungwa, across different habitats and land use strategies, including in photographic tourism, trophy hunting tourism, and community-managed areas. I provide the first spatially explicit density estimates for a lion population in Tanzania, and discuss what findings reveal about lion population ecology and conservation requirements, both in the landscape and elsewhere. I explore how the novel methods employed can be used to improve lion population monitoring and management across the species' range.

In **Chapter 6** I collate data from a variety of methods, including spoor surveys, systematic camera trapping, community camera trapping, and direct observation by photographic tourism operators, to provide some of the first insights into the conservation status of Ruaha-Rungwa's understudied cheetah population. I then discuss findings within ecological, conservation, and monitoring contexts.

Finally, as large carnivore population surveys and monitoring may not be occurring evenly, or where they are most needed, in **Chapter 7** I carried out a review of peer-reviewed large African carnivore population assessments published over the last two decades (2000-2020). I use generalised linear mixed models and generalised linear models to identify taxonomical and geographical research gaps and biases, and employ findings to identify future research opportunities.

In **Chapter 8**, I synthesise findings of the Chapters investigating Ruaha-Rungwa's large carnivores (Chapters 3 – 6), discussing what they reveal about their status and conservation management. I explore newly identified threats, and recommend corrective actions and future research priorities for the area's large carnivores. Through these insights, I aim to provide conservation managers, practitioners, and researchers in the landscape with a resource that can be employed to help improve the conservation outlook of the study populations.

Chapter 9 is the general discussion and conclusion of the thesis. Here, I outline the wider implications of my results for African large carnivore conservation, and recommend research that would further improve understanding of the themes treated in this thesis. I conclude by discussing limitations of this study, and defining priorities and challenges for conservation in modern African landscapes.



The Mzombe River, which forms the boundary between Ruaha NP and Rungwa South OA and Rungwa GR, and between Lunda-Mkwambi GCA and Kizigo GR.

The Mzombe is a key source of dry season surface water in the landscape, with the area exhibiting some of the highest wildlife densities in the complex between June and November.

CHAPTER 2

Literature Review



2.1. EASTERN AFRICA'S LARGE CARNIVORE GUILD

This thesis focuses primarily on five large carnivores: the lion (*Panthera leo*), leopard, (*Panthera pardus*) cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*), and spotted hyaena (*Crocuta crocuta*). Together with the striped hyaena (*Hyaena hyaena)*, these species comprise the eastern African large carnivore guild. An overview of each species, with a focus on their habitat use and spatial ecology, conservation status, and threats is provided below.

2.1.1. Lion

The lion is the largest of the African carnivores, with males typically weighing between 150 and 250 kg and females between 120 and 182 kg (Estes, 1991) The species is also the most social of the *Felidae* family, with most individuals living in resident groups ('prides'; Hunter, 2015). Females in a pride are normally all related, descending from females that have lived in the same area for generations. Male offspring, on the other hand, remain in the pride until sexual maturity is reached (26 – 35 months; Smuts et al., 1978), at which point they are forced to emigrate. They then adopt a nomadic lifestyle within territories of established prides, often forming coalitions with other related or, occasionally, unrelated males, and eventually competing with established pride males for territory (Estes, 1991). Although prides can be large in highly productive areas, with the typical pride numbering about 13 lions in the Serengeti (Tanzania) and Kruger (South Africa) National Parks (NPs; Schaller, 1972; Smuts et al., 1978), in most areas prides average four to six adult lions (Sunquist & Sunquist, 2002).

Lions can consume a great variety of prey species, and will readily scavenge if the opportunity arises. However, their size and gregarious habits are particularly well adapted to predation on larger ungulates (Hunter, 2015). Hayward & Kerley (2005) report mean mass of preferred prey species at 290 kg, with African buffalo (*Syncerus caffer*), common wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*), and gemsbok (*Oryx gazella*) all found to be significantly preferred where available. In the Serengeti NP, wildebeest comprised the majority of lions' diet, while in Manyara (Tanzania) and Kafue (Zambia) NPs, buffalo made up over 60% of lion kills (Mitchell et al., 1965; Schaller, 1972). Predations on animals as large as sub-adult African bush elephants

(*Loxodonta africana*) have also been recorded (Joubert, 2006). Nevertheless, lions are highly adaptable in their hunting strategies, as demonstrated by the fact that, when buffalo availability fell in Kafue NP, lions readily targeted medium-sized prey such as lechwe (*Kobus leche*), puku (*Kobus vardonii*) and common warthog (*Phacochoerus africanus;* Creel et al., 2018).

2.1.1.1. *Habitat use & spatial ecology*

Lions are mostly found in open woodlands, thick bush, and grassland complexes, although they can persist in semi-deserts, deserts, forests, and in mountains up to 5,000 m if sufficient prey is available. The species has a relatively broad habitat tolerance, and was historically absent only from tropical rainforests and the interior of the Sahara desert (Estes, 1991).

Across their range, lion habitat use has been investigated through a variety of methods, including radio telemetry and GPS collars (e.g. Schuette, Creel, et al., 2013; Schuette, Wagner, et al., 2013), direct observation (e.g. Schaller, 1972), camera trapping (e.g. Everatt et al., 2014) or spoor surveys (e.g. Everatt et al., 2015, 2019; Henschel et al., 2016, 2020). As a result of rising anthropogenic threats (Bauer et al., 2016), focus is increasingly being placed on investigating lion ranging patterns in anthropogenically disturbed areas. Lions have been shown to prefer using protected areas (PAs) over grazing zones (Van der Weyde et al., 2018), varying their spatial patterns based on the intensity of use of boundary areas by people and livestock (Schuette, Creel, et al., 2013; Schuette, Wagner, et al., 2013), and at times to be restricted to PAs as part of avoidance strategies of pastoralists (Ogutu et al., 2005; Oriol-Cotterill et al., 2015; Schiess-Meier et al., 2007). Similarly, lions have been found to avoid agricultural landscapes, suggesting particular sensitivity to habitat conversion for agriculture (Mkonyi et al., 2018; Valeix et al., 2012). If necessary, however, lions will still use both agricultural (Gatta, 2016) and pastoral (Oriol-Cotterill et al., 2015) lands, and can exhibit flexible habitat use patterns in human-dominated landscapes, avoiding areas of high human use during the day and selecting for habitat near people when feeding at night (Suraci et al., 2019). Avoidance of human-impacted areas has been suggested to vary at the level of the individual (Snyman et al., 2018), and human density-dependence effects have also been identified, with areas exhibiting human densities above 25 people/km² believed to be unsuitable for the species (Riggio et al., 2013). In Limpopo NP (Mozambique), habitat use by

lions at the coarser home range selection scale was strongly influenced by both distance to settlements and availability of preferred prey, while lions strongly avoided bushmeat poachers at a finer spatial scale (Everatt et al., 2015; although Brown & Marks (2007) suggest that lions can be attracted to poaching camps). Within human-impacted PAs, patrol staff numbers have been shown to play a key role in determining lion persistence (Henschel et al., 2016).

Several studies have noted a positive association between lions and water, with proximity to rivers and riparian areas identified as an important factor underlying lion space use, particularly at a finer scale. Riparian areas provide dense cover for both hunting and shade, and the linear features offer greater opportunities to encounter prey seeking water and food resources (Abade et al., 2014b; Davidson et al., 2012; De Boer et al., 2010; Hopcraft et al., 2005). Indeed, lions have been shown to feed in in areas with high prey 'catchability', rather than necessarily high prey density (Hopcraft et al., 2005; Kittle et al., 2016), with water described as a passive trap for prey which strongly influences lion distribution (Davidson et al., 2012). Abundance of large prey nevertheless remains a key factor in shaping lion habitat use, at multiple spatial scales (Davidson et al., 2012; Everatt et al., 2014; Henschel et al., 2016). Exceptions to this have however been noted in highly disturbed areas, where lions selected for sites further from permanent water, likely to decrease exposure to human activity (Mkonyi et al., 2018).

Some studies have also investigated associations between lions and specific vegetation types. Lions in Majete Wildlife Reserve (Malawi), in addition to selecting for riverine areas, also actively avoided high-altitude miombo woodlands (Briers-louw, 2017). In Kafue NP, lions preferred areas in mixed woodland over thicker miombo woodlands or more open grasslands, possibly as a result of the heterogeneous nature of the habitat being better suited to stalk-and-pounce hunting (Midlane et al., 2014). On the other hand, there is also evidence that lions can exhibit preference for more open habitat, sometimes even selecting strongly for this (Davidson et al., 2012), potentially as it enables lions to hunt better cooperatively (Miller et al., 2018). Even where lions mostly inhabits open areas, however, kills are preferentially made in thickets, highlight the importance of dense vegetation for kill sites (Davidson et al., 2012; Davies et al., 2016) and of accounting for scale in habitat use studies (Everatt et al., 2015). Other studies found no preference for any particular habitat type (Snyman et al., 2018), although this

could have been a result of lions forced to utilise all available habitats as a result of high levels of human encroachment (something also noted for other large carnivores – e.g. leopard; Strampelli et al., 2018a).

Overall, research suggests that lions will generally select for areas with relatively greater availability of prey at coarser spatial scales (Everatt et al., 2014, 2015), while finer scale habitat selection by lions appears to place higher importance on availability of features that facilitate hunting (Davidson et al., 2012; Everatt et al., 2015; Mosser et al., 2009; Valeix et al., 2010). Nevertheless, uncertainty remains regarding scale-specific variations of these effects, and how they are affected by, and vary with, levels and types of anthropogenic pressures.

Finally, both the size of established lion pride territories and the density of a lion population appear to be dependent a range of factors, particularly prey availability and habitat quality. In the high-productivity, prey-rich habitats of Serengeti NP and southern Kruger NP, average home range sizes were found to be circa 200 km^2 and 100 km^2, respectively (Funston et al., 2003; Schaller, 1972). In lower quality habitats, home ranges can however be considerably larger, with pride territories recorded to be as large as 950 km^2 in unprotected areas near Amboseli NP (Kenya; Dolrenry, 2013), ~1,450 – 4,550 km^2 in the semi-desert of the Kgalagadi Transfrontier Park (South Africa-Botswana-Namibia; Funston, 2011), and up to 5,870 km^2 in the hyper-dry skeleton coast of Namibia (Stander, 2019). Conversely, lions have been recorded reaching population densities as high as 38 per 100 km^2 in the prey-rich Ngorongoro crater (Tanzania), 17 per 100 km^2 in Kruger NP, and 14 per 100 km^2 in Serengeti NP (Belant et al., 2016; Ferreira & Funston, 2010; Kissui & Packer, 2004); nevertheless, most lion populations exhibit densities of 0.5 to 4 individuals per 100 km^2 (Bauer et al., 2016), with densities also being generally positively associated with lower levels of human disturbance (Farr et al., 2017).

2.1.1.2. *Conservation status*

The lion is classified as 'Vulnerable' by the IUCN (Bauer et al., 2016). In historical times, lions ranged through most of sub-Saharan Africa through to northern Africa, Greece, the Caucasus, the Middle East, and as far east as eastern India (Hunter, 2015). Today, only sub-Saharan populations persist, as well as a single isolated subpopulation in the 1,400 km^2 Gir forest of India. Riggio et al. (2013) and Bauer et

al. (2016) estimate current lion range at 1.6 million km^2, or only approximately 8% of the species' historical range, while Wolf & Ripple (2017) instead place this figure at ~6%.

In 1975, Myers et al. estimated that about 200,000 lions remained in Africa, down from 400,000 in the 1950s. This is believed to have fallen to less than 100,000 by the early 1990s (Frank et al., 2006), and to less than 40,000 a decade later (Chardonnet, 2002). In recent decades, population declines are believed to have been particularly severe in unfenced populations outside of southern Africa, with Packer et al. (2013) arguing this to be due to the rapid increase in human population densities in West and East Africa. Riggio et al. (2013) estimated 32,000 lions remaining across Africa, although estimates of many populations are based on expert opinion or extrapolations from other areas, and are likely to be imprecise. As a result, Bauer et al. (2016) believe current lion abundance in Africa to be closer to 20,000 individuals.

The main threats to African lion populations today are habitat loss through conversion and fragmentation, retaliatory or pre-emptive killing to protect livestock and human life, and prey base depletion (Bauer et al., 2020). While little data is available on the exact number of lions killed due to conflict with local communities, this is believed to be a primary threat to lion populations in pastoralist areas across Africa, particularly as their scavenging behaviour makes them vulnerable to poisoning (Bauer et al., 2020; Dickman et al., 2014). Persecuted populations are often concurrently also threatened by prey base depletion as a result of increasingly commercialised bushmeat trades, which have led to the collapse of prey populations across large parts of Africa, particularly in East Africa (estimated 52% decline between 1970 and 2005) and West Africa (85%; Lindsey et al., 2013). In addition, poorly-managed trophy hunting has been identified as a source decline for some lion populations, including in Tanzania (Brink et al., 2016; Packer et al., 2010), Zimbabwe (Groom et al., 2014), Cameroon (Croes et al., 2011), and Zambia (Rosenblatt et al., 2014). Finally, illegal trade in lion body parts for medicinal purposes is a growing threat to African lion populations (Everatt, Kokes, et al., 2019), with these being used particularly in West and Central Africa (N'Diaye, 2014; Sogbohossou et al., 2011) and in Asia, to produce medicinal wines which traditionally contained tiger bone (Coals, Moorhouse, et al., 2020;

although recent studies suggest incidents to be opportunistic rather than targeted – Coals, Dickman, et al., 2020).

See Appendix 2.1 for a more detailed overview of the status, current knowledge, and trophy hunting of lion in Tanzania.

2.1.2. Leopard

The leopard is the most wide-ranging member of the *Panthera* genus, distributed across much of sub-Saharan Africa, through south-west Asia and the Caucus into India, China, and the Russian Far East (Hunter, 2015). Leopards have a polygynous mating system, with a single male home range overlapping with several female home-ranges, and are solitary, associating only to mate (Estes, 1991).

Leopard diet is extremely variable between and within populations. Generally, ungulate prey weighing 10 – 40kg are preferred if available (Hayward, Henschel, et al., 2006), but prey as small as insects, reptiles, birds, and small mammals is consumed. Leopards have also been known to occasionally kill prey weighing more than twice their body weight, including adult greater kudu (*Tragelaphus strepsiceros*) and giraffe calves (Hunter, 2015). In Serengeti NP, leopard kills included over 30 different species, compared to 12 for lions, and in Zimbabwe's Matopos NP, 72% of leopard scats were found to contain remains of mammals <5 kg in size (Estes, 1991). Nevertheless, leopard populations usually share a diet dominated by a few species of locally abundant ungulates. Leopards are the only large carnivore to regularly cache larger kills for later consumption, dragging them up trees or into dense vegetation to avoid kleptoparasitism by lions or spotted hyaena (Hayward, Henschel, et al., 2006).

2.1.2.1. *Habitat use & spatial ecology*

The geographical success of the leopard can largely be attributed to its high levels of habitat tolerance (Hunter, 2015). Although in Africa leopards are believed to be most successful in woodlands, mixed grassland savannahs, forests, and riparian zones (Bailey, 1993), they also occur in mountain habitats, coastal scrub, swamps, shrubland, semi-deserts, and deserts, and range from sea level to as much as 4,600 m on Mt. Kenya (Stein et al., 2020).

Several studies have highlighted the frequently complex relationships between landscape heterogeneity and the ecology of the African leopard. Marker & Dickman (2005) found leopard abundance to be correlated with prey biomass, and female leopards in Kruger NP were noted to configure their home ranges around patches of prey-rich habitat (Bailey, 1993). Elsewhere, however, leopards have been shown to preferentially hunt in areas of intermediate vegetation cover, where prey are easier to catch, even if not necessarily more abundant (Balme et al., 2007; Pitman et al., 2013). Generally, a preference for dense habitats has been observed (Miller et al., 2018), and multiple studies have identified associations with riparian vegetation and water (Abade et al., 2014b; Bailey, 1993; Briers-louw, 2017; Burton et al., 2012; Pitman et al., 2013; Satterfield et al., 2017). Leopards have also been shown to disproportionately use areas with rugged terrain (Miller et al., 2018; Pitman et al., 2013), likely to maximise hunting success and denning opportunities, and to minimise kleptoparasitism (Bailey, 1993; Balme et al., 2007). Despite these associations, leopards may exhibit considerable plasticity in their habitat use, a pattern observed in Limpopo NP, where leopard occurrence was not strongly predicted by any of the environmental, conspecific or anthropogenic covariates tested (Strampelli et al., 2018a).

The species is similarly unusual among large carnivore for its relatively high tolerance of human-modified landscapes, particularly in Asia, where with sufficient cover and prey it has been known to persist in plantations, agricultural landscapes, and even densely-populated urban environments (Athreya et al., 2014; Stein et al., 2020). Nevertheless, although they can persist in multiple-use habitats better than most sympatric species (Van der Weyde et al., 2018), leopards will avoid anthropogenic disturbance if possible (Pitman et al., 2017; Strampelli et al., 2018a; Van Cleave et al., 2018). Furthermore, unlike in Asia, research on how African leopards respond to people and the mechanisms that govern such responses is still lacking, and the behaviour and population responses of leopards in heavily human-impacted African landscapes remains equivocal. In Phinda GR (South Africa) leopard density declined from the core of the PA to the border, and was lowest in adjacent non-protected areas (Balme, Slotow, et al., 2010). Negative relationships between human presence and leopard densities have also been observed in Gabon (Henschel et al., 2011), Zambia (Rosenblatt et al., 2016), Namibia (Marker & Dickman, 2005), and Tanzania (Havmøller et al., 2019). However, Balme et al., (2010)

found that, despite an increased risk of mortality, leopards in Phinda GR did not avoid non-protected areas, which may have therefore functioned as an ecological trap. Similarly, in South Africa's Cederberg Mountains leopard movements did not seem influenced by human activity (Martins, 2010), and leopards have been shown to use the same prey-rich areas as bushmeat poachers, with whom they often share an overlapping dietary niche, in impacted habitats (Henschel et al., 2011; Marker & Dickman, 2005; Strampelli et al., 2018a). Considerable uncertainty therefore remains on the exact nature and scale of response of leopards to anthropogenic threats in human-shaped African landscapes.

Finally, leopards show a considerable degree of variation in home range size, which appears to be highly dependent on habitat quality and prey availability. Home range size has been found to vary from as little as 14 km^2 for females in very productive areas of Kruger NP to as large as 2,750 km^2 for males in the extremely dry and prey-sparse southern Kalahari (Botswana; Hunter, 2015). For similar reasons, leopard densities also vary considerably between populations, from as low as 0.6 – 0.7 per 100 km^2 in the Kgalagadi Transfrontier Park, the Cederberg Mountains, and game farms in South Africa (Bothma & Le Riche, 1984; Constant, 2015; Martins, 2010), to as high as 12.7 and 14.5 per 100 km^2 in the N'wanetesi concession of Kruger NP and in a small fenced reserve in Namibia, respectively (Maputla et al., 2013; Noack et al., 2019).

2.1.2.2. *Conservation status*

The leopard is globally listed as 'Vulnerable' by the IUCN (Stein et al., 2020). Although still locally common in certain parts of sub-Saharan Africa, it is increasingly patchily distributed on the continent, and has been locally extirpated from areas densely populated by humans or which have undergone intense habitat conversion (Hunter et al., 2013). By the turn of the century, Ray et al. (2005) estimated that leopards had disappeared from at least 37% of their range in Africa, a figure which was revised to 61% more recently (Stein et al., 2020). There are no reliable continent-wide estimates for the species, with the most commonly cited estimate of 700,000 leopards in Africa (Martin & De Meulenaer, 1988) generally not considered reliable (Marker & Dickman, 2005; Norton, 1990). Nevertheless, African populations are suspected to have declined considerably over the past decades (Stein et al., 2020).

Habitat conversion to agriculture and resulting fragmentation remain the main threat to African leopard populations (Stein et al., 2020). Arguments have been made that leopards in Africa, unlike in Asia, have limited levels of ecological resilience to habitat fragmentation, and that while male leopards can successfully traverse fragmented and suboptimal habitat (Fattebert et al., 2013), African leopards generally require large contiguous habitat with low human disturbances to successfully reproduce (Balme, Slotow, et al., 2010). In addition, the collapse of prey populations in many areas of the continent is believed to be another key driver of range contractions (Lindsey, Balme, Becker, et al., 2013). Furthermore, even where prey populations are still relatively intact, competition with humans for prey often places further pressures on leopard populations (Henschel et al., 2011; Strampelli et al., 2018a). Leopards can also suffer persecution in retribution for real or perceived livestock loss (Stein et al., 2020), and in parts of southern Africa are targeted for the illegal trafficking of leopard skins for cultural regalia (Hunter et al., 2013).

Finally, poorly managed trophy hunting is believed to have been an important cause of decline for some leopard populations. Packer et al. (2010) argued that unsustainable harvest levels led to declines of leopard populations in hunting concessions in Tanzania, while Balme, Slotow, et al. (2009) and Pitman et al. (2015) showed that unsustainable trophy hunting was a key driver of leopard population declines in the KwaZulu-Natal and Limpopo provinces of South Africa, respectively. Hunting has also been shown to disrupt the social structure and spatial dynamics of leopard populations and contribute to infanticide (Balme, Slotow, et al., 2009; Balme et al., 2012; Packer et al., 2009). These findings have led to an increased conservation concern, with Zambia placing a two-year moratorium on leopard hunting in 2013, Botswana suspending all trophy hunting in 2014, and South Africa placing a zero quota for leopard hunting in 2016, 2017, and 2019 (Department of Environmental Affairs of the Republic of South Africa, 2017; Minister of Forestry Fisheries and the Environment, 2020). Research on leopards in hunting areas remains, however, particularly poor, with Balme, Hunter, et al. (2010) arguing that no range country has a proper regulatory framework that combines leopard population information with a detailed understanding of the impacts of hunting on populations.

Finally, a large proportion of leopards in Africa are believed to occur outside of formal PAs (Hunter et al., 2013). This highlights the need for effective conflict mitigation measures for the species, and for a shift from the current PA-centric approach to landscape level conservation planning frameworks for African leopard populations (Swanepoel *et al.* 2014).

See Appendix 2.1 for a more detailed overview of the status, current knowledge, and trophy hunting of leopard in Tanzania.

2.1.3. Cheetah

The fastest terrestrial mammal, the cheetah is able to reach speeds of up to 112 km/h over short distances (Sharp, 1997). With the exception of the lion, a greater degree of sociality has been observed among cheetah than in any other large felid: both males and females of the same litter often stay together for up to six months after independence (Caro, 1994), and males can remain together indefinitely, forming coalitions and defending territories, also at times in conjunction with unrelated males (Caro & Collins, 1986). Female cheetah are tolerant of other females, and do not maintain fixed territories, instead having large overlapping home ranges (Caro, 1994).

Cheetah mostly select for small-medium ungulates, with the main components of their diet varying across their range, from Thomson's gazelle (*Eudorcas thomsonii*) on the Serengeti plains (Schaller, 1968), to impala (*Aepyceros melampus*) in the savannah woodland mosaics of Kruger NP (Mills & Biggs, 1995), lesser kudu (*Tragelaphus imberbis*), gerenuk (*Litocranius walleri*), and dik-dik (*Madoqua spp.*) in the arid bushland of northern Kenya (Mills & Biggs, 1995), puku on the Zambian floodplains (Mitchell et al., 1965), and springbok (*Antidorcas marsupialis*) on the dry plains of the Kgaladadi Transfrontier NP (Mills & Biggs, 1995). Male coalitions have also been known to take down considerably larger prey, including adult wildebeest and hartebeest (*Alcelaphus buselaphus*; Caro, 1994), while ground-dwelling birds and small mammals have also been recorded as occasional prey items. Unlike many other African predators, cheetah rarely scavenge (Caro, 1994; Schaller, 1968). As a result of their smaller size, cheetah can lose up to 10% of their kills to larger or more organised sympatric predators, particularly spotted hyaena and lions (Hayward, Hofmeyr, et al., 2006). Cheetah

are nevertheless efficient hunters, and are able to survive in areas of comparatively low prey densities (Belbachir et al., 2015; Caro, 1994).

2.1.3.1. *Habitat use & spatial ecology*

Although historically associated with open grassland savannah habitats (Caro, 1994; Durant, 1998), cheetah can persist across varied vegetation structures and occupy a range of habitats, including open woodland savannahs (Broomhall, 2006; Mills et al., 2004), bush savannah and thick scrublands (Houser et al., 2009), and even hyper-arid deserts such as the Sahara (Belbachir et al., 2015). In fact, there is increasing evidence that cheetah may preferentially select for mixed habitats consisting of both woodlands or woody cover and open patches, in order to have cover for stalking and still be able to give chase, thus increasing their hunting success (Broomhall, 2006; Gros & Rejmánek, 1999; Klaassen & Broekhuis, 2018; Mills et al., 2004; Muntifering et al., 2006; Purchase & du Toit, 2000; Rostro-García et al., 2015). Woody cover is also argued to reduce kleptoparasitism and cub mortality from sympatric large carnivores, by providing safe denning sites (Caro, 1994; Laurenson, 1995; Mills et al., 2004); indeed, Broomhall (2001) found that, in Kruger NP, woodland savannah cheetah populations had greater viability than grassland populations. Even in mostly open grassland habitats, such as the Maasai Mara NR (Kenya), cheetah select for medium levels of vegetation cover (Pettorelli et al., 2009) and high density of edges between open and semi-closed habitat (Klaassen & Broekhuis, 2018). The reduced visibility of woodlands could also play a role in reducing rates of lion-inflicted mortality on adult cheetahs, by providing safe resting and concealment opportunities (Broekhuis et al., 2013; Mills et al., 2004). Cheetah are the least dominant of the large African carnivore guild, and in areas of high lion densities they have been shown to employ more wooded habitats, and to avoid areas of high prey density, riparian habitat, and water bodies, where they are most at risk (Durant, 1998; Pettorelli et al., 2009; see ‘2.1.7. Interspecific interactions: The role of sympatric predators in habitat use’). Cheetah are particularly well adapted to living in arid environments, not being obligate drinkers, and have been estimated to travel an average of 82 km between drinks of water in the Kalahari Desert, satisfying moisture requirements by drinking blood or urine of prey, or eating melons (Labuschagne, 1979). Furthermore, while cheetah will actively avoid human disturbance (Broekhuis et al., 2019), if enough

prey is available evidence suggests that they can persist in landscapes impacted by cultivation and livestock (Andresen et al., 2014; Pettorelli et al., 2009). Finally, cheetah habitat selection is increasingly being shown to be scale dependent; in the Maasai Mara, human footprint density and formal protection were the main influences on cheetah habitat selection at the home range selection scale, while environmental variables, such as stalking cover and open patches for chasing, had more influence at finer scales (Klaassen & Broekhuis, 2018).

In areas where their main prey species are non-migratory, males and female cheetahs have overlapping ranges that are similar in size (Broomhall et al., 2003). Although these can be very large (average of 1,642 km^2 in Namibian farmlands and 1,583 km^2 in the Sahara; Belbachir et al., 2015; Marker, 2002), intensively-used core areas can be as small as 14% of the total home range (Marker, 2002), possibly as a result of the species' need to remain mobile and avoid competition with larger predators (Broekhuis et al., 2013; Durant, 1998, 2000a; Rostro-García et al., 2015).

Cheetah naturally occur at relatively low population densities, generally existing at 10 – 30% of densities of lion and leopard, even in prime habitat (Durant et al., 2007). The highest recorded density in non-intensively managed populations reserves is of 2.5 cheetah per 100 km^2 in the prey-rich Serengeti NP (although here they can spike to seasonal densities of up to 40 per 100 km^2; Caro, 1994). Nevertheless, for most populations, densities are low: estimates of 0.2 per 100 km^2 on Namibian farmland (Marker, 2002) and of ~1.9 per 100 km^2 in Kruger NP have been recorded (Marnewick et al., 2014), while in the Sahara densities have been estimated to be as low as 0.23 – 0.55 per 10,000 km^2 (Belbachir et al., 2015).

2.1.3.2. *Conservation status*

Cheetah are listed as 'Vulnerable' by the IUCN, although there have been recent recommendations for the species to be uplisted to 'Endangered' (Marker et al., 2017). Historically, cheetahs were found over much of the African continent and across the Middle East and the Caucasus through to India; today, however, they are believed to be present in only 9% of their historical range. Outside Africa, remnant populations persist only in Iran (Durant et al., 2017).

Myers (1975) was the first to discuss the range wide decline experienced by cheetah as a result of habitat loss, estimating that African populations had plummeted from an estimated 40,000 in 1960 to 7,000 – 23,000 by 1975. Marker & Penzhorn (1998) estimated 12,000 – 15,000 adult individuals in Africa, and, in 2017, Durant et al. estimated a total of only 7,100 adult and adolescent cheetahs remaining across the continent. The largest connected population is believed to number ~3,949 individuals spread across the Kavango-Zambezi Transfrontier Conservation Area, spanning five countries. This is followed by an estimated 710 adults in the Serengeti/Mara/Tsavo landscape; 450 in the Samburu-Laikipia landscape in Kenya; 250 in the Omo Mago/Borena PA system in Ethiopia; 217 individuals in the Bahr/Salmat system in Chad and C.A.R.; and 200 in the Ruaha-Rungwa landscape. Nevertheless, the majority of these areas lack robust population abundance or density assessments, and a high level of imprecision is expected (Durant et al., 2015). It is also believed that an estimated 77% of current cheetah range is outside protected areas (Durant et al., 2017).

Various threats have been identified as playing a role in the observed decline in cheetah range. As a result of their comparatively lower densities, cheetah require larger areas than most other African carnivores to persist, and are therefore particularly susceptible to habitat loss and fragmentation (Marker et al., 2017). Under the right conditions, however, cheetah have been shown to persist in heavily human-modified landscapes (Andresen et al., 2014; Marker et al., 2017); this, together with their excellent dispersal abilities (Boast, 2014), highlights the potential for non-protected or partially-protected areas to complement fully-protected areas, ensuring connectivity and gene flow between cheetah sub-populations (Durant et al., 2015; Marker et al., 2017). Nevertheless, cheetahs living outside or on the edge of PAs are often at risk from conflict with pastoralists, being often targeted in retaliation to predation of livestock (Dickman et al., 2014; Thorn et al., 2013; although they are advantaged by the fact they rarely scavenge, and are therefore less susceptible to poisonings – Caro, 1994). Cheetah can also indirectly suffer in impacted areas as a result of loss of prey due to hunting and high livestock densities (Marker et al., 2017), or from direct mortality as bycatch in snares set for bushmeat (Lindsey, Balme, Becker, et al., 2013). Finally, certain cheetah sub-populations are threatened by roadkill and unregulated tourism, and trapping of live cubs for trade has been reported as a key driver of their

disappearance across much of their former range in Asia (Durant et al., 2015). While little information is available on the trade of cheetah cubs in Africa, eastern Africa (particularly Somaliland, Ethiopia and northern Kenya) is believed to be the area most at risk, with cubs being reported as being exported primarily to the Gulf States (Durant et al., 2015; Marker et al., 2017).

See Appendix 2.1 for a more detailed overview of the status and current knowledge of cheetah in Tanzania.

2.1.4. African wild dog

The African wild dog (hereafter: wild dog) is a medium-sized (15-30 kg) canid (Hunter, 2019). Wild dogs have strong social bonds, and live in packs of up to 20 – 40 adults, although mean adult pack size was found to be 4.8 – 8.9 across five ecosystems. Both males and females disperse, in single sex groups (Creel & Creel, 2002).

Wild dogs are hypercarnivores, eating no plant food or insects, and only very rarely scavenging (Creel & Creel, 2002). Although wild dogs can take prey as small as hares and gazelle fawns, and as large as adult zebra and sable, they specialise in hunting the most common medium-sized (14 – 45 kg) antelope in the area (e.g. impala; reedbuck, *Redunca spp.*; Uganda kob, *Kobus kob thomasi*; lechwe; springbok; Estes, 1991). Schaller (1972) recorded that only 11% of kills made by wild dogs in the Serengeti during his study weighed over 65 kg, with 75% of kills being of Thomson's gazelle, while in Kruger NP impala made up 87% of wild dog kills recorded by Pienaar (1969). Wild dogs are very successful hunters, with up to 90% of hunts ending in a kill (compared to 27 – 30% for lion and 25 – 30% for spotted hyaena; Creel & Creel, 2002).

2.1.4.1. *Habitat use & spatial ecology*

Wild dogs are generalists, and are able to persist in a wide range of environmental conditions and habitats as long as sufficient prey is available (Woodroffe & Sillero-Zubiri, 2020). While they seem to reach their highest densities in wooded savannahs (e.g. in Selous GR; Creel & Creel, 1996), they can also succeed in habitats as diverse as grasslands (Kühme, 1965), dense montane & upland forests (Dutson & Sillero-Zubiri, 2005), and deserts (Woodroffe & Sillero-Zubiri, 2020). While wild dogs will

drink regularly if water is available, their long large intestine permits them to absorb moisture from food extremely efficiently, and they can go without drinking for long intervals (Estes, 1991).

Nevertheless, while adaptable, several studies have shown a preference of wild dogs for areas with a high proportion of woodland habitat, a high number of habitat classes, and rugged terrain, the latter being particularly evident when choosing a denning site (Jackson et al., 2014; Mills & Gorman, 1997; Shumba et al., 2018; van Dyk & Slotow, 2003). This preference, as well as an observed avoidance of water sources, of areas with high proportions of bushland, and of edges between grassland and woodland habitats, has been suggested as a coexistence mechanism with larger sympatric carnivores (Creel & Creel, 2002; Jackson et al., 2014; van Dyk & Slotow, 2003). In Selous GR, the reduced visibility of miombo woodlands is believed to help reduce kleptoparasitism and mortality by lions (Creel, 2001), and preference for woodlands has also been suggested as a coexistence strategy in other wooded ecosystems (e.g. Kruger NP; Mills & Gorman, 1997). Indeed, habitat use patterns of larger sympatric predators are increasingly being identified as a key factor in shaping wild dog habitat use (see '2.1.7. Interspecific interactions: The role of sympatric predators in habitat use').

Wild dogs disperse over particularly large distances (Cozzi et al., 2020), and have considerably larger home ranges than would be expected on the basis of their body size (Gittleman & Harvey, 1982). Although during denning periods packs are confined to a relatively small area, this increases drastically during the rest of the year (Creel & Creel, 2002). Home ranges in the Serengeti were estimated at 1,500 – 2000 km^2 (Creel & Creel, 2002), compared to 50 – 260 km^2 during denning, while in Kruger NP they were estimated at 885 km^2, with the same pack ranging over only 80 km^2 when denning (Burrows et al., 1995). Although home ranges of different wild dog packs can overlap, they rarely enter one another's core area (Creel & Creel, 2002). As is to be expected, the species' wide ranging behaviour translates into population densities which are generally low. In northern Botswana, density estimates ranged from 3.5 wild dogs per 100 km^2 (including both adults & yearlings) in the wetter Okavango delta to as low as 0.5 per 100 km^2 in drier habitats. In the Selous GR, densities were estimated to fluctuate between 3.5 and 4.6 adults and yearlings per 100 km^2 (average of 3.8 per 100 km^2; Creel &

Creel, 2002), while in Kruger NP a mean density of 0.7 wild dogs per 100 km^2 was estimated using spatially explicit methods (Marnewick et al., 2014).

2.1.4.2. *Conservation status*

Historically, wild dogs were found across most of sub-Saharan Africa, from mountain summits to deserts, with the possible exception of lowland rainforests and hyper-arid deserts (Schaller, 1972). Over the past century, however, wild dogs have disappeared from much of their former range, suffering a decline second only to the Ethiopian wolf in terms of range contraction for an African carnivore (93%; Wolf & Ripple, 2017). Today, wild dogs have been virtually eradicated from northern and western Africa; furthermore, only remnant populations persist in central and north-eastern Africa, and even in eastern and southern Africa the species is mostly restricted to pockets of low human density. The largest remaining populations are believed to occur in the Kavango-Zambezi Transfrontier Conservation Area, in the Selous-Niassa ecosystem of southern Tanzania and northern Mozambique, and in the Ruaha-Rungwa ecosystem, although no reliable population abundance estimates are available for any of these populations. Overall, only approximately 6,600 adult wild dogs are estimated to remain in Africa, although, as a result of few populations being surveyed, inaccuracies are expected with these estimates (Woodroffe & Sillero-Zubiri, 2020).

Due to their wide-ranging habits, wild dogs are extremely sensitive to habitat fragmentation, and this has been identified as the most pressing threat faced by the species (Woodroffe & Ginsberg, 1999). Their wide-ranging behaviour also leads wild dogs to suffer particularly strongly from edge effects, even in large PAs (Cozzi et al., 2020), and their naturally low densities make them particularly susceptible to predation and kleptoparasitism by lions. Other threats include retaliatory killings as a result of conflict with livestock owners, accidental killings by snares and road accidents, and infectious diseases, particularly rabies (Creel & Creel, 2002; Woodroffe & Sillero-Zubiri, 2020). Wild dog packs have been known to be rapidly decimated by rabies outbreaks, with the disease able to affect several packs over a large area over a short amount of time (e.g. in Botswana, Alexander et al., 2010; and in Kenya, Woodroffe & Donnelly, 2011). This, combined with the fact that the majority of wild dog sub-

populations in Africa are estimated to number fewer than 20 packs, makes the species particularly susceptible to extremely rapid local extinction.

Nevertheless, the long-range dispersal capabilities of wild dogs can also result in populations reappearing unexpectedly and rapidly increasing in size, resulting in natural recoveries (e.g. in Samburu & Laikipia, Kenya, Woodroffe, 2011; in Save Valley Conservancy, Zimbabwe, Pole, 2000; and in the Serengeti, Marsden et al., 2012). This provides hope for the recovery of populations, and highlights the importance of maintaining meta-population connectivity, and of understanding how wild dogs can employ anthropogenically-impacted corridors to improve long-term population survival prospects.

See Appendix 2.1 for a more detailed overview of the status and current knowledge of African wild dog in Tanzania.

2.1.5. Spotted hyaena

The spotted hyaena is the largest extant member of the *Hyaenidae*, with individuals weighing up to 90 kg. Females are generally larger than males (Hunter, 2019). Spotted hyaena are highly gregarious and polygynous, with territorial social communities ('clans') dominated by females and communal dens (but no cooperative provisioning of offspring; Estes, 1991). Although clans can number up to 80 individuals, members do not often remain together, instead foraging alone or in small groups (Kruuk, 1972). Clans as small as 3 individuals have been recorded in very arid habitats of southern Africa (Mills & Hofer, 1998).

Spotted hyaena display greater plasticity in its hunting and foraging behaviour than most African carnivores. Individuals can hunt alone, in small parties of 2 – 5 individuals, or in large groups. During a hunt, spotted hyaena often run through ungulate herds to select an individual to attack, with the young or incapacitated being usually targeted (Kruuk, 1972). Spotted hyaena generally select for prey with a body mass range of 56 – 182 kg, and wildebeest, zebra, greater kudu, impala, springbok, and gemsbok are all the most commonly hunted prey in different parts of their range (Kruuk, 1972; Mills & Hofer, 1998). Spotted hyaena will also readily scavenge, and, unlike other large carnivores, have the capacity

to eat and digest skin, bone, and animal waste. The species often steals kills from leopard, cheetah, wild dog, and, in certain cases, lion (Estes, 1991; Kingdon, 1988; Kruuk, 1972).

2.1.5.1. *Habitat use & spatial ecology*

Spotted hyaena are habitat generalists, dwelling in semi-deserts, savannah, open woodland, dense dry woodland, and mountainous forests up to 4,000 m (Bohm & Höner, 2015). They are, however, generally scarce or absent in extreme desert conditions and tropical rainforests, although they may make deep incursions into forested areas where logging roads provide access (Henschel & Ray, 2003; Mills & Hofer, 1998). Spotted hyaena have been show to select for areas near water, possibly as the dense riparian habitat associated with riverine areas can provide hunting cover, preferential denning sites, and, in anthropogenically impacted areas, concealment opportunities (Abade et al., 2014b; Boydston et al., 2003; Kolowski & Holekamp, 2009; Schuette, Creel, et al., 2013; Schuette, Wagner, et al., 2013).

The relationship of spotted hyaena with humans is ambivalent, with its exact dynamics remaining unclear and warranting further research attention. On the one hand, the species has been shown to actively avoid pastoralists, diminishing utilisation of grazing areas when human presence increased, and to select against areas near settlements and PA boundaries, and increase to use of dense shrubland when livestock densities increase (Boydston et al., 2003; Burton et al., 2012; Green & Holekamp, 2019; Kolowski & Holekamp, 2009; Schuette, Creel, et al., 2013; Schuette, Wagner, et al., 2013). Elsewhere, however, studies found that spotted hyaena associated with greater human population densities or livestock abundance, suggesting that the species may be benefit from vicinity to humans, such as by scavenging discarded food or carcasses (Mkonyi et al., 2018; Yirga et al., 2013, 2017). Indeed, livestock was found in 96% of spotted hyaena scats in the vicinity of pastoralist residences in Serengeti NP (Kruuk, 1972), and extremes are found in some areas, with hyaena concentrating at very high densities around urban waste dumps (e.g. in northern Ethiopia; Yirga et al., 2015) or persisting in densely urbanised areas (e.g. the city centre of Lilongwe, Malawi; pers. obs.). It has also been theorised that, in areas of very high lion densities, more anthropogenically disturbed patches allow spotted hyaena to reach higher population densities, as a result of their higher behavioural plasticity combined with competitive release effects (Farr et al., 2017).

Territory size of clans is highly variable, ranging from 30 km^2 in the Ngorongoro Crater to over 1,000 km^2 in the Kalahari, although mean clan home range size from 18 published studies was 175 km^2 (Mills & Hofer, 1998). Similarly, spotted hyaena population densities have been shown to vary widely, ranging from 0.5 – 0.6 individuals per 100 km^2 in semi-deserts such as the southern Kalahari (Mills, 1990), to as high as 32 per 100 km^2 in the Selous GR (Creel & Creel, 1996) and 41 per 100 km^2 in the most prey-rich areas of Kruger NP (Ferreira & Funston, 2016). Peak densities of between 59 and 200 per 100 km^2 have been recorded in the extremely productive Ngorongoro crater (Höner et al., 2005).

2.1.5.2. *Conservation status*

The spotted hyaena is listed as 'Least Concern' by the IUCN, with the species historically being widespread throughout sub-Saharan Africa. While still relatively widely distributed, their current distribution is increasingly patchy, especially in western and central Africa, where it is mostly restricted to PAs. Nevertheless, being considered extinct in only two countries where they historically occurred (Algeria and Togo), the species' conservation outlook is better than that of any other large African carnivore. The total continental population was tentatively estimated at 27,000 – 47,000 individuals, based on known population densities extrapolated to the wider range. The largest population is believed to be that of the Serengeti ecosystem, estimated at 7,700 – 8,700 individuals (Bohm & Höner, 2015).

The main threat to spotted hyaena populations is habitat loss and conversion, although their high adaptability and resilience can allow them to persist in areas of relatively high human densities (Bohm & Höner, 2015). As a result of their scavenging habits, spotted hyaena are also highly at risk from poisonings, especially of livestock carcasses in retaliation for depredations (Dickman, 2008). Individuals are also often caught in wire snares set out for bushmeat: about 400 adult spotted hyaena are believed to be killed each year in the Serengeti by snares (comprising about 50% of all adult mortality for the population; Hofer et al., 1996), and 18% of all spotted hyaena in Mkhuze GR (South Africa) were estimated to have neck snares or neck snare wounds (Hunnicutt et al., 2016). Finally, spotted hyaena can be killed by vehicles along roads, and are hunted as trophies across some of their range. As a result of generally not being considered a desirable species by trophy hunters, impacts of sport hunting are likely to be marginal for most populations; Hunnicutt et al. (2016), however, found

that in Phinda GR unsustainable trophy hunting was the largest threat for the subpopulations, thus highlighting the need for further research into the effect of trophy hunting on spotted hyaena populations. This is particularly the case since, being larger than males, females are often targeted by hunters (professional hunter, pers. comm.); given the species' social structure, further research is required on the impact this might have on populations.

See Appendix 2.1 for a more detailed overview of the status, current knowledge, and trophy hunting of spotted hyaena in Tanzania.

2.1.6. Striped hyaena

The striped hyaena, classified by the IUCN as 'Near Threatened', is a widespread *Hyaenid*, occurring through central Asia, the Middle East, and all regions of Africa except southern Africa (Hunter, 2019). Although few population assessments have been carried out across its African range, the species is believed to occur at particularly low densities (AbiSaid & Dloniak, 2015).

Although present in the study landscape, and therefore included in this section for completeness, striped hyaena is not one of the primary study species of this thesis (but see Appendix II for research on striped hyaena in Ruaha-Rungwa carried out alongside this thesis).

2.1.7. Interspecific interactions: The role of sympatric predators in habitat use

2.1.7.1. *African wild dog & other predators*

Several studies have shown that African wild dogs are negatively affected by lion and spotted hyaena kleptoparasitism (Creel & Creel, 1996; Kruuk, 1972; Speakman et al., 2016). In areas of high sympatric predator densities these impacts can be particularly strong (Gorman et al., 1998), with Creel & Creel (1996) arguing that, in areas where wild dogs regularly suffered high competition at kills, such as the Serengeti or Ngorongoro, they are relatively unsuccessful. In addition, although their social structure can provide wild dogs with an effective defence against some sympatric carnivores (e.g. spotted hyaena and leopard), lion are a major source of mortality for both adults and pups (Creel & Creel, 2002).

As a result of this, both spatial and temporal partitioning seem to play a role in how wild dogs coexist with larger sympatric predators. The fact that wild dogs exhibit mostly crepuscular hunting habits, for example, has been identified as an important source of temporal partitioning, reducing the likelihood of direct interference competition with mostly nocturnal species such as lion and spotted hyaena (Creel & Creel, 2002; Dröge et al., 2016; Mills & Biggs, 1995). In addition, a number of studies suggested that wild dogs avoid areas heavily used by lions, or exhibiting high lion densities, thereby also employing spatial partitioning as a coexistence strategy (Creel & Creel, 2002; Dröge et al., 2016; Marneweck et al., 2019; Mills & Gorman, 1997). In Kruger NP, Mills & Gorman (1997) noted that wild dogs did not favour habitats with high impala density – although impala comprised 71% of their prey – as these were also favoured by lions. Similarly, wild dogs in the Selous GR avoided areas heavily used by lions, hunting disproportionately often in habitats where they had significantly reduced rates of encounter with prey (Creel, 2001), and Groom et al. (2016), Mbizah et al. (2012), and Romañach & Lindsey (2008) all found that wild dogs selected for areas of lower impala densities. Dröge et al. (2016) suggest that such spatial niche partitioning may be critical for competitive coexistence of wild dogs with dominant competitors, and the large territories of wild dogs have also been reasoned to facilitate avoidance of high-risk areas (Creel & Creel, 2002).

This large-scale displacement from optimal hunting areas would be expected to carry heavy demographic costs (Gorman et al., 1998). Indeed, there is evidence that both lion and spotted hyaena can have population-level impacts on wild dog density and distribution, potentially being the main factor limiting wild dog in some areas (Creel & Creel, 1996, 1998; Dröge et al., 2016; Groom et al., 2016; Mills & Gorman, 1997; Swanson et al., 2014). In Etosha NP (Namibia), a reintroduced pack was completely eliminated by lions, while a lion population crash in the 1960s resulted in a temporary increase in wild dog sightings, only for wild dogs to vacate the area again once lions recovered (Woodroffe & Ginsberg, 1997). Swanson et al. (2014) similarly noted that, over the three decades where Serengeti's lion population nearly tripled, wild dogs progressively declined, first occupying low lion density areas and eventually abandoning the wider area as the lion population increased further. They also found that lion density was the best predictor of wild dog densities in small, fenced South African

reserves. Groom et al. (2016) found that pack size significantly decreased as lion densities increased, and a number of studies indicate that wild dog densities appear to be lowest where spotted hyaena and lions are most abundant (Creel, 2001; Creel & Creel, 1996; Mills & Gorman, 1997; Vanak et al., 2013).

It has been hypothesised that habitat type may play a part in determining the extent to which wild dogs can coexist with lions and spotted hyaena. The fact that wild dogs are able to coexist with lions in many wooded ecosystems (e.g. miombo woodlands in Selous, Creel & Creel, 2002; mopane woodlands in Kruger, Mills & Gorman, 1997), while instead having often gone locally extinct in more open habitats (e.g. Serengeti, Etosha, Liuwa Plains, Ngorongoro; Dröge et al., 2016), suggests that the reduced visibility in woodlands may decrease rates of lion-inflicted mortality and kleptoparasitism (Creel, 2001), and that, due to the associated difficulty in ensuring spatial avoidance, the species may be prone to competitive exclusion in more open, uniform ecosystems (Dröge et al., 2016).

Finally, the wild dog-leopard relationship has received little research attention, despite the fact that the two species exhibit a 67% overlap in preferred prey species, indicating a high potential for interspecific competition (Hayward & Kerley, 2008). Although individual wild dogs are approximately half the weight of an adult male leopard, their greater sociality increases their competitive dominance (Kingdon, 1988). Leopards have been known to kill and consume adult wild dogs (Hayward, Henschel, et al., 2006), but anecdotal accounts of wild dog packs mobbing individual leopards suggest that the dominance hierarchy may be fluid and context-specific (Estes et al., 2011; Kingdon, 1988). In one of the few studies investigating the relationship, Rafiq et al. (2020) found little evidence of leopards modifying their space use as a result of wild dog occurrence.

2.1.7.2. *Cheetah & other predators*

As a result of their light build, cheetah are physically weaker than all sympatric competitors sharing their habitat (Estes, 1991). Cheetahs therefore often lose kills to spotted hyaena or lions, with 9 – 14% of kills in the Serengeti lost to larger predators (Caro, 1982). Lion were also found to be responsible for 78% of all recorded juvenile cheetah predation in the Serengeti (Laurenson, 1995), and both lions and spotted hyaena, as well as occasionally leopards, have been recorded to kill adult cheetahs (Caro, 1994).

Consequently, pressure from sympatric carnivores has been suggested as a key driver of cheetah spatial, temporal, and behavioural ecology (Maddox, 2003). The species' diurnal behaviour, for example, has been explained as an adaptation to this competition pressure (Caro, 1994), with Marnewick et al. (2006) and Belbachir et al. (2015) providing evidence that, in areas where competition is lower, cheetah are more nocturnal. Bissett & Bernard (2007) found that female cheetahs showed temporal and spatial avoidance of lions by hunting at dawn and dusk, and by positioning their home ranges away from lions. In the Serengeti, cheetahs were shown to avoid areas with high densities of their preferred prey, as these were also favoured by lions and spotted hyaena, and it was argued that sympatric effects forced cheetahs into areas of lower prey and predator density (Durant, 1998, 2000a, 2000b). Durant (1998) suggest that the mobility of cheetah is key to their continued coexistence with larger predators, and that their large home ranges are similarly an avoidance response to sympatric predators.

Several studies have argued that such strong sympatric competition can have population-level effects on cheetah, particularly by suggesting that the high rates of cub mortality inflicted by lion and spotted hyaena can suppress cheetah density (Durant, 1998; Laurenson, 1995). In Namibia, McVittie (1979) noted that cheetah sighting were inversely proportional to sightings of other predators, and Kelly et al. (1998) that cheetahs seen more frequently close to lions had a lower reproductive success. Hanby & Bygott (1995) similarly argued that, in Serengeti NP, an increase in lion and spotted hyaena densities led to reductions in cheetah populations inside the park.

However, recent research suggests that the effect of lion and spotted hyaena on the demography of cheetah populations is not always clear. Contrary to previous findings, Swanson et al. (2014) showed that, although the Serengeti lion population nearly tripled over three decades, cheetah numbers remained largely unchanged during this time. They also found that cheetah densities were not significantly negatively related to lion densities across South African private fenced reserves, and therefore argued that neither high levels of lion-inflicted mortality nor behavioural avoidance inflict sufficient demographic consequences to translate into population-level effects. Similarly, Gigliotti et al. (2020a) found that high lion abundance did not always exert negative effects on cheetah populations. Broekhuis et al. (2013) found that cheetahs were actually more likely to occur in areas with high long-

term risk of encountering lion, and that, within these areas of shared use, cheetahs avoided risk on short time scales, by positioning themselves further from the lions and hyaena than expected by chance. Vanak et al. (2013) also demonstrated a high degree of overlap between cheetah and lion home ranges, and found that cheetah sought out prey-rich areas regardless of long-term lion-risk or recent lion presence, adopting very fine scale avoidance measures instead. Swanson et al. (2016) and Rostro-García et al. (2015) similarly found that cheetahs are able to use patches of preferred habitat by avoiding lions on a short-term basis and through scale-dependent habitat selection, and Dröge et al. (2016) noted that cheetah showed no detectable avoidance of areas heavily used by dominant competitors, instead avoiding competitors temporally by being more diurnal. Thus, recent research suggests that, instead of large-scale displacement, cheetah may employ fine-scale spatial and temporal avoidance strategies to minimise risk from sympatric predators without reducing their access to key resources.

Taken together, these findings challenge the perception of cheetahs as 'refuge species' that can only persist in marginal areas of low sympatric predator densities (Caro & Stoner, 2003; Durant, 1998; Laurenson, 1995). Nevertheless, uncertainty remains regarding the exact dynamics and impacts of interspecific effects on cheetah habitat use and long-term persistence. For example, it is possible that effects are density dependent: while Swanson et al. (2016) found that cheetah generally positively associated with lions, this was not the case in areas with very high lion use, and cheetahs also avoided areas of extremely high spotted hyaena use. Lions have similarly been argued to be the primary cause of cheetah extinction in small, fenced reserves when existing at very high densities (Buk et al., 2018).

Finally, interspecific effects of competitors on cheetah are also likely to vary with habitat. Broomhall (2001) suggested that pressures inflicted on cheetah by sympatric competitors were likely to be lower in more mixed savannah woodland habitats, where increased cover facilitated the hiding of cubs. Similarly, Mills et al. (2004) suggest that cheetahs appear to be kleptoparasited less in more wooded habitats, and may select for such areas as a result. The reduced visibility of woodlands has also been argued to potentially reduce rates of lion-inflicted mortality on cheetah (Bissett & Bernard, 2007). Dröge et al. (2016) suggest that open environments with a simple prey set promote competitive exclusion, and Broekhuis et al. (2013) and Klaassen & Broekhuis (2018) noted that cheetahs were better

able to use the same areas as lions in more wooded habitat. However, other research found that increased habitat complexity did not reduce cheetah cub mortality from lion (Gigliotti et al., 2020b). Thus, more research on the density dependence of interspecific exclusion effects, and on how these vary across habitat types, is required to elucidate the exact dynamics of these potentially important effects.

2.1.7.3. *Leopard & other predators*

Across their African range, leopards are vulnerable to kleptoparasitism, injury, and direct morality from lions, spotted hyaena, and potentially wild dogs (Estes, 1991; Kingdon, 1988). Research suggests that leopard activity and distribution patterns can be affected by interspecific competition with sympatric large carnivores (Carter et al., 2015; Vanak et al., 2013), and leopards have been found to adopt various strategies to coexist with dominant competitors; arboreal caching of prey ('hoisting'), for example has been suggested as a key adaptive response to intraguild competition (Bailey, 1993).

Recent research has investigated in more depth the relationship between leopards and lions, which can represent a significant source of mortality for leopards (Bailey, 1993). The majority of these studies appear to suggest limited impact of lions on the coarser spatiotemporal patterns of leopards: in Kruger NP, Maputla et al. (2015) found that movements of leopards were not strongly affected by lion presence, and similar results were obtained by Vanak et al. (2013) and Rafiq et al. (2020). Strampelli et al. (2018a) found that in a heavily human-impacted habitat lion and leopard space use were positively correlated, suggesting that spatial partitioning was not strong enough to prevent leopards from sharing less impacted areas of the landscape with lions. Balme et al. (2017) and Bashant et al. (2020) also found that leopards appeared to suffer few costs from coexisting with lions, and that, while leopards did react to lions, this did not occur at a spatial scale that would result in broad-scale displacement, or prevent leopards from accessing key resource. Miller et al. (2018) argue that minor differences in spatial occupancy, combined with dietary partitioning (also identified by Maputla et al. (2015) as a key co-existence mechanism), enable leopards to share the same spatiotemporal niche as lions without undergoing population suppression effects.

Other studies, however, suggest that the impact of lions on leopard spatial decisions may not be insignificant. Contrary to results obtained in Kruger NP, Maputla et al. (2015) found that in nearby Timbavati GR lion movements appeared to significantly influence those of male leopards, suggesting site-specific differences in responses; the authors hypothesise that this could be a result of higher lion densities in Timbavati, potentially suggesting density-dependence of effects. Furthermore, Packer et al. (2009) found that, in Selous GR, hunting blocks with the highest lion harvest intensities showed the greatest increases in leopard harvests, and argue that lower lion densities may have been benefitting the leopard population. Thus, although most available evidence suggests that dietary niche partitioning is likely to be the main factor enabling leopards to coexist spatiotemporally with lions, the exact impact of lions on leopard behavioural ecology, demography, and population density is likely to be both site and habitat specific, as well as possibly density-dependent (Kumar et al., 2019), and remains unclear.

2.1.7.4. *Spotted hyaena & other predators*

Lions often represent the greatest source of natural mortality for spotted hyaena (Kruuk, 1972), with lion induced mortality found to account for up to 71% of spotted hyaena deaths in Etosha NP (Trinkel & Kastberger, 2005; Watts & Holekamp, 2008).

However, evidence that lion spatial or population dynamics influence those of spotted hyaena is inconclusive. Watts & Holekamp (2008) state that lions can suppress hyaena populations through extensive food stealing, and Green et al. (2017) found that a decrease in lion population led to a concomitant increase in that of spotted hyaena in an anthropogenically disturbed area. On the other hand, Swanson et al. (2016) found that lion and spotted hyaena used the same areas, suggesting that similar space use patterns may be driven by mutual attraction to shared prey, while Périquet et al. (2015) argue that the relationship between the two species is a complex mixture of facilitation and competition. In a comprehensive review of spotted hyaena–lion interactions, the authors found strong evidence for costs to both species through exploitation and interference competition (including through diet overlap, intraguild predation, and kleptoparasitism), but also identified benefits to both species from scavenging opportunities. They suggested that dietary niche partitioning and processes affecting scavenging opportunities facilitate coexistence, allowing both species to concentrate their hunting in areas of high

prey availability. Dröge et al. (2016) found that, in their study area, habitat use and activity patterns of spotted hyaena were positively correlated with those of lions, although they also noted avoidance by spotted hyaena of areas most heavily used by lions. The authors agree with Périquet et al. (2015) in suggesting that spotted hyaena and lions exhibit both beneficial and harmful influences on each other, so that the net effect is complex.

2.1.7.5. *Lion & other predators*

Lions will kill leopard, wild dog, cheetah, and spotted hyaena if the chance arises, but seldom consume them (Schaller, 1972). In many areas, lions interact most often with spotted hyaena, with either species seizing the kill of the other if conditions are favourable (Estes, 1991).

There is no definite evidence that lion space use is influenced by the spatial patterns of spotted hyaena or any other intraguild member, and Kittle et al. (2016) found that lion movement was unconstrained by that of spotted hyaena in Serengeti NP. Nevertheless, there are likely to be subtle effects of spotted hyaena presence on lion spatiotemporal dynamics, which may impact lion at finer scales. These are unlikely however to result in population-level effects, with lion and spotted hyaena population densities generally being positively correlated (Creel & Creel, 1996; Kissui & Packer, 2004).

2.2. LARGE CARNIVORE ASSESSMENTS FOR CONSERVATION MANAGEMENT

2.2.1. Why sample large carnivores? Population assessment & monitoring

Mammals are experiencing a global decline (Brodie et al., 2021), with large carnivores in particular undergoing substantial range contractions (Wolf & Ripple, 2017). In this context, status assessments of large carnivore populations are necessary to guide conservation planning, and to allow the adoption of an adaptive management approach (Balme, Hunter, et al., 2010). In the absence of such information, decisions are often based on expert opinion or educated guesses, and it can be challenging to identify areas of high conservation concern, prioritise investments, and assesses the effectiveness of management interventions (Blake & Hedges, 2004). Failure to provide reliable population assessments can also promote the use of biased management approaches dictated by non-scientific incentives (e.g. public interest or trophy hunting), hindering the implementation of ecologically-meaningful planning (Artelle et al., 2013; Popescu et al., 2016) and potentially misleading the prioritisation of conservation actions (Darimont et al., 2018; Moqanaki et al., 2018).

Generally, two broad questions are addressed when investigating large carnivore population parameters: (1) where is the species found, and why is it found there? (i.e. the population's spatial distribution); and (2) how many of the species are there? (i.e. the population's density or abundance; Karanth & Nichols, 2017). Both of these questions are relevant to this thesis.

2.2.2. How many? Capture-recapture models for large carnivore density estimation

Population densities are often considered the most useful metric of status for conservation management, as they enable comparisons over time and between sites, where population size on its own may be of limited use (May, 1999; Rich et al., 2014). However, large carnivores are often cryptic, nocturnal, wide ranging, and occur at naturally low densities, making them difficult to detect or observe (Barea-Azcón et al., 2007; O'Connell et al., 2011; Wilson, 2001).

As a result of this, camera traps are particularly well-suited to gain insights into large carnivore populations (Karanth & Nichols, 2017; Noss et al., 2013). Karanth (1995) then Karanth & Nichols

(1998) were the first to employ camera traps to determine population parameters of large carnivores, applying closed model capture-recapture (C-CR) statistical frameworks to camera trap data to estimate density of a tiger (*Panthera tigris*) population in India. C-CR models use capture-frequency data derived from photographed animals identified through their unique pelage markings, before dividing the value by some approximation of the effective sampling area (ESA) to estimate population density (Karanth & Nichols, 1998). An estimate of the ESA is typically obtained by adding a boundary strip to the trapping area, equal to either half or the full mean maximum distance moved (MMDM) by captured individuals, which is also estimated from the camera trap data (Borchers & Efford, 2008). The ad-hoc nature of the ESA estimation process, however, has been argued to have little theoretical basis, and has resulted in density estimates obtained using this method being questioned (Efford et al., 2004; Royle et al., 2009). Specifically, studies have reported that H/MMDM buffers are prone to underestimating the ESA, and consequently overestimating density (Soisalo & Cavalcanti 2006; Rich et al., 2014).

In light of this, Borchers & Efford (2008) and Royle & Young (2008) both independently proposed an alternative approach which does not rely on the estimation of the area sampled, termed spatially explicit capture-recapture (SECR). SECR models overcome the limitations of C-CR by incorporating information on the spatial locations of capture histories and detectors (e.g. camera traps), and using the locations at which individuals are detected to fit a spatial model of the detection process, deriving probability density functions based on distance from individual activity centres. The capture histories are also used to model the decline in probability of detection as a function of increased distance from the derived home range centres, which is usually assumed to be half-normal (Efford et al., 2008). Two parameters model the shape of the function: g0, the probability of detection at the hypothetical centre of an individual's home range, and sigma (σ), a function of the scale of animal movement (Borchers & Efford, 2008; Royle et al., 2009). SECR models have been developed in both likelihood-based (Efford et al., 2008) and Bayesian (Royle et al., 2009) frameworks; while the Bayesian approach is advantageous when modelling encounter data conditioned on covariates, the likelihood alternative is considered more appropriate for simpler analyses, as it is considerably faster and the methods have not shown any significant difference in terms of density estimates (Kalle et al., 2011; Noss et al., 2012).

Since their inception, SECR models have been applied to camera trap data to estimate population densities of most individually identifiable large carnivores, including tiger (Kalle et al., 2011; Wang et al., 2018), jaguar (*Panthera onca* – Tobler & Powell 2013; Boron et al., 2016), leopard (Rosenblatt et al., 2016; Strampelli et al., 2018b), cheetah (Boast et al., 2015; Brassine & Parker, 2015), spotted hyaena (Fouché et al., 2020), and striped hyaena (O'brien & Kinnaird, 2011). The lack of easily identifiable pelage patterns on lions, however, has resulted in such models being less readily applicable to camera trap data of the species, and their application to lion is therefore lagging behind (Green et al., 2020).

Instead, a number of alternative methods have become commonly employed to survey lion populations. In particular, since complete counts through intensive monitoring of populations (e.g. Brink et al., 2012; Ogutu & Dublin, 2002) are often not logistically or financially possible, index-based surveys that estimate lion abundance or density indirectly, usually from response rates to audio lures (call-in surveys – e.g. Ferreira & Funston, 2010; Kiffner et al., 2009; Midlane et al., 2015) or track densities (spoor counts – e.g. Funston et al., 2010; Winterbach et al., 2016; Henschel et al., 2020), have become widely implemented across the species' range (Braczkowski, Gopalaswamy, Elliot, et al., 2020). Spoor counts, in particular, have been argued to be a relatively time-efficient and cost-effective method to survey lion populations over large, often remote areas (Henschel et al., 2020). However, although such index-based surveys are insightful when alternatives are lacking (Karanth & Nichols, 2002), and are more resource-efficient than intensive visual monitoring (e.g. Blackburn et al., 2016; Loveridge et al., 2016; Rosenblatt et al., 2014), it has also been argued that these cannot account for variability and biases in detection (Hayward et al., 2015; Hayward & Marlow, 2014) and can lack precision (Kane et al., 2015), resulting in their suitability having been questioned (Anderson, 2001; Balme, Hunter, et al., 2009; Belant et al., 2019b; Dröge et al., 2020; Elliot & Gopalaswamy, 2016; Gopalaswamy et al., 2015; Midlane, 2014; Rosenblatt et al., 2014; Thorn et al., 2010).

Possibly as a result of these uncertainties, recent years have seen the first applications of SECR models to lion populations. Unlike for other large carnivores, however, most instances have involved direct observation data rather than camera traps, with this collected through an unstructured spatial sampling design (Braczkowski, Gopalaswamy, Nsubuga, et al., 2020; Elliot et al., 2020; Elliot & Gopalaswamy,

2016). At the same time, similar spatial mark-resight (SMR) models (Efford, 2019; Rich et al., 2014; Sollmann et al., 2013), which estimate the density of partially marked populations (e.g. from natural characteristics, such as whisker spot patterns, or artificial marks, such as scars) by incorporating spatial data from marked, unmarked, and marked but not identifiable individuals, have been employed to estimate lion population density from camera trap data in Niokolo-Koba NP, Senegal (Kane et al., 2015), and in Moremi GR, Botswana (Rich et al., 2019). SMR models however, unlike SECR models, do not currently allow for the modelling of hybrid finite mixtures, such as sex, as covariates (Efford, 2019); for species where spatial patterns differ considerably between sexes, such as lion (Loveridge et al., 2009), this is currently an important limitation, and encourages further investigation into the applicability of SECR models to lion camera trap data, in addition to the further development of SMR models. Overall, the application of SECR models to camera trap data of lion is a novel technique which holds considerable promise for accurate and reliable lion population surveying and monitoring (Elliot & Gopalaswamy, 2016).

2.2.3. Where, and why? Distribution, occupancy, and habitat use modelling

2.2.3.1. *Occupancy as an alternative population status metric*

Despite the clear value of robust density assessments, estimating population densities of large carnivores through SECR modelling over particularly vast areas is resource consuming, both in terms of time and cost, and is not always logistically feasible for vast African conservation landscapes (Henschel et al., 2020). In contrast, presence-absence data can be collected cost-effectively and rapidly across large areas (Karanth et al., 2011; Mackenzie et al., 2017), including for large African carnivores (Everatt, Moore, et al., 2019; Henschel et al., 2016, 2020; Petracca et al., 2019). Mackenzie et al. (2002) developed occupancy models that use replicated detection/non-detection surveys to estimate the detection probability of a species, and subsequently derive unbiased estimates of occupancy, or site use. Such models explicitly account for the imperfect detection of a species (i.e. that failure to detect a species does not necessarily reflect absence), thus avoiding the biased estimates and misleading inferences which would result from neglecting to account for this. Although occupancy models have been applied to a vast range of data, including direct sightings and counts (Ruiz-Gutiérrez et al., 2010),

interview questionnaires (Farhadinia et al., 2018), and even epidemiological assays (Mackenzie et al., 2017), for large carnivores camera trap data (e.g. Strampelli et al., 2018b) and sign (spoor) data (e.g. Henschel et al., 2016) are generally the easiest to obtain, and thus the most suitable. Spoor surveys, in particular, have been found to outperform most comparable presence-absence data collection methods in terms of efficiency, precision, effort, and cost, particularly over large scales (Thorn et al., 2010).

When absolute abundance or density estimates are particularly difficult to obtain, as can be the case for carnivores over large landscapes, estimation of the proportion of the landscape occupied or used by a species can provide a robust alternative state variable, which can be compared and monitored over sites and time (Mackenzie et al., 2017). Indeed, as a result of their cost-effectiveness and efficiency, occupancy surveys have been argued to have the potential to be an important tool for long-term, large-scale monitoring of large carnivores: Karanth et al., (2011) suggest that occupancy models applied to landscape-scale sign surveys can be employed to survey and monitor tiger populations over vast areas, and Henschel et al. (2016), Everatt, Moore, et al. (2019), and Petracca et al. (2019) show that the same can be achieved for African large carnivore populations, robustly estimating a population status parameter at spatial scales at which estimating density through spatially explicit methods (e.g. SECR) may be logistically and financially prohibitive.

2.2.3.2. *Occupancy modelling to study habitat use patterns*

In addition to being a useful tool for assessing population status, occupancy analyses allow modelling of covariates to explain heterogeneity in occupancy and detectability. This allows for investigations into the habitat use of the target species, by determining associations between variables of interest (whether these be biotic, anthropogenic, or management related) and occurrence (Mackenzie et al., 2002).

Empirical investigations into the habitat use of large African carnivores have been carried out using a variety of data sources (e.g. direct sightings, Pettorelli et al., 2009; radio-telemetry or satellite/GPS collars, Oriol-Cotterill et al., 2015; Suraci et al., 2019; interview questionnaires, Evangelista et al., 2018; sign/spoor surveys, Everatt et al., 2015) and analytical techniques (e.g. environmental niche factor analyses (ENFA), Pettorelli et al., 2009; utilisation distributions, Snyman et al., 2018; Maxent, Abade

et al., 2014; boosted regression trees, Evangelista et al., 2018; support vector machines, Abade et al., 2014), including occupancy modelling (e.g. Everatt, Moore, et al., 2019; Henschel et al., 2016; Strampelli et al., 2018a). However, unlike presence-only species distribution or habitat suitability modelling algorithms (e.g. ENFA, Maxent), occupancy models explicitly account for imperfect detection and unequal sampling effort within the modelling process (Mackenzie et al., 2002), and have thus being argued to be more suitable for such investigations (Mackenzie et al., 2017).

In recent years, occupancy modelling has been employed to determine habitat use associations for a number of large carnivores, including tiger (Karanth et al., 2011; Linkie et al., 2010), jaguar (Petracca et al., 2013; Sollmann et al., 2013), lion (Henschel et al., 2016; Petracca et al., 2019), cheetah (Andresen et al., 2014; Mkonyi et al., 2018), leopard (Searle et al., 2020; Strampelli et al., 2018a), and spotted hyaena (Petracca et al., 2019), at various spatial scales. They have also been used to investigate other patterns whose understanding can help management, such as livestock depredation (Puri et al., 2020).

2.2.3.3. *Two-species modelling to study co-occurrence patterns*

An additional important question in spatial ecology is whether interspecific interactions influence distribution and abundance of species, and to what extent (Brodie et al., 2017; Bullock et al., 2000). Although the gold standard to test this would be to experimentally remove one species and monitor whether this affects status parameters of others (Munger & Brown, 1981), this is often not feasible in practice, particularly over large scales.

As a result, in the context of large carnivores, GPS/VHF collars combined with a range of statistical analyses have been identified as an effective way to study interspecific interactions (Dröge et al., 2016; Vanak et al., 2013). However, these typically assess individual-level mechanisms, and do not provide insights on population-level dynamics that facilitate intraguild co-occurrence (Karanth et al., 2017). Co-occurrence models that employ presence-absence data within an occupancy framework can provide an avenue to test such interactions at coarser scales, while also accounting for imperfect detectability, something which most quantitative alternatives historically employed to investigate co-occurrence fail to do (see Brodie et al. (2017) for a review of such methods). Over recent years, a number of alternative

parametrisations of two-species occupancy models have been developed, to suit a diverse range of contexts (Mackenzie et al., 2004; Richmond et al., 2010; Rota et al., 2016; Waddle et al., 2010)

Nevertheless, such methods, while relatively well established to investigate intraguild interactions between large carnivores in the Americas (e.g. Gutiérrez-González & López-González, 2017; Sollmann et al., 2012) and Asia (e.g. Karanth et al., 2017; Steinmetz et al., 2013; Sunarto et al., 2015) are yet to become commonplace in African systems, with only a handful of published studies employing these analytical tools (Cusack et al., 2016; Miller et al., 2018). In addition, these have exclusively been applied to temporally-replicated camera trap data, which is often collected over areas < 1,000 km^2. Although such models should be applicable to spatially-replicated sign based datasets, and several such datasets already exist (e.g. Everatt, Moore, et al., 2019; Henschel et al., 2020; Petracca et al., 2019), these opportunities are yet to be explored. Given that sign-based presence-absence data can be collected over vast areas relatively efficiently and effectively, considerable potential exists to employ these models to assess population-level interspecific interactions between large African carnivores. Furthermore, such interactions have seldom been empirically examined across gradients of resource availability and anthropogenic pressures at these scales (Karanth et al., 2017), which are those most relevant for management (Petracca et al., 2019). Addressing this knowledge gap, and better understanding how anthropogenic pressures or resource scarcity affect existing avoidance mechanisms, will be important for effective multi-species conservation planning in modern systems.

2.3. STUDY AREA: THE RUAHA-RUNGWA LANDSCAPE

The Ruaha-Rungwa conservation complex is located in south-central Tanzania, and covers ~50,000 km^2 in the Iringa, Dodoma, Singida & Tabora districts (Fig. 2.1). An overview of the Ruaha-Rungwa ecosystem, including its land tenure, ecological characteristics, large carnivore populations, and threats to its biodiversity is provided below.

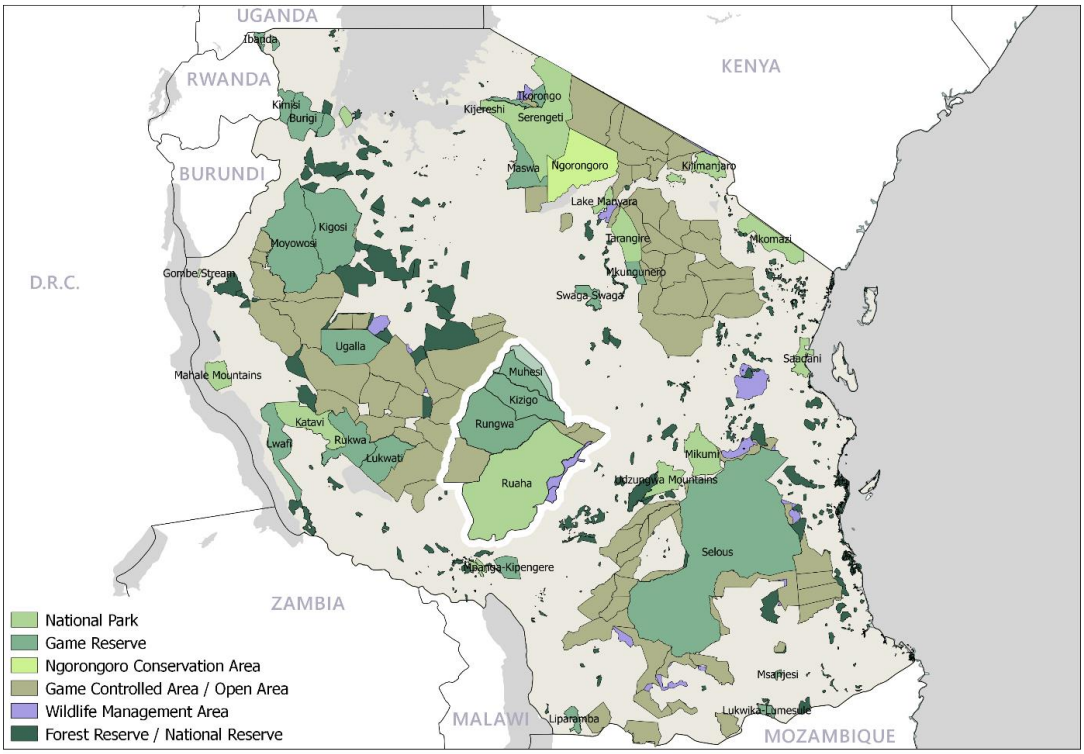


Figure 2.1. The Ruaha-Rungwa landscape in the national conservation context. Recent (2019) upgrades of certain GRs to NPs (Ugalla, Kigosi, Burigi, Kimisi, Ibanda GRs, and part of Selous GR) are not depicted due to uncertainties regarding new boundaries.

2.3.1. Protected area complex

Tanzania's network of PAs comprises a wide range of designations, including: National Parks (NPs), Game Reserves (GRs), Game Controlled Areas (GCAs), Open Areas (OAs), Wildlife Management Areas (WMAs), Forest Reserves (FRs), and Nature Reserves (NRs). NPs are reserved for non-consumptive utilisation (e.g. photographic tourism), and no settlement or resource utilisation of any type is permitted within their boundaries (MNRT, 2007). NPs are generally also the best protected of

Tanzania's PAs in terms of on-the-ground law enforcement. GRs in Tanzania are currently managed exclusively for trophy hunting, and, as in NPs, any permanent human settlements, grazing of livestock, or other extraction of natural resources is prohibited (MNRT, 2007). Law enforcement levels vary greatly, but GRs generally receive the most conservation attention and funding after NPs (Stoner et al., 2007). Sources and extents of both legal and illegal anthropogenic activities within GCAs and OAs vary considerably, but law enforcement is generally poor, with few dedicated resources for management and onsite law enforcement (Lobora et al., 2017; Stoner et al., 2007). Finally, WMAs are Tanzania's newest PA category, and aim to promote wildlife management at the village level by allowing communities and private land holders to decide how the land should be managed and revenue accrued (e.g. photographic tourism, trophy hunting, other types of resource extraction, etc.; MNRT, 2007; USAID, 2013). However, their effectiveness at realising tangible benefits for participating communities has been questioned, as has their ability to effectively conserve wildlife (Bluwstein et al., 2016; Kicheleri et al., 2018; Moyo et al., 2016; USAID, 2013; but see Lee, 2018). For a more detailed description of Tanzania's conservation landscape, including additional information on the different PA categories and the country's main biodiversity conservation challenges, see Appendix 2.1.

The Ruaha-Rungwa landscape comprises one NP (Ruaha), three GRs (Rungwa, Kizigo, and Muhesi), two community-managed WMAs (MBOMIPA and Waga), one GCA (Lunda-Mkwambi), and one OA (Rungwa South). The system is completely unfenced, with wildlife able to move freely between PAs, and between PAs and unprotected areas. The complex borders with unprotected land to the east and south, and with a other less-strictly protected areas (GCAs and OAs) to the west and north (Fig. 2.2).



Figure 2.2. The study area of this thesis, the Ruaha-Rungwa landscape (white border). Both the effective (dark green) and official (light green) boundaries of Muhesi GR are shown. The shaded area to the east of the PAs comprises unprotected village lands that are included within the study area of this study. Brown areas outside of the white border are other PAs (GCAs and OAs) which are generally not considered part of the Ruaha-Rungwa landscape, and are not included in this study.

The area first received formal protection under German rule, with the Saba Game Reserve gazetted in 1912 (later renamed to Rungwa Game Reserve by the British in 1946; Mercer, 2005). Ruaha NP was then gazetted in 1966, when the southern part of the reserve was excised and elevated to NP status, before being extended in 1974. In 2008, the park was further extended to include Usangu GR, making it, until the recent establishment of Nyerere NP, the largest NP in Tanzania at 20,226 km^2. As in all NPs in Tanzania, only photographic tourism is permitted. However, part of the area annexed in 2008 in south-western Ruaha NP still comprises areas of large-scale agriculture, livestock ranching, and permanent human settlements (Fig. 2.3). While formally part of the NP, the boundary dispute between park management and communities in the area is ongoing (TAWIRI, 2019), resulting in these areas not being treated as part of the PA by NP management, and thus leading the effective park boundary to differ from the formally delineated one (TANAPA, 2009). Ruaha NP also experiences additional

anthropogenic impacts in the form of encroachment by livestock and a range of illegal resource extraction activities (bushmeat poaching, logging, fishing, burning for honey gathering). Intensities of these vary across its extent, but are generally greater closer to its boundary (TAWIRI, 2019; this study).

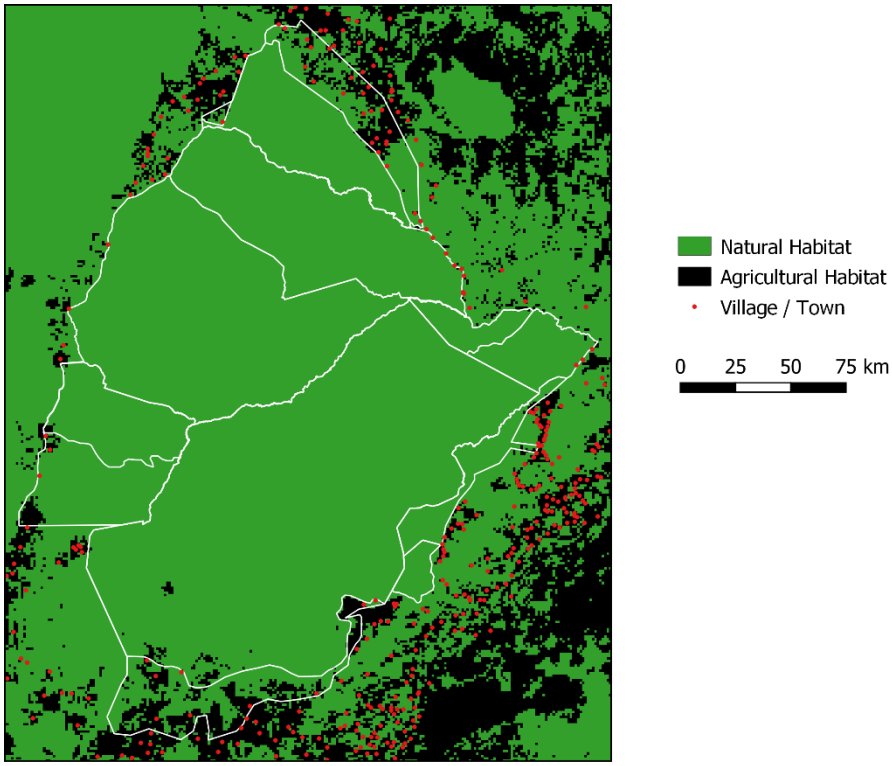


Figure 2.3. Natural and agricultural (converted) habitat (Jacobson et al., 2015), and human centres, in the Ruaha-Rungwa PA complex. Both gazetted and effective boundaries are shown for Ruaha NP and Muhesi GR. The agricultural habitat depicted within the effective Ruaha NP boundary was abandoned following the annexation of Usangu GR into Ruaha NP in 2008, and does not currently have human presence.

The three GRs (Rungwa, Kizigo and Muhesi) are managed as a single entity, and are reserved for trophy hunting. Each GR is sub-divided into multiple hunting blocks, some of which are actively leased and partly managed by hunting operators, and some which are instead vacant and not hunted, and which are fully under TAWA management (Fig. 2.4). Illegal anthropogenic disturbances are similar to those in Ruaha NP (livestock grazing, logging, bushmeat poaching, poaching, fishing, burning for honey gathering), and also additionally include mining (Hariohay et al., 2019). Impacts are greatest in Muhesi and in some areas of Kizigo GR (TAWIRI, 2019; this study). On-the-ground law enforcement is overall generally lower than in the NP, and greater in blocks which are managed by hunting operators (this study). Rungwa is the largest of the three GRs, at 9,175 km^2, and is divided in six hunting blocks, five

of which were actively hunted during the study period. Kizigo GR is the second largest, at circa 5,140 km^2, and is divided into four block (three of which were hunted). Muhesi GR is the smallest; while according to the some official sources it measures circa 4,550 km^2, between 2017 and 2018 new boundaries were delineated by TAWA, as a result of encroachment into the PA (Fig. 2.4, 2.5). Per these new boundaries, the GR now covers approximately 2,720 km^2. Muhesi is divided into two hunting blocks, neither of which was hunted at the time of the study.

The conservation complex also includes a number of less-strictly protected areas. Lunda-Mkwambi GCA (1,720 km^2), to the north-east of Ruaha NP, comprises one actively hunted block within its boundaries ('Lunda-Mkwambi North'). MBOMIPA (947 km^2) and Waga (344 km^2) are two community-led WMAs bordering Ruaha NP to the east, where both photographic tourism and trophy hunting are permitted, although neither were occurring at the time of study. Finally, in Rungwa South OA (3,873 km^2), to the north-west of Ruaha NP, both trophy hunting and other limited legal resource extraction (logging, fishing) are permitted. The area is divided into two hunting blocks (Rungwa OA (S) and Rungwa Mzombe), with only the former being actively hunted during the study period (Fig. 2.4). On-the-ground law enforcement varies within these PAs, but is generally low. A notable exception is the northern part of MBOMIPA WMA, where regular anti-poaching patrols are implemented through funding from independent NGOs (STEP, 2019). The type and intensity of anthropogenic disturbances also vary between and within these PAs, but include most forms of illegal resource extraction (bushmeat poaching, logging, fishing, burning for honey gathering) and illegal grazing of livestock, and are generally greater than in the NP and GRs (TAWIRI, 2019; this study).

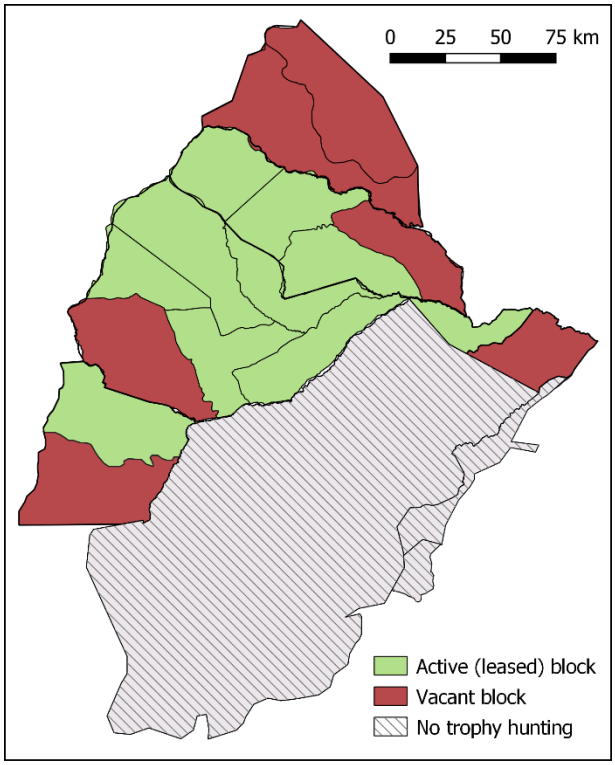


Figure 2.4. Tenure of hunting blocks in the Ruaha-Rungwa landscape. Although MBOMIPA and Waga include trophy hunting in their management plans, at the time of study this was not occurring due to ongoing disputes regarding land tenure, rather than blocks being vacated (i.e. purposefully not leased) by hunting operators. The old boundaries of Muhesi GR are depicted, as these coincide with hunting block delineation. Although the block depicted as vacant in Rungwa was leased by hunting operators for the 2018 season, they did not have a presence during the hunting season and no hunting took place.

Finally, the study area includes unprotected village lands to the south and east of Ruaha NP and MBOMIPA and Waga WMAs. This area is characterised by varying levels of human development, settlements, agriculture, pastoralism, and both legal and illegal natural resources extraction (e.g. logging, fishing, bushmeat poaching). The human population comprises a diverse combination of small-scale farmers, agro-pastoralists, and migrant pastoralists (Dickman, 2008). A wide diversity of wildlife is present (Dickman, 2008), although densities are believed be decreasing due to uncontrolled hunting and human population growth, while livestock numbers are increasingly rapidly (Dorward, 2018). The area exhibits particularly high levels of human-carnivore conflict (Abade et al., 2014a; Dickman, 2008; Dickman et al., 2014; Dorward, 2018; see ‘2.3.5.2. Threats to biodiversity & large carnivores in Ruaha-Rungwa’ below).

2.3.2. Physiography & topography

The Ruaha-Rungwa landscape comprises undulating plateaus and rolling hills with occasional outcrops, low mountains in the south and west, open, seasonally-flooded plains, and some moderately high hills to the east of Ruaha NP. A ridgeline runs from the south-west to the north-east of Ruaha NP, sloping down to the Great Ruaha river valley in the east and the Mzombe river valley in the west.

The largest rivers in the landscapes are the Great Ruaha, the Mzombe, and the Kizigo Rivers, which act as key reservoirs of dry season surface water (Fig. 2.5), as between July and November most tributaries dry up completely. Elevation in the ecosystem varies from 696 m in the Great Ruaha river valley to 2,171 m on mountain peaks in the south-west of the park (ESA, 2009).

2.3.3. Biomes & habitats

Ruaha-Rungwa sits at the intersection of three ecoregions: southern *Acacia-Commiphora* bushland & thickets, where *Acacia* and thorny *Commiphora* trees dominate productive grasslands, leading to high concentrations of large mammals; Central Zambezian miombo woodlands, that cut across southern and central Africa, and are one of the largest ecoregions on the continent; and Eastern miombo woodlands, which extend from northern Mozambique into the easternmost areas of the landscape (Fig. 2.5; Olson et al., 2001). Miombo habitats occur on relatively nutrient-poor soils, leading to lower primary productivity and generally lower densities of mammals (Frost, 1996), and consist of woodlands dominated by *Brachystegia*, *Julbernardia* and *Isoberlina* interspersed with grassy wetlands (‘mbugas’, or ‘dambos’), which act as critical surface water reservoirs in the dry season.

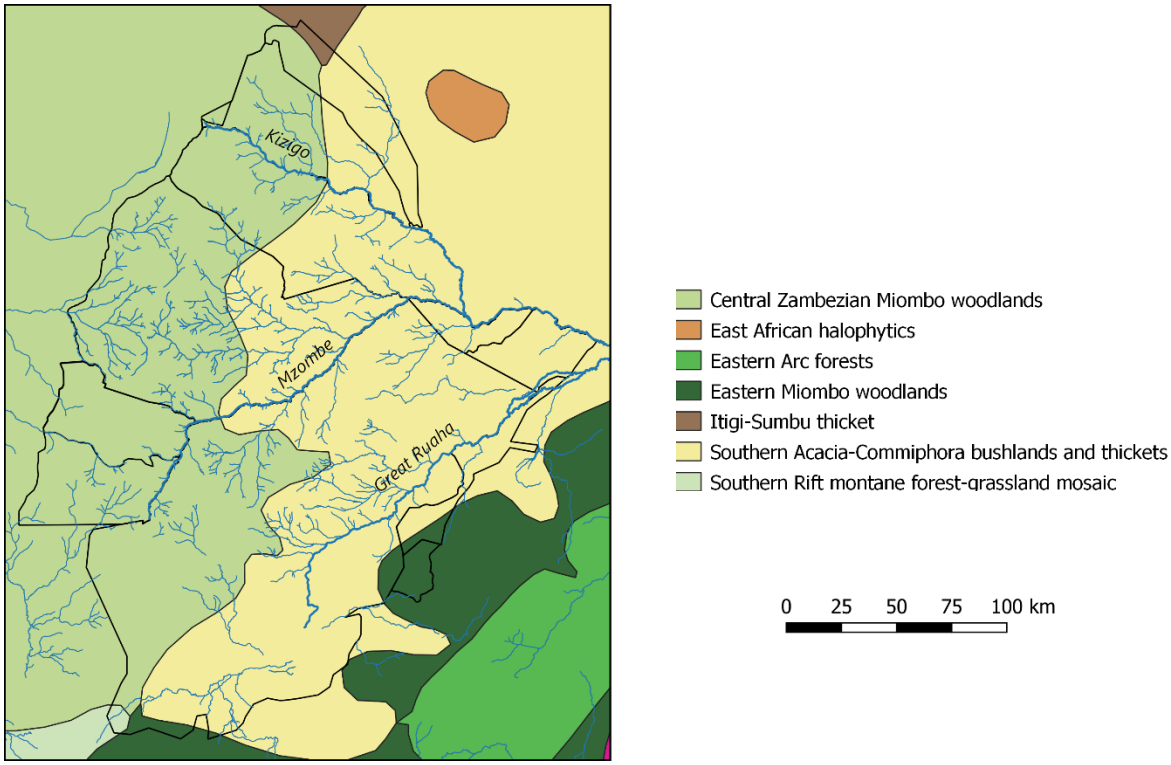


Figure 2.5. Ecoregions (Olson et al., 2001) and major rivers of the Ruaha-Rungwa conservation landscape (map not representative of river networks outside of the PA complex).

2.3.4. Climate

The climate of the region is semi-arid to arid, with both the miombo and *Acacia-Commiphora* habitats experiencing extremely seasonal, highly localised, and spatially varied rainfall. However, while in the *Acacia-Commiphora* habitats rainfall follows a bimodal pattern, with short rains from November to December and long rains from March to May, miombo habitats experience a single, prolonged rain season from November to March. Average annual precipitation varies considerably across the landscape, from 450 mm in the eastern Ruaha NP to nearly 900 mm in Rungwa South OA (Fick & Hijmans, 2017). Temperature ranges between 16 and 40°C, with the hottest months generally being October and November (Barnes, 1983).

2.3.5. Biodiversity

As a result of being the only protected area system covering the transition between the east African *Acacia-Commiphora* zone and the typically southern African miombo woodlands zones, the Ruaha-Rungwa landscape is exceptionally rich in biodiversity. The area is classified as one of outstanding

biodiversity and is one of the 'Global 200' ecoregions (Olson & Dinerstein, 1998). The ecosystem supports more than 1,700 species of plants, 570 of birds, and nearly 200 of mammals, including almost all of eastern Africa's large mammal species, and Tanzania's largest elephant population (estimated at 15,521 in 2018; TAWIRI, 2019). Large ungulates include important populations of African buffalo, Maasai giraffe (*Giraffa camelopardalis tippelskirchii*), plains zebra, common waterbuck (*Kobus ellipsiprymnus*), Lichtenstein's hartebeest (*Alcelaphus buselaphus lichtensteinii*), both greater and lesser kudu, common eland (*Tragelaphus oryx*), and both typically southern-hemisphere species such as roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) antelopes, and northern-hemisphere ones such as Grant's gazelle (*Nanger granti*). Small-medium sized ungulates include impala, bushbuck (*Tragelaphus scriptus*), common (*Sylvicapra grimmia*) and red forest (*Cephalophus natalensis*) duiker, Sharpe's grysbok (*Raphicerus sharpei*), steenbok (*Raphicerus campestris*), Kirk's dik-dik (*Madoqua kirkii*), klipspringer (*Oreotragus oreotragus*), oribi (*Ourebia ourebi*), and Southern (*Redunca arundinum*) and Bohor (*Redunca redunca*) reedbuck. All large carnivores typical of the eastern African savannah are present, including lion, leopard, cheetah, African wild dog, and both spotted and striped hyaena, as well as a range of mesocarnivores (Foley et al., 2014).

2.3.5.1. *Current knowledge of Ruaha-Rungwa's large carnivore guild*

Relatively little is known about Ruaha-Rungwa's large carnivore populations, even though the landscape is considered high-priority for large carnivore conservation at both national and continental scales (Mills et al., 2001; TAWIRI, 2009, 2016). Most empirical research carried out on large carnivores in the complex has focused on human-carnivore interactions and conflict to the east of Ruaha NP and MBOMIPA WMA (Fig. 2.6; Abade et al., 2014a; Dickman, 2008; Dickman et al., 2014; Dorward, 2018). Exceptions to this are research on lion and leopard occurrence in eastern Ruaha NP, MBOMIPA WMA, and non-protected village lands to the east (Abade et al., 2018, 2020), a predictive distribution modelling effort based on opportunistic sightings (Abade et al., 2014b), research investigating the effects of camera trap placement on capture rates of mammal communities (Cusack et al., 2015), and an investigation into human-carnivore conflict to the south-west of Rungwa GR (Fig. 2.6; Hariohay et al., 2017). In addition, due to the high levels of human-carnivore conflicts in village lands to the east of

Ruaha NP and MBOMIPA and Waga WMAs, the Ruaha Carnivore Project was established in 2010, to study and mitigate these interactions and increase local tolerance for large carnivores (RCP, 2020). Nevertheless, the majority of the landscape, and of its large carnivores, remain unstudied (Fig. 2.6).

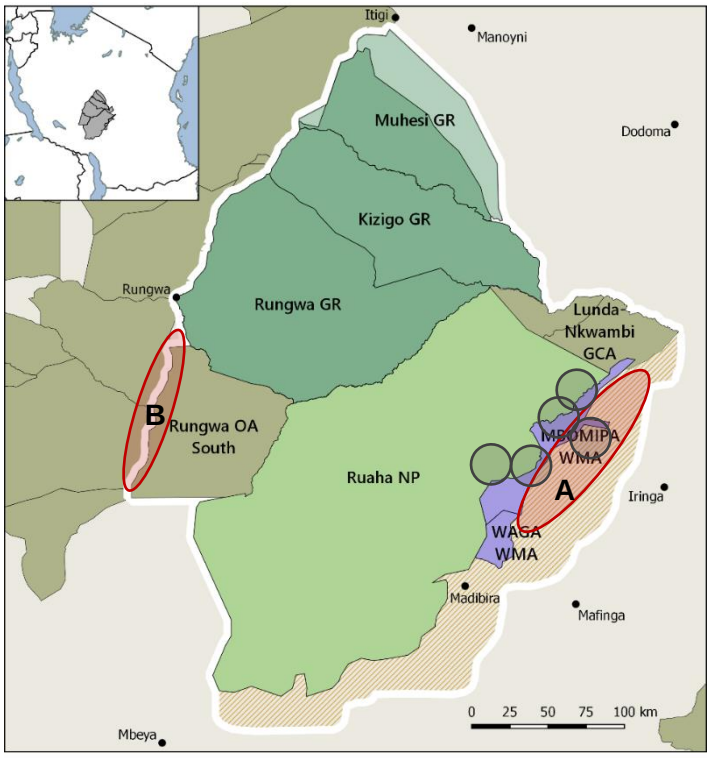


Figure 2.6. The Ruaha-Rungwa landscape (white border encloses the study area of this thesis). Grey circles show approximate locations of camera trapping for previous habitat use or methodological studies (Abade et al., 2018, 2020; Cusack et al., 2015). (A) The approximate study area of previous human-carnivore conflict research (Abade et al., 2014a; Dickman, 2008; Dickman et al., 2014; Dorward, 2018), and the main area of operation of the Ruaha Carnivore Project (RCP). (B) The location of a recent study into human-carnivore conflict (Hariohay et al., 2017).

Ruaha-Rungwa is part of central and western Tanzania's Lion Conservation Unit (LCU; Riggio et al., 2013), and lions are known to occur in all PAs within the complex, as well as in adjacent protected and unprotected areas (Abade et al., 2014b; Dickman, 2008; Hariohay et al., 2017; Mesochina et al., 2010; MNRT, 2016; TAWIRI, 2009). However, little information on population status, density, abundances, and distribution is available. Chardonnet (2002) provides an estimate of 3,360 lions for the complex, by hypothesising a density of 8 lions per 100 km^2, but provides no information as to how this figure was derived, while Bauer & Van Der Merwe (2004) were not able to estimate the size of the population in their range wide assessment. In 2006, the IUCN Cat Specialist Group suggested that around 4,500

lions may persist in the whole of central and western Tanzania (IUCN/SSC Cat Specialist Group, 2006), before Mesochina et al. (2010) estimated, through extrapolations from densities of known populations elsewhere and expert opinion, the total population within Ruaha-Rungwa at 1,485 individuals (part of a wider estimate of 3,779 individuals in central and western Tanzania, of which only 2,235 were estimated to be within PAs). These estimates were later also quoted by Riggio et al. (2013) in their range wide assessment. In 2018, the IUCN Cat Specialist Group estimated 1,962 lions within both Ruaha-Rungwa and the Katavi populations, citing Foley et al. (2014) as reference, although the latter appears to be simply reporting the estimates from Mesochina et al. (2010). Nevertheless, all estimates are based on expert opinion, and no empirical assessments are available for Ruaha-Rungwa's lion population. One possible exception to this might be an unpublished estimate cited in a governmental report (MNRT, 2016), which estimates a density of 6 lions per 100 km^2 in Rungwa GR; however, neither the report nor information on how these estimates were obtained are publicly available. As a result of this lack of data, obtaining further insights into what is likely one of the region's most important lion populations is considered a national conservation priority for the species (TAWIRI, 2009), and an important requirement to inform both its local and range wide management (EU, 2017a).

Relatively recent presence records are available for leopard from Ruaha NP, and from Rungwa, Kizigo and Muhesi GRs, Lunda-Mkwambi GCA, and Rungwa South OA (Abade et al., 2014b; Hariohay et al., 2017; MNRT, 2018; TAWIRI, 2009), while camera trap surveys in 2014 and 2015 confirmed presence in MBOMIPA WMA and in adjacent village lands (Abade et al., 2018). As for lion, however, no population status or large-scale distribution assessments have been carried out in the landscape.

Cheetah are known to occur in both the NP and the GRs in Ruaha-Rungwa, and have been recorded in Lunda-Mkwambi GCA (Dickman, 2008; TAWIRI, 2016). Camera trap surveys in 2014 also confirmed presence in MBOMIPA WMA, and in village lands to the east of Ruaha NP (RCP, unpublished data). No information is available regarding cheetah presence in the ex-Usangu GR (now incorporated into Ruaha NP) or in Rungwa South OA, and presence of the species in the GCAs and OAs to the west and north-west of the landscape, towards the Katavi-Ugalla population, is similarly unknown. The presence of a connectivity corridor linking the two populations is considered possible, but has not been confirmed

(TAWIRI, 2016). No cheetah population abundance, density, or distribution studies have been carried out in Ruaha-Rungwa; although Durant et al. (2017) estimated the overall population at 200 adults, which would make it the fourth largest in eastern Africa, this relied on extrapolations from densities elsewhere, and should be treated with caution (as indicated by the authors). Nevertheless, the population is believed to be of global importance (Durant et al., 2015), and is considered second only to that of the Serengeti in terms of importance for the species in Tanzania. As a result, obtaining further information on cheetah status in Ruaha-Rungwa was deemed to be of the highest priority for the species in Tanzania's first cheetah National Action Plan (TAWIRI, 2009).

Knowledge of the status and distribution of African wild dog in the landscape is also very limited. Although the population is hypothesised to be the third largest in Africa, with the latest status assessment for the species estimating it at 500 individuals (Woodroffe & Sillero-Zubiri, 2020), this involved considerable guesswork, and it is not clear what area the estimate covers. No detailed distribution, abundance, or density estimates are available, although the first National Action Plan carried out for the species stated that the population was likely to be stable at the time (TAWIRI, 2009). The main sources of data for the landscape were photographs from tourists, lodges, and TANAPA questionnaire surveys, which suggested that wild dogs were sighted more often outside Ruaha NP than in the core touristic area of the NP (TAWIRI, 2009). Nevertheless, wild dogs are believed to be resident in all PAs in the landscape, although their presence in south-western Ruaha NP (formerly Usangu GR) and in MBOMIPA is presently considered 'Possible' (TAWIRI, 2016). Obtaining additional information on the distribution and population status of Ruaha-Rungwa's wild dogs is considered 'high priority' for the species in the country (TAWIRI, 2009).

Spotted hyaena records are available from most PAs in the landscape (TAWIRI, 2009), and they are known to use unprotected areas to the east of Ruaha NP (Abade et al., 2014b; Dickman, 2008; Dorward, 2018). As is the case for the other large carnivore species, no empirical population or distribution assessments have however been carried out. Finally, striped hyaena presence in the landscape was still uncertain as of 2009, with only unconfirmed records available (TAWIRI, 2009). Presence of the species

was eventually confirmed in south-eastern Ruaha NP (RCP, 2013), although its exact distribution in the landscape remains unknown.

Finally, although empirical data is again severely lacking, large carnivore populations in Ruaha-Rungwa are believed to likely still be contiguous with populations to the west, in Katavi NP and Rukwa and Lukwati-Piti GRs, through Piti East OA and Chunya-Lukwati OA, as well as with Ugalla GR to the north-west, through a series of GCAs and OAs (Fig. 2.1; Damien, 2019; Jones et al., 2009; Riggio & Caro, 2017). However, little is known about the status of these corridors, with no functional connectivity studies having been carried out, and there is evidence that these areas are at risk from rapidly increasing deforestation (Lobora et al., 2017; TAWIRI, 2019; Appendix III). Historical corridors connecting Ruaha-Rungwa to Swaga Swaga GR and to Serengeti-Ngorongoro in the north, on the other hand, are believed to have been severed. Connectivity between the Usangu area of Ruaha NP and Mpanga Kipengere GR, through the Igando-Igawa wildlife corridor, is uncertain but possible. Finally, historical connectivity to the east, through a corridor to Udzungwa Mountains and Mikumi NPs, is believed to possibly still occur, but is also uncertain (Jones et al., 2009; Riggio & Caro, 2017).

2.3.5.2. *Threats to biodiversity & large carnivores in Ruaha-Rungwa*

Large-scale cultivation & drying of the Great Ruaha River

Although historically flowing year round, since 1993 the Great Ruaha River has ceased to flow for increasingly extended periods in the dry season. This has been shown to be a result of extensive upstream irrigation schemes for rice cultivation in the Usangu wetlands, both outside and inside the current extent of Ruaha NP (Fig. 2.3; Kashaigili et al., 2007; Lankford et al., 2004). Environmental issues were not taken into consideration at the time of project appraisal (African Development Bank, 1997). The reduced environmental flow has been shown to be insufficient to maintain basic ecological functioning of the Great Ruaha (Kashaigili, 2008; Kashaigili et al., 2007), and to have impacted the ecology of Ruaha NP in a number of ways, including through the elimination of over 60% of dry season habitat in Ruaha NP and of 77% of the Ihefu swamp, in the Usangu wetlands (Coppolillo et al., 2008; Kashaigili et al., 2005). The lower availability of dry season surface water is likely to have played a key

role in the observed decrease in Ruaha-Rungwa's ungulate populations over the last few decades (Barnes & Douglas-Hamilton, 1982; Kashaigili et al., 2005; Mtui et al., 2016; Stommel et al., 2016; Stoner et al., 2006; TAWIRI, 2015, 2019).

Following governmental concern due to the reduced flow's impact on power generation in the downstream Mtera hydroelectric dam, in 1998 the core of the wetland was gazetted as part of a new GR (Usangu GR), leading to the forced expulsion of fishermen and pastoralists in the area. This was followed by additional expulsions of livestock and settlements in 2006 – 2007, and the upgrading and annexation of the GR into the expanded Ruaha NP in 2008 (Walsh, 2012). Nevertheless, both large-scale industrial cultivation programmes and human agro-pastoralist settlements are still present within what is now south-west Ruaha NP (Fig. 2.5; TAWIRI, 2019). Despite numerous recommended corrective actions (e.g. Kashaigili, 2008; Kashaigili et al., 2005, 2007; Lankford et al., 2004; Walsh, 2012), current policy is argued to have limited effectiveness in managing the use of the river's water for irrigation, and to be poorly enforced (Sokile et al., 2003).

Subsistence agriculture, pastoralism, and human-carnivore conflict

As a result of the lack of physical barriers between PAs and unprotected community lands, large carnivores are free to range in the latter, creating potential for conflict. In particular, the area to the east of Ruaha NP and MBOMIPA WMA has been the target of a number of human-carnivore interaction studies, which revealed significant conflicts between pastoralists and large carnivores (Abade et al., 2014a; Dickman, 2008; Dickman et al., 2014; Dorward, 2018). The area is inhabited by over 60,000 people within 21 villages (Green & Adams, 2015), from at least 35 different ethnic groups, including Maasai, Barabaig, Hehe, Sukuma and Bena. Many of these rely largely, and often solely, on livestock (primarily cattle, goats, and donkeys), and the area was found to exhibit some of the highest incidences of human-carnivore conflict in Africa (Dickman, 2008). Real and perceived risk of livestock depredation led to pastoralists exhibiting largely negative attitudes towards large carnivores (Dickman et al., 2014), and retaliatory and ritual killings, through both spearing and poisonings, are common (Dickman, 2008). These findings led to the establishment of the Ruaha Carnivore Project, which focuses primarily on the implementation of conflict mitigation strategies in the area (RCP, 2013, 2020).

Unprotected and boundary areas elsewhere in the landscape, on the other hand, have received little research attention, although a recent study by Hariohay et al. (2017) near the boundaries of Rungwa GR and Rungwa South OA suggests that such conflicts are likely to occur around much of the PA complex.

Land conversion for subsistence agriculture is also a threat, especially in the boundary areas of Muhesi GR, south-west Ruaha NP, and MBOMIPA WMA (TAWIRI, 2019), and is the most pressing long-term threat outside of strictly-protected areas (NPs and GRs), including in possible connectivity corridors to the west, north-west, and east (Jones et al., 2009; Riggio & Caro, 2017).

Illegal resource extraction

As discussed (see '2.3.1. Protected Area complex'), resource extraction pressures in the study area vary across its extent, being generally more prevalent close to PA boundaries and in the less-strictly protected areas (GCA, OA, and WMAs), and include: logging, bushmeat poaching through snaring and shooting, fishing, burning for honey gathering, and mining (Hariohay et al., 2019; Knapp et al., 2017; TAWIRI, 2019). In addition, Ruaha-Rungwa suffered extensive poaching of elephants for ivory between 2009 – 2015 (Beale et al., 2017), which caused the population to collapse from approximately 40,000 (the second largest population in Africa) to ~15,000 by 2015 (TAWIRI, 2015, 2019).

By removing natural habitat, illegal logging is a particularly serious threat for large carnivores in the landscape. The highest intensities occur in parts of Kizigo and Muhesi GRs, and in Rungwa South OA, and both legal and illegal logging are a key threat to the intactness of the GCAs and OAs connecting Ruaha-Rungwa to complexes in the west and north-west (TAWIRI, 2019). Furthermore, although exact data is lacking, bushmeat poaching is likely to also be a particularly impactful threat for large carnivores in boundary areas. In addition to removing prey base, potentially forcing large carnivores to target livestock and thus increasing potential for conflict with pastoralists (Dickman, 2008), snaring can also result in direct mortality of large carnivores as by-catch; indeed, at least two lions and one leopard were found to have died in snares around a single village outside of Ruaha NP, over a period of only six months (RCP, unpublished data).

Trophy hunting

Trophy hunting is permitted in Rungwa, Kizigo, and Muhesi GRs, Lunda-Mkwambi GCA, and Rungwa South OA. While permitted in MBOMIPA and Waga WMAs, and part of the management plans of both (MBOMIPA, 2006), it was not taking place in either at the time of study. In 2018, when the majority of the data collection for this thesis was carried out in hunting areas, 8 out of 12 blocks in GRs were actively managed and hunted by hunting operators, as was the hunting block in Lunda-Mwakmbi GCA, and one of the two blocks in Rungwa South OA (Fig. 2.6). Non-hunted (vacant) blocks were not utilised, and their management was solely the responsibility of TAWA. See Appendix 2.1 for a detailed description of the trophy hunting industry and land tenure in Tanzania, and additional background on recent hunting block abandonment trends in the country.

Lion, leopard, and spotted hyaena are hunted in the complex, as are all large ungulates (with the exception of giraffe, due to this being the national animal), with quotas for each species and block set annually by TAWA (MNRT, 2016; see Appendix 2.1 for additional details on the trophy hunting industry in Tanzania). Although publicly available data is sparse, in 2014 average lion offtake rates in Rungwa-Kizigo-Muhesi were of 0.27 lions per 1,000 km^2 (MNRT, 2016), considerably lower than in 2011 (0.68 per 1,000 km^2), and below the 0.5 per 1,000 km^2 recommended by Packer et al. (2010). Approximately 21 lions are believed to be on quota annually for the three GRs (Lyakurwa et al., 2020), while no data is publicly available for leopard or spotted hyaena quotas or offtake during the study period, or for lion in the GCA and OA.

2.4. APPENDICES

Appendix 2.1. Conservation & Large Carnivores in Tanzania

APPENDIX 2.1 – CONSERVATION & LARGE CARNIVORES IN TANZANIA

S2.1. TANZANIA'S BIODIVERSITY CONSERVATION LANDSCAPE

Tanzania boasts one of the highest proportions of protected land of any African country (UNEP-WCMC, 2018), with areas with at least some level of protection estimated to comprise approximately 48% of the country's terrestrial area (Riggio et al., 2019), equivalent to almost three times the Convention on Biological Diversity's Aichi Target 11 of 17% protection of terrestrial areas (CBD, 2010). Partly as a result of this, Tanzania is one of the world's most biodiverse countries (Caro & Davenport, 2016), supporting two of the world's 35 globally recognised biodiversity and endemism hotspots (Mittermeier et al., 2011), 18 different ecoregions (Olson et al., 2001), a third of Africa's total plant species (Sharrock et al., 2014), and the twelfth highest number of bird species by country (Sharrock et al., 2014). The country is also home to at least 340 mammal species, including important populations of threatened and charismatic large mammals (Foley et al., 2014). These include what are believed to be Africa's largest remaining number of wild lions (Bauer et al., 2016), and globally important populations of leopard, cheetah, African wild dog (including what are believed to be two of the continents' three largest populations; Woodroffe & Sillero-Zubiri, 2020), spotted hyaena, and striped hyaena. Wildlife plays numerous social and economic roles in the country, ranging from the cause of widespread human-wildlife conflict to a source of (often illegal) sustenance for millions of rural villagers, to underpinning a national tourism industry that earned over US$6.6 billion per year in 2019 and accounted for approximately 10% of the country's Gross Domestic Product (WTTC, 2020).

Tanzania's extensive network of protected areas comprises a wide range of designations, including: National Parks (NPs), Game Reserves (GRs), Game Controlled Areas (GCAs), Open Areas (OAs), Wildlife Management Areas (WMAs), Forest Reserves (FRs), and Nature Reserves (NRs). Overall legislation is guided by the Wildlife Policy (MNRT, 1998, 2007) which confirms the government's overall right of ownership of wildlife: 'In recognition of the importance of conservation of biological diversity to the livelihood of mankind, the state will retain the overall ownership of wildlife.'

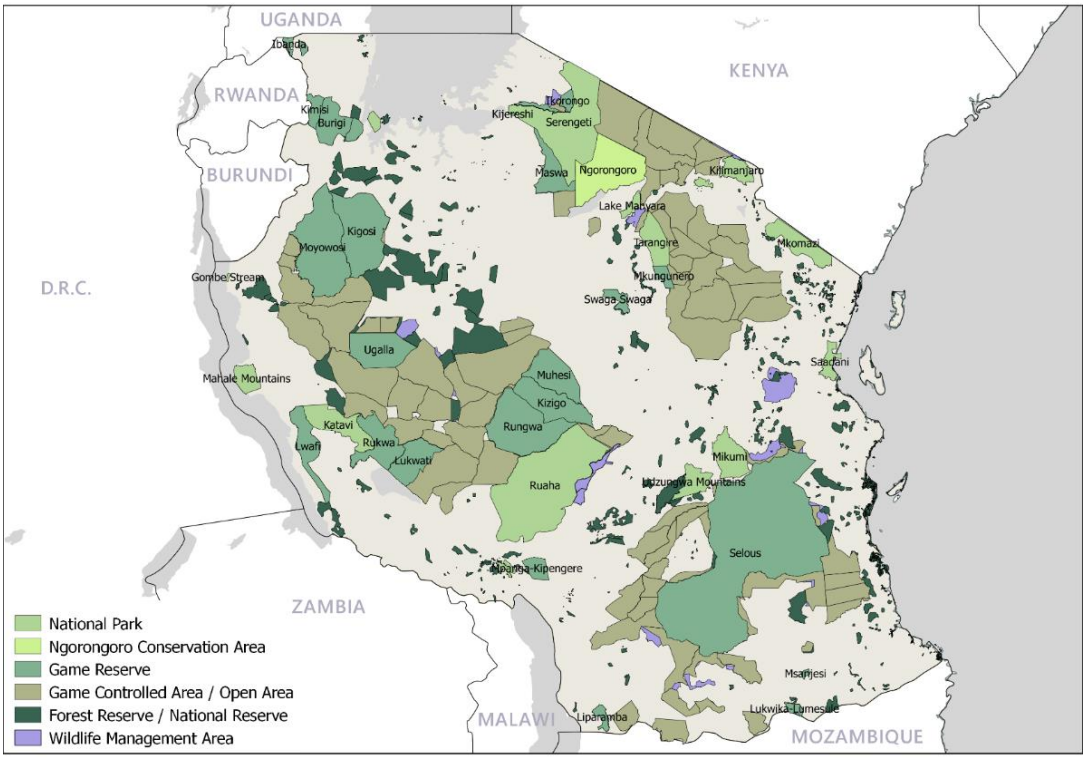


Figure S2.1. Tanzania's Protected Area (PA) network. Recent (2019) upgrades of some GRs to NPs (e.g. Ugalla GR, Kigosi GR, part of Selous GR) are not depicted due to uncertainties regarding new boundaries.

The country counts 22 National Parks (NPs), together covering an area of circa 103,970 km^2, or 11% of the country's total land area. Five of these, accounting for approximately half of this area, were gazetted in 2019 through the upgrade of existing Game Reserves, including what is now Tanzania's largest NP (Nyerere NP, 30,893 km^2; until recently the largest was Ruaha NP, at 20,226 km^2). NPs are reserved for non-consumptive utilisation (e.g. photographic tourism), and no settlement or resource utilisation of any type is permitted within their boundaries (MNRT, 2007). NPs are generally also the best protected of Tanzania's PAs in terms of on-the-ground law enforcement. The Ngorongoro Conservation Area (NCA; 8,292 km^2) similarly only permits photographic tourism, with the exception of Maasai pastoralists, who are permitted to reside and graze their livestock within its boundaries. Protection levels are comparable to those in NPs (Lobora et al., 2017; MNRT, 2007; Stoner et al., 2007).

The country also comprises 19 Game Reserves (GRs), covering an area of circa 77,000 km^2, or 8% of the country's land area. The largest is Selous GR, at ~20,000 km^2, followed by Moyowosi GR (11,489 km^2) and Rungwa GR (9,175 km^2). GRs in Tanzania are currently managed exclusively for trophy

hunting, and, as in NPs, any permanent human settlements, grazing of livestock, or other extraction of natural resources is prohibited (MNRT, 2007). Law enforcement levels vary greatly, but GRs generally receive the most conservation attention and funding after NPs (Stoner et al., 2007). Together, NPs, GRs, and the NCA have therefore been referred to as 'fully protected areas' (Lobora et al., 2017), 'strict protected areas' (Riggio et al., 2019), or 'core protected areas' (MNRT, 2007), due to the greater restrictions on resource use and generally higher levels of law enforcement, and together cover ~20% of Tanzania's terrestrial surface (MNRT, 2016).

In addition, Tanzania also counts 44 Game Controlled Areas (GCAs) and a number of Open Area (OAs), together covering approximately 202,959 km^2, or 21.5% of its total area (although discrepancies exist with regards to denominations, sizes, and boundaries of some PAs in Tanzania, particularly for GCAs, OAs, Forest Reserves (FRs), and Wildlife Management Areas (WMAs), leading to these figures varying in the literature; FZS, 2018; Mesochina et al., 2010; MNRT, 2012b, 2016, 2018; Riggio et al., 2019). Historically, the status of GCAs was not legally clear, and resource extraction activities (logging, grazing for livestock) were permitted alongside trophy hunting. In 2009, however, am amendment of the Wildlife Conservation Act granted them a similar protection status to GRs (Parliament of the United Republic of Tanzania, 2009). Nevertheless, these new regulations appear to not always be enforced, with human settlement and other forms of anthropogenic disturbance still ongoing in some GCAs (FZS, 2018). OAs, instead, are areas with wildlife resources within village lands that are adjacent to formally protected areas, or creating a link between other PAs. Wildlife resources within are protected by the law; however, human activities such as settlement, cultivation, grazing, cutting of trees and firewood collection for domestic use is allowed. The type and extent of use is governed by individual villages' land use plans. OAs permit trophy hunting and are the only land management type to allow resident hunting – i.e. hunting by Tanzanian nationals for consumptive use (MNRT, 2007).

Overall, sources and extents of both legal and illegal anthropogenic activities within GCAs and OAs vary considerably, but law enforcement is generally poor, with few dedicated resources for management and onsite law enforcement (Lobora et al., 2017; Stoner et al., 2007). As a result, GCAs and OAs have

been referred to as ‘lesser protected areas’ (Lobora et al., 2017), ‘less-strictly protected areas’ (Riggio et al., 2019), and ‘semi-protected’ areas (Appendix III).

There are also currently around 38 Wildlife Management Areas, Tanzania’s approach to community-based natural resource management (CBNRM), gazetted across the country (MNRT, 2007). These are at different stages of development, and are estimated to cover about 4% of Tanzania’s total land area (Kicheleri et al., 2018). First implemented in 1998 (MNRT, 1998), WMAs are the most novel conservation-oriented land management strategy in the country, and consist of areas of village land set aside for wildlife conservation. WMAs aim to promote wildlife management at the village level by allowing communities and private land holders to decide how the land should be managed and revenue accrued (e.g. photographic tourism, trophy hunting, other types of resource extraction, etc.; MNRT, 2007; USAID, 2013). However, their effectiveness at realising tangible benefits for participating communities has been questioned, as has their ability to effectively conserve wildlife (Bluwstein et al., 2016; Kicheleri et al., 2018; Moyo et al., 2016; USAID, 2013; but see Lee, 2018). Some WMAs have been established within or in place of GCAs or OAs, leading to further discrepancies with regards to boundaries and the amount of land protected under the different land management types.

Finally, Tanzania also protects 570 FRs, covering approximately 87,000 km^2 (9% of its total land area), and 6 Nature Reserves (NR), covering ~2,000 km^2, where limited natural resource extraction is permitted under license (MNRT, 2007). As in the case of GCAs and OAs, protection in FRs and NRs is generally very low (Oberosler et al., 2019; Stoner et al., 2007), and regulations regarding resource extraction vary between areas and tend to be unclear (FZS, 2018). In some cases, FRs overlap with other protected areas (particularly GCAs, OAs, or WMAs; MNRT, 2016).

Management of Tanzania’s PAs is divided between a number government agencies. NPs are managed by TANAPA (Tanzania National Parks Authority), a parastatal and, since 2018, paramilitary agency. Responsibility for the management of GRs, GCAs, and all wildlife outside of PA boundaries falls to TAWA, also a parastatal and paramilitary agency. Management of OAs is under the jurisdiction of local District Game Officers (DGOs), although TAWA can provide anti-poaching and other support. Management of WMAs falls to local communities, which are expected to collaborate with TANAPA

and/or TAWA. Finally, FRs are managed by the Tanzania Forest Service Agency (TFS), while the NCA is under the jurisdiction of the Ngorongoro Conservation Area Authority (NCAA; MNRT, 2007).

Nevertheless, despite the high proportion of protected land, Tanzania's natural resources face increasing threats from rapidly growing anthropogenic pressures (Caro & Davenport, 2016). The country is experiencing extremely rapid human population growth, with the population increasing from 18.6 million in 1980 to 60.4 million in 2020, and expected to exceed 100 million by 2040 (UN, 2020). Furthermore, population growth has been particularly high along the boundaries of wildlife areas, being highest in wards located <5 km from PAs (Wittemyer et al., 2008). This has led to deforestation accelerating markedly in the past 15 years, with the country losing >37% of its woodland and forest habitat since 1990 (Packer et al., 2009), and seeing 32% of its terrestrial area converted to anthropogenic land uses (Jacobson et al., 2015), with the rate of loss increasingly rapidly (Appendix III).

Although most of this loss has been outside of PAs (Appendix III), habitat conversion for agricultural production and deforestation is also increasing within PAs, particularly less-strictly protected, multi-use PAs (GCAs, OAs, FRs, WMAs; Riggio et al., 2019; Appendix III). Bushmeat poaching is also believed to be increasing in the country (Jambiya et al., 2007), and there have been concomitant declines in herbivore populations, with these also being greatest in less-strictly protected areas (Mtui et al., 2016; Oberosler et al., 2019; Newmark, 1996; Stoner et al., 2006, 2007). Although little data is available, large carnivores are believed to also be increasingly targeted by poisonings as a result of conflicts with pastoralists, particularly around and within less-strictly protected areas (RCP, unpublished data). Such trends are worrying since many less-strictly protected areas in Tanzania still contain important wildlife populations (Caro, 1999; Lobora et al., 2017), and their close proximity to NPs and GRs helps to facilitate seasonal movements (Jenkins et al., 2002) and maintain connectivity between core PA complexes (Jones et al., 2009). The fact that limited funding has contributed to minimal law enforcement in most of these areas, making them unable to provide the levels of protection necessary to safeguard wildlife and their habitat (Pelkey et al., 2000; Riggio et al., 2019; Stoner et al., 2007), is therefore a particular timely and important conservation concern for the country (Lobora et al., 2017).

Due to these increasing pressure on wildlife resources, the government of Tanzania has recently begun exploring novel possibilities for wildlife management and revenue generation, including the establishment of game ranching for both consumptive and non-consumptive uses, which will allow the capture of animals from wild populations, as well as game meat processing and selling facilities (MNRT, 2020a, 2020b). Although novel and as yet untested in the country, the declared objective is to use these strategies to generate a legitimate alternative to wildlife trade and consumption; the exact mechanisms of the proposed system, however, are as of yet unclear.

S2.1.1. Trophy hunting in Tanzania

S2.1.1.1. *Trophy hunting as a conservation tool*

In general, sustainable trophy hunting (also known as 'sport', 'tourist, or 'safari' hunting) has the potential to foster conservation of wildlife, particularly by creating incentives for conservation and the retention of land under wildlife-based uses (Lindsey et al., 2012). This is particularly relevant to large carnivores, which, as a result of their low densities and wide ranging habits, require large areas to survive (Woodroffe & Ginsberg, 1998). Furthermore, large carnivores are at high risk of conflict with humans (Lindsey, Roulet, et al., 2007; Loveridge et al., 2007), and revenues from trophy hunting have been shown to have the potential to increase local tolerance of large carnivores (Nelson et al., 2013) and reduce their persecution (Frank et al., 2006). As a result, financial benefits from hunting have been argued to be essential for providing economic incentives for local communities to conserve large carnivores (Dickson et al., 2009; Lindsey et al., 2006). It has also been argued that the industry creates value for, and thus incentivises the conservation of, areas that photographic tourists would not visit, as a result of remoteness, low wildlife densities, and unsuitability of habitat (Baldus & Cauldwell, 2004; Di Minin et al., 2016), and that it achieves this with a relatively low environmental footprint (Di Minin et al., 2016). These types of PAs are generally classified by the IUCN as Categories IV to VI (Leader-Williams et al., 1996), and account for over 85% of PAs in Tanzania (MNRT, 2016).

If poorly managed or additive to other sources of anthropogenic mortality, however, trophy hunting can have strong deleterious effects on wildlife populations, including for large carnivores, potentially to

such an extent that they are no longer viable (Creel et al., 2016; Packer et al., 2010). In this context, overharvesting and other unsustainable hunting practices have been shown to be common across Africa (e.g. Creel et al., 2016; Rosenblatt et al., 2014), including in Tanzania (Brink et al., 2016; Gayo et al., 2020; Packer et al., 2010), and have been used to argue for the phasing out of trophy hunting. Overall, however, the debate on the value of sport hunting as a conservation tool is increasingly emotive and polarised, with societal, ethical, and biological considerations having been brought forward by proponents of both sides (Bauer et al., 2019; Dickman et al., 2019). However, a lack of scientific data on the ecological and economic impact of trophy hunting continues to preclude objective discourse (Lindsey, Frank, et al., 2007; Mayaka et al., 2005), and more empirical research on the topic is urgently required, to ensure that potentially far-reaching management and policy decisions are based on scientifically-defensible evidence (Macdonald et al., 2017).

S2.1.1.2. *Background to trophy hunting in Tanzania*

Trophy hunting has been occurring in Tanzania since the 19th century (aside from a ban between 1973 and 1978; MNRT, 2016), although the current structure of governance emerged in the 1960s (Leader-Williams et al., 1996). The tourist hunting sector in Tanzania is governed by the Wildlife Conservation Act, No. 5 of 2009, the Wildlife Conservation (Tourist Hunting) Regulations of 2010 (now 2015), and the Wildlife Conservation (CITES Implementation) Regulations of 2005 (MNRT, 2016). Trophy hunting is conducted in designated areas, termed 'hunting blocks', which can be legally declared by the government anywhere that is not a NP. In most cases, however, the boundaries of hunting blocks coincide with those of a GR, GCA, OA, FR, or WMA, with most comprising either the complete PA, or a sub-set of it (MNRT, 2016; UNEP-WCMC, 2015). Individual hunting blocks are leased from the government by hunting operators; historically, this was for a period of 5 years (FZS, 2018), although recently tenure was increased to either 10 or 15 years, depending on the block's category (TAWA, 2018, 2019). Each hunting block is placed in one of three categories (I, II, III), based on their perceived quality, with different fees for each category (TAWA, 2019). Overall, depending on the source, between 264,000 km^2 and 304,400 km^2 of Tanzania, approximately one quarter to one third of the country, are presently eligible for trophy hunting (Booth, 2017; FZS, 2018; MNRT, 2018). A total of 74 species of

wildlife may be shot on license by hunters, who cannot be citizens or residents, under the guidance of a government-approved professional hunter (MNRT, 2016). The majority of government revenue from the trophy hunting industry is from buffalo, lion, and leopard trophies (Baldus & Cauldwell, 2004).

The government of Tanzania views trophy hunting as an important revenue earner and a key tool in wildlife conservation, with the country's Wildlife Policy stating that 'hunting is an economically viable and sustainable use of wildlife that is consistent with the policy of high quality, yet low density tourism that can contribute significantly to the national economy' (MNRT, 2007). The current government policy is that Tanzania's rapidly increasing human population, and associated demand for agro-pastoral land, lead to both consumptive (e.g. hunting tourism) and non-consumptive (e.g. photographic tourism) uses of wildlife being essential to conserve the country's natural habitats (MNRT, 2018). Specifically, hunting areas are argued by the government to create economic value while securing natural ecosystems and their services (MNRT, 2016).

In 2017, fees from over 1000 trophy hunters are believed to have brought over US$13 million in direct accrued revenue to the Tanzanian government (although the overall economic value of the hunting industry is argued to be considerably greater; MNRT, 2018). Trophy hunting is the primary source of revenue for TAWA, which since 2016 retains 100% of hunting revenues (MNRT, 2018), and nearly 80% of TAWA/TWPF's anti-poaching budget comes from hunting revenues (MNRT, 2016). In addition, hunting operators are partly responsible for the management of leased hunting blocks, and are required to carry out anti-poaching and other habitat protection activities (MNRT, 2007). Total contributions to anti-poaching and other protection activities by all operators in Tanzania between 2013 and 2015 was estimated at ~US$3.7 million (Booth, 2017; MNRT, 2016). Finally, it has also been argued that the trophy hunting industry brings considerable direct benefits to communities surrounding PAs: hunting operators are legally required to contribute a minimum of US$5,000 towards community investment and participation per concession per year (Booth, 2017), and total contributions from hunting operators in rural community development between 2013 – 2015 were estimated at US$1.8 million (MNRT, 2016). Where trophy hunting occurs in WMAs, communities should receive between 60 – 65% of the total income from hunting activities (Booth, 2017; MNRT, 2016, 2018). Nevertheless,

over the last two decades significant concerns have been raised regarding the transparency and governance of the industry in Tanzania, particularly with regards to block allocation, sustainability of quotas, and effective enforcement of regulations (Booth, 2017; EU, 2017a; Packer, 2009, 2010; UNEP-WCMC, 2015; USFWS, 2015). These concerns were ultimately cited as drivers of import bans, enacted in 2015, which saw the ban on the import of elephant trophies (in the U.S. and EU) and of lion trophies (in the U.S.) from Tanzania (USFWS, 2015; see 'Trophy hunting of lion in Tanzania' below for more details). The government of Tanzania denies these allegations (MNRT, 2016).

In 2015, an increasing number of hunting blocks began to be abandoned and returned by hunting operators to the government (TAWA) for management; by 2018, nearly 50% of hunting blocks (numerically and by area) had been vacated (FZS, 2018). This has particularly been the case for blocks in less-strictly protected areas, such as GCAs and OAs (Booth, 2017). Reasons brought forward for this are multiple; the aforementioned import bans (USFWS, 2015), and resulting uncertainty, have been cited as key drivers by outfitters and the government (FZS, 2018; MNRT, 2018 – see 'Trophy hunting of lion in Tanzania' below), as approximately 43 – 45% of clients originate from the U.S. (Booth, 2017; MNRT, 2018). Encroachment by humans and livestock, and the resulting impact on wildlife populations, has also been cited as a key driver (Booth, 2017), as have shifting ethical norms in Western society, anti-hunting campaigns, and economic recessions (MNRT, 2018). Recently, a new system of online block auctioning was developed, to attempt to increase both the allocation of vacant blocks and the transparency in the allocation process (TAWA, 2018, 2019), but with mixed success (MNRT, pers. comm.). The Tanzanian government argues that block vacancies have led to insufficient protection of wildlife in abandoned blocks, and that the decrease in hunting revenues has affected its ability to secure its wildlife populations, due to the lack of incentives derived from its sustainable use (MNRT, 2016, 2018). Novel research suggests that vacant blocks are significantly more at risk of habitat loss, thus providing some evidence for such claims, although it also indicates that mechanisms of loss are likely to be complex (Appendix III). Regardless of the underlying drivers, due to the vast size of the area covered by abandoned hunting blocks, research into both the ecological and socio-economic impacts of these significant and rapid shifts in the Tanzanian conservation landscape is urgently required.

S2.2. LARGE CARNIVORES IN TANZANIA

S2.2.1. Lion

S2.2.1.1. *Status & current knowledge of the lion in Tanzania*

Tanzania is believed to be the country with the greatest number of remaining lions (Bauer et al., 2016; Riggio et al., 2013), with the species still being fairly well distributed across PAs in the country, as well as some unprotected areas. In northern Tanzania, lions are present in Serengeti, Tarangire, Manyara, and Mkomazi NPs, as well as in Ngorongoro CA, Loliondo GCA, and Maswa, Grumeti, and Ikorongo GRs. Lions are believed to also be relatively well distributed across unprotected areas in the region, having been recorded over 100 km to the east of Tarangire NP, and occasionally in Lake Natron and West Kilimanjaro. They are also well distributed in central and western Tanzania, including in Ruaha, Katavi, and Mahale NPs, and in Rungwa, Kizigo, Muhesi, Ugalla, Kigosi, Moyowosi, and Rukwa-Lukwati-Piti GRs. Lions are also believed to still be present between these areas, in the lesser-protected and semi-protected areas (GCAs, OAs, and FRs) linking the different NPs and GRs in the region (Mesochina et al., 2010), although no precise distribution data is available. In southern Tanzania, lions are present in Mikumi, Udzungwa Mountains, and Nyerere (ex-Selous GR) NPs, the Selous GR, and the Kilombero GCA. Lions are also present in Saadani NP, on the coast, and possibly in the north-west of the country (Biharamulo, Burigi, Ibanda and Rumanyika GRs), in Swaga Swaga GR, and around Dodoma, Itigi, and Tabora towns, in central Tanzania, although their continued presence in these areas is uncertain (TAWIRI, 2009). In addition, a large number of attacks on people were reported until recently outside of some PAs (particularly Selous GR – Kushnir et al., 2010; Packer, 2005), some as far as near the border with Mozambique, suggesting important populations of lions outside of PAs at least until the mid-2000s. Indeed, Packer et al. (2009) note that in Tanzania, unlike in most other range countries, significant numbers of lion were found outside of protected areas, although it is unclear whether this is still the case. Mesochina (et al., 2010) suggested that the majority (55%) of the species range in Tanzania was in non-gazetted areas, although approximately 81% of the total population is thought to be within protected areas, divided between NPs (21.5 – 24%) and hunting areas (i.e. GRs,

GCA, and OAs; 57%). The same effort estimates country-wide population at 16,800, although the majority of estimates for individual populations were obtained through extrapolation from densities elsewhere, thus introducing considerable uncertainty (Braczkowski, Gopalaswamy, Elliot, et al., 2020). Recent country-wide genetic analyses suggest that the lion populations across the country seem to have gradually decreased in size over recent decades (Smitz et al., 2018), and suggest the presence of three separate lion clusters in Tanzania (northern, southern, and central-western).

Nevertheless, despite the species still being relatively widespread in the country, considerable knowledge gaps remain on the status of most of Tanzania's lion populations (EU, 2017a; Mesochina et al., 2010; Riggio et al., 2013). Furthermore, most research has focused on populations in the northern Tanzania, which has led to a better knowledge of lion population status in this region. Maddox (2003) employed call-in surveys to estimate lion densities at 28 (95% confidence intervals: 9 – 55) per 100 km^2 on the Serengeti plains, 21 (10 – 29) per 100 km^2 in the Ngorongoro Conservation Area, and 37 (12 – 87) per 100 km^2 in Loliondo GCA (TAWIRI, 2009). Also in Serengeti NP, Packer et al. (2005) found that lion densities varied between 3 – 6 per 100 km^2 in the short grass plains to between 20 – 30 per 100 km^2 along the rivers, as well as between years, while Belant et al. (2016) estimated a density of 14.4 lions per 100 km^2 using call-ins, and Belant et al. (2017) one of ~23 per 100 km^2 using call-ins and n-mixture models. Belant et al. (2019) also estimated density in the same area, using spoor counts, with estimates of between 35 – 41 lions per 100 km^2, while Durant et al. (2011) estimated densities of 9.9 per 100 km^2 through distance sampling. The Ngorongoro crater population, also relatively well studied, was estimated at 30 lions per 100 km^2 by Kissui et al. (2010), and was also shown to fluctuate temporally. Nevertheless, even in the better-studied north, status estimates are localised to a few populations (Serengeti NP and Ngorongoro CA), rather than evenly distributed in the region.

Elsewhere in the country, recent population data is sparse, with a few exceptions. Kiffner et al. (2009) employed call-ins to estimate a lion density of 4 (2 – 10) per 100 km^2 in Katavi NP, and Brink et al. (2012) employed the same methodology to estimate densities of between 2 – 10 lions per 100 km^2 in different areas of the Selous GR. Finally, Crosmary et al. (2018) estimated lion densities of 2.1 – 5.1 per 100 km^2 over about one fifth of the Selous GR, using spoor counts. Older population density

estimates include Rodgers (1974), who estimated estimate lion density at 8 per 100 km^2 in eastern Selous GR, and Creel & Creel (1997) and Spong (2002), who estimated densities of 13 and 16 lions per 100 km^2 in northern Selous GR, respectively. No other published density estimates for populations in Tanzania are available; although some governmental reports mention past surveys in Tarangire NP, Rungwa GR, Luganzo GCA, and Moyowosi GR (MNRT, 2016), no information on methods or results is publicly available. Overall, it is estimated that only 8% of lion range in Tanzania has been subjected to any type of survey work (UNEP-WCMC, 2015).

Lions in Tanzania face similar threats affecting lion populations elsewhere in Africa (Bauer et al., 2020). Although habitat loss and fragmentation remains the main threats (MNRT, 2016), ritual, pre-emptive, and retaliatory killings, particularly by pastoralist tribes such as the Maasai and the Barabaig, can reach particularly high intensities in certain parts of Tanzania (Dickman et al., 2014). Around Tarangire NP and in the Ngorongoro CA, Maasai pastoralist kill lions in direct proportion to the number of cattle lost to lions (Ikanda & Packer, 2008; Kissui, 2008). To the east of Ruaha NP, 35 lions were killed in 2011 over an area of less than 500 km^2 (Ruaha Carnivore Project, unpublished data), and 22 lions were poisoned over one year in a single hunting block in the Selous GR (Packer et al., 2010). Overall, it is estimated that about 200 lions are killed by communities in retaliation for livestock losses or human attacks, or preventively, each year across Tanzania, while targeted poaching for body parts for traditional medicine is believed to cause the mortality of between 10 – 20 individuals per years (MNRT, 2016). Trophy hunting has also been identified as a threat for certain lion populations in the country (Brink et al., 2016; Packer et al., 2010; see below), although the Tanzanian government disagrees that impacts from hunting are having detrimental effects on lion populations in Tanzania (MNRT, 2016). Finally, particularly high levels of lion attacks on humans have been recorded in certain areas of Tanzania (Packer, 2005), with over 870 recorded attacks between 1990 and 2009 (Kushnir et al., 2010). Lion attacks on humans have however decreases in recent years (MNRT, pers. comm.), although drivers of this change are as of yet unclear. Approximately 10 lions are killed through official problem animal control (PAC) actions each year (MNRT, 2016).

S2.2.1.2. *Trophy hunting of lion in Tanzania*

Tanzania is Africa's most popular destination in for lion trophy hunting (based on individuals hunted per year; Lindsey et al., 2013), with the species estimated to be hunted on between 34 – 61% of its Tanzanian range (Mesochina et al., 2010). Only foreign tourists can hunt lion in Tanzania, and only males can be hunted. The number of lions hunted is regulated through a fixed annual quota for each individual hunting area ('block') established by the parastatal Tanzania Wildlife Management Authority (TAWA), which manages trophy hunting areas in Tanzania (MNRT, 2016). Quotas are revised annually, and are based on various sources of information, including opinions regarding quota sustainability by TAWA officers and PA managers, input from the Tanzania Wildlife Research Institute (TAWIRI) and other experts, recommendations by hunting operators, and available population and distribution survey data and reports (MNRT, 2016). Lion hunting is estimated to contribute approximately US$1 million per year directly through trophy fees to the Tanzanian economy, and an additional US$1.4 million through other fees (Mesochina et al., 2010; MNRT, 2016). The government trophy fee for lion in Tanzania is currently US$4,900 (to be paid in addition to other, non-trophy or species related fees; MNRT, 2012).

In the early 2000s, lion hunting in Tanzania started coming under scrutiny due to fears of unsustainable hunting practices. Between 2005 and 2009, 38% of hunting blocks were receiving quotas of over 2.5 lions per 1,000 km^2 each year, with 10% receiving quotas higher than 5 per 1,000 km^2. Offtakes were similarly high, with 32% of hunting blocks harvesting more than 1 lion per 1,000 km^2 per year, and 18% more than 2 per 1,000 km^2, with peaks of 5 per 1,000 km^2. The highest levels of offtake were recorded in and around the Selous GR, along the boundaries of Serengeti and Tarangire NPs, and in Lukwati and Rungwa GRs (Mesochina et al., 2010). In 2009, Packer et al. noted that trophy hunting quotas for lions in Tanzania had not been based on rigorous quantitative analyses of harvest patterns, and that a substantial proportion of Tanzania's lion trophies in 2006 – 2008 consisted of sub-adult males, a sign of over-exploitation (Allendorf & Hard, 2009; Packer et al., 2009). Indeed, Packer et al. (2010) found that lion harvests had declined by circa 50% across the country between 1996 and 2008, and that hunting areas with the highest initial harvests suffered the steepest declines. Excessive offtake was argued to

have been the primary driver of a decline in lion abundance in both trophy-hunting areas and adjacent non-hunting PAs (Kiffner et al., 2009; Packer et al., 2010), and to be responsible for skewed sex ratios around Katavi NP (Kiffner et al., 2009) and Selous GR (Brink et al., 2012). As a result, Packer et al. (2010) recommended that annual quotas be limited to 0.5 lions per 1000 km^2 (1 per 1,000 km^2 in the Selous GR), arguing that, although guidelines based on percentage of population harvested already existed (Baldus & Cauldwell, 2004; Caro et al., 2009; Whitman et al., 2004), the lack of population abundance data made these not suitable in Tanzania.

Following this research, several modifications to the quota system were adopted, implemented in the 2010 and 2015 Wildlife Conservation (Tourist Hunting) Regulations (MNRT, 2016). An age limit was set, and only male lions older than six years were allowed to be hunted, as per recommended practice (Begg et al., 2018; Whitman et al., 2007). Trophies of lions between four and six years could still be exported but resulted in penalties, including lowered quotas for the hunting block the following year, while lions younger than four could not be exported and would result in severe penalties for the operator (up to US$10,000; Booth, 2017; MNRT, 2016). Capacity building of the hunting sector was carried out through workshops on lion ageing for hunting operators (although evidence suggests operators still find lion ageing challenging; Gayo et al., 2020), and quotas were also considerably reduced, with the adoption of Packer et al. (2010)'s recommendations (quotas of 0.5 lions/1,000 km^2, with the exception of Selous GR, set at 1 lions/1,000 km^2). This led to offtakes also being significantly reduced over the following years, with the number of lions hunted decreasing from a peak of 278 in 2006 to 39 in 2015, and the proportion of hunted lions over 6 years of age rising from only 3.5% in 2011 to 33.3% in 2014 (Booth, 2017; MNRT, 2016). Furthermore, a monitoring and control programme was reported to have been established to follow up on lion hunting activities (UNEP-WCMC, 2015), although it is unclear how the impacts on populations are monitored (EU, 2017b). The Ministry of Natural Resources and Tourism (MNRT) also reported that a new aged-based quota system was adopted, which allocates quotas to each area according to the age of the lions harvested in the previous hunting season (UNEP-WCMC, 2015). Overall, although Lindsey et al. (2013) state that it is not known whether decreased offtakes are not at least partly due to continued population declines, the increased regulations adopted

are believed to have been beneficial for Tanzania's lion populations, although more research is required to determine their overall effectiveness (EU, 2017a, 2017b).

In 2015, however, the USFWS ESA Final Rule on Lion uplisted the species and banned import of trophies in the U.S. from lions hunted in Tanzania (USFWS, 2015). The effectiveness of import bans on conserving lion populations has been a source of debate. While these and other similar restrictions may reduce a direct source of mortality for lions, and potentially allow populations depleted due to over-hunting to recover (Lindsey et al., 2012), practitioners have argued that such bans may be overall detrimental, by rendering trophy hunting less viable in many areas, and thus removing or reducing the economic justification to retain large blocks of land for wildlife. It has also been argued that bans reduce funds for anti-poaching and tolerance for lions, and, since hunting is often conducted in areas where photographic tourism is often unviable, risk leading to conversion of hunting areas to less conservation-compatible land uses, such as agriculture and pastoralism (Booth, 2010; Di Minin et al., 2013, 2016; Dickman et al., 2019; Lindsey et al., 2012). In the case of Tanzania, U.S. hunting tourists represent the majority of clients, especially for lion (between 48 – 60% of lion hunts between 2012 and 2016; MNRT, 2016). Because of this, Lindsey et al. (2012) considered Tanzania to be highly economically vulnerable to a ban, recommending that interventions should instead focus on improving management. Indeed, hunting associations and the Tanzanian government claim that the U.S. import ban was a key factor in causing approximately one third of all concessions to be returned to the government by hunting operators over a single year (2016), for an area totalling approximately 60,000 km^2 (MNRT, 2016), or ~12% of the lion's estimated range in Tanzania (Mesochina et al., 2010; this area has since increased – FZS, 2018; see 'S2.1.1. Trophy hunting in Tanzania'). Similarly, all management expenses by TAWA, who are responsible for managing hunting areas in Tanzania, have to be met from the Tanzania Wildlife Protection Fund (TWPF), which is replenished by revenues from the hunting sector, and this income is believed to have dropped by circa 30% following import bans enacted by the EU (for elephant trophies) and the USA (lion, elephant; EU, 2017a, 2017b; MNRT, 2016). Nevertheless, empirical research on the drivers of the observed trends in block abandonment, and on its effects on lion populations, is lacking.

S2.2.2. Leopard

S2.2.2.1. *Status & current knowledge of the leopard in Tanzania*

Leopards are considered widespread throughout Tanzania (MNRT, 2018), with the country likely being home to one of Africa's largest remaining populations (Stein et al., 2020). Leopards have been estimated to still occur in between 76% and 90% of Tanzania's terrestrial surface, with the species believed to be present in most NPs and GRs, and in many GCAs and OAs (MNRT, 2018; although distribution estimats were mostly based on older records). The species is also likely to be present in unprotected areas with low human density and availability of natural habitat (Foley et al., 2014; TAWIRI, 2009).

Nevertheless, relatively little empirical research has been carried out on leopards in Tanzania, and the exact distribution and status of most populations is unknown (TAWIRI, 2009). Notable exceptions to this include: two recently published studies, that employed camera trapping and spatially explicit capture-recapture (SECR) modelling to estimate densities of 4.2 leopards per 100 km^2 in Udzungwa Mountains NP (Havmøller et al., 2019) and 5.4 – 5.7 per 100 km^2 in Serengeti NP (Allen et al., 2020); an effort by Crosmary et al. (2018), who sampled about one fifth of Selous GR using spoor counts, and found leopard densities of between 1.7 and 3.8 leopards per 100 km^2; and unpublished density estimates from Maswa GR (5.22 leopards per 100 km^2), the Maasai steppe (2.3 per 100 km^2) and Tarangire NP (7.9 per 100 km^2; MNRT, 2018), although no information is publicly available on how these were obtained. For the majority of the country, however, distribution and population abundance or density data are lacking, and for this reason robust country-wide estimates are not available. In an export quota amendment request to CITES, the Tanzanian government estimated the country-wide leopard population at ~39,000 (MNRT, 2018), based on Martin & De Meulenaer (1988)'s population estimates, in turn based on the relationship between leopard density and rainfall, and widely considered to be an overestimate (Norton, 1990; Nowell & Jackson, 1996; Strampelli et al., 2018b). Country-wide population abundance was later re-assessed at 19,673 based on extrapolation from the density estimates cited above (MNRT, 2018), although considerable guesswork was again involved.

Threats to leopard in Tanzania include most of those faced by the species across the rest of its African range, including habitat and prey base loss, and both direct and indirect persecution (e.g. poisoning or trapping for killing livestock, and accidental capture in bushmeat poaching snares; Stein et al., 2020). It has also been argued that overharvesting of leopard through trophy hunting is a threat to certain populations in Tanzania (Packer et al., 2010), although, as for lion, the government denies this (MNRT, 2018). Records suggest that 4 – 15 leopards are killed annually in Tanzania in problem animal control operations, while there are no known record of trade in leopard bone, and poaching for the illegal trade in skins is not considered a serious threat in the country (MNRT, 2018).

S2.2.2.2. *Trophy hunting of leopard in Tanzania*

Tanzania is one of the world's most popular destinations for sport hunting of leopards, with a total export quota set at 500 individuals, the highest in Africa (CITES, 2020; although this has never been realised in recent years – MNRT, 2018). Quotas are set by TAWA, and, much like quotas for lion (see 'Trophy hunting of lion in Tanzania' above), are revised annually, through the same methodology. Leopards are harvested over an estimated range of 304,400 km^2, equivalent to circa 77% of their estimated protected range in the country (MNRT, 2018). Prior to 2011, Tanzania exported an average of 303 leopard trophies per year (Packer et al., 2010), but exports have decreased considerably since, down to 119 in 2017 (MNRT, 2018). Only male leopards with a body length of over 130 cm (from the tip of the nose to the base of the tail) can be harvested. The Tanzanian government sees trophy hunting of leopard as 'contributing significantly to the conservation of this species and its habitat' (MNRT, 2018). The government trophy fee for leopard in Tanzania is currently US$3,500 (MNRT, 2012b).

Similarly to lion, however, over the past decade there have been rising concerns about potential overharvesting of leopard in hunting areas in the country (Brink et al., 2012; Packer et al., 2010). Spong et al. (2000) showed that about 30% of Tanzania's documented leopard trophies, at the time of the study, were female, and Packer et al. (2010) suggested that trophy hunting may have driven a decline in leopard abundance in several areas in and around Selous GR. As a result, they recommended an annual leopard harvest not exceeding 1.0 leopards per 1000 km^2, with the exception of the Selous GR, where an annual offtake of up to 3.0 leopards per 1000 km^2 was recommended. The Tanzanian

government argues that current quotas reflect this and are below this threshold, although it does appear that offtake intensity estimates are based on Tanzania's estimated leopard country-wide range, rather than these being calculated at the individual population level (MNRT, 2018).

Unlike in South Africa, there is no current age limited implemented in Tanzania, with the aforementioned minimum length being the only requirement (MNRT, 2018). Packer et al. (2009) suggest that an age minimum would be beneficial for leopard populations in Tanzania, with a safe minimum age being 7 years, although they concede that the difficulties associated with estimating leopard age in the field makes this unlikely. Overall, like in much of its range outside of South Africa (Jacobson et al., 2016), little research has been carried out on hunted leopard populations in Tanzania.

S2.2.3. Cheetah

S2.2.3.1. *Status & current knowledge of the cheetah in Tanzania*

The cheetah has witnessed a particularly drastic range contraction in eastern Africa, with only 6.2% of its original range estimated to still be occupied (compared to southern Africa's 22.8%; Durant et al., 2015). In Tanzania, cheetah were historically present throughout the country, with the possible exception of some coastal areas (TAWIRI, 2009), and the country has always been considered an important stronghold for the species (Gros, 2002; Myers, 1975).

Presently, cheetah are known to occur in much of the northern part of the country, including most PAs and unprotected areas in the Maasai Steppe, and along the border with Kenya. Two further populations are confirmed to exist in the country, in south-central and in western Tanzania. The first is in the Ruaha-Rungwa system, with confirmed presence in Ruaha NP and Rungwa, Kizigo, and Muhesi GRs, as well as Lunda-Mkwambi GCA and MBOMIPA WMA, while the second is in the Katavi-Ugalla system, which includes Katavi NP and Ugalla GR, as well as Msima and Mlele GCAs (TAWIRI, 2009, 2016). A total of 1,060 cheetah were estimated to remain across Tanzania, in these three populations, although estimates were obtained by extrapolating from known densities elsewhere, and should therefore be treated with caution (Durant et al., 2015).

Large gaps, however, exist in the current knowledge of cheetah distribution elsewhere in the country. The area between the Ruaha-Rungwa and Katavi-Ugalla populations consists for the most part of hunting concessions, in relatively intact habitat. However, it is unknown if cheetah occur here, and whether a linkage between the two resident populations is present. Cheetah distribution is also unknown in the Moyowosi-Kigosi complex, in north-western Tanzania, and in the Selous-Mikumi-Udzungwa system. Cheetah have been recorded in the Selous GR, with the last confirmed sighting in the late 1990s (TAWIRI, 2009), and in Mikumi NP, with the last confirmed observation also in the 1990s (Gros, 2000; Graham Mercer, pers. comm.); however, it is not known whether these belonged to resident populations that are still present in low numbers, resident populations that are extinct, or vagrants from now-degraded corridors to the west or north.

Until now, virtually all cheetah research in the country has taken place on the Serengeti population, including the only population density assessments carried out in the country (2 – 2.5 cheetah per 100 km^2; Durant et al., 2011, 2017). Obtaining further insights into the distribution and status of cheetah populations elsewhere in Tanzania is therefore considered a national conservation priority for the species (TAWIRI, 2009, 2016).

Finally, as a result of their wide-ranging habits, 44% of confirmed and 63% of possible cheetah range in Tanzania falls outside of NPs (TAWIRI, 2016). This highlights the importance of conservation activities outside of PAs for the species (Marker et al., 2017), and the need to better understand the extent to which populations range outside of core areas. Given the species' naturally low population densities, populations inside strongly protected PAs (NPs, GRs) are almost certainly dependent on partially protected areas (GCAs, OAs, WMAs), and conservation investments in the latter are therefore critical if these are to be successfully conserved in the long-term (Marker et al., 2017; TAWIRI, 2009).

S2.2.4. African wild dog

S2.2.4.1. *Status & current knowledge of the African wild dog in Tanzania*

The historical geographical distribution of wild dogs in Tanzania likely included the majority of the country, as suggested by their habitat adaptability (wild dogs are the only large mammal to have been

sighted on the summit of Mt. Kilimanjaro; Thesiger, 1970). Although the species has disappeared from much of its former range in the country, wild dogs are believed to still be present across 31% of Tanzania, a greater proportional area than in any other country in eastern Africa. Remaining wild dogs are believed to be divided into three populations: a southern population, centred around Nyerere NP and Selous GR; a western-central population, encompassing Ruaha-Rungwa, Katavi-Ugalla, and Moyowosi-Kigosi, and possibly the GCAs and OAs in between (wild dogs were recently confirmed to occur in Rungwa River FR, between Ruaha-Rungwa and Katavi-Ugalla; Damien, 2019); and a northern population, covering the Maasai Steppe, Mkomazi NP, and Loliondo and Maswa GRs. Whether there is still connectivity between these resident populations in not known, although it is believed possible (TAWIRI, 2016). Most published empirical research on wild dogs ecology in Tanzania was carried out in the Selous GR, in the form of a long-term ecological study in the 1990s (Creel & Creel, 1996, 1998, 2002), and research is lacking at a national level (Wilfred, 2017). Although a tentative estimate of 1,800 – 1,900 individuals was made for the country, this involved considerable guesswork to fill the many knowledge gaps (Woodroffe & Sillero-Zubiri, 2020).

Threats to Tanzania's wild dog populations are similar to those faced by the species elsewhere in Africa, including habitat loss & fragmentation, prey base depletion, retaliation as a result of livestock depredation, and accidental killings by snares or vehicles (Wilfred, 2017). Approximately 60% of confirmed wild dog range in Tanzania lies outside of NPs (TAWIRI, 2016); thus, as for cheetah, adjacent strongly protected hunting areas (i.e. GRs), as well as partially-protected (GCAs, OAs, WMAs) and non-protected areas, will be essential to secure the future of wild dogs in Tanzania (particularly given the species' high vulnerability to extinction in smaller PAs; Woodroffe & Ginsberg, 1998).

S2.2.5. Spotted hyaena

S2.2.5.1. *Status & current knowledge of the spotted hyaena in Tanzania*

Spotted hyaena are widespread across Tanzania, with the species known to occur in nearly all NPs and GRs in the country (with the exception of Gombe NP). They are also likely to be present in most of the country's GCAs and OAs, as well as some FRs. There are numerous records of spotted hyaena outside

of PAs, and they are believed to still be present close to Tabora, Singida, and possibly Dodoma towns. Nevertheless, although exact distribution data is lacking, it is likely that the species' range in Tanzania has contracted considerably in the last few decades, as a result of habitat loss, prey base depletion, and targeted killings (particularly through poisonings) following depredation on livestock (TAWIRI, 2009).

Despite its wide distribution, little information is available on spotted hyaena population density and trends in the country (TAWIRI, 2009). The only density estimates available for Tanzania are from the Selous GR (32 individuals per 100 km^2; Creel & Creel, 1996), Serengeti NP (60 – 80 per 100 km^2; Hofer & East, 1995), and the Ngorongoro crater (133 – 240 per 100 km^2; Höner et al., 2005; Kruuk, 1972), although densities in Ngorongoro are believed to have decreased slightly since (TAWIRI, 2009).

S2.2.5.2. *Trophy hunting of spotted hyaena in Tanzania*

Spotted hyaena are hunted for trophies in Tanzania, with quotas for each hunting block set annually by TAWA (although no data on quotas and offtakes are publicly available). However, the species is only rarely sought out by hunters, and most hunts occur opportunistically when baiting for lion or leopard (professional hunter, pers. comm.). No research has been carried out on the impact of trophy hunting on spotted hyaena populations in Tanzania. The government trophy fee for spotted hyaena in Tanzania is currently US$550, or almost only one tenth of that for lion (MNRT, 2012b).

S2.2.6. Striped hyaena

Striped hyaena are believed to be widely distributed in northern and central Tanzania, with Ruaha NP believed to be the southernmost limit of the species' range. Nevertheless, exact distribution, densities and trends are unknown, with most insights based on opportunistic sightings (TAWIRI, 2009).



The Great Ruaha River is the lifeblood of southern Ruaha-Rungwa. Adjacent areas exhibit some of the highest large carnivore densities recorded in Africa.

The environmental flow of the river, however, is threatened by large-scale upstream cultivation and irrigation. These have led to a considerable loss of dry season wildlife habitat, and will lead to even greater impacts if not appropriately addressed.

CHAPTER 3

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



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

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ABSTRACT

Large carnivores are increasingly restricted to human-impacted landscapes, which exhibit vast heterogeneity in biotic resources and anthropogenic pressures. Understanding habitat use of large carnivores and their prey in these modern systems 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 eastern African large carnivore guild, their prey, and illegal human activity across the 50,000 km^2 Ruaha-Rungwa landscape in south-central 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 management types and anthropogenic impact gradients. Habitat conversion to agriculture and prey availability, more so than 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. African wild dog were instead limited within protected areas by habitat features, avoiding areas of high sympatric predator density. The species was also the large carnivore exhibiting the lowest tolerance to habitat conversion, while spotted hyaena and leopard were the most adaptable, 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. Taken together, these results highlight the importance of adopting an integrated approach to conservation planning in mixed-used landscapes characteristic of modern Africa.

3.1. INTRODUCTION

African large carnivore research and conservation has historically been centred around the concept of protected areas (PAs) as isolated islands of wilderness, insulated from anthropogenic disturbances (Adams, 2013). However, while intact, strictly-protected areas remain critical to the survival of most large carnivore populations (Balme et al., 2010; Karanth & Chellam, 2009), many large carnivores now also persist in, and rely on, unprotected or semi-protected areas, so that the future of these species cannot rely on strictly-protected areas alone (Ripple et al., 2014; Woodroffe & Ginsberg, 1998). Indeed, modern African conservation landscapes exhibit vast heterogeneity in biotic resources, anthropogenic pressures, management strategies, and protection levels (DeFries et al., 2007; Lockwood et al., 2006; Riggio et al., 2019), and most large carnivore populations are now exposed to a range of anthropogenic impacts, including habitat loss through conversion to agriculture, competition with livestock, prey-base depletion through bushmeat poaching, and mortality from persecution, bycatch, and trophy hunting (Bauer et al., 2016; Bohm & Höner, 2015; Durant et al., 2015; Stein et al., 2020; Woodroffe & Sillero-Zubiri, 2020). As a result of their naturally low densities, wide ranging nature, and potential for conflict with humans, however, large carnivores are particularly vulnerable to such pressures (Cardillo et al., 2004; Woodroffe & Ginsberg, 1998), and in Africa they have experienced severe population declines over the past 40 years, with range contractions estimated at 94% for lion (*Panthera leo;* Wolf & Ripple, 2017), 48 – 67% for leopard (*Panthera pardus;* Jacobson et al., 2016), 91% for cheetah (*Acinonyx* jubatus; Durant et al., 2015), 93% for African wild dog (*Lycaon pictus*, hereafter: wild dog*;* Wolf & Ripple, 2017), and 24% for spotted hyaena (*Crocuta crocuta;* Wolf & Ripple, 2017). Understanding large carnivore spatial dynamics and habitat requirements in modern, human-disturbed landscapes, now comprising the majority of their remaining range, is therefore essential to ensure their effective conservation into the 21st century (Athreya et al., 2013; Balme et al., 2014).

While there has been research into the impact of different forms of anthropogenic disturbance on the ecology of individual large carnivore species, including habitat conversion (Abade et al., 2020; Boron et al., 2016), pastoralism (Everatt, Moore et al., 2019; Ogutu et al., 2005; Schuette, Creel, et al., 2013), bushmeat poaching (Everatt et al., 2015; Henschel et al., 2011), conflict with humans (Masseloux et al.,

2018; Schuette, Wagner, et al., 2013), and trophy hunting (Creel et al., 2016; Croes et al., 2011; Davidson et al., 2011; Loveridge et al., 2007; Mweetwa et al., 2018; Packer et al., 2010), multiple stressors can lead to impacts greater than would be expected through individual effects alone, so focusing on single effects can be misleading. As a result, the extent to which these pressures interplay and compare with biotic resources in shaping large carnivore space use remains poorly understood (Balme et al., 2014; Everatt et al., 2019). Comprehending these dynamics, and identifying the limits of species' tolerances in these novel, multi-dimensional systems, is critical if intact large carnivore communities are to successfully persist in increasingly heterogeneous and impacted habitats (Balme et al., 2014; Klaassen & Broekhuis, 2018).

In addition, it is also becoming increasingly clear that, for conservation strategies to be successful in the long-term, objectives must be aligned with the needs for economic development and access to natural resources of both local communities and national governments (Sayer, 2009; Tallis et al., 2009). There is therefore an urgent need to evaluate which models that deliver both biodiversity conservation and human development benefits can be integrated within successful large carnivore conservation frameworks (Millenium Ecosystem Assessment, 2005; UN, 1987). This is particularly pressing in Tanzania, which is home to some of Africa's largest remaining wilderness areas (UNEP-WCMC & IUCN, 2018) and globally important populations of large carnivores (Bauer et al., 2016). Although almost half of the country's terrestrial area is under some form of legal protection – more than any other African country (UNEP-WCMC & IUCN, 2018) – rapid human development, and the associated increased demand for agro-pastoral land, is placing Tanzania's vast PA network and its wildlife under increasingly severe pressure (Lobora et al., 2017; Riggio et al., 2019; UN, 2017).

Many of Tanzania's PAs are employed for trophy hunting, which has the potential to maintain large carnivores and their habitats by providing economic incentives and creating value for wildlife in areas often unsuitable for photographic tourism, with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2007, 2012). However, if poorly managed or additive to other sources of anthropogenic mortality, trophy hunting can have a detrimental impact on populations, and can contribute to local extinctions (Creel et al., 2016; Packer et al., 2010; Rosenblatt et al., 2014).

Tanzania is Africa's most popular destination for trophy hunting of wild lion, leopard, and other charismatic species (CITES, 2020; Packer et al., 2010), with hunting permitted in approximately one third of the country (circa 300,000 km^2; MNRT, 2016, 2018; Riggio et al., 2019). Nevertheless, little research has been carried out to determine the impact of the practice on large carnivore populations in the country (but see Brink et al., 2016; Packer et al., 2010). This has led to increased conservation concern, culminating in a ban on the import of lion trophies from Tanzania into the U.S. (USFWS, 2015), and calls for further research on the impacts of trophy hunting on Tanzania's large carnivores (EU, 2017). Furthermore, an increasing proportion of hunting blocks has been vacated by hunting operators and returned to the government for management in recent years, with approximately half of the country's 150 hunting blocks being abandoned between 2014 and 2018 (FZS, 2018). The impacts of this significant land management change on large carnivores, however, are also yet to be assessed.

At almost 50,000 km^2, the Ruaha-Rungwa conservation complex in south-central Tanzania is a vast mosaic of fully-protected, semi-protected, and unprotected areas, subject to a wide spectrum of both legal and effective on-the-ground protection. With its components under a variety of management strategies, and experiencing a range of sources and intensities of human pressure, Ruaha-Rungwa provides an ideal setting in which to investigate large carnivore spatial ecology and assess the relative success of competing management strategies in a human-impacted, multiple-use setting characteristic of much of modern Africa. To do so, we employed occupancy modelling (Mackenzie et al., 2002) applied to sign-based presence/absence transect data to determine the relative impact of biotic, anthropogenic, and management factors in shaping the habitat use of five large carnivore species (lion, leopard, cheetah, wild dog, and spotted hyaena), their prey, and illegal human activity in Ruaha-Rungwa. We explore how this varied at multiple spatial scales, and across land management types and anthropogenic disturbance gradient. We then discuss what our findings reveal about the habitat use requirements of large carnivores and their prey, and maintaining intact large carnivore guilds in modern, multiple-use African landscapes. We conclude by providing insights regarding the potential role of trophy hunting as a conservation tool in the region, and the conservation implications of ongoing hunting block abandonment in Tanzania.

3.2. METHODS

3.2.1. Study area

Ruaha-Rungwa is a large mixed PA system in south-central Tanzania. The landscape is comprised of: strictly protected Ruaha National Park (NP; 20,226 km^2), the second largest in East Africa, where only photographic tourism is permitted; strictly protected Rungwa, Kizigo, and Muhesi Game Reserves (GRs; 9,175 km^2, 5,140 km^2, and 2,720 km^2, respectively), further sub-divided into zones ('hunting blocks'), where only trophy hunting is permitted; less-strictly protected Lunda-Mkwambi Game Controlled Area (GCA; 1,720 km^2), also reserved for trophy hunting; less-strictly protected community-managed MBOMIPA and WAGA Wildlife Management Areas (WMAs; 947 and 344 km^2, respectively), where both photographic tourism and trophy hunting are permitted, although neither were taking place at the time of study; and less-strictly protected Rungwa South Open Area (OA; 3,870 km^2), where trophy hunting and additional resource extraction by local communities (e.g. logging, fishing) are permitted. Management of the different PAs is divided among a number of parastatal agencies, and hunting operators are also required to contribute to the management of their respective hunting blocks through protection activities (e.g. anti-poaching; MNRT, 2007, 2016). On-the-ground law enforcement is highest in the strictly protected NP and GRs, and lower in the OA, GCA, and WMAs. The complex is surrounded by unprotected village lands to the south and east, and by a number of additional OAs and GCAs to the west and north (Fig. 3.1). No physical barriers restricting movement of wildlife (e.g. fences) are present in the landscape.

Vegetation cover comprises a mosaic of *Acacia-Commiphora* open savannah/bushland and central Zambezian and Eastern *Brachystegia*-dominated miombo woodland, complemented by riverine forests and floodplain grasslands (Olson et al., 2001). Rainfall is distinctly seasonal, with over 90% of the area's annual rainfall occurring between December and April, and average annual precipitation varies considerably across the landscape, from 450 mm in eastern Ruaha NP to nearly 900 mm in Rungwa South OA (Fick & Hijmans, 2017). Surface water availability in the landscape is highly seasonal, with the majority of smaller tributaries drying up completely in the late dry season. The Great Ruaha River

is the largest in the region, and runs along Ruaha NP's south-eastern border; although historically a perennial river that flowed year-round, upstream large-scale cultivation has affected the flow of the river, and since 1993 it has ceased to flow in the dry season (Mtahiko et al., 2006). Other key sources of dry season surface water include the Mzombe and Kizigo Rivers (Fig. 3.1). Altitude in the ecosystem ranges from 696m to 2,171m (ESA, 2009).

The large mammal assemblage of Ruaha-Rungwa includes most species characteristic of the eastern African savannah and woodland (Foley et al., 2014). The area is believed to harbour globally important populations of lion (IUCN Red List Status: Vulnerable), cheetah (Vulnerable) and African wild dog (Endangered), and regionally important populations of leopard (Vulnerable), spotted hyaena (Least Concern), and striped hyaena (*Hyaena hyaena*; Near Threatened) (IUCN, 2020; TAWIRI, 2009), although to date little research has been carried out into these populations. The area also supports most species of East African ungulates, and a globally important population of African bush elephant (*Loxodonta africana;* Chase et al., 2016; TAWIRI, 2019).

Anthropogenic pressures within the PA complex include: land clearing for settlement and subsistence agriculture in unprotected areas and in parts of south-western Ruaha NP and Rungwa South OA; bushmeat poaching; fishing; burning for honey gathering; legal and illegal logging; and illegal mining. Although they vary considerably across the PA system's extent, impacts are generally greatest in less-strictly protected areas (GCA, OA, WMAs) and in part of the GRs (TAWIRI, 2019). Trophy hunting is permitted in Rungwa, Kizigo, and Muhesi GRs, Lunda-Mkwambi GCA, and Rungwa South OA; here, lion, leopard, and spotted hyaena are legally hunted, as are most ungulates (MNRT, 2016). However, four of twelve hunting blocks within the GRs (33%) were vacant at the time of the study, with no trophy hunting taking place. Finally, although protection is generally highest within the NP, human settlements and intensive agriculture are present in south-west Ruaha NP. The area was annexed to the NP in 2008, yet as a result of boundary disputes several thousand people still reside within the gazetted boundaries of the NP (Sirima, 2016; TAWIRI, 2019). As a result, the effective boundaries of the NP (those considered by PA management) do not correspond to the gazetted boundaries in this area (Fig. 3.1).

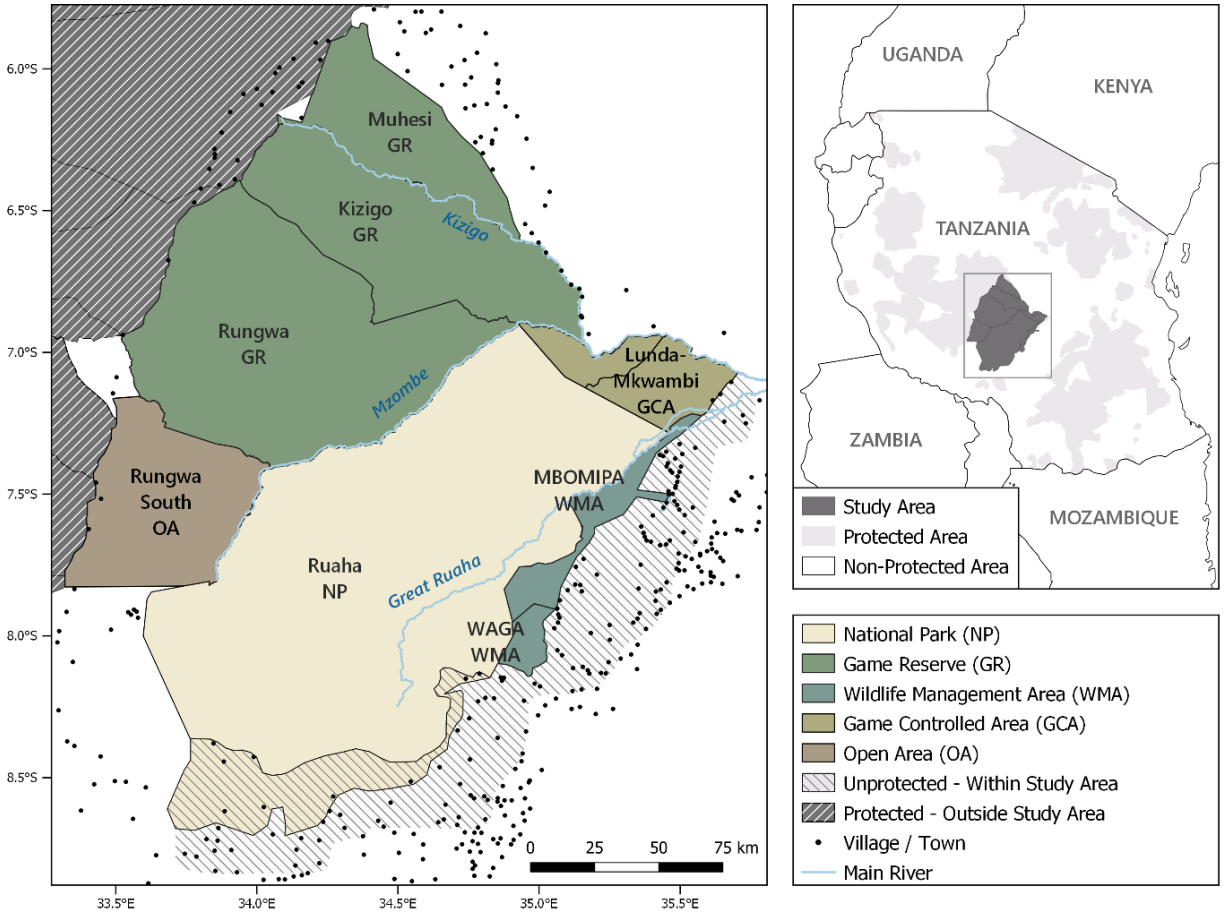


Figure 3.1. The Ruaha-Rungwa conservation landscape (A), located within the wider context of Tanzania's protected area network (B). Both the gazetted and effective boundaries for Ruaha NP, which differ, are represented. Note that while the boundary between Lunda-Mkwambi North and South, the two component blocks of the GCA, is depicted, the Rungwa South OA and Rungwa Mzombe OA blocks are presented under a single nomenclature ('Rungwa South OA').

3.2.2. Study design

We employed an occupancy modelling framework to model the distribution of large carnivores, their prey, and illegal human activity from presence/absence sign (spoor) transect data, and obtain inferences on their habitat use. Occupancy models use spatially or temporally replicated detection/non-detection surveys ('sampling occasions') to estimate the probability of detecting a species (p), and derive unbiased probabilities of sites being occupied or used by the species (ψ), while explicitly accounting for imperfect detection and variable survey effort (Mackenzie et al., 2002). Although our primary interest lay in large carnivore habitat use, prey and illegal human activity occurrence were first modelled, to be in turn employed as explanatory covariates in the large carnivore models. This allowed

us to investigate how heterogeneity in prey and illegal human activity site use affected large carnivore occurrence, and how these effects compared with each other and with other variables (as per Everatt et al., 2015, 2019).

Habitat selection is a hierarchical process, ranging from distribution and home range selection to the temporary use of resource patches and feeding sites within the home range (Johnson, 1980; Schaefer & Messier, 1995). As such, habitat use can be investigated at multiple spatial scales by sampling at different biologically-meaningful dimensions (Baldwin & Bender, 2008; O'Neill et al., 2020; Sunarto et al., 2012). Understanding the role of scale in habitat use is important for conservation planning, and investigations limited to a single scale may fail to recognize the importance of key habitat components (Davidson et al., 2012; Dickson & Beier, 2002; Nams et al., 2006). For example, Everatt et al., 2015 found that lion seemed to avoid bushmeat poachers when making third order (temporary use selection scale) choices, but not second order (home range selection scale) ones. Similarly, Ciarniello et al., 2007 demonstrated how designing PAs for grizzly bears, *Ursus arctos*, based solely on habitat selection at the third order would exclude features whose importance only became evident at a coarser scale. We therefore investigated habitat use at two spatial scales: the first corresponding approximately to home range selection and persistence (HRS), and the second to temporary use selection within the home range (TUS; equivalent to Johnson (1980)'s second and third order of habitat selection, respectively).

3.2.2.1. *Home Range Selection (HRS) scale*

We employed a study design comprising five nested sampling grids to examine habitat use of large carnivores at the home range selection (HRS) scale, and model prey and illegal human activity distribution at the same scale (Table 3.1; Fig. 3.2). A nested configuration was employed to assess how habitat use associations varied across gradients of human impact and between land management types, and to allow for higher resolution when modelling habitat use within PAs (by removing effects of coarser-level pressures, such as habitat conversion to agriculture in unprotected areas). All grids comprised 225 km^2 grid cells, each equivalent to a sampling unit (hereafter: site). The size of the sampling site is representative of the approximate scale at which large carnivores make second order habitat use decisions (Henschel et al., 2016; Karanth et al., 2011), and is appropriate for decision-

making by PA managers (Petracca et al., 2019). We acknowledge that this will vary slightly by species; however, as there is no theoretical basis for sampling units being required to be the size of species' home ranges (MacKenzie et al., 2017), we reasoned that this was an appropriate scale to model habitat use at a scale approximate to second-order use by an entire large carnivore guild.

This study design was employed to carry out five single-species occupancy analyses for each of the five target large carnivore species (lion, leopard, cheetah, African wild dog, spotted hyaena) – one for each sampling grid. In addition, probability of use estimates of prey species and illegal human activity, to be employed as covariates in the large carnivore models, were obtained for each sampled site through a single occupancy analysis employing the largest sampling grid (HRS-ALL; Table 3.1).

It should be noted that, throughout this study, habitat use represents not only selection, but also ability to persist (therefore differing slightly from Johnson's (1980) definition). Non-use should therefore be interpreted as species either actively selecting against an area *or* selecting favourably, but being unable to persist.

Table 3.1. Home range selection (HRS) scale nested sampling grids. See Fig. 3.1 for visual representations.

Grid	Study Area	Approx. Size (km^2)	Rationale
A. HRS-ALL	Complete landscape, including unprotected village lands	50,000	Compare high-level effects (protection, habitat conversion & settlements, prey availability)
B. HRS-PA	PAs only	40,000	Compare anthropogenic, biotic & management factors (including trophy hunting) within PAs
C. HRS-PAS	Areas of PAs with regular on-the-ground law enforcement only	25,000	Compare anthropogenic, biotic & management factors (including trophy hunting) within well-protected PAs
D. HRS-NAT	Areas of Ruaha NP with regular on-the-ground law enforcement only	13,000	Compare biotic habitat use drivers in a quasi-natural setting
E. HRS-HUNT	Hunting PAs only	25,000	Assess effect of block occupancy & vacancy

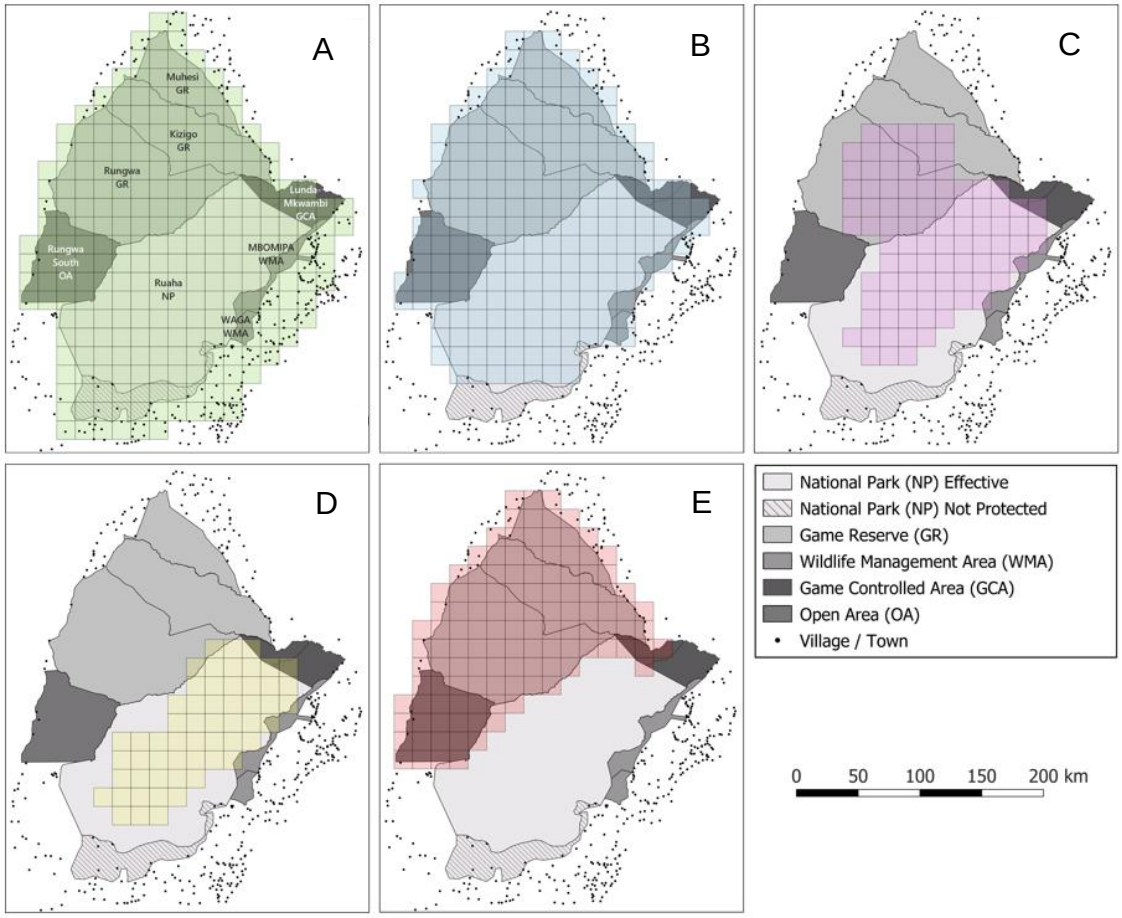


Figure 3.2. The five different sampling grids employed to investigate habitat use of large carnivores at the home range selection (HRS) scale; A = complete landscape (HRS-ALL); B = PAs only (HRS-PA); C = areas of PAs with regular law enforcement only (HRS-PAS); D = areas of Ruaha NP with regular law enforcement only (HRS-NAT); and E = hunting PAs only (HRS-HUNT). Coloured area shows the portion of the landscape included in each grid.

3.2.2.2. *Temporary Use Selection (TUS) scale*

We employed a sixth and final sampling design to investigate habitat use at the temporary use selection within the home range (TUS) scale. Here, sites were defined as a 2 km stretch of road, as this was deemed biologically meaningful to the scale at which large carnivores make short-term habitat use decisions (Duangchatrasiri et al., 2019; Everatt et al., 2015; Sunarto et al., 2012). For covariate extraction and calculation purposes, the area within a 250 m buffer around each 2 km segment of survey transects was employed, thus covering an area of ~1 km^2 (mean area for all sites: 1.12 km^2). For each species, we included only transects within HRS sites where the species was detected (i.e. with a $\psi^{(Cond.)} = 1$), as this signified with certainty that these areas formed part of at least one home range, and ensured

that areas with no presence at a coarser scale were not erroneously interpreted as being avoided at this finer scale.

At both scales, standard assumptions of an occupancy modelling approach were met (Mackenzie et al., 2002); however, we were able to relax the closure assumption at both scales due to interpreting the occupancy estimator (ψ) as the probability of site use, rather than the proportion of area occupied (MacKenzie et al., 2017).

3.2.3. Data collection

We conducted vehicle-based sign ('spoor') transect surveys across Ruaha-Rungwa, to collect detection/non-detection data on large carnivores, their prey, and illegal human activity. Large carnivores carry out extensive movements along road networks (Mckenzie et al., 2012); as a result, sign-based surveys are an effective and efficient method to collect presence/absence data for large carnivores over vast areas, including for lion (Everatt et al., 2014, 2019; Henschel et al., 2016; Petracca et al., 2019), leopard (Crosmary et al., 2018; Petracca et al., 2019) cheetah (Andresen et al., 2014; Williams, 2016), wild dog (Henschel et al., 2020; Petracca et al., 2019) and spotted hyaena (Bauer & Henschel, 2015; Mkonyi et al., 2018), as well as being suitable for collecting data on both ungulates and illegal human activity (Everatt et al., 2015, 2019; Petracca et al., 2019).

Spoor data of five large carnivores (lion, leopard, cheetah, wild dog, and spotted hyaena) and eight ungulate species (buffalo (*Syncarus caffer)*, giraffe (*Giraffa camelopardis)*, plains zebra (*Equus quagga*), eland (*Taurotragus oryx*), sable (*Hippotragus niger*), roan (*Hippotragus equinus*), greater kudu (*Tragelaphus strepsiceros*; hereafter: kudu), and impala (*Aepyceros melampus*)), as well as of signs of human presence, was collected. Because of the difficulty associated with differentiating between sable and roan spoor, and their similar habitat preferences (Estes, 1991), they were pooled and treated as one species ('roan & sable').

Surveys were carried out over two dry seasons, between 7 July and 29 November 2017, and 29 June and 21 November 2018. The survey team consisted of a driver and two experienced trackers seated on custom-made seats on the bull-bar of the vehicle. The vehicle was driven at a maximum speed of 10

km/h, and surveying was carried out between dawn and approximately 10:00 am, before a high-standing sun made detection difficult. If there was evidence of a vehicle using the road during the previous night, transects were postponed, and if another vehicle travelled on the road during surveying, the transect was ended. Transects varied in length based on the amount of roads present within each site, with a minimum of 6 km and a maximum of 20 km surveyed at each HRS site (differences in sampling effort are accounted for in the modelling process; Mackenzie et al., 2002). During surveying, we divided each transect into 500 m segments, and recorded whether sign of each species of interest was detected or non-detected (1 or 0) within each 500 m segment. As probability of detecting tracks depends on the quality and type of the road surveyed (Funston et al., 2010), we also noted the quality of road surveyed, and how recently this had last been used by vehicles. Road quality was given a grade between 1 and 4 (1 = best; 4 = worst), and vehicle use intensity was estimated between 0 – 3 (0 = no vehicles in 4+ days, 1 = no vehicles yesterday, 2 = vehicles yesterday, 3 = vehicle passed today; transect is ended).

3.2.4. Site use covariates

We identified a range of predictor variables (covariates) to explain heterogeneity in the occurrence of large carnivores, prey, and illegal human activity in the landscape, at both spatial scales investigated (HRS & TUS; Table 3.2 – 3.8. See Appendix 3.1 for more detailed covariate justifications and calculation methods, and Appendix 3.2 for covariate maps). For large carnivores, covariates were either biotic (availability of prey, vegetation type, and landscape features) or abiotic (anthropogenic disturbances and management). For each species, the specific prey species included as covariates varied by analysis, and were based on prey preferences described in the literature (Appendix 3.1). Not all covariates tested at the HRS scale were employed in the TUS analysis; covariates which did not exhibit heterogeneity within most individuals' home ranges (e.g. land management type) were not included, as we reasoned most individuals would not be able to make decisions at this scale (i.e. which areas of the home range to use) based on these.

Site use models were also built for each prey species and for illegal human activity, at each spatial scale (HRS & TUS), to obtain probability of use estimates for each site. However, for prey and human activity we treat the two spatial scales as scales of undefined biological relevance, which are nevertheless

referred to as the HRS and the TUS scales, for simplicity. Unlike for large carnivores, all covariates hypothesised to affect site use were modelled at both spatial scales.

All covariates, for all species, were extracted at the sampling unit level, such that each 225 km^2 (HRS) or ~1 km^2 (TUS) site had a covariate value equal to the mean of all raster pixel values within that site, using the 'Zonal Statistics' tool in QGIS 3.6.3. As large carnivore habitat use may depend on characteristics that may change seasonally (Cozzi et al., 2013), all covariates were collected at – or representative of, if extracted through remote sensing – the time of surveying. See Appendix 3.1 for additional details on the extraction process for each covariate.

Table 3.2. Covariates hypothesised to influence habitat use by lion at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to lion occurrence	Measurement (site level)	Data source	Published evidence of effect	Spatial Scale	Relevant Arrays (HRS)	Hypothesised effect on site use
Biotic – Prey[1]								
Preferred prey (buffalo) site use	Buff	Availability of preferred prey / buffalo	Probability of site use of buffalo[2]	This study	Everatt et al., 2015; Hayward & Kerley, 2005	HRS & TUS	HRS-ALL HRS-PA, HRS-PAS HRS-NAT HRS-HUNT	+
Alternate prey site use	SecPrey	Availability of alternate prey	Mean probability of site use of other prey species (zebra, giraffe, roan & sable, kudu, impala)[2]	This study	Everatt et al., 2015; Hayward & Kerley, 2005	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Zebra site use	Zeb	Availability of zebra	Probability of site use of zebra[2]	This study	Hayward & Kerley, 2005	HRS & TUS	HRS-PAS HRS-NAT	+
Kudu site use	Kud	Availability of kudu	Probability of site use of kudu[2]	This study	Hayward & Kerley, 2005	HRS & TUS	HRS-PAS[3] HRS-NAT[3]	+
Roan & Sable site use	Sbl	Availability of roan & sable	Probability of site use of roan & sable[2]	This study	Hayward & Kerley, 2005	HRS & TUS	HRS-PAS HRS-NAT	+
Giraffe site use	Gff	Availability of giraffe	Probability of site use of giraffe[2]	This study	Hayward & Kerley, 2005	HRS & TUS[2]	HRS-PAS[2] HRS-NAT[2]	+
Impala site use	Imp	Availability of impala	Probability of site use of impala[2]	This study	Hayward & Kerley, 2005	HRS & TUS	HRS-PAS HRS-NAT	+
Mean prey site use	AllPrey	Availability of all prey	Average probability of site use of all prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)[2]	This study	Hayward & Kerley, 2005	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Biotic – Other								
Tree cover	C	Habitat features facilitating prey capture	% cover (woodland or bushland)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	Hopcraft et al., 2005	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Riparian habitat	R	Habitat features facilitating prey capture	Mean Euclidian distance to nearest riparian habitat	Rivers & drainage lines GIS layer (hand digitised)	Hopcraft et al., 2005	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Habitat type	H	Habitat features facilitating prey capture, nutritional variation	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	Midlane et al., 2014	HRS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	/
Abiotic – Anthropogenic Impacts								
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al*., 2015)	Bauer et al., 2016	HRS	HRS-ALL	-
Distance to human settlements	DistV	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	Settlements & hamlets GIS layer (hand digitised)	Bauer et al., 2016; Petracca et al., 2019	HRS	HRS-ALL	+
Distance to PA boundary	Bound	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	IUCN WDPA, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Bauer et al., 2016; Petracca et al., 2019	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Illegal human use	Hum	Targeted or accidental snaring, behavioural avoidance	Probability of site use of illegal human activity[2]	This study	Everatt et al., 2015, 2019	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Abiotic – Management								
Legal protection	PA	Protection from targeted or accidental mortalities, prey base protection	% site legally protected	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Henschel et al., 2016; Packer et al., 2013	HRS	HRS-ALL	+
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[4]	This study	Henschel et al., 2016; Packer et al., 2013	HRS	HRS-ALL, HRS-PA HRS-PAS HRS-HUNT	+
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	Henschel et al., 2016; Packer et al., 2013	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Trophy hunting (permitted)	Hnt	Offtake mortalities	% site where hunting is permitted	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Croes et al., 2011; Packer et al., 2010	HRS	HRS-ALL HRS-PA HRS-PAS	-
Trophy hunting (occurring)	Mgd	Offtake mortalities	% site in actively managed hunting area	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Croes et al., 2011; Packer et al., 2010	HRS	HRS-ALL HRS-PA HRS-PAS HRS-HUNT	-

[1] Species considered preferred were included in all HRS and TUS analyses, while those taken regularly but not preferentially were included only in HRS-PAS, HRS-NAT and TUS analyses (based on Hayward et al., 2005)
[2] Site-specific probability of use for each prey species and for illegal human activity were obtained by modelling these within an occupancy modelling framework. See 'Methods' for additional details on the modelling strategy employed
[3] Covariate initially included in this analysis but removed due to low heterogeneity in values between sites in the sampling grid
[4] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.3. Covariates hypothesised to influence habitat use by leopard at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to leopard occurrence	Measurement (site level)	Data source	Published evidence of effect	Spatial Scale	Relevant Arrays (HRS)	Hypothesised direction of effect
Biotic – Prey[1]								
Preferred prey (impala)	Imp	Availability of preferred prey / impala	Probability of site use of impala[2]	This study	Hayward et al., 2006	HRS & TUS	HRS-ALL HRS-PA HRS-PAS[4] HRS-NAT[4] HRS-HUNT	+
Kudu	Kud	Availability of greater kudu	Probability of site use of kudu[2]	This study	Hayward et al., 2006	HRS & TUS	HRS-PAS[3] HRS-NAT[3]	+
Roan & Sable	Sbl	Availability of roan & sable	Probability of site use of roan & sable[2]	This study	Hayward et al., 2006	HRS & TUS	HRS-PAS[4] HRS-NAT[4]	+
All prey	AllPrey	Availability of all prey	Average probability of site use of all prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)[2]	This study	Hayward et al., 2006	HRS & TUS	HRS-ALL HRS-PA HRS-PAS[3] HRS-NAT[3] HRS-HUNT	+
Biotic – Other								
Cover	C	Habitat features facilitating prey capture	% cover (woodland or bushland)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	Balme et al., 2007; Henschel et al., 2020	HRS & TUS	HRS-ALL HRS-PA HRS-PAS[4] HRS-NAT[4] HRS-HUNT	+
Riparian habitat	R	Habitat features facilitating prey capture	Mean Euclidian distance to nearest riparian habitat	Rivers & drainage lines GIS layer (hand digitised)	Burton et al., 2012	HRS & TUS	HRS-ALL HRS-PA HRS-PAS[4] HRS-NAT[4] HRS-HUNT	+
Habitat type	H	Habitat features facilitating prey capture, nutritional variation	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	Kane et al., 2014	HRS	HRS-ALL HRS-PA HRS-PAS[3] HRS-NAT[3] HRS-HUNT	/
Abiotic - Anthropogenic Impacts								
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al*., 2015)	Stein et al., 2016	HRS	HRS-ALL	-
Distance to human settlements	DistV	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	Settlements & hamlets GIS layer (hand digitised)	Strampelli et al., 2018; Petracca et al., 2019	HRS	HRS-ALL	+
Distance to PA boundary	Bound	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Stein et al., 2016; Petracca et al., 2019	HRS & TUS	HRS-PA HRS-PAS[4] HRS-NAT[4] HRS-HUNT	+
Illegal human use	Hum	Targeted or accidental snaring, behavioural avoidance	Probability of site use of illegal human activity[2]	This study	Henschel et al., 2011	HRS & TUS	HRS-PA HRS-PAS[3] HRS-NAT[3] HRS-HUNT	-
Abiotic – Management								
Legal protection	PA	Protection from targeted or accidental mortalities, prey base protection	% site legally protected	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Madsen & Broekhuis, 2018	HR	HRS-ALL	+
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[5]	This study	Madsen & Broekhuis, 2018	HR	HRS-ALL HRS-PA HRS-HUNT	+
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	Madsen & Broekhuis, 2018	HRS& TUS	HRS-ALL HRS-PA HRS-PAS[4] HRS-NAT[4] HRS-HUNT	-
Trophy hunting (permitted)	Hnt	Offtake mortalities	% site where hunting is permitted	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Packer et al., 2010	HR	HRS-ALL HRS-PA HRS-PAS[4]	-
Trophy hunting (occurring)	Mgd	Offtake mortalities	% site in actively managed hunting area	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Packer et al., 2010	HR	HRS-ALL HRS-PA HRS-PAS[4] HRS-HUNT	-

[1] Species considered preferred were included in all HRS analyses, as well as TUS, while those taken regularly but not preferentially were included only in HRS-PAS, HRS-NAT and TUS analyses (based on Hayward et al., 2006a)
[2] Site-specific probability of use for each prey species and for illegal human activity were obtained by modelling these within an occupancy modelling framework. See 'Methods' for additional details on the modelling strategy employed
[3] Covariate initially included in this analysis but removed due to low heterogeneity in values between sites in the sampling grid
[4] Analysis planned but not carried out due to low heterogeneity in detections
[5] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.4. Covariates hypothesised to influence habitat use by cheetah at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to cheetah occurrence	Measurement (site level)	Data source	Published evidence of effect	Spatial Scale	Relevant Arrays (HRS)	Hypothesised direction of effect
Biotic – Prey[1]								
Preferred prey (impala)	Imp	Availability of preferred prey / impala	Probability of site use of impala[2]	This study	Andresen et al., 2014; Hayward, Hofmeyr, et al., 2006	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	+
Kudu	Kud	Availability of kudu	Probability of site use of kudu[2]	This study	Hayward, Hofmeyr, et al., 2006	HRS & TUS	HRS-PAS[3] HRS-NAT[3]	+
Roan & Sable	Sbl	Availability of roan & sable	Probability of site use of roan & sable[2]	This study	Hayward, Hofmeyr, et al., 2006	HRS & TUS	HRS-PAS HRS-NAT	+
All prey	AllPrey	Availability of all prey	Average probability of site use of all prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)[2]	This study	Hayward, Hofmeyr, et al., 2006	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT[3]	+
Biotic – Other								
Cover	C	Habitat features facilitating prey capture	% cover (woodland or bushland)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	Bissett & Bernard, 2007; Pettorelli et al., 2009	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	+
Riparian habitat	R	Habitat features facilitating prey capture	Mean Euclidian distance to nearest riparian habitat	Rivers & drainage lines GIS layer (hand digitised)	Broomhall et al., 2003; M. G. L. Mills et al., 2004	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	-
Habitat type	H	Habitat features facilitating prey capture, nutritional variation	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	Broomhall et al., 2003; M. G. L. Mills et al., 2004	HRS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	/
Distance to major river	Riv	Avoidance of areas of high densities of dominant competitors	Mean Euclidian distance to nearest large river	Rivers & drainage lines GIS layer (hand digitised)	Durant, 1998; Pettorelli et al., 2009	HRS, TUS?	HRS-ALL HRS-PA HRS-PAS HRS-NAT	+
Abiotic - Anthropogenic Impacts								
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al*., 2015)	Durant et al., 2015	HRS	HRS-ALL	-
Distance to human settlements	DistV	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	Settlements & hamlets GIS layer (hand digitised)	Andresen et al., 2014; Petracca et al., 2019	HRS	HRS-ALL	+
Distance to PA boundary	Bound	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Klaassen & Broekhuis, 2018; Madsen & Broekhuis, 2018	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	+
Illegal human use	Hum	Targeted or accidental snaring, behavioural avoidance	Probability of site use of illegal human activity[2]	This study	Klaassen & Broekhuis, 2018; Madsen & Broekhuis, 2018	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	-
Abiotic – Management								
Legal protection	PA	Protection from targeted or accidental mortalities, prey base protection	% site legally protected	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Klaassen & Broekhuis, 2018; Madsen & Broekhuis, 2018	HRS	HRS-ALL	+
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[5]	This study	Klaassen & Broekhuis, 2018; Madsen & Broekhuis, 2018	HRS	HRS-ALL HRS-PA HRS-HUNT[4]	+
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	Klaassen & Broekhuis, 2018; Madsen & Broekhuis, 2018	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT[4]	-
Trophy hunting (permitted)	Hnt	Disturbance / prey offtake	% site where hunting is permitted	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Durant et al., 2015	HRS	HRS-ALL HRS-PA HRS-PAS	-
Trophy hunting (occurring)	Mgd	Disturbance / prey offtake	% site in actively managed hunting area	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Durant et al., 2015	HRS	HRS-ALL HRS-PA HRS-PAS HRS-HUNT[4]	-

[1] Species considered preferred were included in all HRS analyses, as well as TUS, while those taken regularly but not preferentially were included only in HRS-PAS, HRS-NAT and TUS analyses (based on Hayward et al., 2006b)
[2] Site-specific probability of use for each prey species and for illegal human activity were obtained by modelling these within an occupancy modelling framework. See 'Methods' for additional details on the modelling strategy employed
[3] Initially included in this analysis but removed due to low heterogeneity in values between sites in the sampling grid
[4] Analysis planned but not carried out due to low heterogeneity in detections
[5] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.5. Covariates hypothesised to influence habitat use by African wild dog at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to wild dog occurrence	Measurement (site level)	Data source	Published evidence of effect	Spatial Scale	Relevant Arrays (HRS)	Hypothesised direction of effect
Biotic – Prey[1]								
Preferred prey (impala)	Imp	Availability of preferred prey / impala	Probability of site use of impala[2]	This study	Hayward, O'Brien, et al., 2006	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Preferred prey (kudu)	Kud	Availability of kudu	Probability of site use of kudu[2]	This study	Hayward, O'Brien, et al., 2006	HRS & TUS	HRS-ALL, HRS-PA[3] HRS-PAS3 HRS-NAT[3] HRS-HUNT[3]	+
Roan & Sable	Sbl	Availability of roan & sable	Probability of site use of roan & sable[2]	This study	Hayward, O'Brien, et al., 2006	HRS & TUS	HRS-PAS HRS-NAT	+
All prey	AllPrey	Availability of all prey	Average probability of site use of all prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)[2]	This study	Hayward, O'Brien, et al., 2006	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Biotic – Other								
Cover	C	Habitat features facilitating prey capture	% cover (woodland or bushland)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	M. G. L. Mills & Gorman, 1997; Shumba et al., 2018	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Riparian habitat	R	Habitat features facilitating prey capture	Mean Euclidian distance to nearest riparian habitat	Rivers & drainage lines GIS layer (hand digitised)	Creel & Creel, 2002; M. G. L. Mills & Gorman, 1997	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Habitat type	H	Habitat features facilitating prey capture, nutritional variation	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	M. G. L. Mills & Gorman, 1997; Shumba et al., 2018	HRS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	/
Distance to major river	Riv	Avoidance of areas of high densities of dominant competitors	Mean Euclidian distance to nearest large river	Rivers & drainage lines GIS layer (hand digitised)	Creel & Creel, 2002; M. G. L. Mills & Gorman, 1997	HRS, TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Abiotic - Anthropogenic Impacts								
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al*., 2015)	Van Der Meer et al., 2014	HRS	HRS-ALL	-
Distance to human settlements	DistV	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	Settlements & hamlets GIS layer (hand digitised)	Van Der Meer et al., 2014;	HRS	HRS-ALL	+
Distance to PA boundary	Bound	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	IUCN WDPA (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Van Der Meer et al., 2014; Petracca et al., 2019	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT	+
Illegal human use	Hum	Targeted or accidental snaring, behavioural avoidance	Probability of site use of illegal human activity[2]	This study	Woodroffe & Sillero-Zubiri, 2020	HRS & TUS	HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Abiotic – Management								
Legal protection	PA	Protection from targeted or accidental mortalities, prey base protection	% site legally protected	IUCN WDPA, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Van Der Meer et al., 2014	HRS	HRS-ALL	+
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[4]	This study	Van Der Meer et al., 2014	HRS	HRS-ALL HRS-PA HRS-HUNT	+
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	Van Der Meer et al., 2014	HRS & TUS	HRS-ALL HRS-PA HRS-PAS HRS-NAT HRS-HUNT	-
Trophy hunting (permitted)	Hnt	Offtake mortalities	% site where hunting is permitted	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Woodroffe & Sillero-Zubiri, 2020	HRS	HRS-ALL HRS-PA HRS-PAS	-
Trophy hunting (occurring)	Mgd	Offtake mortalities	% site in actively managed hunting area	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Woodroffe & Sillero-Zubiri, 2020	HRS	HRS-ALL HRS-PA HRS-PAS HRS-HUNT	-

[1] Species considered preferred were included in all HRS analyses, as well as TUS, while those taken regularly but not preferentially were included only in HRS-PAS, HRS-NAT and TUS analyses (based on Hayward et al., 2006c)
[2] Site-specific probability of use for each prey species and for illegal human activity were obtained by modelling these within an occupancy modelling framework. See 'Methods' for additional details on the modelling strategy employed
[3] Covariate initially included in this analysis but removed due to low heterogeneity in values between sites in the sampling grid
[4] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.6. Covariates hypothesised to influence habitat use by spotted hyaena at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to spotted hyaena occurrence	Measurement (site level)	Data source	Published evidence of effect	Spatial Scale	Relevant Arrays (HRS)	Hypothesised direction of effect
Biotic – Prey[1]								
All prey	AllPrey	Availability of all prey	Average probability of site use of all prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)[2]	This study	Hayward, 2006	HRS & TUS	HRS-ALL HRS-PA[3] HRS-PAS3 HRS-NAT[3] HRS-HUNT3	+
Buffalo	Buff	Availability of buffalo	Probability of site use of buffalo[2]	This study	Hayward, 2006	TUS	/	+
Kudu	Kud	Availability of kudu	Probability of site use of kudu[2]	This study	Hayward, 2006	TUS	/	+
Impala	Imp	Availability of impala	Probability of site use of impala[2]	This study	Hayward, 2006	TUS	/	+
Roan & Sable	Sbl	Availability of roan & sable	Probability of site use of roan & sable[2]	This study	Hayward, 2006	TUS	/	+
Giraffe	Giff	Availability of giraffe	Probability of site use of giraffe[2]	This study	Hayward, 2006	TUS**	/	+
Zebra	Zeb	Availability of zebra	Probability of site use of zebra[2]	This study	Hayward, 2006	TUS	/	+
Biotic – Other								
Cover	C	Habitat features facilitating prey capture	% cover (woodland or bushland)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	Boydston et al., 2003	HRS & TUS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-NAT[3] HRS-HUNT[3]	-
Riparian habitat	R	Habitat features facilitating prey capture	Mean Euclidian distance to nearest riparian habitat	Rivers & drainage lines GIS layer (hand digitised)	Kolowski & Holekamp, 2009	HRS & TUS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-NAT[3] HRS-HUNT[3]	+
Habitat type	H	Habitat features facilitating prey capture, nutritional variation	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	Pettorelli et al., 2010	HRS	HRS-ALL HRS-PA[2] HRS-PAS[2] HRS-NAT[2] HRS-HUNT[2]	/
Abiotic - Anthropogenic Impacts								
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al*., 2015)	Burton et al., 2012; Schuette et al., 2013	HRS	HRS-ALL	-
Distance to human settlements	DistV	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	Settlements & hamlets GIS layer (hand digitised)	Petracca et al., 2019	HRS	HRS-ALL	+
Distance to PA boundary	Bound	Persecution, unsuitable habitat	Distance to nearest settlement, with asymptote (Ln)	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Petracca et al., 2019	HRS & TUS	HRS-PA[3] HRS-PAS[3] HRS-NAT[3] HRS-HUNT[3]	+
Illegal human use	Hum	Targeted or accidental snaring, behavioural avoidance	Probability of site use of illegal human activity[2]	This study	Petracca et al., 2019	HRS & TUS	HRS-PA[3] HRS-PAS[3] HRS-NAT[3] HRS-HUNT[3]	-
Abiotic – Management								
Legal protection	PA	Protection from targeted or accidental mortalities, prey base protection	% site legally protected	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al*. (2017)	Burton et al., 2012; Schuette et al., 2013	HRS	HRS-ALL	+
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[4]	This study	Burton et al., 2012; Schuette et al., 2013	HRS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-HUNT[3]	+
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	Burton et al., 2012; Schuette et al., 2013	HRS & TUS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-NAT[3] HRS-HUNT[3]	-
Trophy hunting (permitted)	Hnt	Offtake mortalities	% site where hunting is permitted	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Croes et al., 2011	HRS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-HUNT[3]	-
Trophy hunting (occurring)	Mgd	Offtake mortalities	% site in actively managed hunting area	Tanzania Wildlife Authority (TAWA) *pers comm*.; this study	Croes et al., 2011	HRS	HRS-ALL HRS-PA[3] HRS-PAS[3] HRS-HUNT[3]	-

[1] Species considered preferred were included in all HRS analyses, as well as TUS, while those taken regularly but not preferentially were included only in HRS-PAS, HRS-NAT and TUS analyses (based on Hayward et al., 2006c)
[2] Site-specific probability of use for each prey species and for illegal human activity were obtained by modelling these within an occupancy modelling framework. See 'Methods' for additional details on the modelling strategy employed
[3]Analysis planned but not carried out due to low heterogeneity in detections
[4] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.7. Covariates hypothesised to influence habitat use by prey (ungulate) species at the home range selection (HRS) and the temporary use selection (TUS) spatial scales.

Covariate	Handle	Relationship to ungulate occurrence	Measurement (site level)	Data source	Hypothesised direction of effect
Biotic – Other					
Water	W	Dry season surface water availability	Mean probability of water availability (mean pixel value)	Google Earth (hand digitised)	- (Sbl[1]) + (All others)
NDVI (mean)	NDVIave	Nutritional resources (primary productivity)	Mean NDVI value at site during survey period (mean pixel value)	MCD43A4_NDVI (NASA LP DAAC, https://lpdaac.usgs. gov/)	+ (All)
NDVI (standard deviation)	NDVIstd	Nutritional resources (primary productivity)	Standard deviation of NDVI values at site during survey period (mean pixel value)	MCD43A4_NDVI (NASA LP DAAC, https://lpdaac.usgs. gov/)	+ (All)
Tree cover	C	Nutritional resources (primary productivity)	% cover (woodland only)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	+ (All)
Habitat type	H	Predominant habitat type (*miombo* or *Acacia-commiphora*)	Habitat type (*miombo* or *Acacia-commiphora*) - % site *miombo*	WWF Terrestrial Ecoregions of the World (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)	+ (Sbl) - (Imp[2])
Abiotic - Anthropogenic Impacts					
Habitat conversion to agriculture	Crop	Unsuitable habitat	% converted habitat in cell	Google Earth Grids (Jacobsen *et al.*, 2015)	- (All)
Distance to Human Settlements	DistV	Direct persecution, competition with lviestock	Natural logarithm of mean distance to nearest settlement, with asymptote (Log)	Settlements & hamlets GIS layer (hand digitised)	- (All)
Abiotic – Management					
Legal protection	PA	Protection from targeted or accidental mortalities	% site legally protected	IUCN WDPA (WDPA; https://protectedplanet.net/), Riggio *et al.* (2017)	+ (All)
Strong effective protection	PAS	Protection from targeted or accidental mortalities, prey base protection	% site receiving regular anti-poaching patrols[3]	This study	+ (All)

[1] Sbl: sable & roan
[2] Imp: impala
[3] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

Table 3.8. Covariates hypothesised to influence illegal human activity within PAs in Ruaha-Rungwa at the home range selection (HRS) and the temporary use selection (TUS) spatial scales

Covariate	Handle	Relationship to illegal human use	Measurement (site level)	Data source	Hypothesised direction of effect
Biotic					
Water	W	Dry season surface water availability	Mean probability of water availability (mean pixel value)	Hand digitised	+
All prey	AllPrey	Availability of wild ungulates	Mean probability of site use of six prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)	This study	+
Tree cover	C	Increased attractiveness for logging	% cover (woodland only)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa http://2016africalandcover20m.esrin.esa.int/	+
Other					
Distance to PA boundary	Bound	Increased difficulty of access	Mean distance to nearest PA boundary	IUCN World Database on Protected Areas, modified (WDPA; https://protectedplanet.net/), Riggio *et al.* (2017)	-
Distance to ranger post	Post	Protection from targeted or accidental mortalities, prey base protection	Distance to nearest range post, with asymptote (Ln)	This study	+
Strong effective protection	PAS	Avoidance of more strongly protected areas	% site receiving regular anti-poaching patrols[3]	This study	-

[1] Includes regular protection activities by management authorities (TAWA, TANAPA) or others (e.g. NGOs, hunting operators). Assessed through data collected during surveying, and cross-referenced with management authorities (TAWA, TANAPA)

3.2.5. Detection covariates

As some segments failed to reach the full sampling occasion length (see 'Occupancy Modelling' below), we included segment length as a covariate ('effort') hypothesised to influence detection at the HRS scale, in all analyses. In addition, we included an index combining road quality and vehicle use intensity data as a single detection covariate ('substrate'), for all analyses at both the HRS and TUS scales (Table 3.9).

Table 3.9 Covariates hypothesised to influence detection.

Covariate	Handle	Relationship to detection	Measurement (site level)	Data source	Hypothesised effect
Effort	E	Higher effort per sampling occasion should increase detection	Number of 500-m sections in sampling occasion	This study	+
Substrate quality & vehicle use index	S	Better quality substrate and less vehicle use should increase detection	Mean probability of site use of six prey species (buffalo, zebra, roan & sable, impala, kudu, giraffe)	This study	+

3.2.6. Occupancy modelling

3.2.6.1. *Accounting for spatial dependence*

For all analyses in this study, sampling occasions consisted of different spatially replicated transect segments within each site. However, data from track-based surveys carry an inherent risk of spatial autocorrelation, where a lack of independence between observations is observed due to their physical proximity (Markovian dependence; Dale & Fortin, 2014), which must be addressed.

At the HRS scale, the use of occupancy models that explicitly account for spatial dependence in detections (Hines et al., 2010) was precluded by several sampling sites containing independent (non-continuous) transects (Henschel et al., 2016). Instead, for each species, we specifically tested for spatial independence between consecutive sampling occasions in program PRESENCE (Hines, 2006), by increasing sampling occasion length by 500 m increments until (1) the standard single-season occupancy (Mackenzie et al., 2002) outperformed the model accounting for Markovian dependence in detections (Hines et al., 2010); and (2) the two key parameters of the model accounting for correlated detections ($\ominus$, probability of presence on a sampling occasion given absence on previous replicate, and

$\ominus^{I}$, probability of presence on a sampling occasion given presence on previous replicate) were approximately equal (as per Henschel et al., 2016). The length at which this was achieved (which varied by species – see '3.3. Results') was considered the minimum acceptable sampling occasion length for each species, enabling us to avoid spatial auto-correlation biases.

At the TUS scale, sampling occasions consisted of 2 – 4 500 m segments, which were always continuous. This allowed us to address spatial autocorrelation between replicates by employing occupancy models that specifically account and control for correlation in detections in the modelling process (Hines et al., 2010).

3.2.7. Occupancy analyses

Detection/non-detection matrices were constructed for each analysis, for each species, from survey transect data (see Appendix 3.3 for all model input data). These were then analysed using single-season, single-species occupancy models in package *unmarked* (Fiske & Chandler, 2011) in R version 3.5.3 (R Core Team, 2019) at the HRS scale, and in program PRESENCE (Hines, 2006) at the TUS scale (models accounting for correlation in detections are not implemented in R package *unmarked*).

For all analyses, we followed a two-step process to model detection (p) and site use (ψ). First, we modelled covariates hypothesised to influence *p* while holding site use constant (using the most parametrised model of non-correlated covariates), to identify which of the competing detection models best explained the observed heterogeneity in detection probability, based on Akaike Information Criterion (AIC) rankings (adjusted for small sample size (AICc) at the HRS scale; Karanth et al., 2011; MacKenzie et al., 2017). We then modelled ψ by fixing the best ranked detection model, and varying all possible combinations of non-correlated site covariates. Covariates were standardised on a z-scale to facilitate model convergence (Mackenzie et al., 2017) and tested for collinearity using Pearson's correlation test, and were not included in the same model if $r > 0.6$ (Green, 1979; see Appendix 3.4 for correlation tables).

To avoid over-parameterisation, the maximum number of possible covariates within a single model was informed by the rule of thumb of 15 – 25 observations (defined here as detections) per predictor variable

(Green, 1991). If convergence issues arose, the number of covariates in the model was decreased by n = 1 until these were resolved. Univariate models were employed for sampling grids with a small number of sites ($n < 50$).

Models were ranked based on their AIC/AICc scores, and for each analysis we retained a final model set comprising all models with $\Delta AIC/\Delta AICc < 2$, as this indicates substantial empirical support (Burnham & Anderson, 2004). Maximum-likelihood estimates of detection probability (p) and site use (ψ) for each site were obtained by model-averaging parameters from the final model set, based on their relative model weights (Burnham & Anderson, 2004; MacKenzie et al., 2017). For each analysis, the importance of individual covariates in explaining heterogeneity in site use was determined by summing the AIC/AICc weights of all models in which the variable was present in the final model set (Σw; Burnham & Anderson, 2004; MacKenzie et al., 2017). The direction of influence of covariates on site use was determined by the untransformed coefficients (β) of each covariate, and covariates were deemed to have a strong (statistically significant) impact if the β-coefficient $\pm$ 1.96 x standard error (SE) did not include zero (Mackenzie & Bailey, 2004). As per standard practice, β-coefficients were not averaged, with that of the top-ranked and most parametrised models presented instead (MacKenzie et al., 2017).

We assessed goodness-of-fit of the top-ranked and most parameterised model within each final model set (MacKenzie et al., 2017), using the MacKenzie and Bailey goodness of fit test for single-season occupancy models, based on Pearson's chi-square (Mackenzie & Bailey, 2004). Where there was more than one model with the largest number of parameters within the final model set, goodness of fit was tested for the highest ranked of these.

3.3. RESULTS

We surveyed a total of 2,789 km of transects across eight PAs, as well as completely non-protected village lands (Fig. 3.3; Table 3.10). Overall, a total of 185 sites were surveyed at the HRS scale (average survey effort per site = 15.1 km), equivalent to approximately 85% of sites in the landscape. A total of 1484 sites were sampled at the TUS scale (Table 3.11). The number of independent detections varied from a minimum of 13 to a maximum of 545 for the different target species (Table 3.12).

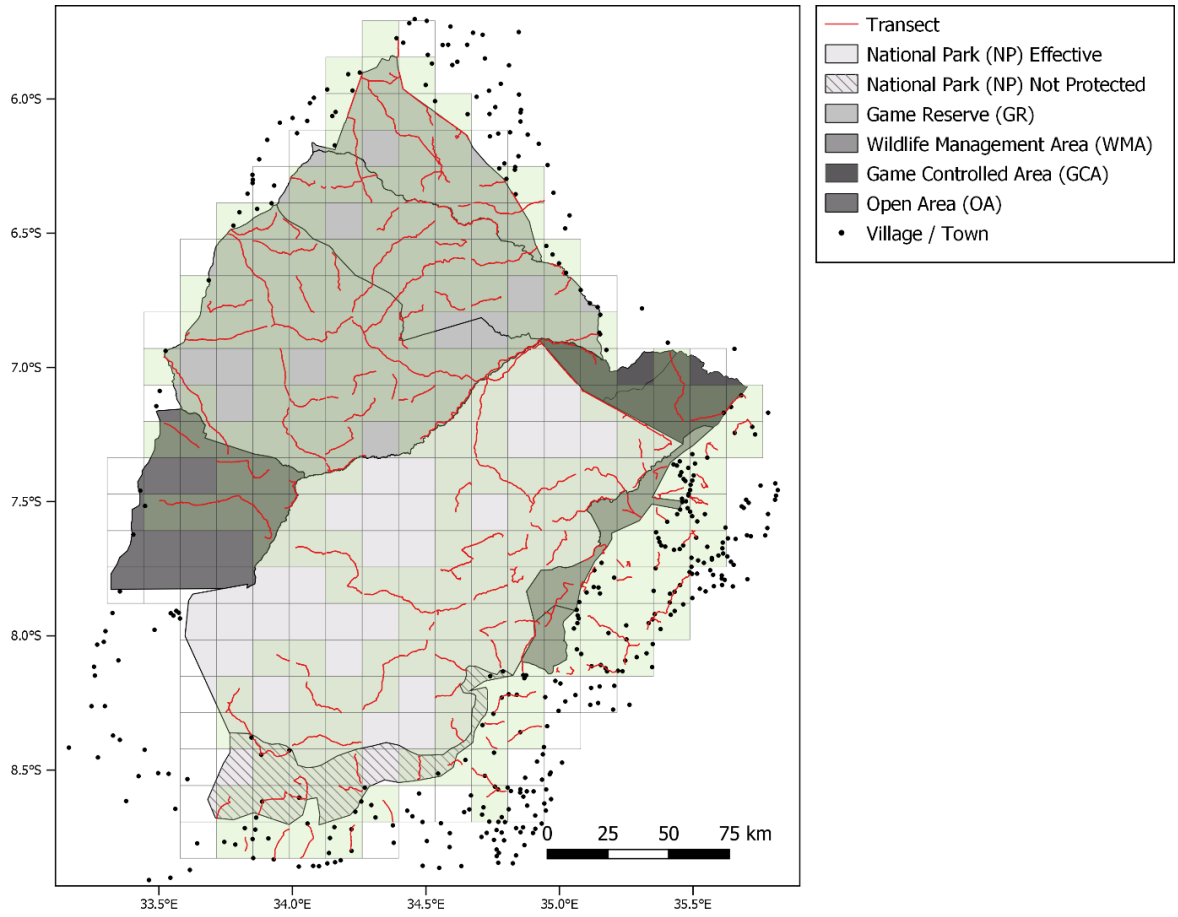


Figure 3.3. Survey transects carried out in the Ruaha-Rungwa landscape, for all home range selection (HRS) scale sampling grids. Surveyed sampling sites are highlighted in green. 2,789 km of transects were sampled in 8 PAs, as well as completely non-protected lands, over two dry seasons (2017 and 2018), in 185 sites at the HRS scale.

Table 3.10. Summary of survey effort within the different components of the Ruaha-Rungwa conservation landscape.

PA	Area (km^2)	Survey effort[1] (km)	Approximate Coverage (%)
Ruaha NP			
(Effective)	17,829	995	74
(Gazetted, non-effective)	2,323	127	97
(Total)	20,152	1,122	77
Rungwa GR	9,056	689	94
Kizigo GR	5,104	385	93
Muhesi GR[2]	2,688	336	92
MBOMIPA & Waga WMAs	1,138	131	100
Lunda-Mkwambi GCA[3]	1,839	161	86
Rungwa S OA	3,751	146	54
Village lands	7,350	413	90

[1] Transects carried out along boundaries between two adjacent PAs were included in total count for both
[2] Effective size
[3] Includes both Lunda-Mkwambi North & South

Table 3.11. Number of sites sampled for each occupancy analysis, for each study species.

Species	Number of Sites (HRS)					Number of Sites (TUS)[1]
	HRS-ALL	HR_PA	HRS-PAS	HRS-NAT	HRS-HUNT	
Prey						
All Species	185	-	-	-	-	1484
Anthropogenic						
Illegal Human Activity	-	144	-	-	-	1211
Large Carnivores						
Lion	185	144	56	40	85	734
Leopard	185	144	56	40	85	1046
Cheetah	185	144	56	40	85	96
Wild Dog	185	144	56	40	85	226
Spotted Hyaena	185	144	56	40	85	1211

[1] For large carnivores, only transects from HRS sites with a ψ Cond. = 1 (i.e. where the species was detected) were used as sites in the TUS scale analyses, while for prey and illegal human activity all were used
HRS = Large carnivore home range selection scale
TUS= Large carnivore temporary use selection within the home range selection scale

Table 3.12. Total detections (number of sampling occasions where species was detected) for all study species, for all home range selection (HRS) scale sampling grids

Species	Total detections – HRS scale
Buffalo	187
Zebra	212
Giraffe	460
Eland	123
Roan & Sable	336
Kudu	545
Impala	283
Illegal Human Activity	164
Lion	163
Leopard	234
Cheetah	13
African Wild Dog	40
Spotted Hyaena	447

For prey species, spatial independence was achieved at 3 – 4 km, depending on species (4 km: buffalo, eland, roan & sable, impala; 3 km: giraffe, kudu). To streamline analyses, a conservative spatial replicate (sampling occasion) length of 4 km was used for all prey species. For illegal human activity, spatial independence was achieved at 4 km, and sampling occasions therefore measured 4 km. For large carnivores, spatial independence was achieved at 1km for cheetah; 4km for wild dog and lion; and 5km for leopard and spotted hyaena. As a result, a conservative length of 5 km was used for spatial replicates for all large carnivore analyses at the HRS scale.

There was no evidence of lack of fit or over-dispersion for the majority of the top and most parametrised models in the final model set (ΔAIC/ΔAICc < 2) for large carnivore, prey, and illegal human use analyses. Where there was evidence of some over-dispersion (c-hat > 1.5), standard errors were adjusted accordingly (Mackenzie et al., 2017; see Appendix 3.8 for complete goodness-of-fit test results).

3.3.1. Prey occupancy

At both HRS and TUS scales, eland occupancy could not be modelled as a result of the combination of relatively low number of detections and the high spatial heterogeneity in these.

The number of 4 km spatial replicates per site was restricted to n = 4 for all prey species at the HRS scale, to reduce the number of NAs in the data and improve model fit (Mackenzie et al., 2017). All prey analyses at the HRS scale therefore employed a maximum of 16 km of transect data per site.

At the HRS scale, effort was found to influence detection probability of giraffe and kudu, while the substrate index impacted detection of roan & sable, kudu, and impala. For buffalo and zebra, the null model (i.e. neither effort nor substrate influencing detection) ranked highest, and was therefore employed in the subsequent site use analyses. At the TUS scale, substrate was found to influence detection probability of buffalo, giraffe, and kudu, while for zebra, roan & sable, and impala the null model, p(.), ranked higher. See Appendix 3.5 for full detection rankings.

The final model set at the HRS scale comprised 1 model for buffalo, 6 for zebra, 5 for giraffe, 4 for roan & sable, 9 for kudu, and 2 for impala. The final model set at the TUS scale comprised 1 model for

buffalo, 6 for zebra, 5 for giraffe, 2 for roan & sable, 1 for kudu, and 2 for impala. See Appendix 3.6 for full occupancy model rankings of prey species.

3.3.1.1. *Relative importance of site use covariates*

For all analyses (including prey, human activity, and large carnivores), only β-coefficients of covariates present within at least one model with strong support (i.e. $\Sigma w > 0$) are presented. If the covariate is present in multiple models in the final set, β-coefficients from both the top and the most-parameterised models including that covariate are presented (Mackenzie et al., 2017).

At the HRS scale, legal protection and availability of natural habitat were the best predictors of occurrence for all prey species (Table 3.13). Of these, legal protection was a better predictor of occurrence of buffalo, zebra, giraffe, and sable and roan, while, for kudu and impala availability of natural habitat explained occurrence best. Dry season surface water availability was a strong predictor of some water-dependent species (buffalo, zebra and impala), and a weak or even negative (kudu) predictor for the others. Primary habitat type (miombo woodlands or *Acacia-Commiphora* bushland and grasslands) was important for some species, with statistically significant, positive relationships observed between buffalo and roan & sable site use and miombo, and between impala occurrence and *Acacia-Commiphora*. Regular on-the-ground law enforcement was a strong predictor of zebra persistence, and significant associations were observed between greater forest cover and buffalo and roan & sable site use, while kudu and impala instead exhibited significant positive associations with more open areas. Greater variation in vegetation composition and growth was a strong positive predictor of roan & sable; giraffe and impala, instead, were conversely strongly associated with areas of lower primary productivity. Similar relationships were observed at the TUS scale (Table 3.13), as were a range of other non-significant covariate effects, at both spatial scales investigated (Tables 3.13, 3.14).

Table 3.13. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining site use (ψ) of six ungulate species in Ruaha-Rungwa at the home range selection (HRS) scale. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and/or the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	*β* (SE*β*) (Top model)	*β* (SE*β*) (Most param.)
Buffalo				
PA	1.00	+	**1.73 (0.40)**	**1.68 (0.40)**
W	1.00	+	**1.13 (0.39)**	**1.11 (0.34)**
H	1.00	+	**1.10 (0.34)**	**0.89 (0.39)**
Zebra				
PA	1.00	+	**1.04 (0.30)**	
PAS	0.89	+	**0.67 (0.23)**	
W	0.21	+	**0.47 (0.20)**	
H	0.34	+	0.33 (0.20)	
NDVIstd	0.23	+	0.35 (0.20)	
C	0.15	+	0.29 (0.21)	
Giraffe				
PA	1.00	+	**2.46 (0.45)**	
NDVIstd	0.66	-	**1.23 (0.57)**	
C	0.37	+	1.73 (0.89)	
W	0.29	-	0.50 (0.34)	
Roan & Sable				
PA	1.00	+	**1.52 (0.30)**	
H	1.00	+	**1.37 (0.31)**	
PA*H	1.00	+	**1.72 (0.68)**	
NDVIstd	0.39	+	**0.63 (0.30)**	
PAS	0.23	-	0.49 (0.28)	
C	0.21	+	0.57 (0.33)	
Kudu				
Crop	1.00	-	**1.80 (0.30)**	**1.62 (0.42)**
NDVIstd	0.36	-	0.50 (0.36)	0.44 (0.34)
DistV	0.32	+	0.58 (0.48)	0.50 (0.47)
C	0.20	-	0.42 (0.39)	0.45 (0.39)
W	0.15	-	0.30 (0.33)	0.30 (0.33)
H	0.07	-	0.17 (0.33)	0.17 (0.33)
Impala				
Crop	1.00	-	**1.63 (0.31)**	
C	1.00	-	**1.78 (0.33)**	
W	0.59	+	**0.75 (0.29)**	
H	0.41	-	**0.74 (0.31)**	

Covariate key: Legal protection (PA); availability of water (W); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); variation in vegetation composition and growth (NDVIstd); forest cover (C); conversion of habitat to agriculture (Crop); logarithmic distance to human settlement (DistV); protected miombo woodland (PA*H)

Table 3.14. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining site use (ψ) of six ungulate species in Ruaha-Rungwa at the temporary use selection (TUS) scale. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and/or the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	*β* (SE*β*) (Top model)	*β* (SE*β*) (Most param.)
Buffalo				
PA	1.00	+		**1.23 (0.35)**
PAS	1.00	+		**0.13 (0.05)**
W	1.00	+		**0.58 (0.06)**
H	1.00	+		**0.18 (0.06)**
C	1.00	-		**0.21 (0.06)**
NDVIstd	1.00	+		**0.21 (0.07)**
Zebra				
PA	1.00	+		**1.25 (0.40)**
PAS	1.00	+		**0.47 (0.07)**
W	1.00	+		**0.17 (0.05)**
NDVIstd	0.71	+		0.13 (0.07)
H	0.69	+		0.11 (0.06)
C	0.58	-		0.13 (0.07)
Giraffe				
PA	1.00	+	**0.96 (0.08)**	**0.96 (0.08)**
PAS	1.00	+	**0.14 (0.05)**	**0.14 (0.05)**
Crop	1.00	-	**0.21 (0.09)**	**0.21 (0.09)**
H	0.18	-	0.03 (0.05)	0.03 (0.05)
W	0.15	-	0.01 (0.04)	0.01 (0.04)
C	0.14	-	0.01 (0.06)	0.01 (0.06)
NDVIstd	0.14	-	0.01 (0.03)	0.01 (0.03)
Roan & Sable				
PA	1.00	+	**1.15 (0.12)**	**1.15 (0.12)**
PAS	1.00	-	**0.27 (0.05)**	**0.26 (0.05)**
H	1.00	+	**0.54 (0.06)**	**0.52 (0.06)**
C	1.00	+	**0.28 (0.06)**	**0.26 (0.06)**
NDVIstd	1.00	+	**0.14 (0.06)**	**0.14 (0.06)**
W	0.48	-	0.07 (0.05)	0.07 (0.05)
Kudu				
PA	1.00	+		**2.41 (0.76)**
Crop	1.00	-		**0.45 (0.09)**
W	1.00	-		**0.32 (0.11)**
H	1.00	-		**0.80 (0.15)**
C	1.00	-		**0.45 (0.16)**
NDVIstd	1.00	+		**0.52 (0.13)**
PAS	1.00	-		1.43 (0.86)
Impala				
PA	1.00	+	**0.56 (0.09)**	**0.52 (0.10)**
Crop	1.00	-	**0.47 (0.09)**	**0.46 (0.09)**
W	1.00	+	**0.36 (0.08)**	**0.33 (0.09)**
H	1.00	-	**0.55 (0.08)**	**0.56 (0.08)**
C	1.00	-	**0.67 (0.10)**	**0.67 (0.10)**
NDVIstd	1.00	-	**0.27 (0.10)**	**0.28 (0.10)**
PAS	0.48	+	0.05 (0.06)	0.11 (0.08)

Covariate key: Legal protection (PA); availability of water (W); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); variation in vegetation composition and growth (NDVIstd); forest cover (C); conversion of habitat to agriculture (Crop); logarithmic distance to human settlement (DistV); protected miombo woodland (PA*H)

3.3.1.2. *Mean probability of detection and site use*

The estimated mean probability of detection ($\bar{\hat{p}}$) and of site use ($\bar{\hat{\psi}}$) for all prey species at both scales are presented in Table 3.15, alongside naïve occupancy estimates. At the HRS scale, the mean probability of site use can also be interpreted as the proportion of the sampled area used by the species (Mackenzie et al., 2017).

Mean site use for most prey species was found to be similar between photographic and hunting areas, and greater in actively-managed blocks compared to vacant ones (see Fig. 3.4 in '3.4. Discussion').

Table 3.15. Estimated naïve occupancy (ψ), mean detection probability ($\bar{\hat{p}}$), and site use ($\bar{\hat{\psi}}$; also interpretable as the proportion of the sampled area used by the species) for ungulate prey species, with associated mean of the standard errors (SE) at the home range selection (HRS) and temporary use selection (TUS) scales. Standard errors have been adjusted for over-dispersion were relevant (Appendix 3.8)

Species	Naïve ψ	$\bar{\hat{p}}$ (SE)	$\bar{\hat{\psi}}$ (SE)
HRS scale			
Buffalo	0.45	0.44 (0.05)	0.49 (0.06)
Zebra	0.47	0.54 (0.07)	0.51 (0.08)
Giraffe	0.77	0.75 (0.02)	0.78 (0.04)
Roan & Sable	0.58	0.77 (0.03)	0.58 (0.07)
Kudu	0.85	0.84 (0.03)	0.86 (0.04)
Impala	0.54	0.64 (0.04)	0.56 (0.08)
TUS scale			
Buffalo	0.21	0.72 (0.08)	0.43 (0.07)
Zebra	0.21	0.48 (0.08)	0.39 (0.07)
Giraffe	0.58	0.76 (0.03)	0.75 (0.03)
Roan & Sable	0.36	0.64 (0.05)	0.54 (0.04)
Kudu	0.64	0.48 (0.03)	0.78 (0.05)
Impala	0.31	0.55 (0.07)	0.38 (0.04)

3.3.2. Illegal human activity occupancy

At both the HRS and TUS scales, the null detection model ranked highest (Appendix 3.5), and was therefore employed in subsequent analyses. The final model set comprised 8 models at the HRS scale and one at the TUS scale (Appendix 3.6).

3.3.2.1. *Relative importance of site use covariates*

Table 3.16. Relative summed model weights (Σw) and β-coefficient estimates, with associated standard errors, of covariates explaining illegal human site use (ψ) at the home range selection (HRS) and temporary use selection (TUS) scales within PAs in Ruaha-Rungwa. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect ($\beta \pm 1.96$ x SE) in the top and/or the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	β (SE$_\beta$) (Top model)	β (SE$_\beta$) (Most param.)
HRS scale				
Bound	1.00	-	**1.67 (0.52)**	**1.70 (0.52)**
PAS	1.00	-	**1.06 (0.38)**	**0.96 (0.37)**
Post	0.80	+	0.63 (0.36)	0.57 (0.37)
C	0.60	-	0.49 (0.36)	0.43 (0.34)
W	0.35	-	0.35 (0.28)	0.30 (0.28)
AllPrey	0.17	-	0.34 (0.49)	0.34 (0.49)
TUS scale				
Post	1.00	+	**0.44 (0.06)**	
Bound	1.00	-	**0.78 (0.09)**	
PAS	1.00	-	**0.91 (0.13)**	
W	1.00	+	**0.19 (0.07)**	
C	1.00	+	**0.13 (0.05)**	
AllPrey	1.00	-	**0.21 (0.05)**	

Covariate key: Logarithmic distance to PA boundary (Bound); Regular on-the-ground law enforcement (PAS); distance to ranger post (Post); forest cover (C); availability of water (W); mean availability of ungulate prey (AllPrey)

At the HRS scale, higher illegal human use was most strongly associated with proximity to PA boundary (Σw=1.00) and a lack of regular on-the-ground law enforcement (Σw=1.00), which both had a significant impact. There was also some evidence that greater illegal human use was associated with increased distance to ranger post (Σw=0.80) and greater forest cover (Σw=0.60), and to a lesser extent with lower availability of water (Σw=0.35) and of ungulates (Σw=0.17), although none of these had a significant effect (Table 3.16).

At the TUS scale, all included predictor covariates exhibited a significant relationship with illegal human activity, and their summed model weights were equal (Σw=1.00). Illegal human activity was strongly positively associated with increasing distance from ranger post, proximity to PA boundary,

and availability of water, and negatively with regular on-the-ground law enforcement, more closed areas, and availability of wild ungulates.

3.3.2.2. *Mean probability of detection and site use*

At the HRS scale, the model-averaged probability of detecting illegal human use given presence at the site was $\bar{p}$= 0.51 (SE=0.03), while the mean probability of site use was estimated at $\bar{\bar{\psi}}$ = 0.53 (SE=0.08), slightly higher than a naïve occupancy estimate of 0.50. This suggests the presence of illegal human activity in approximately half of the sampled areas within PAs in the landscape. Probability of illegal human use was slightly higher within strictly-protected trophy hunting areas (GRs; $\bar{\bar{\psi}}$ = 0.50 (SE=0.07)) than photographic tourism areas (Ruaha NP; $\bar{\bar{\psi}}$ = 0.37 (SE=0.06)). Within GRs, mean probability of illegal human activity was significantly greater in vacant ($\bar{\bar{\psi}}$ = 0.77 (SE=0.07)) than in actively managed ($\bar{\bar{\psi}}$ = 0.34 (SE=0.07)) hunting blocks.

At the TUS scale, the model-averaged probability of detecting illegal human use given presence at the site was $\bar{p}$= 0.54 (SE=0.05), while the mean probability of site use at the TUS was estimated at $\bar{\bar{\psi}}$ = 0.35 (SE=0.04), considerably higher than a naïve occupancy estimate of 0.20.

3.3.3. Large carnivore occupancy

Some preferred prey covariates selected for inclusion (see: '3.1. Methods') were ultimately not included in some analyses, due to prey site use estimates exhibiting little heterogeneity between sites. These were: giraffe site use in the lion HRS-PAS, HRS-NAT, and TUS analyses, and in the spotted hyaena TUS analyses; and kudu site use in the lion, leopard, and cheetah HRS-PAS and HRS-NAT analyses, and in all wild dog HRS analyses except HRS-ALL.

3.3.3.1. *Lion*

Substrate was found to influence detection of lion in all analyses, at both scales, while effort influenced detection in three analyses at the HRS scale (Appendix 3.5). The final model set with ΔAICc < 2 from the top-ranked model comprised 11 models for the HRS-ALL sampling grid, 19 for HRS-PA, 5 for HRS-PAS, 2 for HRS-NAT, 11 for HRS-HUNT, and 10 for TUS (Appendix 3.7).

Relative importance of site use covariates

Across the landscape (HRS-ALL), all correlated competing variables (Crop, AllPrey, SecPrey, PA, and Buff) had a significant relationship with lion occurrence, although there is significantly more evidence for availability of natural habitat being the best predictor of lion occurrence (Σw=1.00; Table 3.17). There is also considerable support for proximity to ranger post being a statistically significant determinant of lion occurrence at this scale (Σw=1.00), and for lion being associated with actively managed hunting areas over vacant ones (Σw=1.00), although this effect is not significant.

Within protected areas (HRS-PA), lion were best predicted by lower illegal human activity (Σw=0.57) and regular on-the-ground law enforcement (Σw=0.37), which both had a significant effect on lion occurrence. There was some evidence that lion were better predicted by buffalo availability (Σw=0.08) than by mean availability of all prey (Σw=0.00) or secondary prey (Σw=0.00), as the former also had a signficant effect in some cases. Higher lion site use within PAs was also generally associated with hunting areas being actively managed (Σw=0.91), *Acacia-Commiphora* habitat (Σw=0.63), and proximity to ranger post (Σw=0.33). There was little evidence of distance to PA boundary (Σw=0.00) or of the overarching management strategy of an area (i.e. photographic versus hunting tourism; Σw=0.00) exhibiting meaningful associations with lion occurrence within PAs.

Within strong effectively-protected areas (HRS-PAS), lion site use was not significantly associated with any covariate, although it did exhibit non-significant associations with proximity to ranger post (Σw=1.00), riparian habitat (Σw=0.41), availability of buffalo (Σw=0.12) and zebra (Σw=0.11), and lower illegal human activity (Hum; Σw=0.10). Illegal human activity and proximity to ranger post exhibited significant relationships in models with some support ($\Delta AIC_c < 7$; Appendix 3.7), however, suggesting a potentially meaningful impact. There again was little evidence of the overarching management strategy of an area (Σw=0.00) having an effect.

Within the core area of Ruaha NP (HRS-NAT), lion occurrence was best explained by higher buffalo site use (Σw=0.65) and proximity to ranger post (Σw=0.35), although only the latter had a significant effect in strongly supported models. Within hunting areas (HRS-HUNT), lion exhibited a strong,

significant association only with actively managed hunting areas (Σw=1.00), in addition to a non-significant association with *Acacia-Commiphora* habitat (Σw=0.85).

Within their home range (TUS), lion were significantly positively associated with areas with greater buffalo site use (Σw=1.00) and closer to riparian habitat (Σw=1.00), as well as generally with greater impala (Σw=0.48) and kudu (Σw=0.41) site use, and with lower roan & sable site use (Σw=0.27).

Table 3.17. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining lion site use (ψ) across different landscape components in Ruaha-Rungwa, at two spatial scales. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	*β* (SE*β*) (Top model)	*β* (SE*β*) (Most param.)
HRS-ALL				
Crop	0.62	-	**1.96 (0.58)**	**1.43 (0.57)**
AllPrey	0.22	+	**1.39 (0.34)**	**1.36 (0.34)**
SecPrey	0.16	+	**1.42 (0.36)**	**1.41 (0.36)**
Post	1.00	-	**0.72 (0.29)**	0.52 (0.27)
Mgd	1.00	+	0.72 (0.42)	0.78 (0.42)
H	0.33	-	0.32 (0.28)	0.32 (0.28)
PAS	0.28	+	0.39 (0.30)	0.44 (0.29)
R	0.13	-	0.19 (0.27)	0.20 (0.27)
C	0.05	-	0.08 (0.32)	0.08 (0.32)
HRS-PA				
Hum	0.58	-	**0.63 (0.28)**	**0.60 (0.27)**
PAS	0.37	+	**0.59 (0.26)**	**0.54 (0.26)**
Buff	0.08	+	**0.52 (0.25)**	0.05 (0.32)
Mgd	0.91	+	0.69 (0.37)	0.73 (0.40)
H	0.63	-	0.49 (0.28)	0.63 (0.34)
Post	0.33	-	0.32 (0.27)	0.29 (0.27)
C	0.18	+	0.35 (0.35)	0.32 (0.35)
R	0.17	-	0.22 (0.26)	0.27 (0.26)
HRS-PAS				
Post	1.00	-	1.25 (0.65)	
R	0.41	-	0.74 (0.46)	
Buff	0.12	+	0.66 (0.62)	
Zeb	0.11	+	0.49 (0.46)	
Hum	0.10	-	0.36 (0.35)	
HRS-NAT				
Post	0.35	-	**1.08 (0.53)**	
Buff	0.65	+	1.34 (0.78)	
HRS-HUNT				
Mgd	1.00	+	**1.16 (0.44)**	**1.05 (0.46)**
H	0.85	-	0.54 (0.37)	0.55 (0.38)
PAS	0.09	+	0.24 (0.42)	0.24 (0.42)
Post	0.08	-	0.17 (0.34)	0.17 (0.34)
Hum	0.07	-	0.18 (0.44)	0.18 (0.44)
SecPrey	0.07	+	0.13 (0.36)	0.13 (0.36)
AllPrey	0.07	+	0.12 (0.37)	0.12 (0.37)

R	0.07	-	0.10 (0.33)	0.10 (0.33)
Buff	0.07	+	0.10 (0.37)	0.10 (0.37)
Bound	0.07	+	0.10 (0.45)	0.10 (0.45)
C	0.07	-	0.40 (0.54)	0.40 (0.54)
TUS				
Buff	1.00	+	**0.25 (0.07)**	**0.28(0.07)**
R	1.00	-	**0.18 (0.07)**	**0.19 (0.07)**
Imp	0.48	+	0.12 (0.06)	0.07 (0.08)
Kud	0.41	+	0.08 (0.06)	0.08 (0.06)
Sbl	0.27	-	0.10 (0.06)	0.11 (0.06)
Post	0.14	-	0.08 (0.06)	0.04 (0.07)
Bound	0.05	-	0.02 (0.06)	0.01 (0.06)
Hum	0.03	-	0.01 (0.06)	0.03 (0.07)

Covariate key: Conversion of habitat to agriculture (Crop); mean prey site use (AllPrey); mean prey site use of secondary prey (SecPrey); buffalo site use (Buff); zebra site use (Zeb); kudu site use (Kud); impala site use (Imp); roan & sable site use (Sbl); distance to riparian habitat (R); distance to ranger post (Post); logarithmic distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site actively managed by hunting operators (Mgd).

3.3.3.2. *Leopard*

As a result of leopard being detected at all but two sites in the HRS-PAS grid (n=54; naïve occupancy=0.96), and at all but one in the HRS-NAT grid (n=39; naïve occupancy=0.98), leopard site use could not be modelled within these grids. This however indicates that, at the spatial scale investigated, leopard were using virtually all strongly effectively protected areas and the core NP.

Both effort and substrate influenced leopard detection, in all analyses (Appendix 3.5). The final model set comprised 13 models for the HRS-ALL sampling grid, 6 for HRS-PA, 13 for HRS-HUNT, and 12 for TUS (Appendix 3.7).

Relative importance of site use covariates

Table 3.18. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining leopard site use (ψ) across different landscape components in Ruaha-Rungwa, at two spatial scales. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect ($\beta \pm 1.96 \times SE$) in the top and the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	β (SE_β) (Top model)	β (SE_β) (Most param.)
HRS-ALL				
DistV	0.67	+	**2.87 (0.55)**	**2.48 (0.53)**
Crop	0.25	-	**4.94 (1.07)**	**4.99 (1.14)**
AllPrey	0.07	+	**2.57 (0.48)**	**2.56 (0.48)**
C	0.57	+	**0.96 (0.42)**	0.47 (0.47)
Hnt	0.69	+	0.88 (0.51)	0.91 (0.53)
Post	0.50	-	0.60 (0.40)	0.67 (0.41)

R	0.18	+	0.50 (0.45)	0.29 (0.49)
H	0.14	-	0.59 (0.39)	0.60 (0.40)
HRS-PA				
PAS	1.00	+	15.82 (16.97)	14.31 (16.19)
Mgd	1.00	+	2.27 (1.63)	2.47 (1.68)
R	0.20	+	0.43 (0.45)	0.43 (0.45)
H	0.14	+	0.24 (0.39)	0.24 (0.39)
Imp	0.12	+	0.15 (0.39)	0.15 (0.39)
C	0.12	+	0.11 (0.42)	0.11 (0.42)
Post	0.11	+	0.06 (0.38)	0.06 (0.38)
HRS-HUNT				
Mgd	0.81	+	6.24 (12.60)	6.24 (12.60)
Post	0.46	+	1.95 (1.11)	1.95 (1.11)
Hum	0.42	-	13.97 (9.98)	13.97 (9.98)
Imp	0.24	+	1.36 (0.87)	1.13 (0.72)
PAS	0.23	+	13.32 (41.13)	13.32 (41.13)
R	0.11	+	0.53 (0.60)	0.53 (0.60)
Bound	0.07	+	2.71 (2.96)	2.71 (2.96)
H	0.05	+	0.48 (0.58)	0.48 (0.58)
TUS				
Bound	1.00	+	**0.14 (0.05)**	**0.13 (0.05)**
C	0.61	+	**0.10 (0.05)**	0.09 (0.05)
Kud	0.44	+	0.08 (0.05)	0.06 (0.05)
AllPrey	0.26	+	0.09 (0.06)	0.06 (0.05)
Post	0.25	+	0.04 (0.05)	0.04 (0.05)
Imp	0.23	-	0.08 (0.05)	0.11 (0.06)
R	0.11	-	0.04 (0.05)	0.04 (0.05)

Covariate key: Conversion of habitat to agriculture (Crop); Logarithmic distance to village (DistV); mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); distance to riparian habitat (R); distance to ranger post (Post); distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; '+ = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting (+) or photographic tourism (-) area (Hnt); site actively managed by hunting operators (Mgd).

Across the wider Ruaha-Rungwa landscape (HRS-ALL), distance to settlement (Σw=0.67) was a better predictor of leopard occurrence than availability of natural habitat (Σw=0.25), mean ungulate availability (Σw=0.08), legal protection (Σw=0.00), or availability of preferred prey (impala; Σw=0.00; Table 3.18). There was also evidence of leopard being generally associated with more closed habitat (Σw=0.57; an effect that was significant at times), with areas designated for hunting (Σw=0.69), and with proximity to ranger posts (Σw=0.50).

Within protected areas (HRS-PA), leopard site use did not exhibit significant relationships with any of the predictor covariates at this scale. It was however generally positively associated with regular on-the-ground law enforcement (Σw=1.00) and with actively managed hunting areas over vacant ones (Σw=1.00). There was no support for distance to boundary (Σw=0.00), photographic or hunting tourism

(Σw=0.00), or illegal human activity (Σw=0.00) being associated with leopard occurrence within PAs at this scale.

The strongest predictor of leopard occurrence within hunting areas (HRS-HUNT) was whether the area was actively managed by hunting operators, rather than vacant (Σw=0.81), although this effect was not significant. There was also some evidence that leopard site use increased with greater distance to ranger post (Σw=0.46), lower illegal human activity (Σw=0.42), greater impala site use (Σw=0.24), and regular on-the-ground law enforcement (Σw=0.23), among others. However, the observed large covariate *β*-coefficients suggest that the high naïve occupancy is probably confounding results to an extent.

Within the home range (TUS), leopard site use was most strongly predicted by increasing distance to PA boundary (Σw=1.00) and availability of cover (Σw=0.61), both of which had a significant effect. Leopard were also generally associated with greater availability of kudu (Σw=0.44) and mean ungulate prey availability (Σw=0.26), among others.

3.3.3.3. *Cheetah*

Within hunting areas, the very low number of cheetah detections (n=5) and resulting low naïve occupancy (0.06) meant that it was not possible to model site use in the relevant sampling grid (HRS-HUNT). This indicates either low occurrence of cheetah in hunting areas, low detectability, or both.

Effort was found to influence cheetah detection in three analyses at the HRS scale, while substrate did not (Appendix 3.5). The final model set comprised 9 models for the HRS-ALL sampling grid, 12 for HRS-PA, 8 for HRS-PAS, 9 for HRS-NAT, and 11 for TUS (Appendix 3.7).

Relative importance of site use covariates

Table 3.19. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining cheetah site use (ψ) across different landscape components in Ruaha-Rungwa, at two spatial scales. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	*β* (SE*β*) (Top model)	*β* (SE*β*) (Most param.)
HRS-ALL				
DistV	1.00	+	**1.09 (0.54)**	**1.18 (0.55)**
Hnt	0.12	-	0.31 (0.40)	0.31 (0.38)
C	0.11	+	0.30 (0.42)	0.30 (0.42)

Riv	0.10	+	0.24 (0.38)	0.24 (0.38)
Imp	0.09	-	0.20 (0.42)	0.20 (0.42)
H	0.09	-	0.18 (0.39)	0.18 (0.39)
Post	0.09	+	0.18 (0.39)	0.18 (0.39)
Mgd	0.09	-	0.11 (0.36)	0.11 (0.36)
R	0.09	-	0.10 (0.39)	0.10 (0.39)
HRS-PA				
Hum	0.14	-	0.60 (0.62)	
PAS	0.12	+	0.52 (0.49)	
Riv	0.10	+	0.53 (0.56)	
C	0.10	+	0.48 (0.54)	
AllPrey	0.09	+	0.60 (0.81)	
Post	0.08	+	0.33 (0.44)	
Imp	0.07	-	0.31 (0.46)	
Hnt	0.07	-	0.19 (0.41)	
Mgd	0.06	+	0.17 (0.40)	
H	0.06	+	0.11 (0.42)	
R	0.05	+	0.08 (0.39)	
HRS-PAS				
Imp	0.20	-	0.76 (0.55)	
C	0.19	+	0.83 (0.62)	
Riv	0.11	+	0.63 (0.59)	
Hnt	0.10	-	0.60 (0.63)	
Hum	0.09	-	0.69 (0.92)	
H	0.08	+	0.44 (0.55)	
Sbl	0.07	+	0.38 (0.55)	
HRS-NAT				
C	0.14	+	0.88 (0.68)	
R	0.14	-	0.90 (0.66)	
Imp	0.14	-	0.78 (0.64)	
Riv	0.13	+	0.84 (0.62)	
H	0.10	+	0.68 (0.60)	
Hum	0.09	-	1.02 (1.09)	
Sbl	0.08	+	0.59 (0.60)	
Bound	0.05	+	0.34 (0.70)	
TUS				
R	0.16	+	0.52 (0.48)	
Bound	0.09	-	0.27 (0.35)	
AllPrey	0.08	+	0.17 (0.37)	
Post	0.08	-	0.17 (0.36)	
Sbl	0.07	+	0.13 (0.36)	
Riv	0.07	-	0.08 (0.34)	
Imp	0.07	-	0.07 (0.36)	
C	0.07	-	0.03 (0.38)	
Kud	0.07	+	0.02 (0.35)	

Covariate key: Logarithmic distance to village (DistV); mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); roan & sable site use (Sbl); distance to riparian habitat (R); distance to ranger post (Post); logarithmic distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting (+) or photographic tourism (-) area (Hnt); site actively managed by hunting operators (Mgd); logarithmic distance to large river (Riv)

There is the most support for distance to settlement (Σw=0.67, significant effect) being a better predictor of cheetah occurrence across the landscape (HRS-ALL) than any of the competing landscape-scale variables (Table 3.19). Within protected areas (HRS-PA), strongly protected areas (HRS-PAS), the core Ruaha NP (HRS-NAT), and within the home range (TUS), there was little evidence of any covariate having a strong impact on cheetah occurrence at this scale, with no significant covariate associations and with the null model either ranking highest or receiving strong support (Appendix 3.7).

3.3.3.4. *African Wild Dog*

Both effort and substrate affected wild dog detection in the three analyses at the HRS scale, and did not at the TUS scale (Appendix 3.5). The final model set comprised 1 model for the HRS-ALL sampling grid, 1 for HRS-PA, 7 for HRS-PAS, 2 for HRS-NAT, 3 for HRS-HUNT and 4 for TUS (Appendix 3.7).

Relative importance of site use covariates

Table 3.20. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining African wild dog site use (ψ) across different landscape components in Ruaha-Rungwa, at two spatial scales. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	*β* (SE*β*) (Top & Param. model)
HRS-ALL			
AllPrey	1.00	+	**3.40 (1.26)**
Riv	1.00	+	**0.94 (0.41)**
HRS-PA			
AllPrey	1.00	+	**1.76 (0.69)**
Riv	1.00	+	**1.00 (0.43)**
HRS-PAS			
Riv	0.79	+	**2.40 (1.12)**
Post	0.32	+	1.45 (1.09)
R	0.18	+	0.97 (0.72)
Imp	0.11	-	1.51 (0.94)
C	0.09	+	1.38 (0.74)
AllPrey	0.09	+	0.35 (0.69)
Hnt	0.09	-	0.42 (0.84)
HRS-NAT			
Riv	0.41	+	**2.20 (1.01)**
R	0.59	+	2.87 (1.56)
HRS-HUNT			
AllPrey	1.00	+	**3.28 (1.20)**
Riv	0.48	+	0.85 (0.50)
H	0.29	+	0.69 (0.49)

TUS			
Kud	1.00	+	**0.51 (0.21)**
Imp	0.64	-	**0.49 (0.22)**
Bound	0.60	+	**0.55 (0.25)**
C	0.36	+	**0.59 (0.25)**
R	0.17	-	0.22 (0.20)

Covariate key: Mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); distance to riparian habitat (R); distance to ranger post (Post); logarithmic distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting (+) of photographic tourism (-) area (Hnt); distance to large river (Riv)

Across the landscape (HRS-ALL), there was the most evidence for wild dog site use being better predicted by mean availability of all ungulate prey (Σw=1.00; Table 3.20) rather than legal protection (Σw=0.00), availability of natural habitat (Σw=0.00), distance to village (Σw=0.00), or preferred prey (Σw=0.00). Similar significant associations between wild dog site use and greater mean availability of ungulate prey were also observed within protected areas (HRS-PA) and hunting areas (HRS-HUNT). Results also provide evidence of a similarly well-supported, statistically significant relationship between wild dog site use and increasing distance to large rivers, observed across the landscape (HRS-ALL; Σw=1.00) and within protected areas (HRS-PA; Σw=1.00), strongly protected areas (HRS-PAS; Σw=0.79), the core Ruaha NP (HRS-NAT; Σw=0.41), and hunting areas (HRS-HUNT; Σw=0.48, here the effect was non-significant). This was the only covariate relationship to have a significant effect within strongly effectively protected PAs (HRS-PAS) and the core area of Ruaha NP (HRS-NAT), suggesting a particularly strong role at these scales.

In addition, there was evidence of non-significant positive associations between site use and increasing distance to riparian habitat within strongly protected areas (HRS-PAS; Σw=0.18) and the core NP (HRS-NAT; Σw=0.59); with increasing distance to ranger post (Σw=0.32) and greater forest cover (Σw=0.32) in strongly protected areas (HRS-PAS); and with miombo habitat (Σw=0.29) in hunting areas. Models with some support (ΔAICc<7) also suggest a significant relationship with lower illegal human activity and regular on-the-ground law enforcement within protected areas (HRS-PA), and with miombo habitat within strongly protected areas (HRS-PAS) and the core NP (HRS-NAT; Appendix 3.7). There was little evidence that PA management strategy (photographic versus hunting tourism) was a predictor of wild dog occurrence.

Within their home range, wild dog site use was significantly positively predicted by greater kudu and impala site use (Σw=1.00 and Σw=0.64, respectively), and by greater distance to PA boundary (Σw=60) and forest cover (Σw=0.36).

3.3.3.5. *Spotted Hyaena*

Spotted hyaena were detected at all sampled sites within the HRS-PA sampling grid (n=144), the HRS-PAS grid (n=56), the HRS-HUNT grid (n=85), and the HRS-NAT grid (n=40). It was therefore not possible to model second order habitat use of spotted hyaena within these grids, as results suggested that, at this spatial scale, spotted hyaena were using virtually all areas within PAs in the landscape.

Both effort and substrate impacted spotted hyaena detection at the HRS scale, and substrate impacted detection at the TUS scale (Appendix 3.5). The final model set comprised 9 models for the HRS-ALL grid and 6 models for the TUS grid (Appendix 3.7).

Relative importance of site use covariates

Table 3.21. Relative summed model weights (Σw) and *β*-coefficient estimates, with associated standard errors, of covariates explaining spotted hyaena site use (ψ) across different landscape components in Ruaha-Rungwa, at two spatial scales. Only models retained in the final confidence set (ΔAICc<2) were considered. Highlighted covariates have a significant effect (*β* ± 1.96 x SE) in the top and the most parameterised model in which they appear.

Site Covariate	Σw	Relationship	β (SE$_\beta$) (Top model)	β (SE$_\beta$) (Most param.)
HRS-ALL				
AllPrey	1.00	+	**2.59 (0.52)**	**2.60 (0.53)**
R	0.68	+	0.59 (0.33)	0.55 (0.44)
Post	0.58	-	0.45 (0.32)	0.46 (0.32)
C	0.38	+	0.61 (0.37)	0.70 (0.46)
H	0.09	-	0.17 (0.48)	0.17 (0.48)
TUS				
Buff	1.00	+	**0.29 (0.04)**	**0.27 (0.05)**
Sbl	1.00	-	**0.13 (0.04)**	**0.13 (0.04)**
R	0.35	-	0.02 (0.04)	0.03 (0.04)
Hum	0.18	-	0.04 (0.04)	0.04 (0.04)
Kud	0.15	-	0.02 (0.04)	0.02 (0.04)
C	0.14	+	0.01 (0.05)	0.01 (0.05)

Covariate key: Mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); buffalo site use (Buff); kudu site use (Kud); roan & sable site use (Sbl); availability of riparian habitat (R); distance to ranger post (Post); probability of illegal human activity (Hum); primary habitat (H; + = miombo woodland; - = *Acacia-Commiphora* grasslands & bushlands); forest and bush cover (C)

There was strong evidence that, at the HRS scale, spotted hyaena site use across the landscape (HRS-ALL) was better determined by mean availability of prey (Σw=1.00, significant effect) than by legal

protection (Σw=0.00), availability of natural habitat (Σw=0.00), or distance to village (Σw=0.00). There was also evidence of occurrence being generally associated with greater distance to riparian habitat (Σw=0.68), proximity to ranger post (Σw=0.58), and more closed habitat (Σw=0.38), although none of these effects were significant (Table 3.21). The species was similarly distributed in both photographic and hunting tourism areas.

Within the home range (TUS), spotted hyaena exhibited a significant positive relationship with buffalo site use (Σw=1.00), and a significant negative association with that of roan & sable (Σw=1.00). Weak general positive relationships were observed with proximity to riparian habitat (Σw=0.35), lower illegal human activity (Σw=0.18), lower kudu site use (Σw=0.15), and greater cover availability (Σw=0.14).

3.3.4. Mean probability of detection and site use of large carnivores

The model-averaged estimates of probability of detection ($\bar{\hat{p}}$) and of site use ($\bar{\hat{\psi}}$) for large carnivores are presented in Table 3.22, alongside naïve occupancy estimates. As for prey, the mean probability of site use can, at the HRS scale, be interpreted as the proportion of the study area (sampling grid) used by the species (Mackenzie et al., 2002).

Table 3.22. Model-averaged mean probability of detection ($\bar{\hat{p}}$), site use ($\bar{\hat{\psi}}$), and naïve occupancy (ψ) for large carnivores at the different scales and sampling grids investigated, with associated mean of the standard errors in brackets (adjusted for over-dispersion were relevant; Appendix 3.8).

	HRS-ALL	HRS-PA	HRS-PAS	HRS-NAT	HRS _HUNT	TUS
Naïve ψ						
Lion	0.45	0.57	0.73	0.78	0.53	0.34
Leopard	0.64	0.82	0.96	0.98	0.84	0.33
Cheetah	0.06	0.07	0.09	0.10	0.08	0.15
Wild dog	0.17	0.22	0.32	0.25	0.22	0.21
Spotted hyaena	0.82	1.00	1.00	1.00	1.00	0.72
$\bar{\hat{p}}$ **(SE)**						
Lion	0.38 (0.20)	0.49 (0.19)	0.55 (0.17)	0.59 (0.16)	0.39 (0.18)	0.79 (0.07)
Leopard	0.47 (0.14)	0.51 (0.13)	-	-	0.84 (0.12)	0.78 (0.05)
Cheetah	0.12 (0.05)	0.07 (0.06)	0.15 (0.12)	0.19 (0.15)	-	0.16 (0.07)
Wild dog	0.17 (0.08)	0.19 (0.08)	0.21 (0.05)	0.17 (0.11)	0.24 (0.00)	0.37 (0.05)
Spotted hyaena	0.80 (0.15)	-	-	-	-	0.91 (0.08)
$\bar{\hat{\psi}}$ **(SE)**						
Lion	0.58 (0.10)	0.70 (0.11)	0.80 (0.11)	0.81 (0.09)	0.70 (0.12)	0.74 (0.14)
Leopard	0.71 (0.08)	0.88 (0.04)	-	-	0.91 (0.07)	0.71 (0.12)
Cheetah	0.16 (0.11)	0.28 (0.28)	0.20 (0.18)	0.19 (0.18)	-	0.29 (0.14)
Wild dog	0.34 (0.10)	0.41 (0.12)	0.55 (0.19)	0.50 (0.15)	0.37 (0.12)	0.26 (0.07)
Spotted hyaena	0.83 (0.06)	-	-	-	-	0.91 (0.04)

Mean site use was significantly greater in miombo woodlands than *Acacia-Commiphora* for wild dog, and was instead similar for all other large carnivores. Similarly, mean wild dog site use was greater in strictly-protected hunting areas (GRs; $\bar{\hat{\psi}}$=0.49 (SE = ± 0.13)) than strictly-protected photographic Ruaha NP ($\bar{\hat{\psi}}$=0.34 (SE = ± 0.12)), but similar for other large carnivores.

Mean site use in actively managed hunting areas was $\bar{\hat{\psi}}$=0.87 (SE = ± 0.08) for lion and $\bar{\hat{\psi}}$=0.96 (SE = ± 0.03) for leopard, compared to $\bar{\hat{\psi}}$=0.50 (SE = ± 0.12) for lion and $\bar{\hat{\psi}}$=0.77 (SE = ± 0.11) for leopard in vacant hunting areas. A similar relationship was observed in non-hunted species (wild dog: $\bar{\hat{\psi}}$=0.60 (SE = ± 0.15) in actively-managed hunting blocks versus $\bar{\hat{\psi}}$=0.32 (SE = ± 0.09) in vacant blocks; cheetah: $\bar{\hat{\psi}}$=0.23 (SE = ± 0.16) in actively-managed blocks versus $\bar{\hat{\psi}}$=0.12 (SE = ± 0.12) in vacant blocks), while spotted hyaena were ubiquitous in both.

3.4. DISCUSSION

Modern African conservation landscapes exhibit vast heterogeneity in biotic resources, anthropogenic disturbances, and management and protection strategies (DeFries et al., 2007; Lockwood et al., 2006; Riggio et al., 2019). Understanding the spatial dynamics of large carnivores and their prey in these novel systems is essential to ensure their effective conservation into the 21st century (Balme et al., 2014; Ray et al., 2005). Here, we employ an integrated, multi-species and multi-scale occupancy framework to provide insights into the habitat use of a large carnivore guild, their prey, and anthropogenic impacts in the 50,000 km^2 multiple-use Ruaha-Rungwa landscape in south-central Tanzania.

In summary, our results provide evidence for habitat conversion to agriculture and prey availability, more so than legal protection, being the main limiting factors for large carnivores at a landscape-scale. While all species exhibited difficulty persisting in highly-converted areas, wild dog exhibited the lowest tolerance threshold to habitat conversion, and spotted hyaena the highest. Lion appeared particularly affected by human disturbance within PAs, even within strongly protected areas, while wild dog were primarily limited by habitat features, appearing to avoid areas of high sympatric predator density. Although leopard and spotted hyaena exhibited high adaptability to a range of habitats and anthropogenic disturbances, our findings reveal that their persistence thresholds may be lower than suggested elsewhere. Large carnivore occurrence within PAs was not associated with either overarching management strategy (photographic vs. hunting tourism), while in hunting areas active management was associated with greater persistence of both large carnivores and their prey. Drier and more forested habitats, which receive lower conservation attention, were particularly important for some species, including the threatened wild dog. Overall, our results highlight the importance of adopting an integrative rather than species-centric approach to large carnivore conservation in African landscapes, in order to capture the complex and diverging requirements of complete carnivore guilds and their prey. Our study also identifies a novel threat to Tanzania's conservation areas, in the form of decreased management investments associated with the abandonment of hunting areas.

3.4.1. Prey habitat use

Kudu and giraffe were found to be the most adaptable of the ungulates considered, exhibiting high flexibility to a range of habitats and resilience to anthropogenic disturbance and lower levels of protection (Fig. 3.4). Both species, together with impala, were the most widespread ungulates in boundary or unprotected areas, whereas buffalo were the rarest. Similarly, kudu and impala were the only prey species that were better predicted by availability of natural habitat than by legal protection. This suggests that, as long as patches of unconverted habitat are maintained, these species can persist as a prey source for large carnivores ranging outside PA boundaries, as well as in more impacted areas within PAs. This resilience is likely a consequence of their greater adaptability (kudu, giraffe; Estes, 1991) or smaller body size (impala). On the other hand, legal protection appeared essential for larger and highly social ungulates (buffalo, zebra, giraffe, and roan & sable), which were unable to thrive in unprotected areas, even where natural habitat was available. Regular on-the-ground law enforcement within PAs was similarly particularly important for these species, further highlighting their greater vulnerability to human pressures (Tables 3.13, 3.14).

Kudu and giraffe were also found to readily occupy drier areas in the landscape, thus also highlighting the species' ecological flexibility (Estes, 1991). On the other hand, water-dependent buffalo, impala, and zebra were strongly associated with dry season surface water and with greater variation in vegetation growth and composition (Tables 3.13, 3.14). Given the importance of buffalo for lion (see below), such seasonal range contractions are likely to also affect large carnivore populations.

Our results also reveal the importance of different vegetation types for certain ungulate species. Impala were strongly associated with *Acacia-Commiphora* habitats at both scales (Tables 3.13, 3.14; Fig. 3.4), likely as a result of their browsing habits (Estes, 1991). Thus, while impala is likely to be an important prey species for carnivores in this habitat, other ungulates of similar body size (e.g. common duiker, *Sylvicapra grimmia*; steenbok, *Raphicerus campestris*; and reedbuck, *Redunca spp.*) are likely to be more important prey species for most large carnivores in miombo woodlands. Roan & sable, on the other hand, were found almost exclusively in miombo woodlands (Tables 3.13, 3.14; Fig. 3.4), and likely act as an important prey resource for larger (lion) or cooperative (wild dog) predators in these

areas. Miombo was also found to be an important habitat for both buffalo and zebra (Tables 3.13, 3.14; Fig. 3.4), likely as a result of its greater dry season surface water availability compared to *Acacia-Commiphora* habitats. Our findings thus indicate that eastern Africa's miombo woodlands, while relatively understudied (Abdallah & Monela, 2007; Davis et al., 2020) and exhibiting relatively low primary productivity (Frost, 1996), are likely to be important for numerous ungulate species, including some generally associated with more open savannah habitats. Finally, buffalo were associated with more open areas at the finer scale considered, which may reflect an attempt to increase vigilance and minimise predation risk by lion.

3.4.2. Illegal human activity in Ruaha-Rungwa

Illegal human activity was significantly greater near PA boundary, decreasing rapidly towards the interior (see Appendix 3.10 for site use maps), and in areas without regular on-the-ground law enforcement, at both scales. This highlights the role of protection activities such as anti-poaching in the study area, and suggests that legal safeguards alone may not be enough to effectively secure biodiversity (Everatt et al., 2014, 2019; Petracca et al., 2019). It is worth noting that approximately half of the area with regular on-the-ground law enforcement was classified as such also due to regular protection activities by hunting operators and conservation NGOs (with the other half, in Ruaha NP, instead being secured primarily through government-funded activities). In addition, within strictly protected hunting PAs (GRs), vacant hunting blocks suffered from considerably greater illegal human disturbance than actively managed blocks (Fig. 3.4). This finding is likely a result of the lack of anti-poaching patrols in the former, and reveals a potentially impactful management role of hunting operators in the landscape.

Illegal human use was slightly lower in non-hunting PAs than in hunting PAs (Fig. 3.4), and lower near ranger posts. Thus, although some posts were unable to carry out regular patrols due to funding limitations (TAWA, pers. comm.), this suggests that the mere presence of these structures can help curtail illegal activities (Moore et al., 2018). Finally, illegal human activity was generally greater in areas of lower ungulate availability, likely reflecting wildlife populations being more impacted in more disturbed areas, which are less strongly protected, farthest from ranger posts, and closest to PA boundary.

3.4.3. Large carnivore habitat use

Across the Ruaha-Rungwa complex (including unprotected village land), spotted hyaena were estimated to use circa 83% of the sampled area in the landscape, leopard 71%, lion 58%, wild dog 32%, and cheetah 16% (Fig. 3.4). Findings thus suggest that the most regionally threatened species, cheetah and wild dog (Wolf & Ripple, 2017), are also those most vulnerable in Ruaha-Rungwa. As expected, spotted hyaena and leopard, species which have shown environmental flexibility and resilience to anthropogenic pressures elsewhere (Henschel et al., 2020; Petracca et al., 2019), were relatively widespread. Lion, although still fairly well distributed, were clearly limited across the landscape, with evidence of top-down limitation even within PAs.

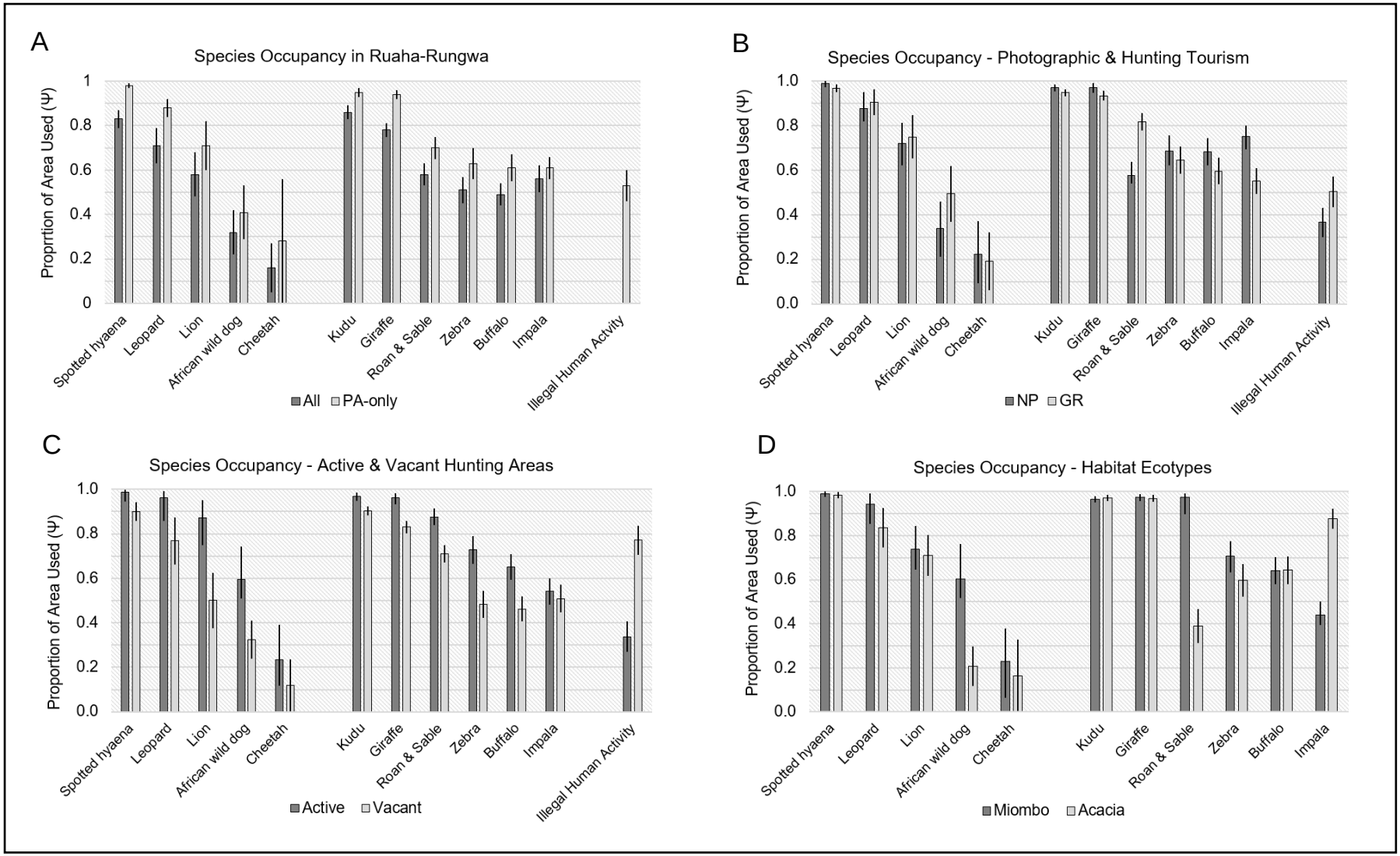


Figure 3.4. Estimated species occupancy ($\bar{\bar{\psi}}$) in Ruaha-Rungwa (A) within the complete Ruaha-Rungwa landscape (including village lands), and within PAs only; (B) within strictly-protected photographic (NP) and trophy hunting (GR) areas; (C) within actively managed versus vacant areas in strictly-protected hunting areas (GRs); (D) within miombo and *Acacia-Commiphora* habitats, within PAs. All estimates are presented with associated mean of the standard errors; occupancy is interpreted as proportion of area used.

3.4.3.1. *Natural habitat & prey are more critical than legal protection*

The availability of natural (unconverted) habitat was a stronger predictor of home range (second order) use than legal protection, for all large carnivores. This is in line with the fact that all target species were detected in village lands, and suggests that it can be possible for these species to persist outside PAs, provided sufficient natural habitat and wild prey are present. While both legal and effective protection are important for large carnivores in impacted landscapes, our results support habitat conversion to agriculture and subsequent prey depletion being the single greatest threats to large carnivore persistence at coarser scales (Wolf & Ripple, 2016), and underscore the importance of conserving patches of natural habitat around and between PAs.

In particular, our findings highlight the difficulty of lion to persist in highly converted and fragmented habitats – an unsurprising finding for such a large and conspicuous felid (Everatt et al., 2019). Lion site use in boundary areas and non-PAs ($\bar{\hat{\psi}}$ = 0.17, SE = ± 0.09) declined rapidly with increasing habitat conversion and decreasing availability of prey (Fig. 3.5), underscoring the critical importance of refuges of unconverted land for lion to persist in marginal habitats (Abade et al., 2020).

Unexpectedly, leopard site use in non-PAs was similar to that of lion ($\bar{\hat{\psi}}$ = 0.19, SE = ± 0.12), with comparable relationships between site use and habitat conversion and prey availability (Fig. 3.5). Although leopard are considered a highly adaptable species (Estes, 1991; Foley et al., 2014), our findings reveal that, while the species is able to endure an intermediate level of human disturbance within PAs, there is a limit to this tolerance. While this mirrors findings elsewhere in Africa (Fattebert et al., 2015; Strampelli et al., 2018), it differs from those obtained elsewhere in the species' global range, where it has been shown to successfully persist in fully agricultural landscapes (e.g. in India; Athreya et al., 2013). Evidence therefore suggests that African leopard populations may exhibit lower levels of tolerance to anthropogenic disturbances, possibly as a result of differences in human cultural norms (Woodroffe, 2000), which can lead to greater persecution and mortality (leopard mortalities have been recorded in the study area from both accidental snaring and targeted poisonings – Dickman, 2008). Further investigation into the persistence thresholds of leopard, and how these vary across regions and

human cultural spectrums (including through studies into the social-carrying capacity of large carnivores – Behr et al., 2017), should therefore be considered a research priority in anthropogenically-disturbed areas of Africa.

Both cheetah and wild dog site use in non-PAs was especially low ($\bar{\hat{\psi}}$=0.03, SE = ± 0.02 and $\bar{\hat{\psi}}$=0.04, SE = ± 0.01, respectively). This confirms that these species are particularly at risk in highly disturbed areas (Winterbach et al., 2013), as highlighted by the sharp decrease in wild dog site use with even minimal levels of habitat conversion, and the relatively high prey availability requirements of the species (Fig. 3.5). Cheetah were similarly very unlikely to persist in proximity to human settlements, suggesting that edge effects are particularly strongly felt by the species (Durant et al., 2017; Klaassen & Broekhuis, 2018), and that excessive development is likely the greatest threat to cheetah outside PAs. The wide ranging nature of both species (Creel & Creel, 2002; Marker et al., 2017) is likely to exacerbate these effects, with individuals moving outside of PAs through converted or depleted areas, where they are most at risk. These findings thus highlight the particular importance of landscape-scale conservation planning (Trombulak & Baldwin, 2010) and of well-protected core areas within mixed-use conservation complexes (Winterbach et al., 2013) for wild dog and cheetah.

As expected, spotted hyaena was the large carnivore with the highest site use in non-PAs ($\bar{\hat{\psi}}$=0.40, SE = ± 0.11), the greatest resilience to both agricultural conversion and prey depletion (Fig. 3.5), and which was detected farthest from PA boundary (21 km; lion: 11 km; leopard: 8 km; wild dog: 4 km; cheetah: 2 km). Nevertheless, even spotted hyaena appeared to have been extirpated from sites with very high levels of habitat conversion, where wild prey are virtually absent. Although the species has been found to persist in areas with little wild prey elsewhere, subsisting on human refuse and livestock (e.g. in Ethiopia; Yirga et al., 2017), our findings suggest that this is not the case in the agricultural landscapes of south-central Tanzania, and that a certain amount of wild prey is necessary for the species to persist in an area (Fig. 3.5). As in the case of leopard, these inferred differences between populations are likely to be, at least in part, related to cultural norms and tolerance; while tolerance for spotted hyaena is high in Ethiopia (Baynes-Rock, 2013), the species is highly persecuted in Ruaha-Rungwa in retaliation for livestock predation (Dickman, 2008). These findings thus further highlight the need for studies aimed

at better understanding the role of human socio-cultural norms in shaping large-carnivore persistence (Behr et al., 2017), to help inform how to best locally implement conservation solutions across sub-Saharan Africa.

Large carnivores are known to respond to thresholds of human density beyond which populations become locally extinct (Woodroffe, 2000), and site-specific ecological resilience thresholds of populations need to be determined to guide conservation and identify ecological traps (Everatt et al., 2019; Winterbach et al., 2013). In Ruaha-Rungwa, we found wild dog to exhibit the lowest tolerance threshold to habitat conversion, with probability of occurrence dropping below 40% at only 4% conversion to agriculture, compared to 15% for lion, 19% for leopard, and 32% for spotted hyaena (Fig. 3.5; the relationship could not be modelled for cheetah due to the low number of detections). Wild dog were also found to require the highest availability of wild prey, and spotted hyaena the lowest (Fig. 3.5). Our results therefore agree with others in suggesting that wild dog, followed by lion, are the large carnivore species with the lowest resilience to habitat conversion to agriculture, as a result of a combination of greater sociality, conspicuousness, and potential for conflict (Winterbach et al., 2013). We encourage use of these identified thresholds to help inform land use, species recovery, and connectivity corridor planning in the region (Foley et al., 2015; Qi et al., 2020).

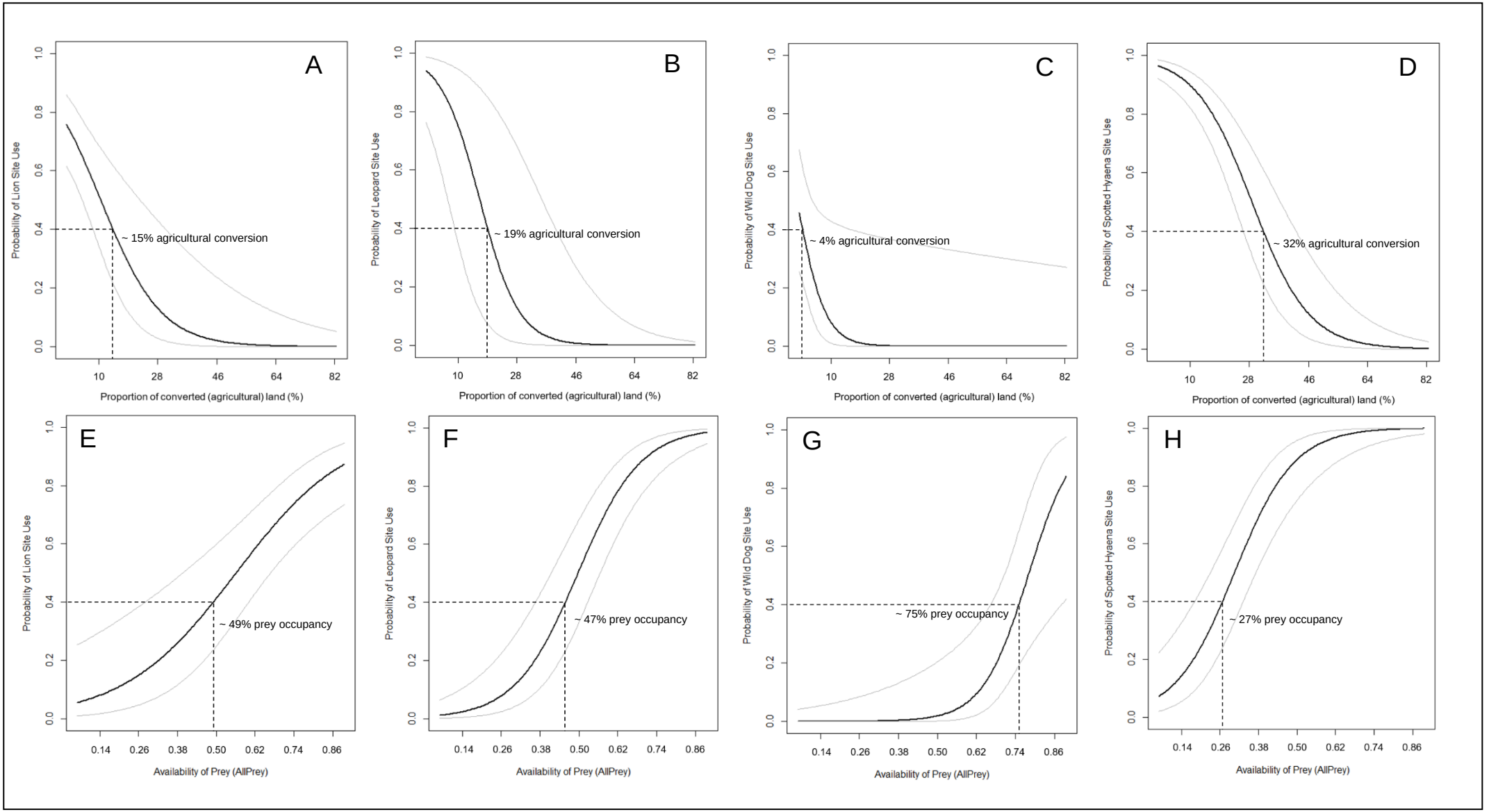


Figure 3.5. Relationship between proportion of site converted to agriculture (cropland) and probability of lion (A), leopard (B), African wild dog (C) and spotted hyaena (D) site use estimates in Ruaha-Rungwa (HRS-ALL, with 95% confidence intervals). Probability of site use ($\widehat{\psi}$) falls under 0.4 once approximately 15% (lion), 19% (leopard), 4% (wild dog) and 32% (spotted hyaena) of the site is converted to agriculture. E-H: Relationship between mean availability of ungulate prey (AllPrey) and probability of lion (A), leopard (B), wild dog (C) and spotted hyaena (D) site use estimates in Ruaha-Rungwa (HRS-ALL, with 95% confidence intervals). Probability of site use ($\widehat{\psi}$) falls under 0.4 once at mean prey site use probabilities of 0.49 (lion), 0.47 (leopard), 0.75 (wild dog) and 0.27 (spotted hyaena). Plots were produced using the top ranked model containing the covariate based on AICc rankings. All other covariates in the model were held at their mean value. Cheetah not included due to large confidence intervals (but see Appendix 3.9).

3.4.3.2. *Human impacts within PAs – Lion are vulnerable even within strongly protected areas*

While natural habitat and prey availability were the most important predictors of large carnivores across the wider landscape, analyses within PAs revealed vulnerabilities to finer-scale human disturbances, as well as additional biotic relationship.

The strongest predictors of home range (second order) use by lion within PAs were lower illegal human activity and regular on-the-ground law enforcement (Table 3.17), with site use declining rapidly with increasing illegal human activity (Fig. 3.6). This suggests that the species is suffering from considerable top-down pressure within PAs, and further highlights the important role of active protection for large carnivores in impacted landscapes (Henschel et al., 2016). Our findings thus align with others in suggesting that, in disturbed areas, anthropogenic rather than ecological variables exhibit the strongest associations with large carnivore habitat use (Petracca et al., 2019). Further evidence for this is provided by the significant associations between lion occurrence and proximity to ranger post (as observed for large carnivores elsewhere – Farhadinia et al., 2018; Ghoddousi et al., 2016), which holds even when sampling across the whole landscape, where the effects of coarser pressures such as habitat conversion are at play, and within the best-protected areas of the landscape (Table 3.17). While these effects may be at least in part due to some ranger posts being located along the main rivers in the landscape, in high prey density areas (TAWIRI, 2019), the consistency of the effect across analyses suggests top-down limitation on lion even within the best-protected areas. This is likely a result of both direct mortality (e.g. through snaring; Everatt et al., 2019; Loveridge et al., 2017, 2020) and indirect effects (prey base depletion, and selection against or inability to persist in prey-depleted areas; Bauer et al., 2020; Wolf & Ripple, 2016). As lion was the large carnivore for which such effects were strongest, our findings suggest a particular vulnerability of the species to human disturbances within PAs, as noted by others (Farr et al., 2017; Petracca et al., 2019). This may be at least partly explained by the fact that, as the dominant competitor within their guild, lion are unlikely to have evolved appropriate strategies for mitigating competition with other species, and may therefore be less able to adapt to competition from humans (Everatt et al., 2019). The lack of significant covariate effects within strongly protected areas

(HRS-PAS), on the other hand, suggests that lions will use most areas in a landscape at the scale investigated, provided a baseline level of effective protection.

There was little evidence, in contrast, of human activity within PAs driving lion habitat use within the home range (TUS scale). Although Everatt et al. (2015) found that lion avoided bushmeat poachers at a similar scale in Mozambique, our results instead suggest that these disturbances have a higher-level effect in Ruaha-Rungwa. This is likely due to very high levels of anthropogenic pressure in certain parts of the landscape preventing lion from occurring in these areas in the first place, as indicated by the observed HRS scale effects.

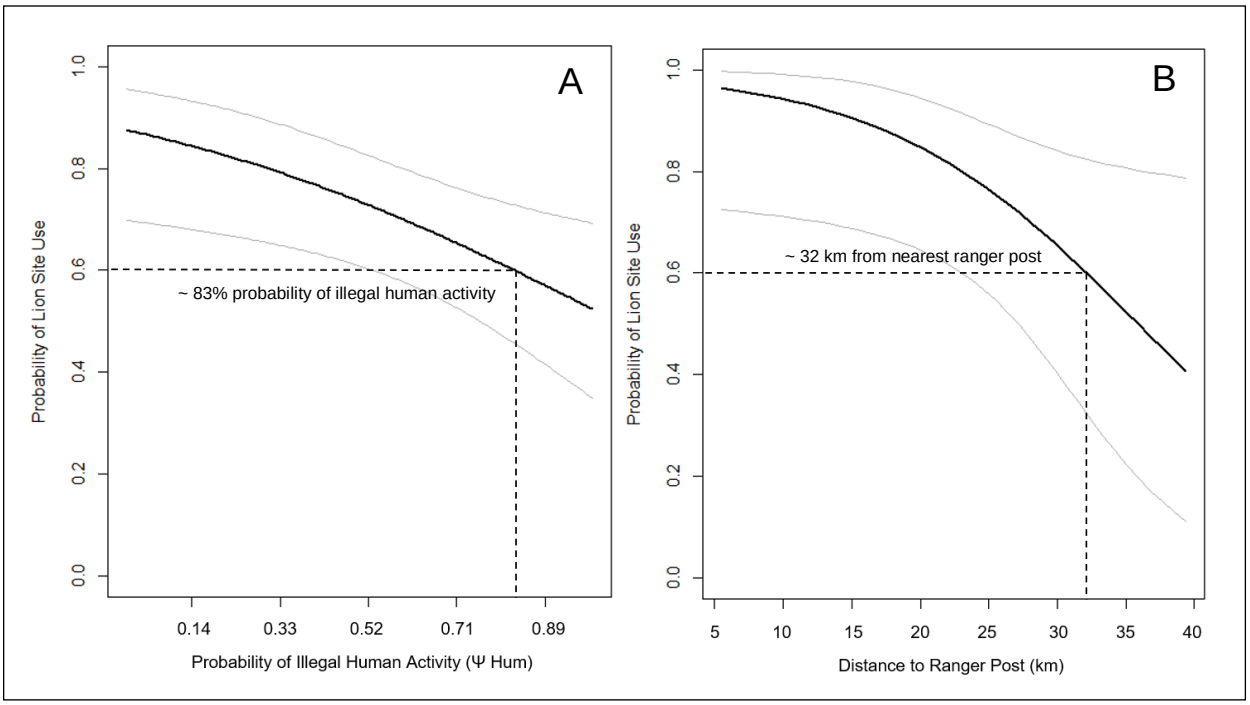


Figure 3.6. Effects of anthropogenic impacts on lion occurrence within PAs in Ruaha-Rungwa. (A) Relationship between probability of illegal human activity and probability of lion site use ($\widehat{\bar{\psi}}$) within PAs (HRS-PA, with 95% confidence intervals). Probability of lion occurrence within protected areas falls <0.6 at high probabilities of illegal human activity (0.83). (B) Relationship between distance to ranger post and probability of lion site use ($\widehat{\bar{\psi}}$) within the core Ruaha NP (HRS-NAT, with 95% confidence intervals). Probability of lion occurrence within the core Ruaha NP falls <0.6 when distance to ranger post is >32 km. Plots produced using the top ranked model containing the covariate based on AICc rankings, with all other covariates in the model held at their mean value.

Top-down limitation within PAs was less apparent for other large carnivores. For both leopard and spotted hyaena, no anthropogenic or management covariate had a strong impact on occurrence within

PAs at the HRS scale. This suggests that these species are able to succeed in less prey-rich and less strongly protected, more impacted areas where lion struggle to persist. Nevertheless, although the relationship was not significant, regular law enforcement was the best predictor of leopard use within PAs, suggesting that leopard are still likely benefitting from higher levels of protection. It is likely that this effect would become more apparent when investigating finer-scale metrics of status, such as population density (Henschel et al., 2011). Within the home range (TUS scale), distance to boundary exhibited a significant, strongly supported relationship with leopard use (Table 3.18), despite showing no effect at the HRS scale. While it is possible that leopards whose home ranges are located near PA boundary are selecting for areas farther from this, this is unlikely to be the case for most individuals in the landscape; instead, the observed effect is likely a result of abundance-induced heterogeneity in detection, with leopard densities (and therefore detection) likely to be greater farther from PA boundary, where edge effects are felt less strongly (Balme et al., 2010; Woodroffe & Ginsberg, 1998).

There was also little evidence of illegal human activity having a strong impact on cheetah or wild dog occurrence within PAs at the HRS scale. Although we observed a significant relationship between wild dog site use and distance to PA boundary at the finer TUS scale, this is also likely a result of abundance-induced heterogeneity. For cheetah, there was also no evidence that any covariate played a strong role in driving habitat use at the TUS scale. This lack of strong effects, at both scales, is likely a result of the low number of cheetah detections, and more research is required to ascertain the extent of impacts of human pressures within PAs. Finally, the lack of evidence for distance to PA boundary impacting large carnivore site use at the HRS scale suggests that sufficient prey and protection can, at least in part, overcome edge effects associated with proximity to boundary.

3.4.3.3. *Effects of biotic resources – African wild dog require areas of lower competitor density*

Our findings provide strong evidence for wild dog being limited within PAs by biotic factors, rather than anthropogenic pressures. Across all HRS scale analyses, the species was strongly associated with areas further from large rivers (Fig. 3.7), but which nonetheless exhibited relatively high levels of prey availability. Although areas near large rivers host the highest concentrations of prey in the dry season

(TAWIRI, 2019), these are also believed to be the areas of the landscape with highest densities of dominant sympatric carnivores (lion and spotted hyaena; Chapter 5; RCP, unpublished data). Taken together, these findings suggest an avoidance of, or inability to persist in, these high-prey but also high competitor density areas by wild dog. Similar avoidance of scarce water resources by wild dog was noted in Zimbabwe by Ndaimani et al. (2016), who also hypothesised the high potential for intraguild competition to be the likely reason for the observed patterns. Instead, wild dog appear to be selecting for areas with intermediate levels of prey availability, but lower densities of sympatric predators. This is further supported by our finding that, within areas with a relatively good baseline levels of prey availability (i.e. strongly protected areas, HRS-PAS, and the core NP, HRS-NAT), distance to large river was the only covariate exhibiting a significant effect on wild dog occurrence, and by the negative association with ranger posts, which were strong predictors of lion use. Mean wild dog site use being significantly greater in sites in miombo compared to those in *Acacia-commiphora* (Fig. 3.4) could similarly be a result of kleptoparasitism and direct mortality from sympatric predators being minimised in woodlands (Mills & Gorman, 1997; Creel & Creel, 2002), and highlights the importance of this habitat for the species in Ruaha-Rungwa. Our results thus add to growing body of evidence that wild dog populations can be suppressed in areas of high sympatric competitor density (Creel & Creel, 1998; Marneweck et al., 2019; Mills & Gorman, 1997), and suggest the presence of such density-dependent limiting effects in Ruaha-Rungwa. More research is recommended to elucidate the finer-scale dynamics of such effects, and determine whether they are a result of spatial avoidance by wild dog of areas with high lion density, inability to persist due to intraguild predation, or a combination of both.

Within the home range (TUS scale), instead, wild dog were significantly associated with areas with higher probability of encountering preferred prey (kudu and impala), greater cover, and proximity to riparian areas. This suggests that, by avoiding dominant competitors at a coarser (HRS) scale, wild dog may not forced to avoid areas of higher prey availability or catchability, also preferred by other sympatric carnivores, at finer spatial scales. This finding brings attention to the importance of scale in habitat use studies, with the same covariate having an opposing effect at the two scales considered.

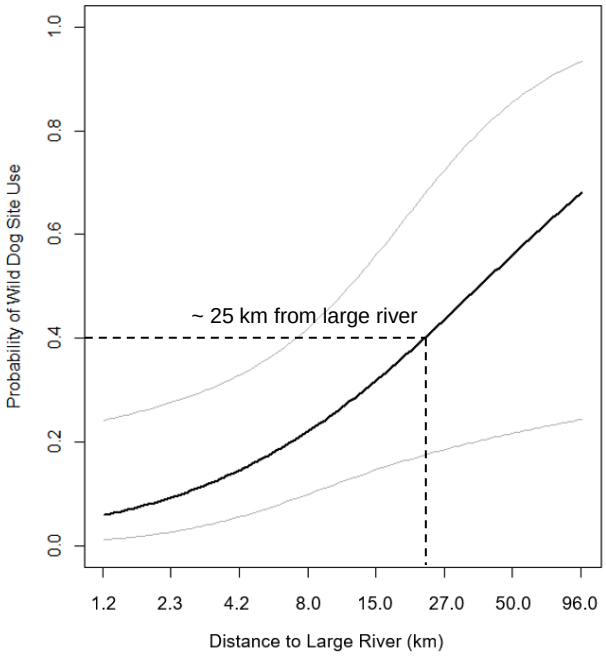


Figure 3.7. Relationship between distance to larger river (in km) and probability of wild dog site use ($\bar{\hat{\psi}}$) within PAs in Ruaha-Rungwa (HRS-PA, with 95% confidence intervals). Wild dog site use increases with greater distance to large rivers, with probability of wild dog occurrence rising >0.4 only when farther than 25 km from large rivers. Plot produced using the top ranked model containing the covariate based on AICc rankings; all other covariates in the model were held at their mean value.

Although lion were mostly limited by top-down pressures at the HRS scale, our results also reveal some important biotic relationships. As found elsewhere (Everatt et al., 2015), buffalo availability was strongly associated with lion occurrence within all PA analyses (Fig. 3.8), and was a better predictor of occurrence than mean prey availability, or any other individual prey species. This suggests that buffalo are particularly important for lion in the landscape, and is the likely explanation for the observed importance of miombo woodlands for lion. Conversely, the lack of significant relationships between lion occurrence and habitat features that can facilitate capture of prey (e.g. riparian habitats) suggests that prey availability is more important than catchability at coarse spatial scales. On the other hand, within the home range (TUS scale), lion appeared to make decisions based on both the availability and catchability of prey: significant associations were observed between lion and areas of their home range

with higher probability of encountering prey (particularly buffalo), and with riparian habitats, where prey are more vulnerable (Balme et al., 2007; Hopcraft et al., 2005).

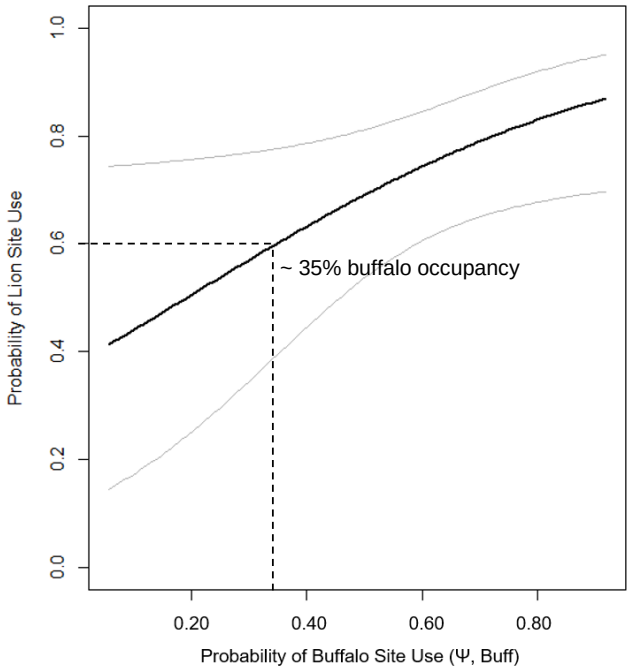


Fig. 3.8. Relationship between probability of buffalo occurrence ($\bar{\hat{\psi}}$) and probability of lion site use ($\bar{\hat{\psi}}$) within protected areas in Ruaha-Rungwa (HRS-PA, with 95% confidence intervals). Probability of lion occurrence falls <0.6 at lower probabilities of buffalo occurrence (0.35). Plots produced using the top ranked model containing the covariate based on AICc rankings. All other covariates in the model were held at their mean value.

Across HRS scale analyses, leopard were associated with greater availability of vegetation cover, reflecting the species' requirement for hunting cover and refuge from sympatric predators (Balme et al., 2007; Burton et al., 2012). However, this relationship was significant only in the landscape-wide sampling grid (HRS-ALL), suggesting that the effect may, at least in part, be an artefact of the greater availability of cover within PAs. The lack of any effect of primary vegetation type on leopard instead confirms that, as long as cover is available, the species can be equally successful across a range of habitats (Estes, 1991). Similarly, the low power of prey covariates in predicting leopard habitat use (as noted elsewhere – e.g. Kafley et al., 2019) is likely a consequence of the species' wide dietary breadth (Hayward, Henschel, et al., 2006), and of not having been able to account for additional, smaller-bodied prey species present in the study area (e.g. common duiker, steenbok, bushbuck, *Tragelaphus sylvaticus*, oribi, *Ourebia ourebi*). Within the home range (TUS scale), availability of cover was again

the most important requirement for leopard. This brings further attention to the importance of accounting for multiple scales, as an analysis restricted to a single scale would have failed to acknowledge the true extent of the covariate's impact on the habitat needs of leopard.

For cheetah, the null model received strong support in all analyses within PAs, at both scales, with no strong covariate associations observed. This suggests either relatively homogeneous habitat use, or insufficient data to model this effectively. While the latter is more likely, the fact that cheetah were detected across a range of habitats and protection gradients nevertheless indicates a certain level of environmental flexibility by the species (Bissett & Bernard, 2007).

Finally, the ubiquity of spotted hyaena within PAs, and the lack of significant relationships with any biotic covariate at the HRS scale, indicates high adaptability to a range of environmental conditions (Fig. 3.4). Within the home range (TUS scale), the significant positive relationship between spotted hyaena and buffalo site use, and negative association with roan & sable, suggests that spotted hyaena are selecting for wetter, more open, prey-rich areas of their home range, likely as a result of these providing better hunting and scavenging opportunities.

3.4.3.4. *Effect of competing management strategies and trophy hunting*

The fact that there was little evidence that whether an area was designated for trophy hunting or photographic tourism had an impact on large carnivore occurrence (Fig. 3.4; Tables 3.17 – 3.21) suggests that neither enterprise is impacting persistence at the scale investigated. These findings mirror those by Mills et (al. 2020), who found comparable occurrence by lions within hunting concessions and national parks in West Africa, at a similar scale to that investigated here.

On the other hand, there was strong evidence that large carnivores and their prey were faring better in actively managed hunting areas compared to those which had been left vacant, with no management or protection activities by hunting operators (Fig. 3.4; Tables 3.17, 3.18). We believe this to likely result from differences in management between actively managed and vacant hunting blocks. In Tanzania, hunting operators are mandated by law to carry out regular protection activities (e.g. anti-poaching patrols) within their blocks (MNRT, 2012); if these are vacated, however, management is returned to

the Tanzania Wildlife Authority (TAWA), which often lacks the resources to effectively protect such large and remote areas, particularly without the income generated from hunting activities (EU, 2017; MNRT, 2012, 2016; TAWA, pers. comm.). This can lead to vacant blocks being rarely patrolled (this study), and to the observed higher levels of disturbance, which negatively impact wildlife occurrence. Less-strictly protected areas, where law enforcement levels were also lower, also exhibited higher illegal human activity and lower occurrence of both herbivores and large carnivores, confirming the pattern noted elsewhere in Tanzania (Oberosler et al., 2019).

3.4.4. Conservation Implications

3.4.4.1. *Ruaha-Rungwa's large carnivore guild and the importance of heterogeneous landscapes*

Our study revealed that the Ruaha-Rungwa ecosystem hosts important populations of lion, leopard, African wild dog, spotted hyaena, and possibly cheetah and striped hyaena, for which more in-depth assessments are required. Although this is in line with prior conjectures (Bauer et al., 2016; Durant et al., 2017; TAWIRI, 2009, 2016), this is the first empirical, landscape-scale status assessment of the complex's large carnivore populations.

Overall, Ruaha NP and Rungwa GR were the PAs with the greatest occurrence of large carnivores in the dry season, due to the combination of greater availability of surface water – and thus prey – and legal protection status and on-the-ground law enforcement. Nevertheless, MBOMIPA WMA and Lunda-Mkwambi GCA, although experiencing high levels of human impacts, were also found to be areas of particular conservation importance, due to the presence of key dry season water refuges. Based on our results, areas with the highest dry season prey densities (i.e. the Great Ruaha and Mzombe River valleys) were identified as the most important for lion in the complex (Appendix 3.10), and likely act as source populations for much of the wider landscape. Their effective protection should therefore be considered a priority for the species.

For wild dog, on the other hand, miombo woodlands (especially in the better-protected Ruaha NP and Rungwa GR), as well as drier areas (e.g. the Ruaha NP escarpment) were instead found to be of critical importance. This is in line with findings from Creel (2001), who suggest that areas of intermediate prey

densities may be ideal for wild dog, given the lower occurrence of sympatric predators. These divergent habitat requirements highlight the importance of adopting an integrated, landscape-scale approach to African large carnivore conservation (Trombulak & Baldwin, 2010), particularly in modern mixed-use systems, and of securing environmentally heterogeneous landscapes, rather than only core areas of higher wildlife densities (Winterbach et al., 2013). Ruaha-Rungwa's miombo woodlands were also found to host important populations of most target species, including some traditionally associated with more open savannah habitat (e.g. lion, cheetah). Although in Ruaha NP miombo woodlands receive less conservation and tourist attention than areas near the Great Ruaha River, as a result of lower wildlife densities and accessibility, and of the vegetation type being unsuitable for photographic tourism (TANAPA, 2009; TAWIRI, 2019), our study reveals these to be of key conservation importance for a range of large carnivore and ungulate species.

For leopard and spotted hyaena, providing baseline levels of protection should be sufficient to ensure their persistence across most of the PA complex. Cheetah, on the other hand, appear to be widely distributed but rare, and finer-scale ranging studies for both cheetah and wild dog should be considered priorities, due to these being both the rarest large carnivores in the complex and the most threatened species overall (Wolf & Ripple, 2017).

At a landscape scale, our results align with previous research in identifying habitat conversion to agriculture as the most pressing long-term threat for Tanzania's wildlife populations (Kiffner et al., 2015). In addition, our findings indicate that illegal human activities are also posing an important threat to Ruaha-Rungwa's large carnivores, even within more strongly protected areas. Efforts should therefore be focused on diminishing these threats, particularly in the most impacted areas (i.e. vacant hunting blocks, south-western Ruaha NP, and less-strictly protected areas; Appendix 3.10), which are likely currently acting as ecological traps (Penteriani et al., 2018). In addition, large carnivores were widespread in boundary areas (Appendix 3.10), and mortalities from both accidental snaring and direct persecution are common in these areas (Dickman et al., 2014). Unprotected areas surrounding the PA complex are therefore also likely acting as population sinks, and conflict-mitigation activities and other initiatives that reduce mortalities in unprotected areas (e.g. increasing tolerance by tying wildlife

presence to financial benefits; RCP, 2019), should be encouraged, and considered conservation priorities for Ruaha-Rungwa's large carnivore populations.

3.4.4.2. *Trophy hunting and the growing threat of hunting area abandonment*

Although overarching land management strategy (i.e. whether an area was designated for photographic tourism or trophy hunting) was not found to impact large carnivore occurrence in Ruaha-Rungwa at the scale investigated (Tables 6 – 10, Fig. 4), we recommend further research to determine whether offtake from hunting is impacting populations in other ways. In Zimbabwe, for example, while trophy hunting was similarly found to not impact leopard site use, it negatively affected the species' abundance (Searle et al., 2020), and similar density-suppressing effects are common (Croes et al., 2011; Mweetwa et al., 2018). We therefore recommend the integration of complementary metrics, such as density estimation, into future status assessments in Ruaha-Rungwa, ideally as part of longer-term monitoring programmes in hunting areas. Nevertheless, our results suggest that large carnivores and their prey can successfully persist in hunting areas, provided these are effectively managed. Taken together, our findings also indicate that on-the-ground law enforcement, rather than an area's overarching management strategy (photographic or hunting tourism), is a better determinant of large mammal persistence.

The fact that vacant hunting blocks experienced high levels of human disturbance, and lower occurrence of both large carnivores and their prey (Fig. 3.4), suggests that the presence of hunting operators can improve the management of wildlife habitats in the absence of other sources of conservation funding, provided these carry out regular protection activities. At the same time, it was not possible to ascertain whether over-hunting played a role in hunting blocks becoming degraded before they were abandoned; this may indeed have been the case, particularly as there is evidence of over-harvesting elsewhere in Tanzania (Packer et al., 2010; Brink et al., 2016). Given that not all hunting operators were observed to invest the same amount of resources into law enforcement (this study), it is possible that poor management on the part of operators may have contributed, at least in part, to vacant blocks becoming degraded prior to being abandoned. Ensuring that hunting operators implement regular anti-poaching activities, which our results show are critical for the prolonged viability of these areas, should therefore be seen as a priority for PA managers.

Nevertheless, regardless of the underlying drivers, our findings reveal that the high levels of human disturbance in vacant hunting blocks are a key conservation threat in Ruaha-Rungwa, as shown by block vacancy being the strongest predictor of absence of lion and leopard in hunting areas. As far as we are aware, this is the first study to investigate the effect of hunting block abandonment on large mammal populations in Tanzania, and our findings have significant conservation implications. Approximately half of Tanzania's hunting areas were vacated by hunting operators between 2014 and 2018, resulting in almost 150,000 km^2 of hunting PAs becoming vacant (FZS, 2018); as a result, if the degradation observed in vacant blocks in Ruaha-Rungwa were indicative of the status of vacant blocks elsewhere in the country, the dereliction of protective management associated with hunting block vacancy would likely presently be one of the greatest threats to Tanzania's biodiversity. We therefore strongly encourage further research into this emerging reality, both in Tanzania and in other areas experiencing similar ongoing patterns of hunting area abandonment (e.g. Zambia, Mozambique; FZS, 2018). In light of these findings, we also caution against attempts to phase out trophy hunting (or, more specifically, protection activities associated with it) without appropriate alternatives already in place (Dickman et al., 2019; Lindsey et al., 2012). Given the size of the areas of concern, both consumptive and non-consumptive conservation-oriented strategies will likely be required (Di Minin et al., 2016; Lindsey et al., 2007), through mechanisms that are both established (photographic tourism, trophy hunting) and innovative (e.g. debt for nature swaps, carbon sequestration payments, a conservation basic income, private philanthropy, joint ventures with the private and/or NGO sector, sustainable livestock-wildlife systems; Buscher & Fletcher, 2020; Crossman et al., 2011; Keesing et al., 2018; Lindsey et al., 2014; Pringle, 2017; Venter et al., 2009; Western et al., 2020). We therefore urgently recommend investments to identify and implement solutions to what is likely to be a novel yet potentially severe threat to Africa's wildlife and its habitats.

3.4.5. Methodological considerations & main study limitations

Probability of detection was generally higher for larger prey species (buffalo, giraffe, roan & sable; Table 3.15); this is to be expected, given that larger tracks should be easier to detect. However, it also suggests that this method may not be ideal to collect presence/absence data on smaller mammals.

In addition, it is worth noting that we grouped together all signs of illegal human presence within a PA, due to an inability to determine with certainty the motive behind the observed incursion. However, different motivations (e.g. bushmeat poaching, logging, mining, livestock grazing, etc.) will have considerably varied impacts on large carnivore habitat use, and pose varying levels of threat to their persistence. As a result, while useful to inform law enforcement priorities, our insights on illegal human activity unfortunately lack the resolution required to identify conservation actions necessary to address the underlying drivers. Future efforts should therefore build upon the findings and methodologies presented here, and attempt to better understand the effect of individual illegal activities within PAs on large carnivore occurrence and persistence.

Finally, due to the low number of detections, it was not possible to obtain many inferences on cheetah habitat use in Ruaha-Rungwa. Our findings thus suggest that spoor-based surveys targeting cheetah should be complemented with additional data collection techniques to improve detection (e.g. camera traps located on scent-marking sites – Andresen et al., 2014). Although spoor surveys have been successfully employed to obtain inferences on cheetah distribution and habitat use over large scales elsewhere (e.g. Kenya – Henschel et al., 2020; Angola – Petracca et al., 2019), ours is not the first spoor survey to result in a low number of cheetah detections (Williams, 2016). It is unclear whether, both in our case and elsewhere, this was a consequence of cheetah being rare, of low detectability, or both. Most likely, a combination of factors is at play, with the effectiveness of road-based spoor surveys likely being dependent on a number of factors, including levels of human activity and both cheetah and sympatric competitor density. For example, in one of the study areas with a relatively high number of cheetah detections, both lion and spotted hyaena were absent (Houser et al., 2009). This might lead cheetah to travel more often along roads, as they would not need to minimise encounters with larger sympatric predators. At the same time, it is also possible that low detections are due to low overall abundance, and that cheetah are not thriving in the landscape; however, given that these were not localised (cheetah was recorded in five of the eights PAs surveyed; see Appendix 3.10 for detection maps of all large carnivores), it appears that the species is relatively widespread in the landscape, albeit likely existing at low densities (Chapter 6). Ultimately, the underlying mechanisms which determine

cheetah road use and detection are unclear, and additional research, ideally involving satellite collars and spanning a number of sites, is encouraged to better clarify these.

With the exception of cheetah, however, our study shows that occupancy modelling applied to spoor surveys is an effective and efficient method for collecting distribution and habitat use data on large carnivores, their prey, and human impacts across large areas, comprising a range of habitats and land management types. We therefore encourage the approach be applied to provide inferences on the status and habitat use of large African carnivore populations in vast conservation areas elsewhere, so that these can be employed to develop targeted and informed conservation management recommendations.

3.5. ACKNOWLEDGEMENTS

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3.6. APPENDICES

Appendix 3.1. Occupancy Covariates Justification & Calculations

Appendix 3.2. Occupancy Covariate Maps

Appendix 3.3. Occupancy Analyses Input Files

Appendix 3.4. Covariate Correlation Testing

Appendix 3.5. Detection Modelling Rankings

Appendix 3.6. Prey & Human Activity Occupancy Modelling Rankings.

Appendix 3.7. Large Carnivore Occupancy Modelling Rankings

Appendix 3.8. Goodness of Fit Tests

Appendix 3.9. Additional Covariate Effects Graphs

Appendix 3.10. Site Use Maps & Large Carnivore Detections

APPENDIX 3.1 – OCCUPANCY COVARIATES JUSTIFICATION & CALCULATIONS

A justification for the selection of the covariates hypothesised to affect large carnivore, prey, and/or illegal human activity site use, as well as a detailed methodology of how individual covariates were extracted and calculated, can be accessed at:

https://github.com/pstrampelli/Occupancy-Covariates-Justification-Calculations

APPENDIX 3.2 – OCCUPANCY COVARIATE MAPS

Maps of the site use covariate employed to model large carnivore, prey, and/or illegal human activity site use can be accessed at:

https://github.com/pstrampelli/Occupancy-Covariate-Maps

APPENDIX 3.3 – OCCUPANCY ANALYSES INPUT FILES

All input files (including detection matrices, site covariates, and detection covariates) for all species, at all scales, can be accessed at:

https://github.com/pstrampelli/Occupancy-Analyses-Input-Files

APPENDIX 3.4 – COVARIATE CORRELATION TESTING

Outputs of covariate correlation tests, which were carried out for each analysis of each species, can be accessed at:

https://github.com/pstrampelli/Covariate-Correlation-Testing

APPENDIX 3.5 – DETECTION MODELLING RANKINGS

Prey

Table S3.1. Model rankings of possible combinations of covariates influencing detection (p) for each prey species at the HRS (home range selection) and temporary use selection (TUS) scales.

Species	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS						
Buffalo	p (E+S)	594.76	0.00	0.36	582.76	7
	p (E)	594.86	0.10	0.35	582.86	6
	p (S)	596.31	1.59	0.16	584.28	6
	p (.)	596.75	2.05	0.13	584.71	5
Zebra	p (.)	626.62	0.00	0.48	616.28	5
	p (E)	627.90	1.28	0.26	615.43	6
	p (S)	628.74	2.12	0.17	616.27	6
	p (E+S)	630.04	3.42	0.09	615.41	7
Giraffe	p (E)	670.00	0.00	0.68	657.53	6
	p (E+S)	671.38	1.38	0.31	671.38	7
	p (.)	678.15	8.15	0.01	557.81	5
	p (S)	680.10	10.10	0.00	667.63	6
Roan/Sable	p (S)	559.25	0.00	0.42	544.62	6
	p (E+S)	560.16	0.86	0.28	543.29	7
	p (.)	560.68	1.43	0.21	548.21	5
	p (E)	562.26	3.01	0.09	547.63	6
Kudu	p (E+S)	540.35	0.00	0.97	525.75	7
	p (S)	546.82	6.47	0.03	534.35	6
	p (E)	556.58	15.84	0.00	544.11	6
	p (.)	569.01	28.27	0.00	558.67	5
Impala	p (S)	636.55	0.00	0.45	624.08	6
	p (E+S)	636.98	0.43	0.36	622.35	7
	p (E)	639.12	2.57	0.13	626.65	6
	p (.)	640.63	4.08	0.06	630.29	5
TUS						
Buffalo	p (S)	2664.83	0.00	0.69	2640.83	12
	p (.)	2666.45	1.62	0.21	2644.45	11
Zebra	p (.)	2810.10	0.00	0.81	2780.10	11
	p (S)	2912.02	1.92	0.19	2785.76	12
Giraffe	p (S)	5862.25	0.00	0.91	5836.25	9
	p (.)	5866.99	4.74	0.09	5846.30	8
Roan/Sable	p (.)	4117.70	0.00	0.84	4095.70	11
	p (S)	4119.69	1.99	0.16	4095.70	12
Kudu	p (S)	6292.17	0.00	1.00	6260.17	13
	p (.)	6308.68	16.51	0.00	6278.68	12
Impala	p (.)	3567.93	0.00	0.83	3533.93	12
	p (S)	3569.91	1.98	0.17	3533.91	13

Covariate key: Effort (E); Substrate quality & use index (S). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Illegal Human Activity

Table S3.2. Model rankings of possible combinations of covariates influencing detection (p) illegal human activity at the home range selection (HRS) scale.

Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS scale					
p (.)	501.47	0.00	0.49	486.84	7
p (S)	503.03	1.56	0.22	486.21	8
p (E)	503.30	1.83	0.20	486.48	8
p (E+S)	504.96	3.49	0.09	485.93	9
TUS scale					
p (.)	1995.26	0.00	0.73	1973.26	11
p (S)	1997.26	2.00	0.27	1973.26	12

Large Carnivores

Table S3.3. Model rankings of covariates influencing detection (p) for lion in each occupancy analysis at the home range selection (HRS) and temporary use selection (TUS) scales.

Analysis	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS-ALL	p (E+S)	575.91	0.00	0.82	552.38	11
	p (S)	578.98	3.07	0.18	557.72	10
	p (E)	612.87	36.96	0.00	591.61	10
	p (.)	620.99	45.08	0.00	601.96	9
HRS-PA	p (E+S)	541.92	0.00	0.89	527.88	7
	p (S)	545.95	4.11	0.11	533.99	6
	p (E)	575.61	33.77	0.00	563.65	6
	p (.)	584.44	42.60	0.00	574.48	5
HRS-PAS	p (S)	251.11	0.00	0.56	241.11	5
	p (E+S)	251.57	0.46	0.44	239.57	6
	p (E)	265.56	14.45	0.00	255.56	5
	p (.)	267.05	15.94	0.00	259.05	4
HRS-NAT	p (S)	181.56	0.00	0.62	173.56	4
	p (E+S)	182.76	1.20	0.34	172.76	5
	p (.)	188.51	6.95	0.02	182.51	3
	p (E)	188.87	7.31	0.02	180.87	4
HRS-HUNT	p (E+S)	312.88	0.00	0.89	298.88	7
	p (S)	317.10	4.22	0.11	305.10	6
	p (E)	331.72	18.84	0.00	319.72	6
	p (.)	337.73	24.85	0.00	327.73	5
TUS	p (S)	2070.75	0.00	1.00	2052.75	9
	p (.)	2093.19	22.44	0.00	2075.19	8

Covariate key: Effort (E); Substrate quality & use index (S); AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Table S3.4. Model rankings of covariates influencing detection (p) for leopard in each occupancy analysis at the home range selection (HRS) and temporary use selection (TUS) scales.

Analysis	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS-ALL	p (E+S)	685.69	0.00	0.95	672.25	9
	p (E)	691.55	5.86	0.05	677.99	8
	p (S)	708.40	22.71	0.00	694.51	8
	p (.)	718.99	33.30	0.00	704.89	7
HRS-PA	p (E+S)	635.25	0.00	0.96	623.30	6
	p (S)	641.78	6.48	0.04	631.78	5
	p (E)	658.55	23.25	0.00	648.55	5
	p (.)	669.70	34.40	0.00	661.70	4
HRS-HUNT	p (E+S)	390.99	0.00	0.89	376.99	7
	p (S)	395.29	4.30	0.10	383.29	6
	p (E)	399.52	8.53	0.01	387.52	6
	p (.)	405.35	14.36	0.00	395.35	5
TUS	p (S)	2916.84	0.00	1.00	2989.84	9
	p (.)	2952.82	35.98	0.00	2936.82	8

Covariate key: Effort (E); Substrate quality & use index (S). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Table S3.5. Model rankings of covariates influencing detection (p) for cheetah in each occupancy analysis at the home range selection (HRS) and temporary use selection (TUS) scales.

Species	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS-ALL	p (E)	123.34	0.00	0.49	115.34	4
	p (E+S)	124.34	1.00	0.30	114.34	5
	p (.)	126.27	2.93	0.11	120.27	3
	p (S)	126.60	3.26	0.10	118.60	4
HRS-PA	p (E)	107.33	0.00	0.42	99.33	4
	p (.)	107.62	0.29	0.36	101.62	3
	p (E+S)	109.29	1.96	0.16	99.29	5
	p (S)	111.00	3.67	0.06	103.00	4
HRS-PAS	p (.)	56.03	0.00	0.33	50.03	3
	p (E)	56.06	0.03	0.32	48.06	4
	p (S)	57.18	1.15	0.19	49.18	4
	p (E+S_	57.57	1.54	0.15	47.57	5
HRS-NAT	p (E)	43.53	0.00	0.51	35.53	4
	p (.)	45.21	1.68	0.21	39.21	3
	p (E+S)	45.53	2.00	0.19	35.53	5
	p (S)	47.1	3.57	0.09	39.1	4
TUS	p (.)	143.40	0.00	0.56	137.40	3
	p (S)	143.91	0.51	0.44	135.91	4

Covariate key: Effort (E); Substrate quality & use index (S). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Table S3.6. Model rankings of covariates influencing detection (p) for African wild dog in each occupancy analysis at the home range selection (HRS) and temporary use selection (TUS) scales.

Analysis	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS-ALL	p (E+S)	250.80	0.00	0.54	243.50	6
	p (E)	251.62	0.82	0.35	244.29	5
	p (S)	254.53	3.73	0.01	247.12	5
	p (.)	257.20	6.40	0.00	249.71	4
HRS-PA	p (E+S)	250.66	0.00	0.54	238.66	6
	p (E)	251.46	0.80	0.36	241.46	5
	p (S)	254.37	3.71	0.08	244.37	5
	p (.)	257.01	6.35	0.02	249.01	4
HRS-PAS	p (E)	138.53	0.00	0.35	128.53	5
	p (.)	139.34	0.81	0.23	131.34	4
	p (E+S)	139.48	0.95	0.22	127.48	6
	p (S)	139.71	1.18	0.20	129.71	5
HRS-NAT	p (S)	69.87	0.00	0.63	59.87	4
	p (E+S)	71.97	2.10	0.22	63.97	5
	p (E)	73.01	3.14	0.13	65.01	4
	p (.)	76.31	6.44	0.02	70.31	3
HRS-HUNT	p (.)	161.08	0.00	0.36	153.08	4
	p (E)	161.47	0.39	0.29	151.47	5
	p (S)	162.14	1.06	0.21	152.14	5
	p (E+S)	162.92	1.84	0.14	150.92	6
TUS	p (S)	2468.83	0.00	0.99	2456.83	9
	p (.)	2479.38	10.55	0.01	2469.38	8

Covariate key: Effort (E); Substrate quality & use index (S). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Table S3.7. Model rankings of covariates influencing detection (p) for spotted hyaena in each occupancy analysis at the home range selection (HRS) and temporary use selection (TUS) scales

Species	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS-ALL	p (E+S)	502.73	0.00	0.99	488.09	8
	p (E)	512.46	9.73	0.01	497.53	7
	p (S)	540.09	37.36	0.00	524.36	7
	p (.)	558.57	55.85	0.00	542.30	6
TUS	p (S)	2070.75	0.00	1.00	2052.75	9
	p (.)	2093.19	22.44	0.00	2075.19	8

Covariate key: Effort (E); Substrate quality & use index (S); AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

APPENDIX 3.6 – PREY & HUMAN ACTIVITY OCCUPANCY MODELLING RANKINGS

Prey – Home range selection (HRS) scale

Table S3.8. Model rankings for prey site use at the home range selection (HRS) scale, based on AICc values. Final set based on models with ΔAICc < 2 for (a) buffalo, (b) zebra, (c) giraffe, (d) roan & sable, (e) kudu, and (f) impala.

a) **Buffalo**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (PA+W+H) p(E+S)	593.23	0.00	1.00	578.23	7

b) **Zebra**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (PA+PAS+NDVIstd) p(.)	626.62	0.00	0.26	616.28	5
2	ψ (PA+PAS+H) p(.)	626.83	0.21	0.23	616.49	5
3	ψ (PA+PAS) p(.)	627.65	1.03	0.15	619.43	4
4	ψ (PA+PAS+C) p(.)	627.70	1.08	0.15	617.36	5
5	ψ (PA+H+W) p(.)	628.19	1.57	0.11	617.85	5
6	ψ (PA+PAS+W) p(.)	628.34	1.72	0.10	618.00	5

c) **Giraffe**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (PA+NDVIstd+C) p(E)	668.17	0.00	0.37	655.70	6
2	ψ (PA) p(E)	669.36	1.19	0.20	661.14	4
3	ψ (PA+W+NDVIstd) p(E)	670.00	1.83	0.15	657.53	6
4	ψ (PA+W) p(E)	670.07	1.90	0.14	659.73	5
5	ψ (PA+NDVIstd) p(E)	670.13	1.96	0.14	659.79	5

d) **Roan & Sable**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (PA+H+NDVIstd+PA*H) p(S)	559.25	0.00	0.39	544.62	7
2	ψ (PA+H+PAS+PA*H) p(S)	560.26	1.01	0.23	545.63	7
3	ψ (PA+H+C+PA*H) p(.)	560.42	1.17	0.21	545.79	7
4	ψ (PA+H+PA*H) p(.)	560.93	1.68	0.17	548.46	6

e) **Kudu**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Crop) p(E+S)	539.28	0.00	0.18	528.94	5
2	ψ (Crop+NDVIstd) p(E+S)	539.36	0.08	0.17	526.89	6
3	ψ (Crop+DistV) p (E+S)	539.91	0.63	0.13	527.44	6
4	ψ (Crop+C) p (E+S)	540.21	0.93	0.11	527.74	6
5	ψ (Crop+NDVIstd+DistV) p (E+S)	540.35	1.07	0.10	525.72	7
6	ψ (Crop+NDVIstd+W) p (E+S)	540.74	1.46	0.09	526.11	7
7	ψ (Crop+C+DistV) p (E+S)	540.75	1.47	0.09	526.12	7
8	ψ (C+H) p (E+S)	541.13	1.85	0.07	528.66	6
9	ψ (Crop+W) p (E+S)	541.21	1.93	0.06	528.74	6

f) **Impala**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Crop+W+C) p(S)	636.55	0.00	0.59	624.08	7
2	ψ (Crop+H+C) p(S)	637.24	0.69	0.41	624.77	7

Covariate key: Legal protection (PA); availability of water (W); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); strong effective protection (PAS); variation in vegetation composition and growth (NDVIstd); forest cover (C); conversion of habitat to agriculture (Crop); natural logarithm of distance to human settlement (DistV); protected miombo woodland (PA*H). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Prey – Temporary use selection (TUS) scale

Table S3.9. Results of model ranking for prey site use at the temporary use selection (TUS) scale, based on AIC values. Final set based on models with ΔAICc < 2 for (a) buffalo, (b) zebra, (c) giraffe, (d) roan & sable, (e) kudu, and (f) impala.

a) **Buffalo**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+PAS+W+H+C+NDVIstd),th1(),p(S),th0pi()	2664.83	0.00	1.00	2640.83	12

b) **Zebra**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+PAS+W+H+C+NDVIstd),th1(),p(.),th0pi()	2810.10	0.00	0.28	2780.10	12
2	ψ,th0(PA+PAS+W+C+NDVIstd),th1(),p(.),th0pi()	2811.18	1.08	0.17	2783.18	11
3	ψ,th0(PA+PAS+W+H),th1(),p(.),th0pi()	2811.22	1.12	0.16	2785.22	10
4	ψ,th0(PA+PAS+W+NDVIstd),th1(),p(.),th0pi()	2811.56	1.46	0.14	2785.56	10
5	ψ,th0(PA+PAS+W+H+C),th1(),p(.),th0pi()	2811.60	1.50	0.13	2783.60	11
6	ψ,th0(PA+PAS+W+H+C+NDVIstd),th1(),p(.),th0pi()	2811.76	1.66	0.12	2783.66	11

c) **Giraffe**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+PAS+CGE),th1(),p(S),th0pi()	5860.65	0.00	0.39	5836.65	9
2	ψ,th0(PA+PAS+CGE+H),th1(),p(S),th0pi()	5862.25	1.60	0.18	5836.25	10
3	ψ,th0(PA+PAS+CGE+W),th1(),p(S),th0pi()	5862.58	1.93	0.15	5836.58	10
4	ψ,th0(PA+PAS+CGE+C),th1(),p(S),th0pi()	5862.64	1.99	0.14	5836.64	10
5	ψ,th0(PA+PAS+CGE+NDVIstd),th1(),p(S),th0pi()th0pi()	5862.25	2.00	0.14	5836.65	10

d) **Roan & Sable**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+PAS+H+C+NDVIstd),th1(),p(.),th0pi()	4117.58	0.00	0.52	4097.58	10
2	ψ,th0(PA+PAS+H+C+NDVIstd+W),th1(),p(.),th0pi()	4117.70	0.12	0.48	4095.70	11

e) **Kudu**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+PAS+Crop+W+H+C+NDVIstd),th1(),p(S),th0pi()	6292.17	0.00	1.00	6260.17	13

f) **Impala**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ,th0(PA+W+Crop+H+C+NDVIstd),th1(),p(.),th0pi()	3567.75	0.00	0.52	3535.75	11
2	ψ,th0(PA+PAS+W+Crop+H+C+NDVIstd),th1(),p(.),th0pi()	3567.93	0.18	0.48	3533.93	12

Covariate key: Legal protection (PA); availability of water (W); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); strong effective protection (PAS); variation in vegetation composition and growth (NDVIstd); forest cover (C); conversion of habitat to agriculture (Crop); natural logarithm of distance to human settlement (DistV); protected miombo woodland (PA*H). AICc = Akaike

Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Human – Home range selection (HRS) & Temporary use selection (TUS) scale

Table S3.10. Results of multivariate model ranking for illegal human site use at the home range selection (HRS) and temporary use selection (TUS) scales, based on AICc values. Final set based on all models with ΔAICc < 2.

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
HRS scale						
1	ψ (Bound+PAS+C+Post) p(.)	500.43	0.00	0.19	487.96	6
2	ψ (Bound+PAS+Post) p(.)	500.57	0.14	0.18	490.23	5
3	ψ (Bound+PAS+W+Post) p(.)	501.08	0.65	0.14	488.61	6
4	ψ (Bound+PAS+W+C+Post) p(.)	501.47	1.04	0.12	486.84	7
5	ψ (Bound+PAS+C) p(.)	501.66	1.23	0.11	491.32	5
6	ψ (Bound+PAS+W+C) p(.)	501.93	1.50	0.09	489.46	6
7	ψ (Bound+PAS+C+Post+AllPrey) p(.)	502.00	1.57	0.09	487.37	7
8	ψ (Bound+PAS+Post+AllPrey) p(.)	502.26	1.83	0.08	489.79	6
TUS scale						
1	ψ (Bound+PAS+Post+W+C+AllPrey) p(.)	1995.26	0.00	1.00	1973.26	11

Covariate key: Availability of water (W); strong effective protection (PAS); forest cover (C); distance to protected area boundary (Bound); distance to ranger post (Post); mean availability of ungulate prey (AllPrey). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

APPENDIX 3.7 – LARGE CARNIVORE OCCUPANCY MODELLING RANKINGS

The final model set for each large carnivore occupancy analysis can be found below (Note that covariate 'Mgd' is presented as 'Htd' in full model rankings outputs).

Additionally, complete model rankings, for all species and at all scales, can be accessed at:

https://github.com/pstrampelli/Full-Occupancy-Model-Rankings/

Lion

Table S3.11. Results of model ranking for lion site use in the different sampling grids, based on AICc values (AIC at the temporary use selection (TUS) scale). Final set based on models with ΔAICc/ΔAIC < 2 for (a) HRS-ALL, (b) HRS-PA, (c) HRS-PAS, (d) HRS-NAT, (f) HRS-HUNT, and (g) TUS.

a) **HRS-ALL**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Crop+Post+Mgd) p(E+S)	568.54	0.00	0.14	554.54	7
2	ψ (Crop+PAS+Post+Mgd) p(E+S)	568.71	0.17	0.13	552.71	8
3	ψ (AllPrey+Post+Mgd) p(E+S)	568.72	0.18	0.13	554.72	7
4	ψ (Crop+PAS+H+Post+Mgd) p(E+S)	569.41	0.87	0.09	551.41	9
5	ψ (AllPrey+H+Post+Mgd) p(E+S)	569.45	0.91	0.09	553.45	8
6	ψ (SecPrey+Post+Mgd) p(E+S)	569.50	0.96	0.09	555.50	7
7	ψ (SecPrey+H+Post+Mgd) p(E+S)	569.75	1.21	0.08	553.75	8
8	ψ (Crop+H+Post+Mgd) p(E+S)	569.83	1.29	0.08	553.83	8
9	ψ (Crop+R+Post+Mgd) p(E+S)	570.08	1.54	0.07	554.08	8
10	ψ (Crop+PAS+R+Post+Mgd) p(E+S)	570.17	1.63	0.06	552.17	9
11	ψ (Crop+C+Post+Mgd) p(E+S)	570.48	1.94	0.05	554.48	8

b) **HRS-PA**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Hum+H+Mgd) p(E+S)	541.92	0.00	0.10	527.92	7
2	ψ (PAS+H+Mgd) p(E+S)	542.08	0.16	0.09	528.08	7
3	ψ (Hum+H+Post+Mgd) p(E+S)	542.53	0.61	0.07	526.53	8
4	ψ (PAS+H+Post+Mgd) p(E+S)	542.63	0.71	0.07	526.63	8
5	ψ (Hum+H+C+Mgd) p(E+S)	542.93	1.00	0.06	526.93	8
6	ψ (Hum+Mgd) p(E+S)	543.06	1.14	0.05	531.06	6
7	ψ (Buff+Post+Mgd) p(E+S)	543.09	1.17	0.05	529.09	7
8	ψ (Hum+R+H+Mgd) p(E+S)	543.21	1.29	0.05	527.21	8
9	ψ (Hum+Post+Mgd) p(E+S)	543.21	1.29	0.05	529.21	7
10	ψ (PAS+Post+Mgd) p(E+S)	543.40	1.47	0.05	529.40	7
11	ψ (PAS+R+M+Mgd) p(E+S)	543.46	1.54	0.04	527.46	8
12	ψ (PAS+M+C+Mgd) p(E+S)	543.52	1.59	0.04	527.52	8
13	ψ (Hum) p(E+S)	543.55	1.63	0.04	533.55	5
14	ψ (PAS+Mgd) p(E+S)	543.56	1.64	0.04	531.56	6
15	ψ (Hum+R+Mgd) p(E+S)	543.68	1.76	0.04	529.68	7
16	ψ (Hum+M+C+Post+Mgd) p(E+S)	543.68	1.76	0.04	525.68	9
17	ψ (PAS) p(E+S)	543.79	1.86	0.04	533.79	5

18	ψ (Hum+R+M+C+Mgd) p(E+S)	543.89	1.97	0.04	525.89	9
19	ψ (Hum+Buff+M+Mgd) p(E+S)	543.90	1.98	0.04	527.90	8

c) **HRS-PAS**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (R+Post) p(S)	251.11	0.00	0.41	502.213	5
2	ψ (Post) p(S)	252.06	0.96	0.26	504.1266	4
3	ψ (Buff+Post) p(S)	252.31	1.20	0.12	504.6117	5
4	ψ (Zeb+Post) p(S)	252.67	1.57	0.11	505.3462	5
5	ψ (Post+Hum) p(S)	252.98	1.87	0.10	505.9617	5

d) **HRS-NAT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Buff) p(S)	181.56	0.00	0.65	173.56	4
2	ψ (Post) p(S)	182.83	1.27	0.35	174.83	4

e) **HRS-HUNT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (M+Mgd) p(E+S)	311.30	0.00	0.19	299.30	6
2	ψ (Mgd) p(E+S)	311.70	0.40	0.15	301.70	5
3	ψ (PAS+M+Mgd) p(E+S)	312.99	1.68	0.09	298.99	7
4	ψ (M+Post+Mgd) p(E+S)	313.05	1.74	0.08	299.05	7
5	ψ (Hum+M+Mgd) p(E+S)	313.14	1.84	0.07	299.14	7
6	ψ (SecPrey+M+Mgd) p(E+S)	313.19	1.88	0.07	299.19	7
7	ψ (AllPrey+M+Mgd) p(E+S)	313.20	1.89	0.07	299.20	7
8	ψ (R+M+Mgd) p(E+S)	313.21	1.90	0.07	299.21	7
9	ψ (Buff+M+Mgd) p(E+S)	313.23	1.92	0.07	299.23	7
10	ψ (Bound+M+Mgd) p(E+S)	313.25	1.95	0.07	299.25	7
11	ψ (M+C+Mgd) p(E+S)	313.30	2.00	0.07	299.30	7

f) **TUS**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ (Buff+R+Imp),θ_0, $\theta_{1,}$ p(S)	2070.75	0	0.23	2052.75	9
2	ψ (Buff+R+Sbl),θ_0, $\theta_{1,}$ p(S)	2071.16	0.41	0.15	2053.16	9
3	ψ (Buff+R+Sbl+Kud),θ_0, $\theta_{1,}$ p(S)	2071.42	0.67	0.12	2051.42	10
4	ψ (Buff+R+Imp+Kud),θ_0, $\theta_{1,}$ p(S)	2071.99	1.24	0.11	2051.99	10
5	ψ (Buff+R+Kud),θ_0, $\theta_{1,}$ p(S)	2072.11	1.36	0.1	2054.11	9
6	ψ (Buff+R+Post+Kud),θ_0, $\theta_{1,}$ p(S)	2072.25	1.5	0.09	2052.25	10
7	ψ (Buff+R),θ_0, $\theta_{1,}$ p(S)	2072.6	1.85	0.07	2056.6	8
8	ψ (Buff+R+Imp+Post),θ_0, $\theta_{1,}$ p(S)	2072.63	1.88	0.06	2052.63	10
9	ψ (Buff+R+Imp+Bound),θ_0, $\theta_{1,}$ p(S)	2072.63	1.88	0.04	2052.63	10
10	ψ (Buff+R+Imp+Hum),θ_0, $\theta_{1,}$ p(S)	2072.73	1.98	0.03	2052.73	10

Covariate key: Conversion of habitat to agriculture (Crop); mean prey site use (AllPrey); mean prey site use of secondary prey (SecPrey); buffalo site use (Buff); zebra site use (Zeb); kudu site use (Kud); impala site use (Imp); roan & sable site use (Sbl); availability of riparian habitat (R); distance to ranger post (Post); distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site actively hunted (Mgd). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Leopard

Table S3.12. Results of model ranking for leopard site use at the different sampling grids, based on AICc values (AIC at the temporary use selection (TUS) scale). Final set based on models with ΔAICc/ΔAIC < 2 for (a) HRS-ALL, (b) HRS-PA, (c) HRS-HUNT, and (d) TUS.

a) **HRS-ALL**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (DistV+C) p(E+S)	679.27	0.00	0.13	667.27	6
2	ψ (DistV+C+Post+Hnt) p(E+S)	679.49	0.23	0.11	663.49	8
3	ψ (DistV+Post+Hnt) p(E+S)	679.72	0.46	0.10	665.72	7
4	ψ (DistV+C+Hnt) p(E+S)	679.73	0.46	0.10	665.73	7
5	ψ (DistV+R+Post+Hnt) p(E+S)	680.21	0.94	0.08	664.21	8
6	ψ (Crop+H+Hnt) p(E+S)	680.23	0.97	0.08	666.23	7
7	ψ (AllPrey+C) p(E+S)	680.27	1.00	0.07	668.27	6
8	ψ (Crop+Hnt) p(E+S)	680.50	1.24	0.07	668.50	6
9	ψ (Crop+H+Post+Hnt) p(E+S)	680.82	1.56	0.06	664.82	8
10	ψ (DistV+C+Post) p(E+S)	680.84	1.57	0.05	666.84	7
11	ψ (DistV+R+C+Post+Hnt) p(E+S)	681.10	1.84	0.05	663.10	9
12	ψ (V+R+C) p(E+S)	681.17	1.90	0.05	667.17	7
13	ψ (Crop+Post+Hnt) p(E+S)	681.18	1.92	0.04	667.19	7

b) **HRS-PA**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (PAS+Mgd) p(E+S)	635.25	0.00	0.31	623.25	6
2	ψ (PAS+R+Mgd) p(E+S)	636.11	0.85	0.20	622.11	7
3	ψ (PAS+H+Mgd) p(E+S)	636.90	1.64	0.14	622.90	7
4	ψ (PAS+Imp+Mgd) p(E+S)	637.10	1.84	0.12	623.10	7
5	ψ (PAS+C+Mgd) p(E+S)	637.18	1.93	0.12	623.18	7
6	ψ (PAS+Post+Mgd) p(E+S)	637.23	1.98	0.11	623.23	7

c) **HRS-HUNT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Hum+Post+Mgd) p(E+S)	390.99	0.00	0.13	376.99	7
2	ψ (Imp+Mgd) p(E+S)	391.35	0.36	0.11	379.35	6
3	ψ (PAS+Imp+Mgd) p(E+S)	391.50	0.51	0.10	377.50	7
4	ψ (Hum+Imp+Mgd) p(E+S)	391.55	0.57	0.10	377.55	7
5	ψ (Hum+Post) p(E+S)	391.63	0.64	0.09	379.63	6
6	ψ (PAS+Post+Mgd) p(E+S)	391.96	0.97	0.08	377.96	7
7	ψ (Bound+Imp+Mgd) p(E+S)	392.30	1.31	0.07	378.30	7
8	ψ (R+Imp+Mgd) p(E+S)	392.43	1.44	0.06	378.43	7
9	ψ (Post+Mgd) p(E+S)	392.51	1.52	0.06	380.51	6
10	ψ (Mgd) p(E+S)	392.76	1.77	0.05	382.76	5
11	ψ (Hum+R+Post) p(E+S)	392.81	1.82	0.05	378.81	7
12	ψ (PAS+Mgd) p(E+S)	392.87	1.88	0.05	380.87	6
13	ψ (Hum+M+Post) p(E+S)	392.92	1.93	0.05	378.92	7

d) **TUS**

	Model	AIC	ΔAIC	W_i	-2*Log	nPars
1	ψ (Kud+C+Bound),θ_0, θ_1, p(S)	2916.84	0.00	0.11	2898.84	9
2	ψ (C+Bound),θ_0, θ_1, p(S)	2917.17	0.33	0.09	2901.17	8

3	ψ (C+Bound+Post),θ_0, $\theta_{1,}$ p(S)	2917.61	0.77	0.08	2899.61	9
4	ψ (Kud+Imp+Bound),θ_0, $\theta_{1,}$ p(S)	2917.62	0.78	0.08	2899.62	9
5	ψ (Kud+C+Bound+Post),θ_0, $\theta_{1,}$ p(S)	2918.01	1.17	0.06	2898.01	10
6	ψ (Bound),θ_0, $\theta_{1,}$ p(S)	2918.05	1.21	0.06	2904.05	7
7	ψ (AllPrey+Imp+Bound),θ_0, $\theta_{1,}$ p(S)	2918.09	1.25	0.06	2900.09	9
8	ψ (Kud+R+C+Bound),θ_0, $\theta_{1,}$ p(S)	2918.12	1.28	0.06	2898.12	10
9	ψ (AllPrey+C+Bound),θ_0, $\theta_{1,}$ p(S)	2918.16	1.32	0.06	2900.16	9
10	ψ (Imp+Bound),θ_0, $\theta_{1,}$ p(S)	2918.22	1.38	0.06	2902.22	8
11	ψ (AllPrey+C+Bound+Post),θ_0, $\theta_{1,}$ p(S)	2918.27	1.43	0.05	2898.27	10
12	ψ (Bound+Post),θ_0, $\theta_{1,}$ p(S)	2918.34	1.50	0.05	2902.34	8
13	ψ (R+C+Bound),θ_0, $\theta_{1,}$ p(S)	2918.55	1.71	0.05	2900.55	9
14	ψ (Kud+Bound),θ_0, $\theta_{1,}$ p(S)	2918.66	1.82	0.04	2902.66	8
15	ψ (AllPrey+Kud+C+Bound),θ_0, $\theta_{1,}$ p(S)	2918.70	1.86	0.04	2898.70	10
16	ψ (AllPrey+Kud+Imp+Bound),θ_0, $\theta_{1,}$ p(S)),θ_0, $\theta_{1,}$ p(S)	2918.82	1.98	0.04	2898.82	10

Covariate key: Conversion of habitat to agriculture (Crop); distance to village (DistV); mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); availability of riparian habitat (R); distance to ranger post (Post); distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting area (Hnt); site actively hunted (Mgd)

Cheetah

Table S3.13. Results of model ranking for cheetah site use at the different sampling grids, based on AICc values (AIC at the temporary use selection (TUS) scale). Final set based on models with ΔAICc/ΔAIC < 2 for (a) HRS-ALL, (b) HRS-PA, (c) HRS-PAS, (d) HRS-NAT, (f) HRS-HUNT, and (g) TUS.

a) **HRS-ALL**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (DistV) p(E)	119.34	0.00	0.23	111.34	4
2	ψ (DistV+Hnt) p(E)	120.63	1.29	0.12	110.63	5
3	ψ (DistV+C) p(E)	120.85	1.51	0.11	110.85	5
4	ψ (DistV+Riv) p(E)	120.95	1.61	0.10	110.95	5
5	ψ (DistV+Imp) p(E)	121.11	1.77	0.09	111.11	5
6	ψ (DistV+M) p(E)	121.13	1.78	0.09	111.13	5
7	ψ (DistV+Post) p(E)	121.16	1.81	0.09	111.16	5
8	ψ (DistV+Mgd) p(E)	121.24	1.90	0.09	111.24	5
9	ψ (DistV+R) p(E)	121.28	1.94	0.09	111.28	5

b) **HRS-PA**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (.) p(E+S)	106.96	0.00	0.14	100.96	3
2	ψ (Hum) p(E+S)	107.33	0.37	0.12	99.33	4
3	ψ (PAS) p(E+S)	107.61	0.65	0.10	99.61	4
4	ψ (Riv) p(E+S)	107.68	0.72	0.10	99.68	4
5	ψ (C) p(E+S)	107.88	0.92	0.09	99.88	4
6	ψ (AllPrey) p(E+S)	108.10	1.14	0.08	100.10	4
7	ψ (Post) p(E+S)	108.35	1.39	0.07	100.35	4
8	ψ (Imp) p(E+S)	108.45	1.49	0.07	100.45	4
9	ψ (Hnt) p(E+S)	108.73	1.77	0.06	100.73	4
10	ψ (Mgd) p(E+S)	108.76	1.80	0.06	100.76	4
11	ψ (M) p(E+S)	108.88	1.92	0.05	100.88	4
12	ψ (R) p(E+S)	108.92	1.96	0.05	100.92	4

c) **HRS-PAS**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Imp) p(.)	56.03	0.00	0.20	50.03	3
2	ψ (C) p(.)	56.10	0.07	0.19	50.10	3
3	ψ (.) p(.)	56.46	0.43	0.16	52.46	2
4	ψ (Riv) p(.)	57.17	1.14	0.11	51.17	3
5	ψ (Hnt) p(.)	57.41	1.38	0.10	51.41	3
6	ψ (Hum) p(.)	57.64	1.61	0.09	51.64	3
7	ψ (H) p(.)	57.78	1.75	0.08	51.78	3
8	ψ (Sbl) p(.)	57.97	1.94	0.07	51.97	3

d) **HRS-NAT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (C) p(E)	45.21	0.00	0.14	39.21	3
2	ψ (R) p(E)	45.26	0.05	0.14	39.26	3
3	ψ (Imp) p(E)	45.28	0.07	0.14	39.28	3
4	ψ (Riv) p(E)	45.37	0.16	0.13	39.37	3
5	ψ (.) p(E)	45.43	0.22	0.13	41.43	2

6	ψ (M) p(E)	46.00	0.79	0.10	40.00	3
7	ψ (Hum) p(E)	46.14	0.93	0.09	40.14	3
8	ψ (Sbl) p(E)	46.38	1.17	0.08	40.38	3
9	ψ (Bound) p(E)	47.17	1.96	0.05	41.17	3

e) **TUS**

	Model	**AIC**	**ΔAIC**	**W_i**	**-2*Log**	**nPars**
1	ψ (.) p(.)	143.14	0	0.18	139.14	2
2	ψ (R) p(.)	143.4	0.26	0.16	137.40	3
3	ψ (Bound) p(.)	144.52	1.38	0.09	138.52	3
4	ψ (AllPrey) p(.)	144.92	1.78	0.08	138.92	3
5	ψ (Post) p(.)	144.93	1.79	0.08	138.93	3
6	ψ (Sbl) p(.)	145.02	1.88	0.07	139.02	3
7	ψ (Riv) p(.)	145.09	1.95	0.07	139.09	3
8	ψ (Imp) p(.)	145.1	1.96	0.07	139.10	3
9	ψ (C) p(.)	145.13	1.99	0.07	139.13	3
10	ψ (Kud) p(.)	145.14	2.00	0.07	139.14	3
11	ψ (Hum) p(.)	145.14	2.00	0.06	139.14	3

Covariate key: Distance to village (DistV); mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); roan & sable site use (Sbl); availability of riparian habitat (R); distance to ranger post (Post); distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting area (Hnt); site actively hunted (Mgd); distance to large river (Riv). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

African Wild Dog

Table S3.14. Results of model ranking for wild dog site use at the different sampling grids, based on AICc values (AIC at the temporary use selection (TUS) scale). Final set based on models with ΔAICc/ΔAIC < 2 for (a) HRS-ALL, (b) HRS-PA, (c) HRS-PAS, (d) HRS-NAT, (f) HRS-HUNT, and (g) TUS.

g) **HRS-ALL**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (AllPrey+Riv) p(E+S)	250.80	0.00	1.00	238.80	6

h) **HR_PA**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (AllPrey+Riv) p(E+S)	250.66	0.00	1.00	238.66	6

i) **HRS-PAS**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (Post+Riv) p(E)	138.53	0.00	0.23	128.53	5
2	ψ (Riv) p(E)	138.70	0.17	0.21	130.70	4
3	ψ (R+Riv) p(E)	139.01	0.48	0.18	129.01	5
4	ψ (Imp+Post) p(E)	139.92	1.39	0.11	129.92	5
5	ψ (C+Post) p(E)	140.35	1.82	0.09	130.35	5
6	ψ (AllPrey+Riv) p(E)	140.41	1.88	0.09	130.41	5
7	ψ (Hnt+Riv) p(E)	140.41	1.88	0.09	130.41	5

j) **HRS-NAT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (R) p(S)	69.57	0.00	0.59	59.87	4
2	ψ (Riv) p(S)	70.33	0.76	0.41	60.33	4

k) **HRS-HUNT**

	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ (AllPrey+Riv) p(S)	161.08	0.00	0.48	153.08	4
2	ψ (AllPrey+M) p(S)	162.10	1.02	0.29	154.10	4
3	ψ (AllPrey) p(S)	162.51	1.42	0.23	156.51	3

l) **TUS**

	Model	AIC	ΔAIC	W_i	-2*Log	K
1	ψ (C+Kud+Bound), θ_0, θ_1, p(S)	2468.83	0.00	0.36	456.83	6
2	ψ (Kud+Bound) p(.), θ_0, θ_1, p(S)	2469.70	0.87	0.24	457.70	6
3	ψ (Kud+Imp) p(.), θ_0, θ_1, p(S)	2469.71	0.88	0.23	459.71	5
4	ψ (R+Kud+Bound), θ_0, θ_1, p(S)	2470.32	1.48	0.17	458.32	6

Covariate key: Mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); availability of riparian habitat (R); distance to ranger post (Post); distance to PA boundary (Bound); probability of illegal human activity (Hum); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); regular on-the-ground law enforcement (PAS); forest and bush cover (C); site in hunting area (Hnt); distance to large river (Riv). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

Spotted Hyaena

Table S3.15. Results of model ranking for spotted hyaena site use at the different sampling grids, based on AICc values (AIC at the temporary use selection (TUS) scale). Final set based on models with ΔAICc/ΔAIC < 2 for (a) HRS-ALL, and (b) TUS.

f) **HRS-ALL**

	Model	AICc	ΔAICc	W_i	-2*Log	K
1	ψ (AllPrey+R+Post) p(E+S)	495.94	0.00	0.22	481.94	7
2	ψ (AllPrey+R) p(E+S)	496.05	0.10	0.21	484.05	6
3	ψ (AllPrey+C) p(E+S)	497.11	1.16	0.12	485.11	6
4	ψ (AllPrey+Post) p(E+S)	497.46	1.51	0.10	485.46	6
5	ψ (AllPrey+C+Post) p(E+S)	497.64	1.70	0.09	483.64	7
7	ψ (AllPrey+R+C) p(E+S)	497.78	1.84	0.08	483.78	7
8	ψ (AllPrey+R+H+Post) p(E+S)	497.81	1.87	0.086	481.81	8
9	ψ (AllPrey+R+C+Post) p(E+S)	497.92	1.98	0.081	481.92	8

g) **TUS**

	Model	AIC	ΔAIC	W_i	-2*Log	K
1	ψ (Buff+Sbl), θ_0, θ_1, p(S)	5264.58	0.00	0.36	5248.58	8
2	ψ (Buff+Sbl+Hum) p(.), θ_0, θ_1, p(S)	5265.90	1.32	0.18	5247.90	9
3	ψ (Buff+R+Sbl) p(.), θ_0, θ_1, p(S)	5266.08	1.50	0.17	5248.08	9
4	ψ (Buff+Sbl+Kud) p(.), θ_0, θ_1, p(S)	5266.25	1.67	0.15	5248.25	9
5	ψ (Buff+C+Sbl), θ_0, θ_1, p(S)	5266.48	1.90	0.14	5248.48	9
6	ψ (Buff+Sbl), θ_0, θ_1, p(S)	5264.58	0.00	0.36	5248.58	8

Covariate key: Mean prey site use (AllPrey); kudu site use (Kud); impala site use (Imp); buffalo site use (Buff); kudu site use (Kud); roan & sable roan site use (Sbl); availability of riparian habitat (R); distance to ranger post (Post); probability of illegal human activity (Hum); primary habitat (H; positive, miombo woodland; negative, *Acacia-Commiphora* grasslands & bushlands); forest and bush cover (C). AICc = Akaike Information Criterion, adjusted for small sample sizes; ΔAICc = Difference between model AICc and that of model with the lowest AICc; Wi = relative model weight; nPars = number of parameters in the model; −2 log = twice the negative likelihood; (.) signifies constant parameter

APPENDIX 3.8 – GOODNESS OF FIT TESTS

Goodness of fit was assessed for the highest ranked and most parameterised model with strong support (ΔAICc < 2). If more than one model contained the same number of parameters, goodness of fit was assessed for the highest ranked of these.

Prey Species

HRS scale

There was no evidence of lack of fit (p-value > 0.05) for any species, but there was some evidence of overdispersion (c-hat > 1.5) for buffalo, zebra, giraffe, and sable. As a result, where presented (e.g. Table 3.15) standard errors were adjusted accordingly.

Table S3.16. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each prey species at the HRS scale.

Species	Model	Model details	p-value	$\hat{c}$
Buffalo	Top	ψ(PA+W) p(E)	0.17	1.41
	Param.	ψ(PA+W+PAS) p(E)	0.15	1.51
Zebra	Top & Param.	ψ(PA+PAS+NDVIstd) p(.)	0.11	1.93
Giraffe	Top	ψ(PA) p(E)	0.10	1.95
	Param.	ψ(PA+W+NDVIstd) p(E)	0.09	1.87
Sable	Top & Param.	ψ(PA+M+NDVIstd) p(S)	0.12	1.70
Kudu	Top	ψ(Crop) p(E+S)	0.39	1.05
	Param.	ψ(Crop+NDVIstd+DistV) p(E+S)	0.35	1.17
Impala	Top & Param.	ψ(Crop+W+C) p(S)	0.44	1.09

TUS scale

There was no evidence of lack of fit (p-value > 0.05) or overdispersion (c-hat > 1.5) for any of the species, with the exception of kudu, for which standard errors were adjusted as a result when presented.

Table S3.17. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each prey species at the TUS scale.

Species	Model	Model details	p-value	$\hat{c}$
Buffalo	Top & Param.	Ψ,th0(PA+PAS+W+H+C+NDVIstd),th1(),p(S),th0pi()	0.19	1.17
Zebra	Top & Param.	Ψ,th0(PA+PAS+W+H+C+NDVIstd),th1(),p(S),th0pi()	0.43	0.99
Giraffe	Top	Ψ,th0(PA+PAS+CGE),th1(),p(S),th0pi()	0.39	0.99
	Param.	Ψ,th0(PA+PAS+CGE+M),th1(),p(S),th0pi()	0.54	0.90
Sable	Top	Ψ,th0(PA+PAS+H+C+NDVIstd),th1(),p(S),th0pi()	0.35	1.10
	Param	Ψ,th0(PA+PAS+H+C+NDVIstd+W),th1(),p(S),th0pi()	0.44	1.01
Kudu	Top & Param.	Ψ,th0(PA+PAS+Crop+W+H+C+NDVIstd),th1(),p(S),th0pi()	0.05	1.97
Impala	Top	Ψ,th0(PA+Crop+W+H+C+NDVIstd),th1(),p(.),th0pi()	0.35	0.97
	Param	Ψ,th0(PA+PAS+Crop+W+H+C+NDVIstd),th1(),p(.),th0pi()	0.31	1.04

Illegal Human Activity

HRS scale

There was no evidence of lack of fit (p-value > 0.05) or overdispersion (c-hat > 1.5).

Table S3.18. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each prey species at the HRS scale.

Model	Model details	p-value	$\hat{c}$
Top	ψ(Bound+PAS+C+Post) p(.)	0.74	0.81
Param.	ψ(Bound+PAS+W+C+Post) p(.)	0.54	0.85

TUS scale

There was no evidence of lack of fit (p-value > 0.05) or overdispersion (c-hat > 1.5).

Table S3.19. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each prey species at the HRS scale.

Model	Model details	p-value	$\hat{c}$
Top & Param.	Ψ,th0(Bound+PAS+Post+W+C+Prey),th1(),p(.),th0pi()	0.19	1.28

Large Carnivores

HRS-ALL

There was no evidence of lack of fit (p-value > 0.05) or overdispersion (c-hat > 1.5), except for spotted hyaena, for which standard errors were therefore adjusted accordingly when presented (e.g. Table 3.21).

Table S3.20. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the HRS-ALL grid

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top	ψ(Crop+Post+HrdW) p(E+S)	0.56	0.92
	Param.	ψ(Crop+PAS+H+Post+Mgd) p(E+S)	0.53	0.87
Leopard	Top	Ψ(V+C) p(E+S)	0.59	0.91
	Param.	Ψ(V+R+C+Post+Hnt) p(E+S)	0.54	0.91
Cheetah	Top	Ψ(V) p(E)	0.49	0.42
	Param.	Ψ(V+Hnt) p(E)	0.55	0.44
Wild dog	Top & Param.	Ψ(AllPrey+Riv) p(E+S)	0.31	1.05
Spotted hyaena	Top	Ψ(AllPrey+R+Post) p(E+S)	0.05	2.42
	Param	Ψ(AllPrey+R+H+Post) p(E+S)	0.05	2.35

HRS-PA

For all species, at this scale, there was no evidence of lack of fit or overdispersion.

Table S3.21. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the HRS-PA grid

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top	ψ(Hum+H+Mgd) p(E+S)	0.14	1.31
	Param.	ψ(Hum+H+C+Post+Mgd) p(E+S)	0.60	0.89
Leopard	Top	Ψ(Hum+Mgd) p(E+S)	0.35	1.08
	Param.	Ψ(PAS+R+Mgd) p(E+S)	0.56	0.90
Cheetah	Top	Ψ(.) p(E)	0.40	0.22
	Param.	Ψ(Hum) p(E)	0.14	1.23
Wild dog	Top & Param.	Ψ(AllPrey+Riv) p(E+S)	0.65	0.68

HRS-PAS

For all species, at this scale, there was no evidence of lack of fit or overdispersion.

Table S3.22. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the HRS-PAS grid.

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top & Param.	ψ(R+Post) p(S)	0.52	0.95
Cheetah	Top & Param	ψ(Imp) p(.)	0.42	0.68
Wild dog	Top & Param	ψ(Post+Riv) p(E)	0.57	0.74

HRS-NAT

For all species, at this scale, there was no evidence of lack of fit or overdispersion.

Table S3.23. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the HR-NAT grid.

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top & Param.	ψ(Buff) p(S)	0.36	1.08
Cheetah	Top & Param.	ψ(C) p(.)	0.51	0.55
Wild dog	Top & Param.	ψ(R) p(S)	0.93	0.35

HRS-HUNT

For all species, at this scale, there was no evidence of lack of fit or overdispersion.

Table S3.24. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the HRS-HUNT grid.

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top	ψ(M+Mgd) p(E+S)	0.75	0.79
	Param.	ψ(PAS+M+Mgd) p(E+S)	0.74	0.79
Leopard	Top & Param.	ψ(Hum+Post+Mgd) p(.)	0.38	1.05
Wild dog	Top & Param.	ψ(AllPrey+Riv) p(.)	0.47	0.91

TUS

For all species, at this scale, there was no evidence of lack of fit or overdispersion.

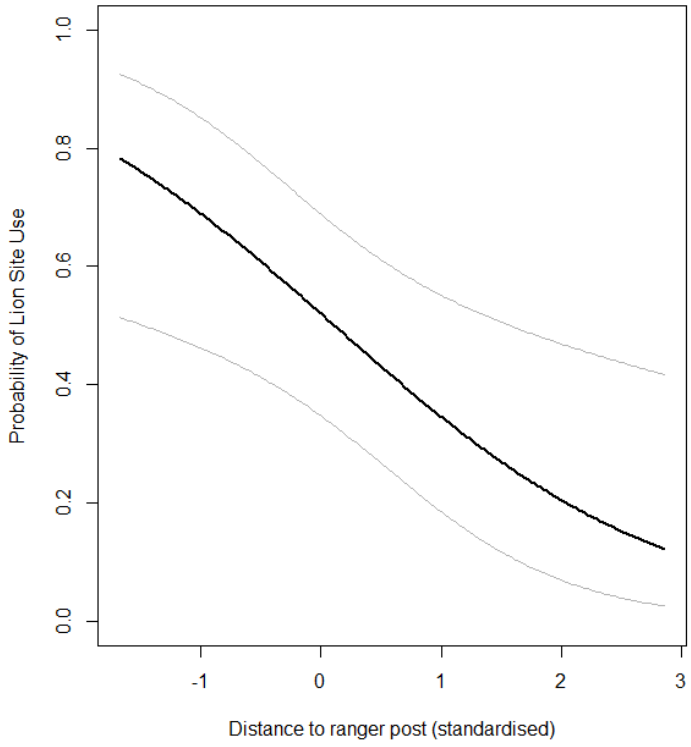
Table S3.25. Goodness of fit for the top and most-parameterised (Param.) model in the final model set for each large carnivores in the TUS analysis.

Species	Model	Model details	p-value	$\hat{c}$
Lion	Top	Ψ(Buff+R+Imp),θ_0, θ_1, p(S)	0.42	1.07
	Param.	Ψ(Buff+R+Post+Kud),θ_0, θ_1, p(S)	0.37	1.05
Leopard	Top	Ψ(Kud+C+Bound),θ_0, θ_1, p(S)	0.34	1.12
	Param.	Ψ(Kud+C+Bound+Post),θ_0, θ_1, p(S)	0.39	1.08
Cheetah	Top	Ψ(.), p(.)	0.70	0.18
	Param.	Ψ(R), p(.)	0.66	0.31
Wild Dog	Top & Param.	Ψ(C+Kud+Bound),θ_0, θ_1, p(S)	0.07	1.48
Spotted hyaena	Top	Ψ(Buff+Sbl),θ_0, θ_1, p(S)	0.36	1.03
	Param.	Ψ(Buff+R+Imp+Hum),θ_0, θ_1, p(S)	0.40	1.04

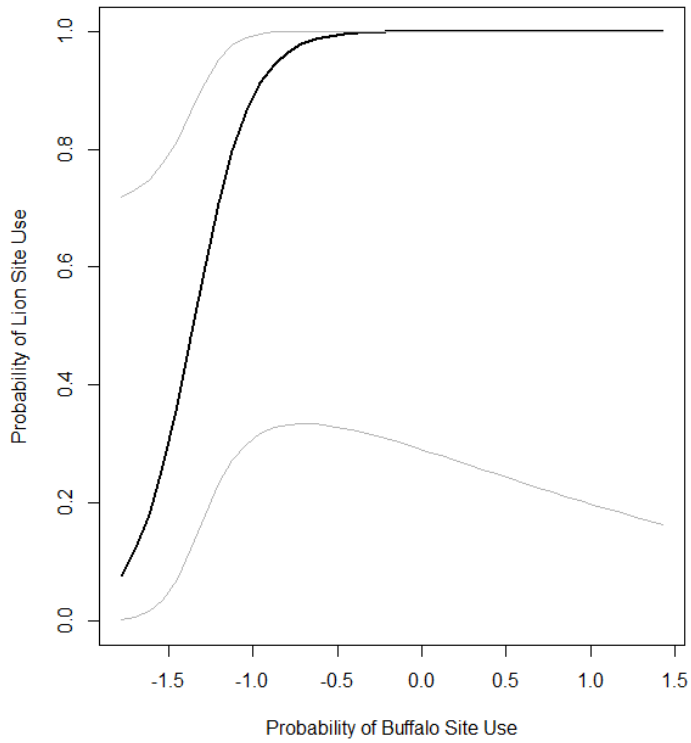
APPENDIX 3.9 – ADDITIONAL SIGNIFICANT COVARIATE EFFECTS GRAPHS

Below are presented graphs of continuous covariates with significant effects that were not included in main body. Plots were produced using the top ranked model containing the covariate based on AICs rankings. All other covariates in the model were held at their mean value. 95% confidence intervals are included. Plots are included of all covariate relationships with robust effects present in the final model set and not in the main text. Only plots from home range selection (HRS) scale analyses included, due to TUS scale analyses being implemented in PRESENCE.

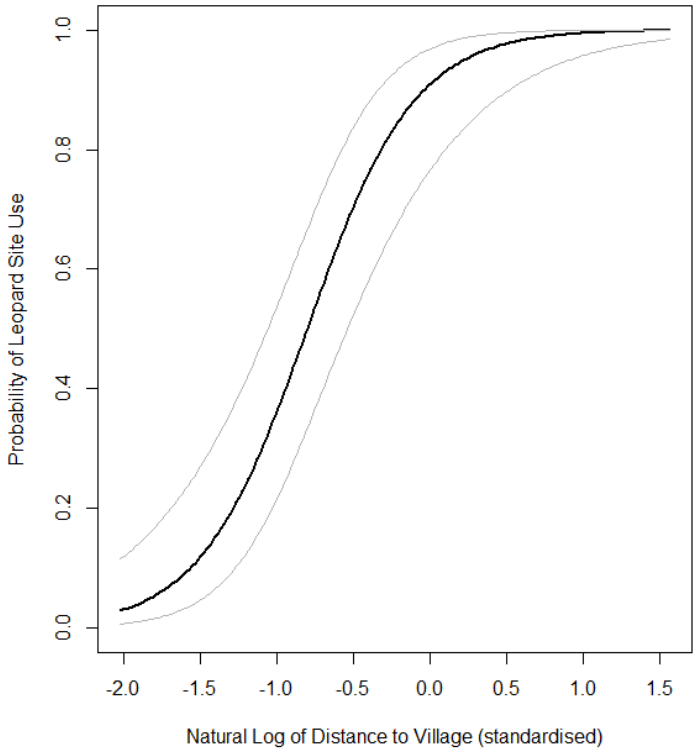
Lion, HRS-ALL – Distance to Ranger Post



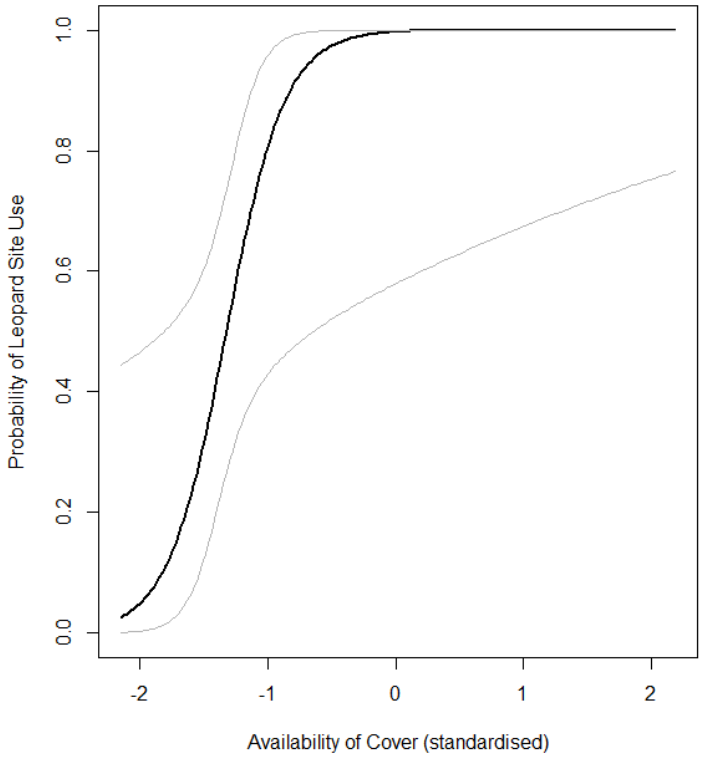
Lion, HRS-NAT – Probability of buffalo site use



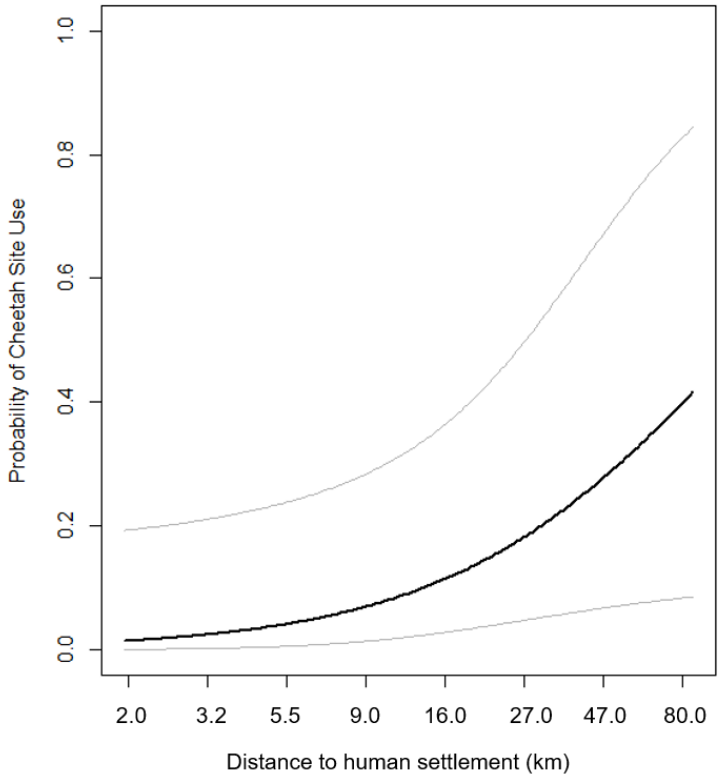
Leopard, HRS-ALL – Distance to Village (Ln)



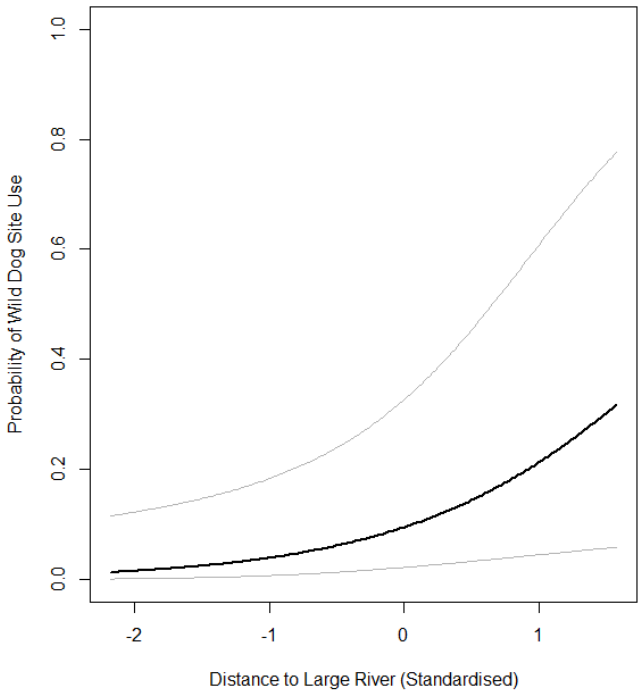
Leopard, HRS-ALL – Availability of cover



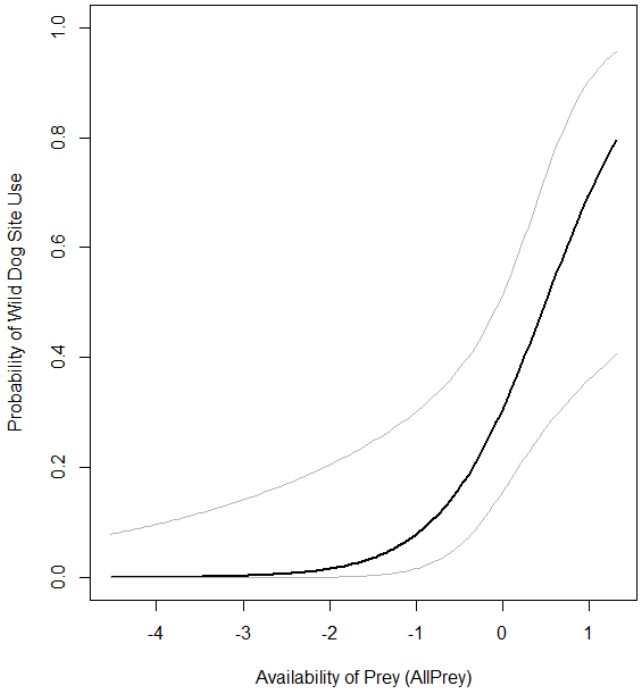
Cheetah, HRS-ALL – Distance to human settlement



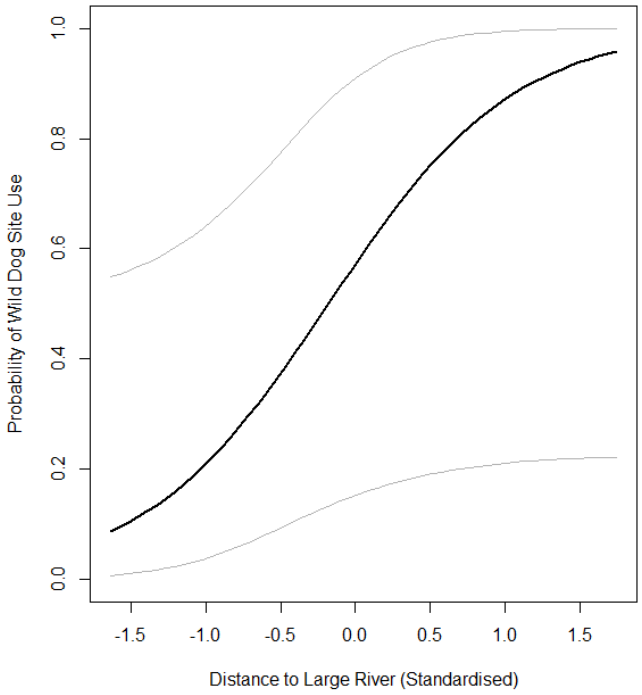
African Wild Dog, HRS-ALL – Distance to Large River



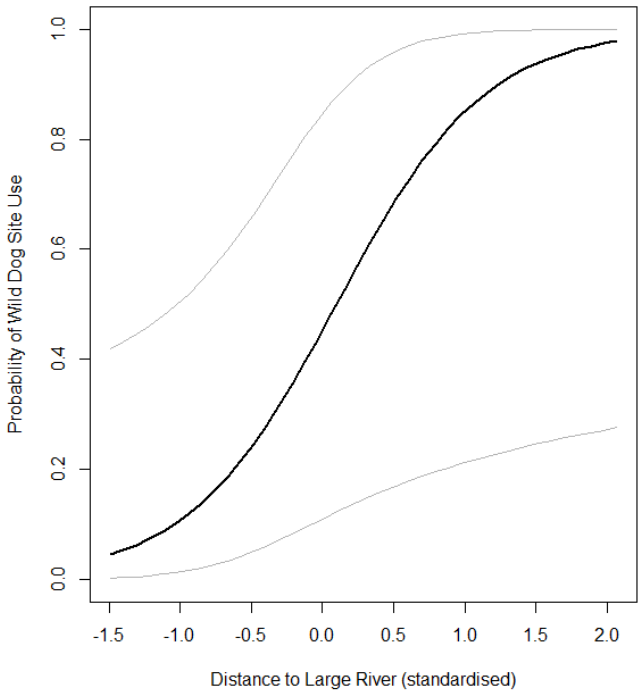
African Wild Dog, HRS-PA – Availability of Prey (AllPrey)



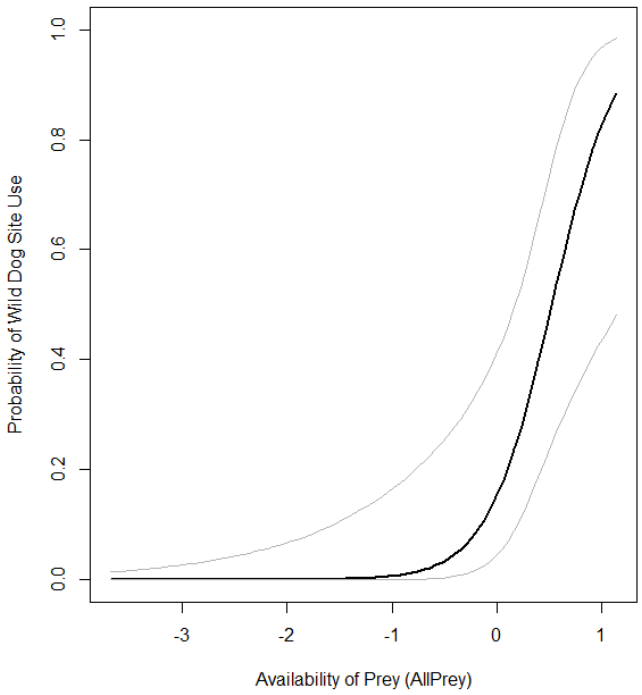
African Wild Dog, HRS-PAS – Distance to Large River



African Wild Dog, HRS-NAT – Distance to Large River



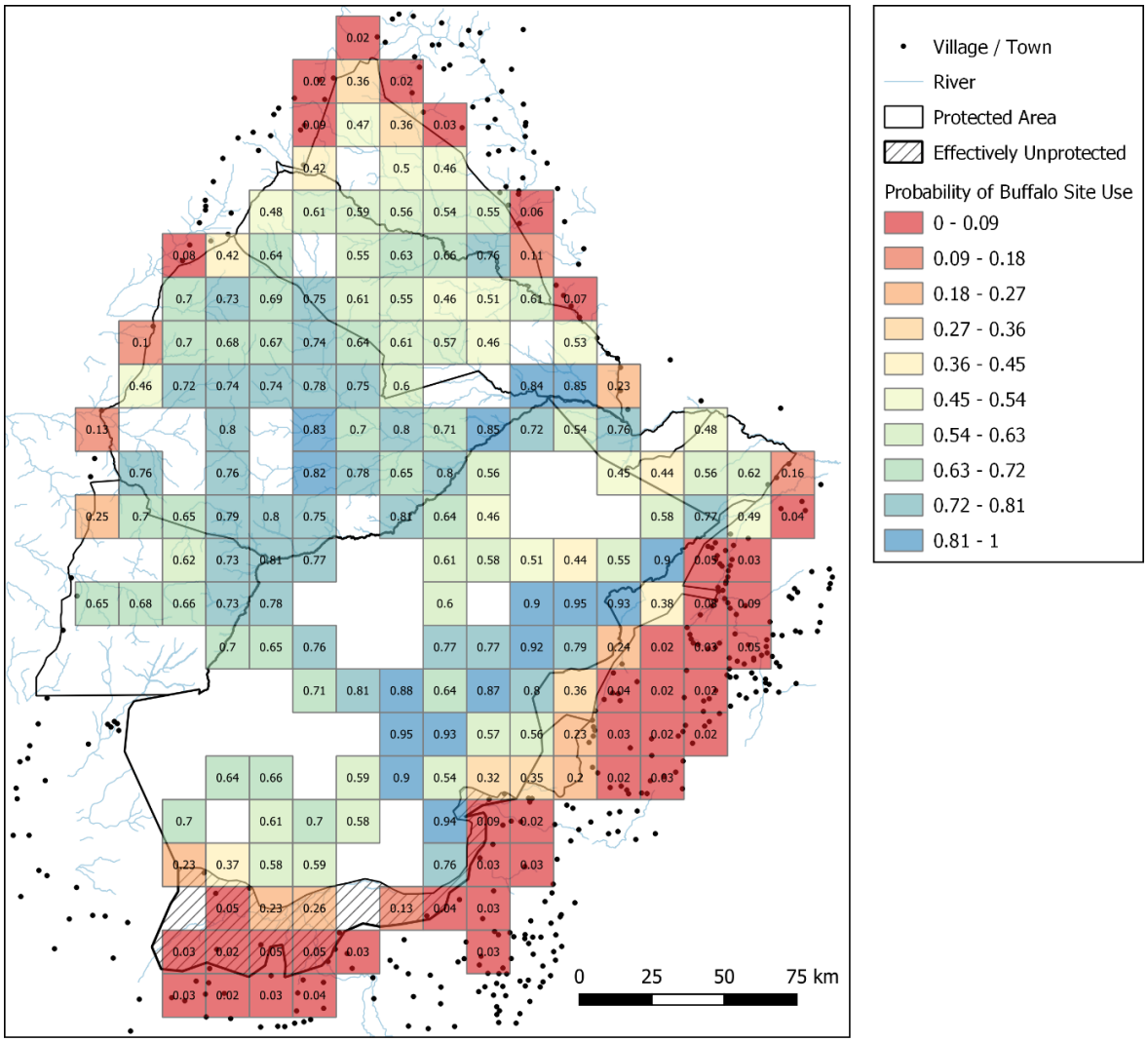
African Wild Dog, HRS-HUNT – Availability of Prey (AllPrey)



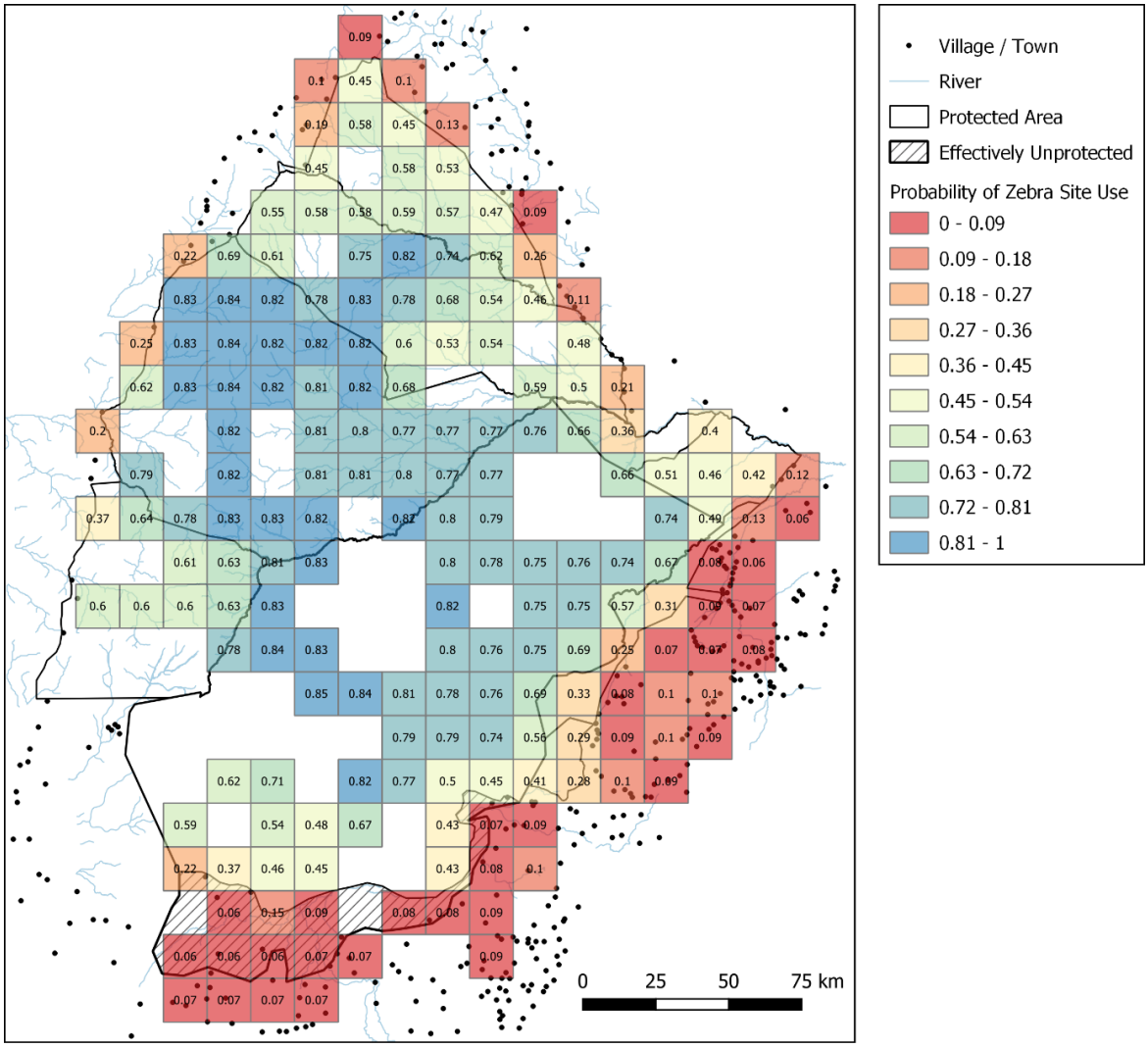
APPENDIX 3.10 – SITE USE MAPS & LARGE CARNIVORE DETECTIONS

The site use estimates presented below were obtained through model-averaging of models with strong support (AIC/AICc<2), as detailed in the methodology, from HRS-ALL analyses.

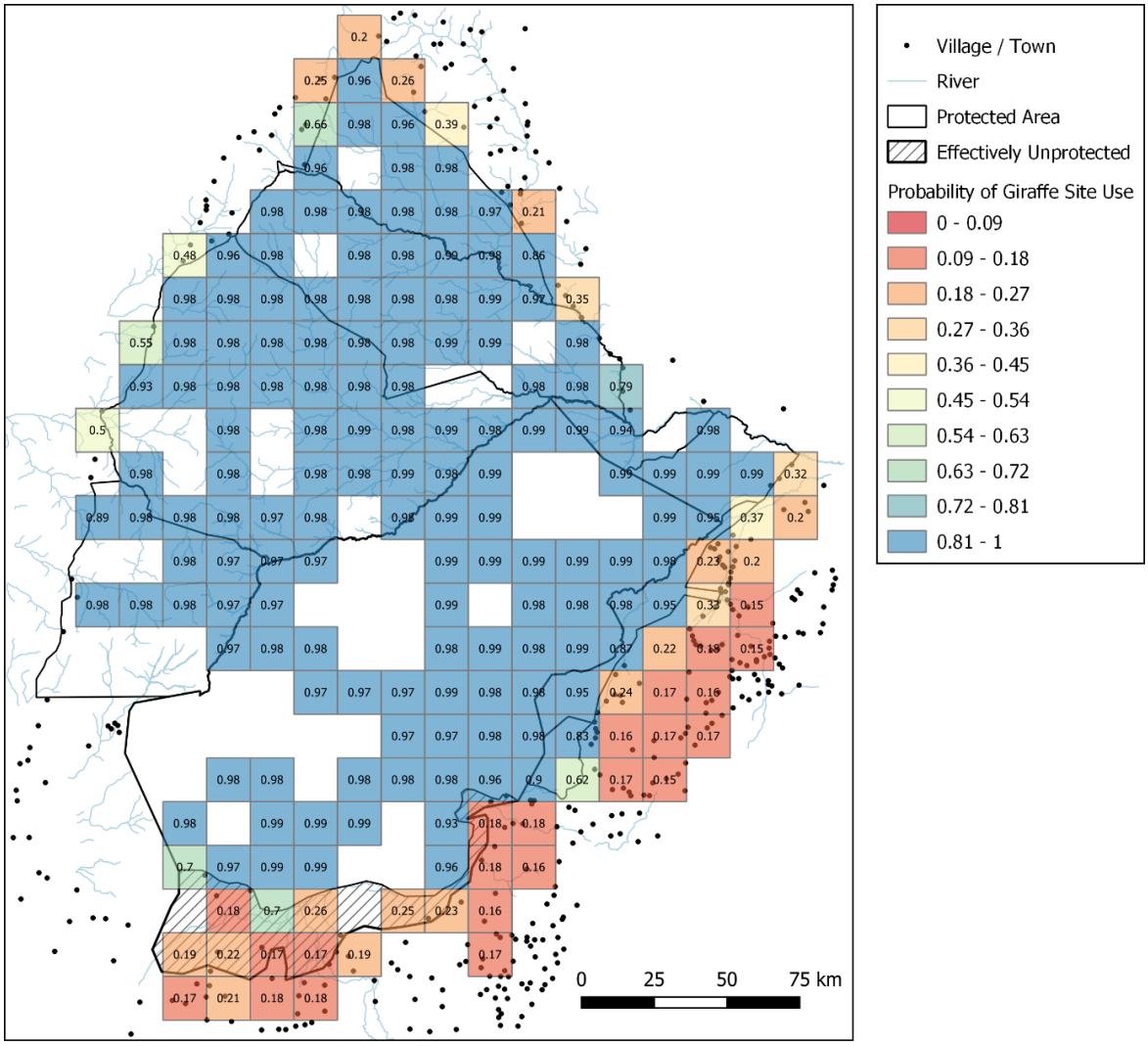
Buffalo



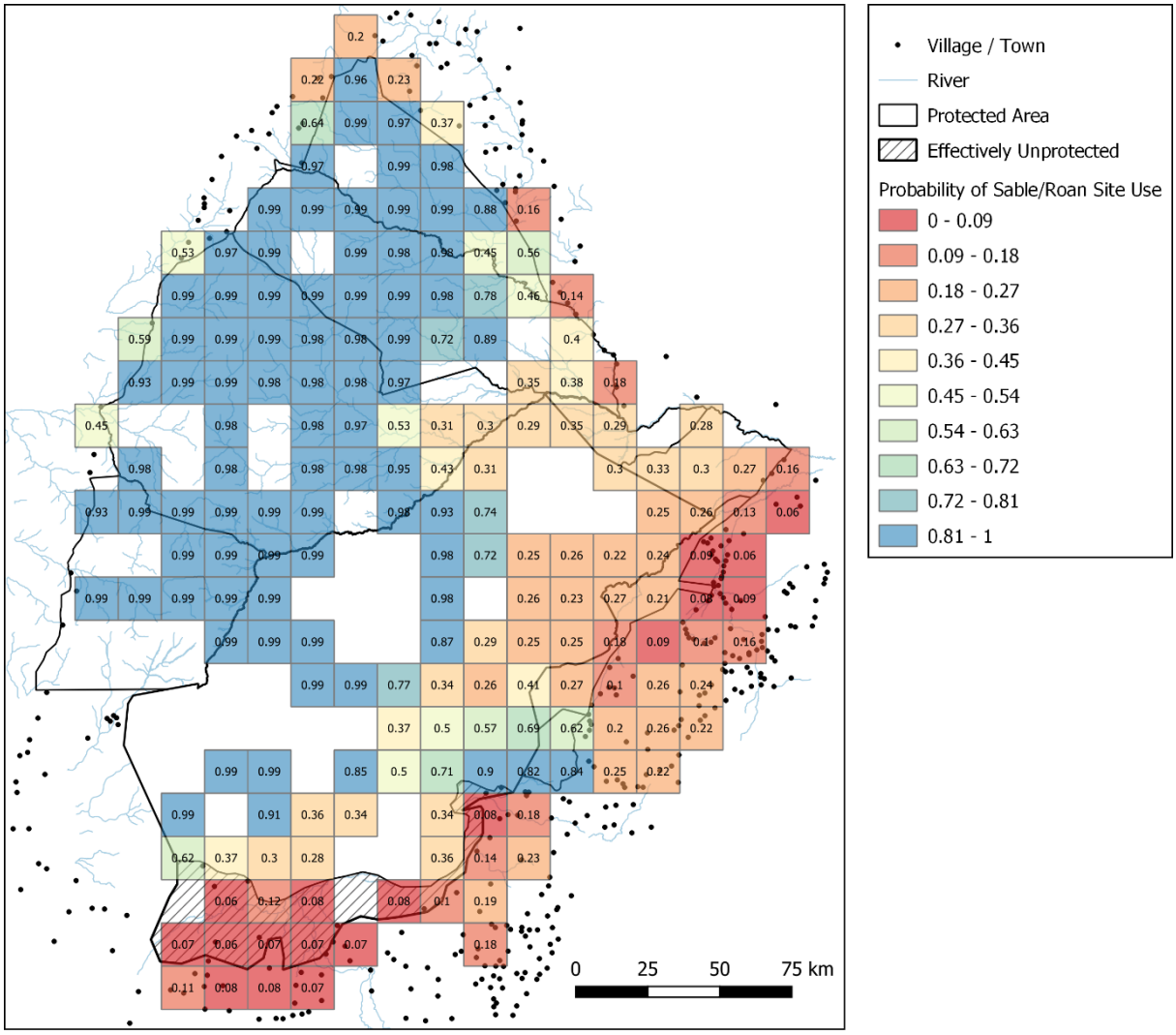
Zebra


Village / Town
River
Protected Area
Effectively Unprotected
Probability of Zebra Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

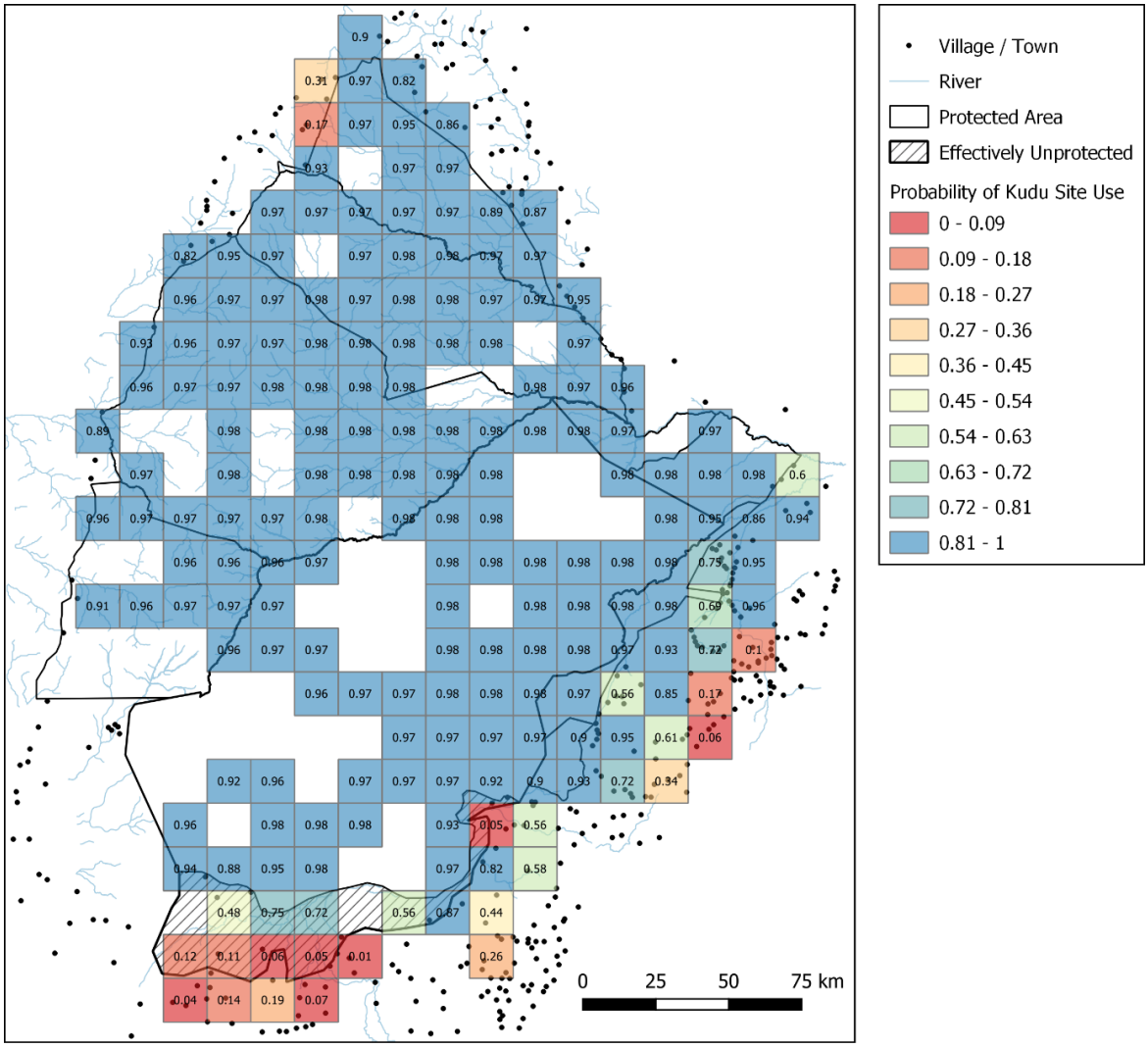
Giraffe


Village / Town
River
Protected Area
Effectively Unprotected
Probability of Giraffe Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

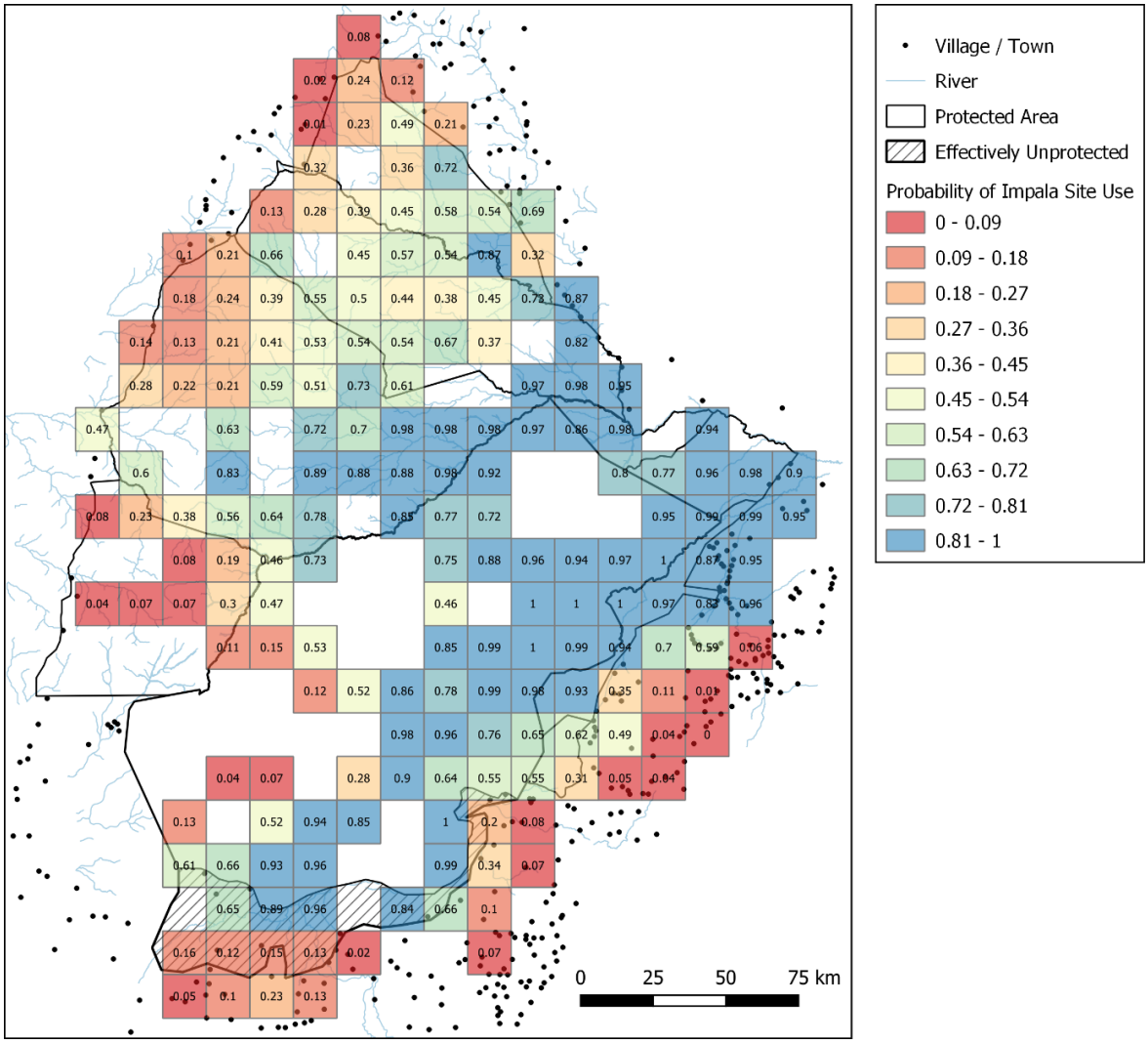
Roan & Sable


Village / Town
River
Protected Area
Effectively Unprotected
Probability of Sable/Roan Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

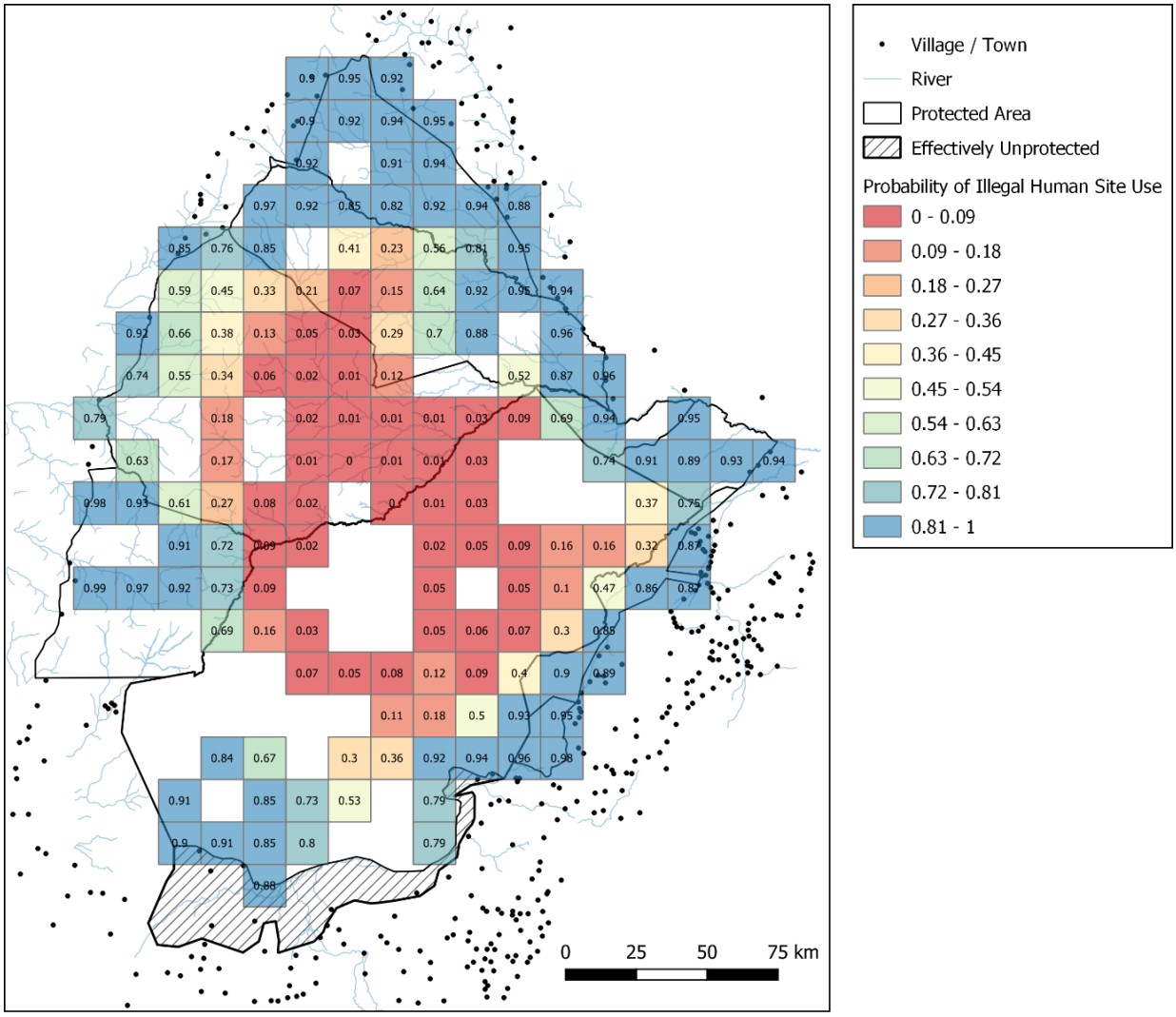
Greater Kudu



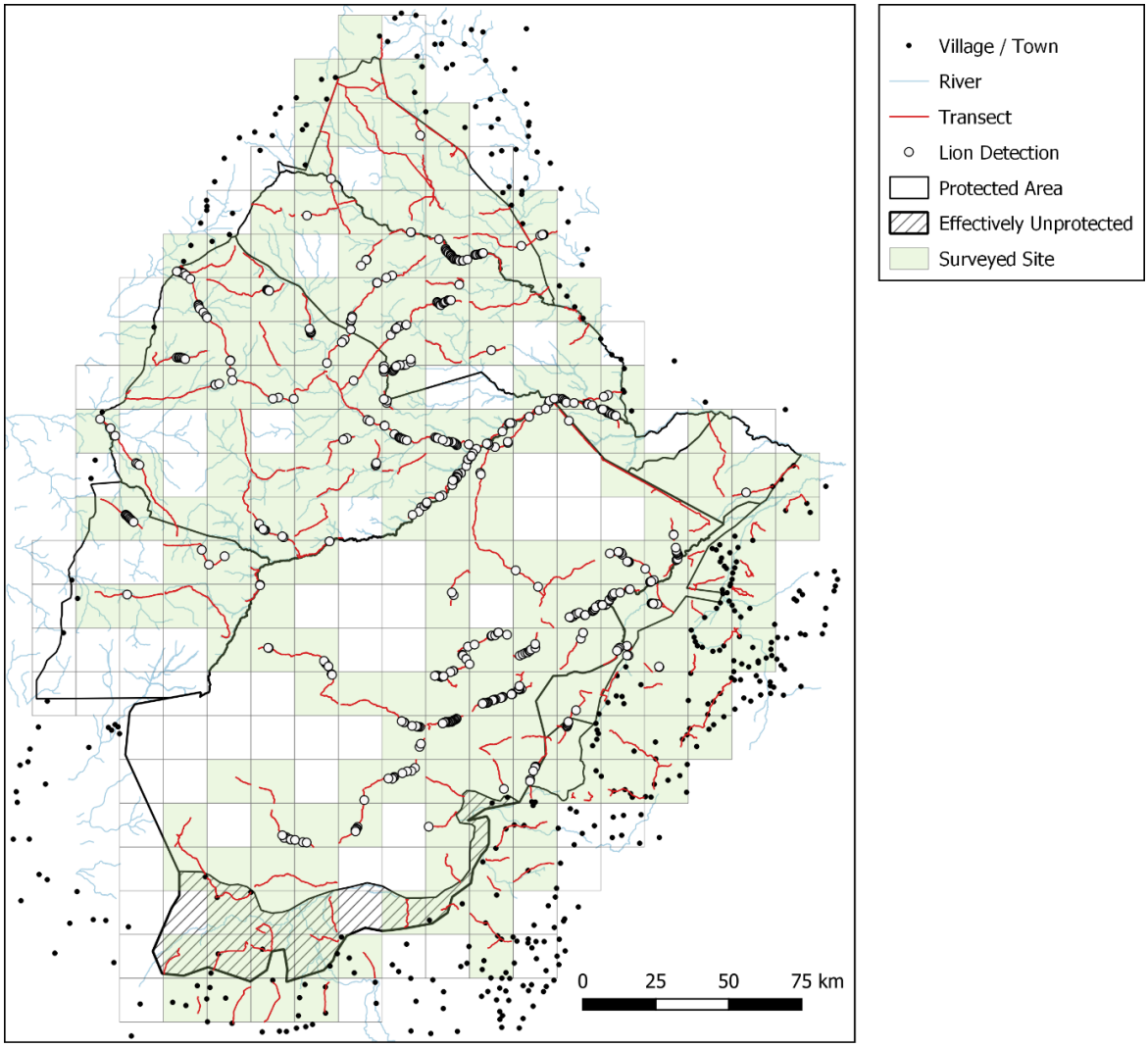
Impala

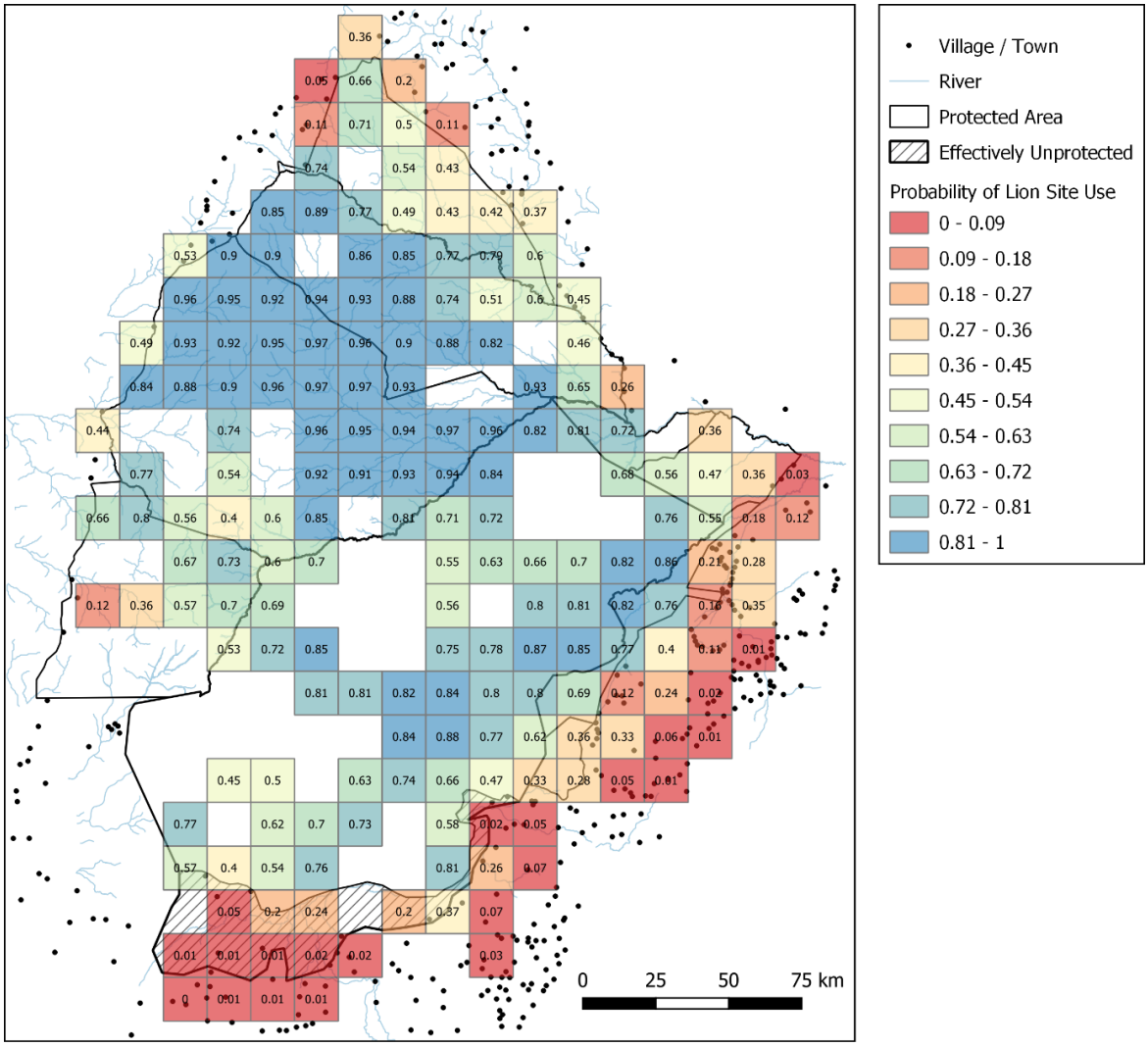

Village / Town
River
Protected Area
Effectively Unprotected
Probability of Impala Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

Illegal Human Activity

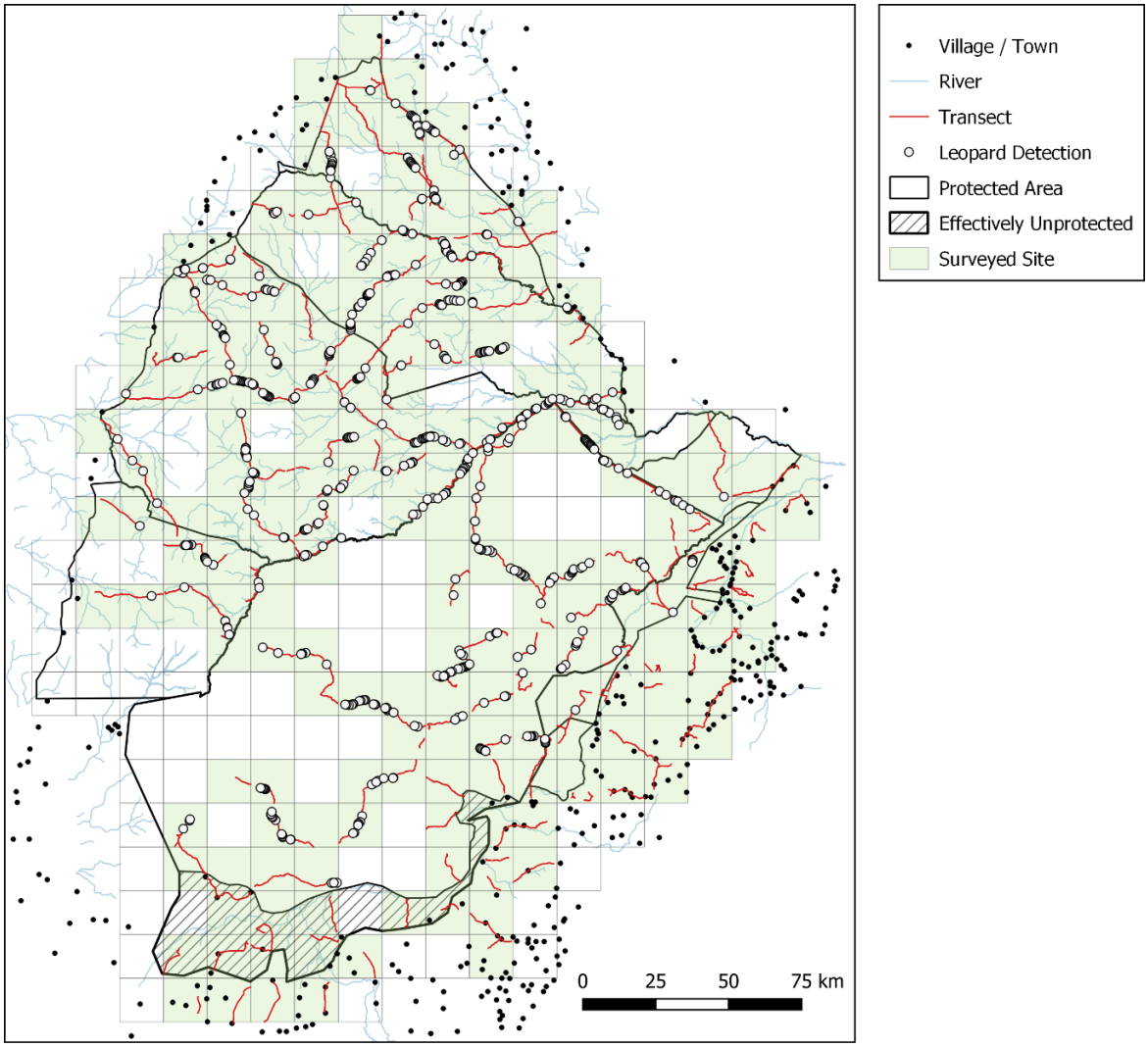


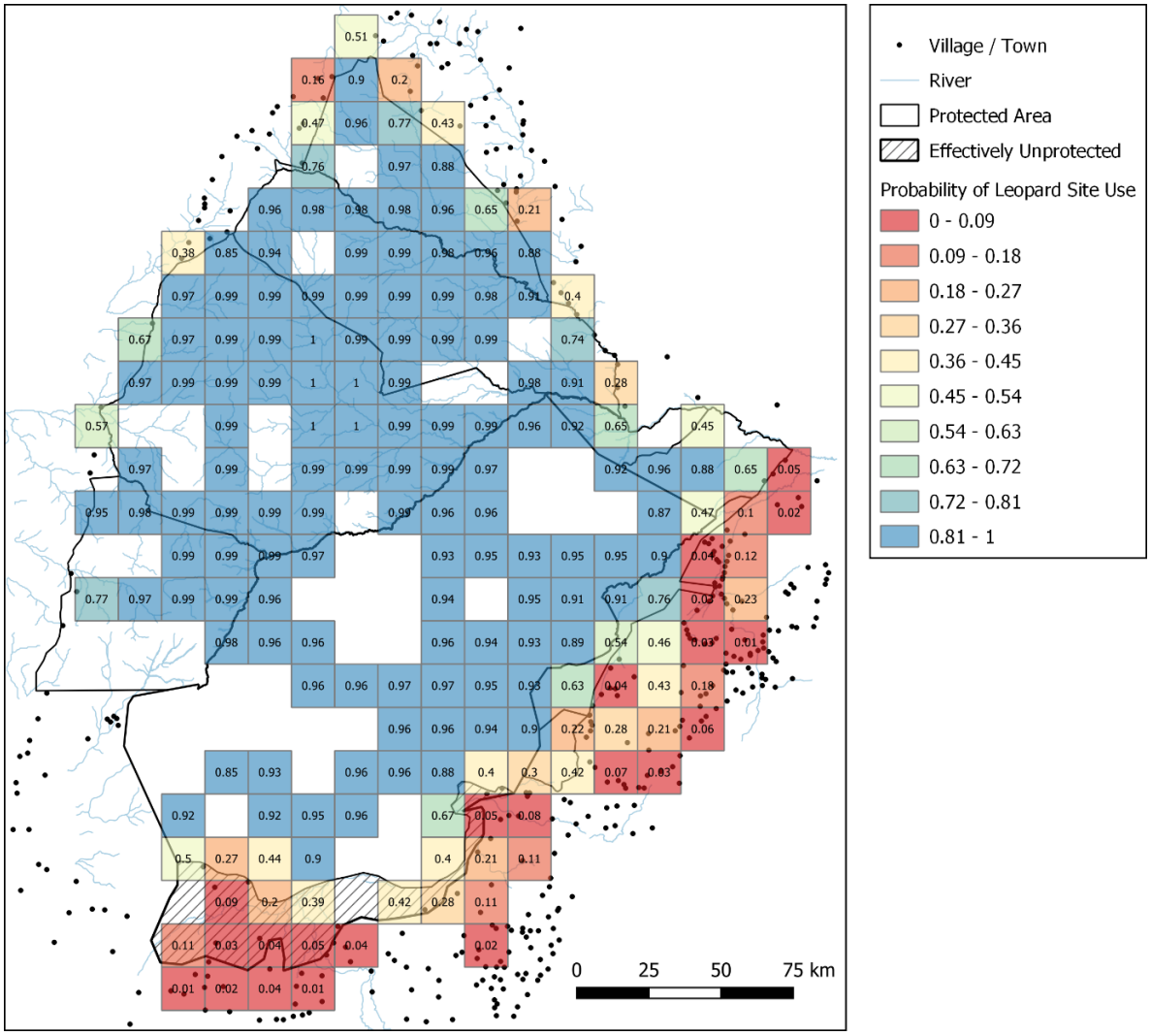
Lion


Village / Town
River
Transect
Lion Detection
Protected Area
Effectively Unprotected
Surveyed Site
0
25
50
75 km

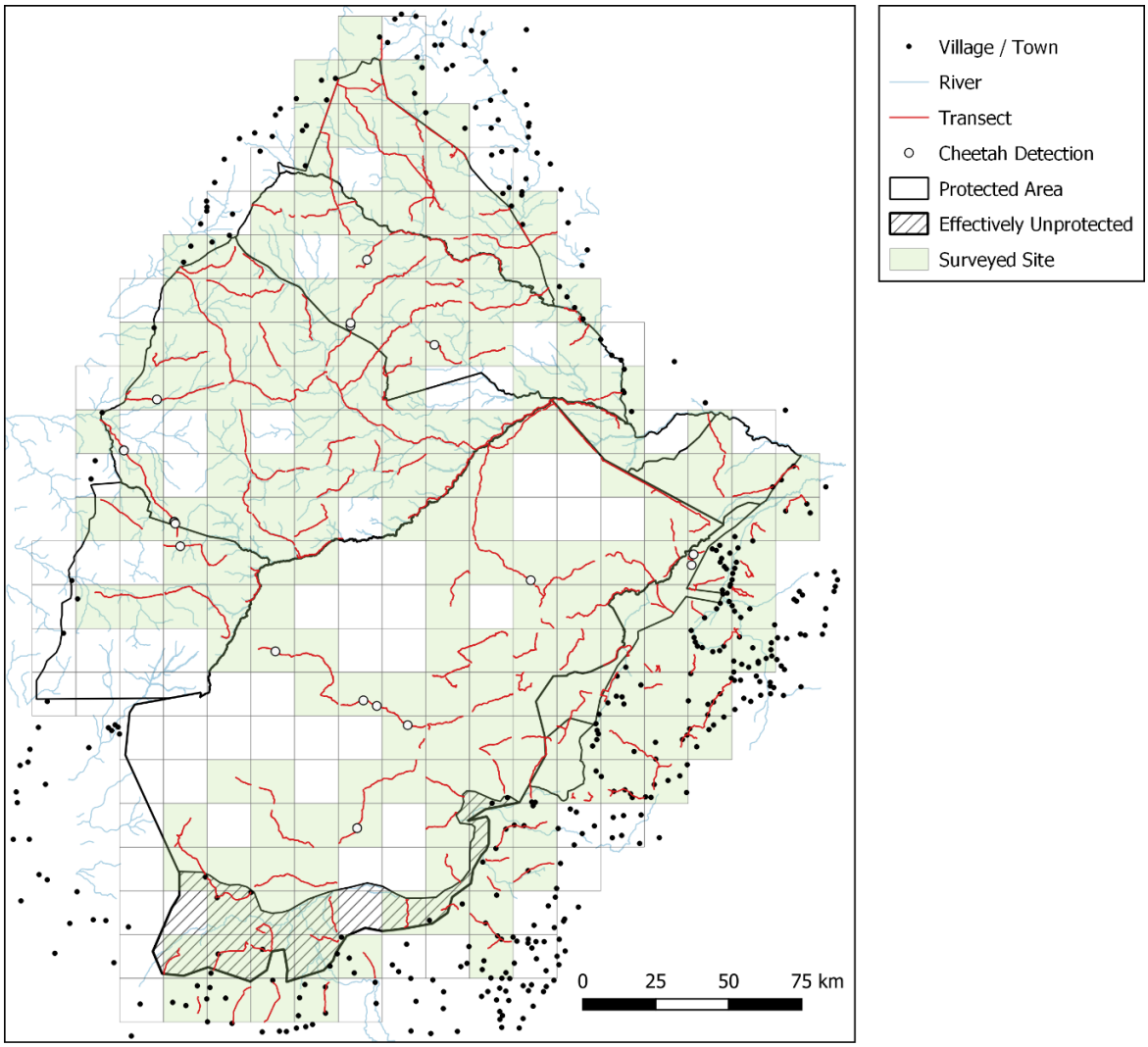

Village / Town
River
Protected Area
Effectively Unprotected
Probability of Lion Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

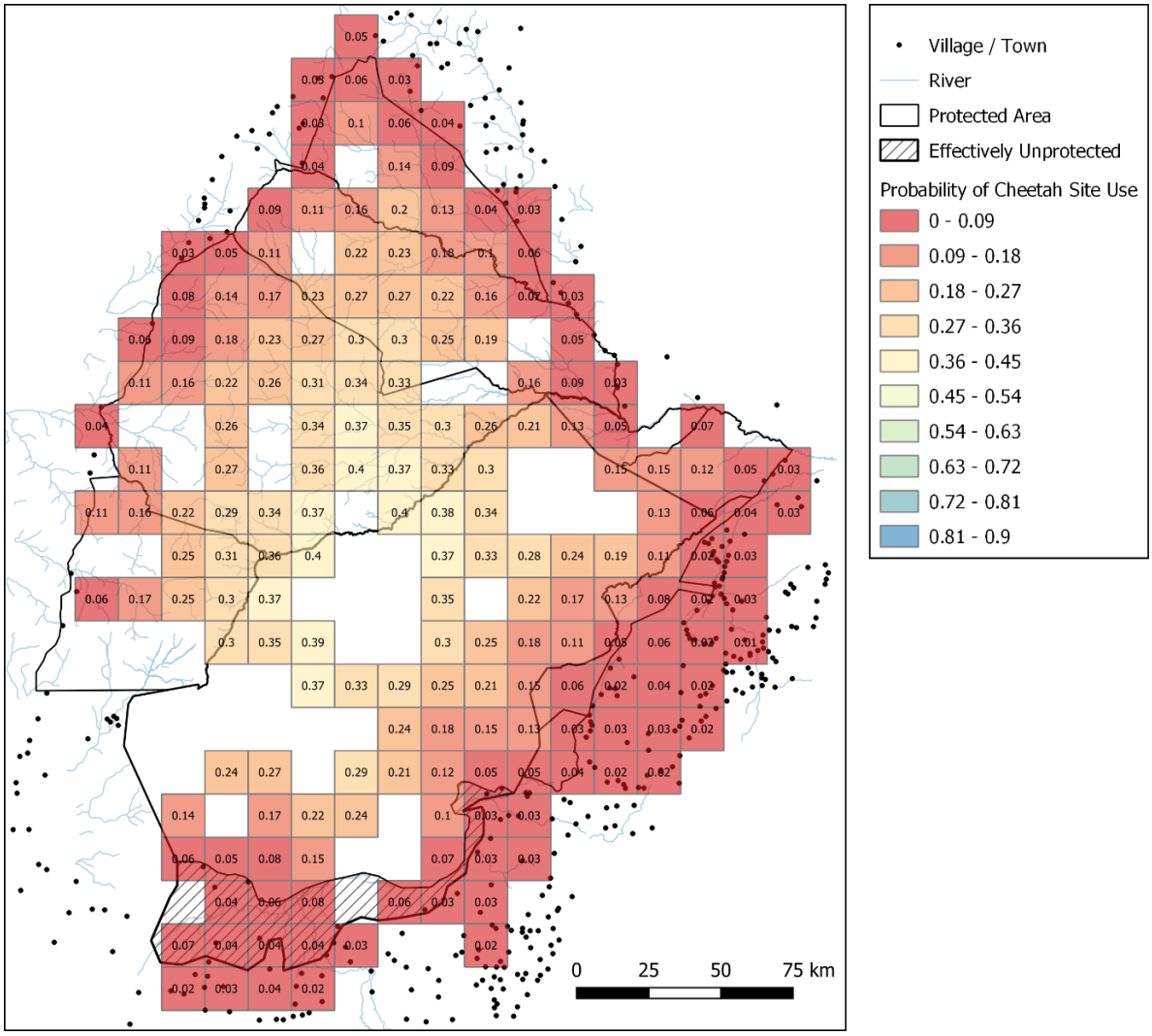
Leopard


Village / Town
River
Transect
Leopard Detection
Protected Area
Effectively Unprotected
Surveyed Site
0
25
50
75 km

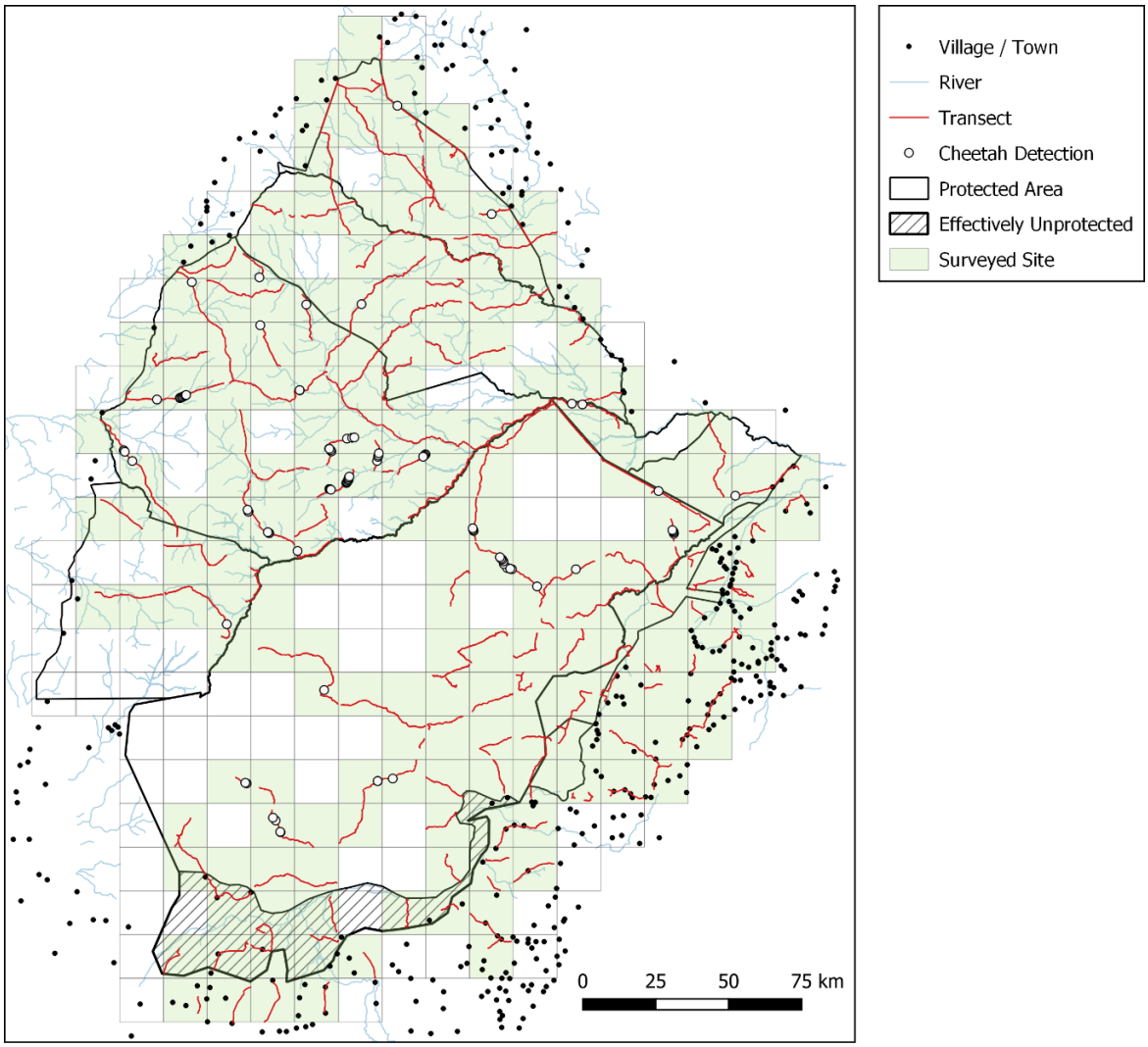

Village / Town
River
Protected Area
Effectively Unprotected
Probability of Leopard Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

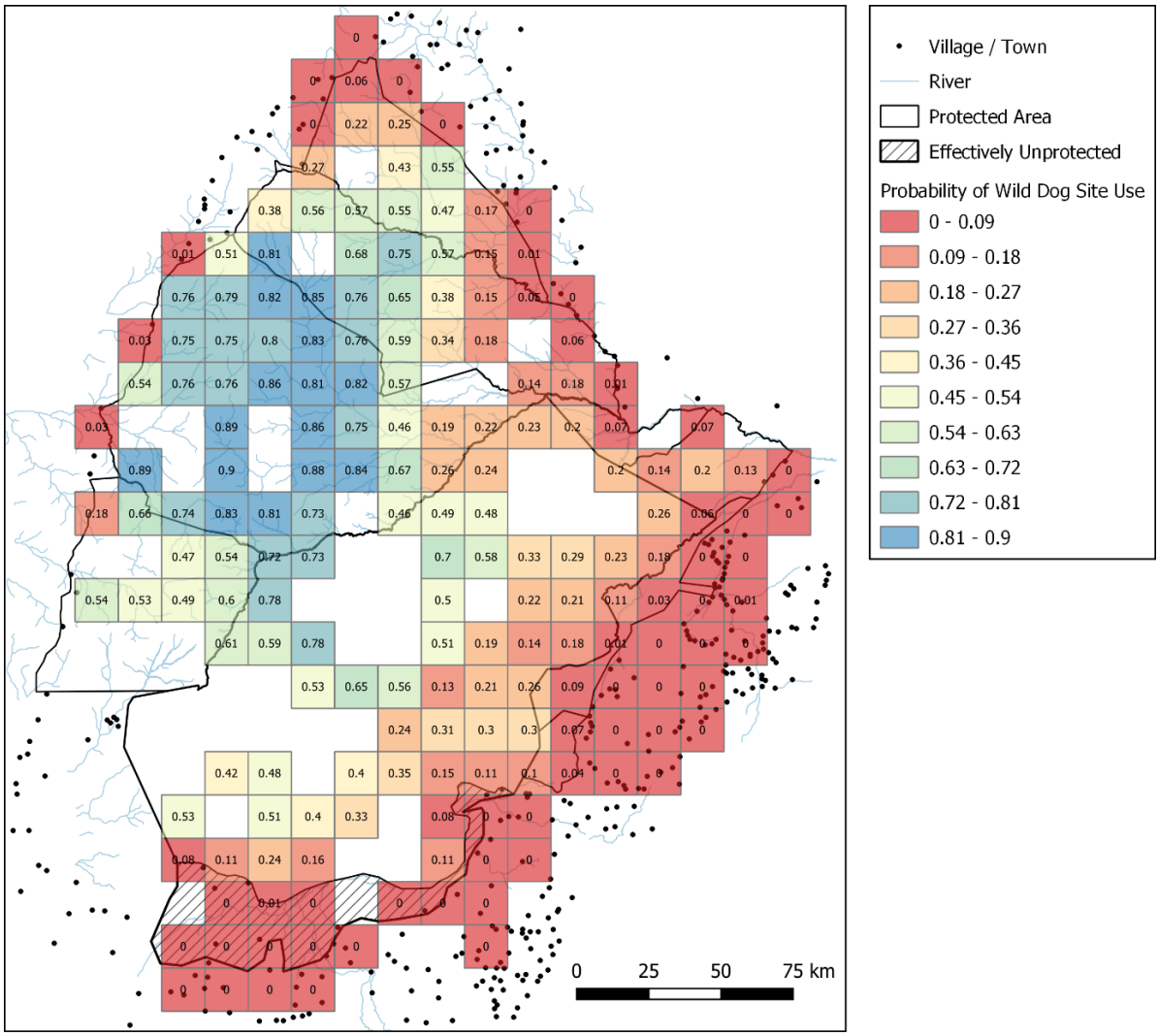
Cheetah


Village / Town
River
Transect
Cheetah Detection
Protected Area
Effectively Unprotected
Surveyed Site
0
25
50
75 km

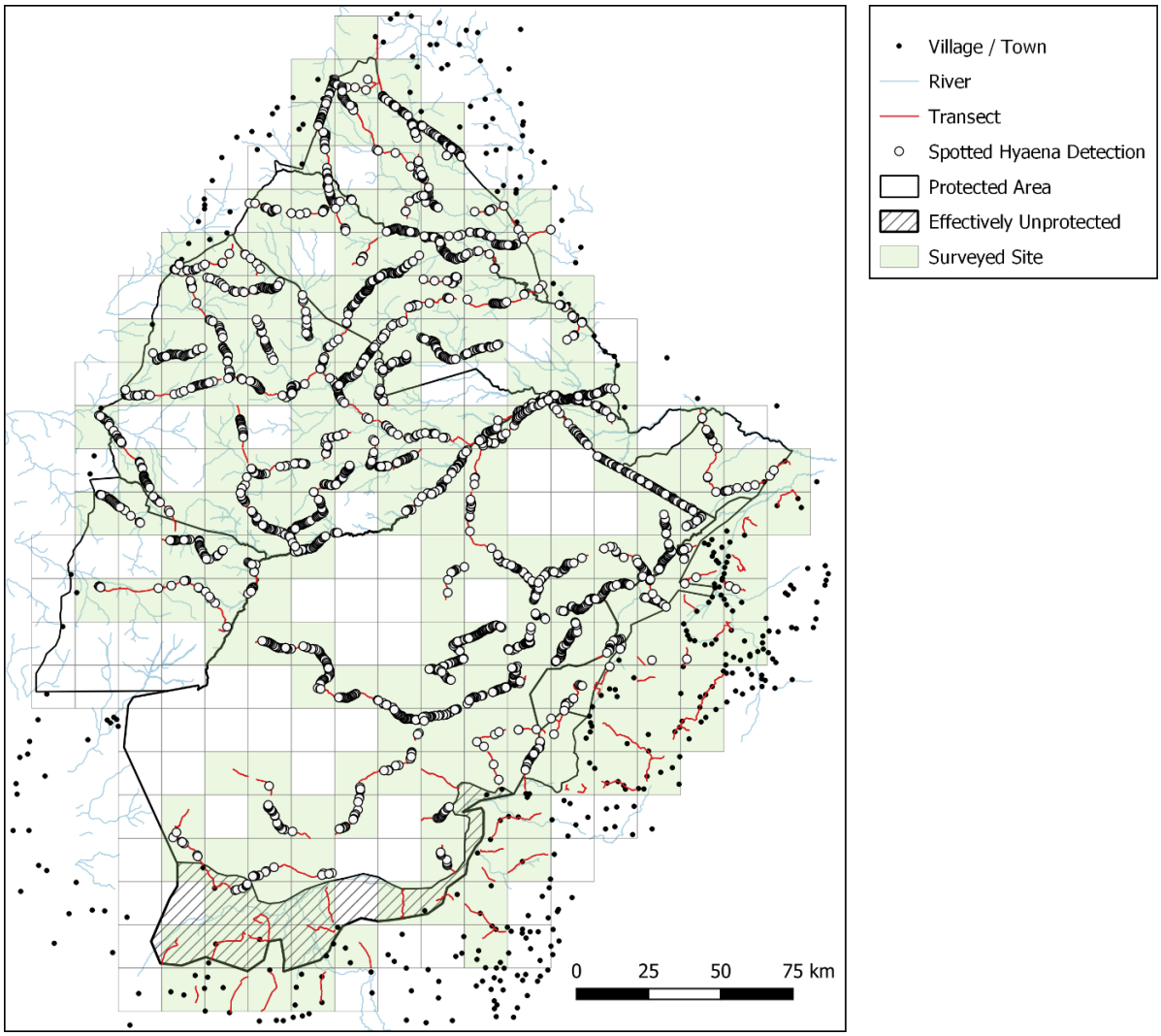

Village / Town
River
Protected Area
Effectively Unprotected
Probability of Cheetah Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 0.9
0
25
50
75 km

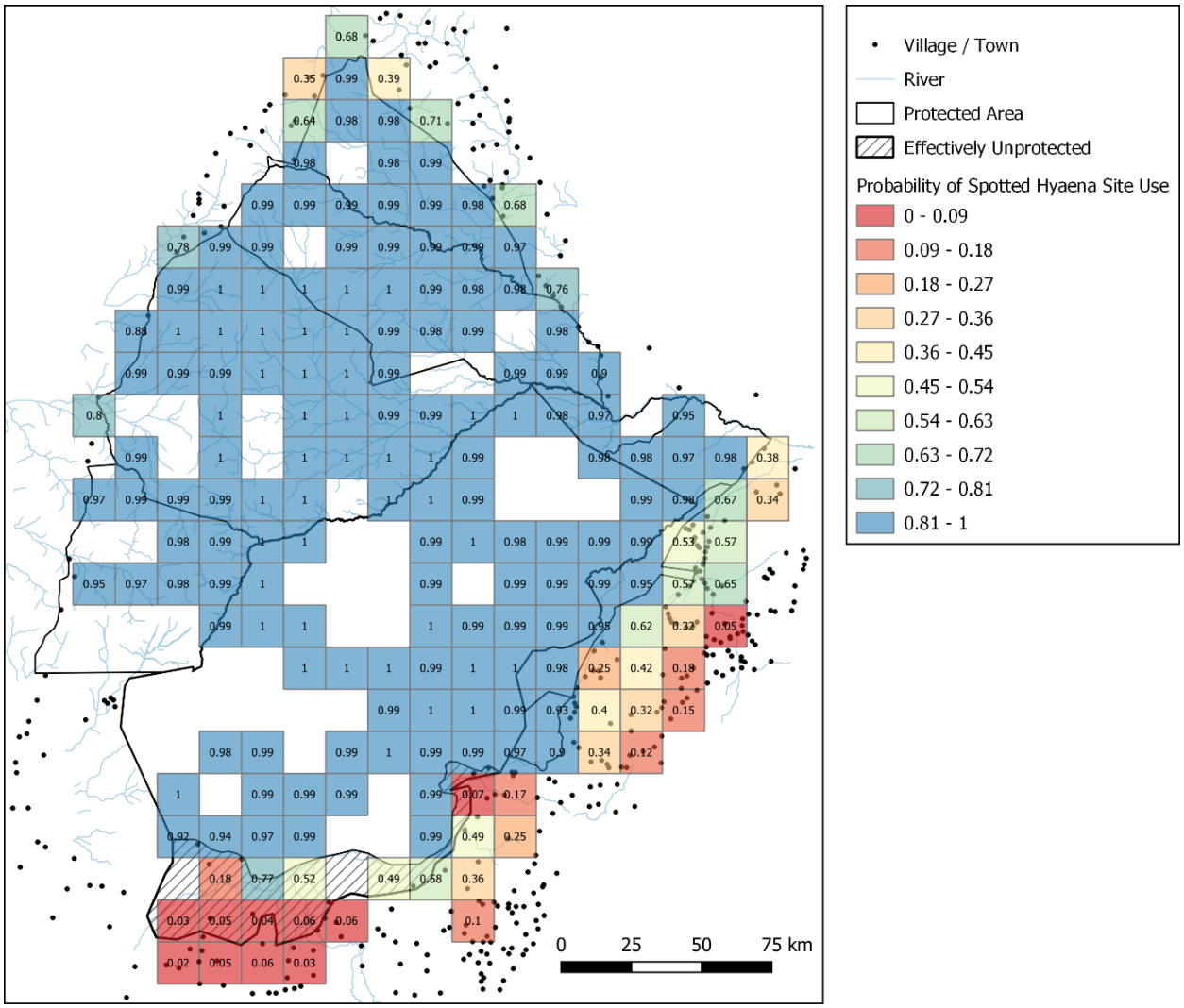
African Wild Dog




Village / Town
River
Protected Area
Effectively Unprotected
Probability of Wild Dog Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 0.9
0
25
50
75 km

Spotted Hyaena




Village / Town
River
Protected Area
Effectively Unprotected
Probability of Spotted Hyaena Site Use
0 - 0.09
0.09 - 0.18
0.18 - 0.27
0.27 - 0.36
0.36 - 0.45
0.45 - 0.54
0.54 - 0.63
0.63 - 0.72
0.72 - 0.81
0.81 - 1
0
25
50
75 km

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Camping along the Great Ruaha River, in southern Ruaha NP, during the 2017 survey season.

As a result of the vastness and remoteness of much of the area, and the need for spoor transects to begin at sunrise, mobile camping was a necessity for much of the survey effort.

CHAPTER 4

Spatial co-occurrence patterns of sympatric large carnivores in a multi-use African system



In preparation for *PLOS ONE*

- RUNNING HEADER -

Co-occurrence of large African carnivores

- TITLE -

Spatial co-occurrence patterns of sympatric large carnivores in a multi-use African system

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ABSTRACT

Interspecific interactions can be a key driver of large carnivore habitat use, and must be accounted for in conservation planning. However, spatial partitioning between African carnivores, and particularly how this varies with scale and anthropogenic impacts, remains poorly understood. Furthermore, most studies take place within small or highly protected core areas, rather than in heterogeneous, mixed-use landscapes characteristic of much of modern Africa. Here, we provide one of the first investigations into population-level competitive interactions among large African carnivores across a gradient of anthropogenic pressure and resource availability. We collected detection/non-detection data for an eastern African large carnivore guild over an area of ~50,000 km^2, in the Ruaha-Rungwa landscape in south-central Tanzania. We then applied conditional co-occupancy models to investigate co-occurrence between lion, leopard, and African wild dog across habitats, land management strategies, and anthropogenic impact gradients, at two biologically meaningful scales. Co-occurrence patterns of cheetah and spotted hyaena could not be modelled. After accounting for habitat and detection effects, we found some evidence of wild dog avoidance of lion at a coarser landscape scale, and strong evidence of fine-scale avoidance. Effects were strongest when more impacted areas of the landscape were included in the analyses. On the other hand, we found no evidence of interspecific exclusion of leopard by lion; rather, positive associations were observed at both scales, suggesting shared habitat preferences, particularly in more human-impacted areas. Although it was not possible to model interspecific interactions between wild dog and leopard at a coarser, landscape scale, we found little evidence of fine scale leopard habitat use being affected by wild dog. Our findings also reveal some interspecific effects on species detection, at both scales. In most cases, habitat use was driven more strongly by habitat effects than by interspecific pressures, even where evidence of the latter was present. Overall, our results help shed light on an assemblage that has been rarely examined at this scale. We also demonstrate, for the first time, the effectiveness of sign-based co-occurrence modelling to describe interspecific spatial patterns of sympatric large carnivores across a gradient of anthropogenic impact. Finally, we discuss the implications of our findings for large carnivore conservation in modern African systems.

4.1. INTRODUCTION

Intraguild competition plays an important role in shaping ecological communities (Caro & Stoner, 2003; Creel, 2001; Palomares & Caro, 1999; Rosenzweig, 1995). Effects are generally asymmetric, with dominant species having the potential to negatively impact subordinates, either directly, through intraguild killing and kleptoparasitism (Balme et al., 2017; Palomares & Caro, 1999), or indirectly, by driving spatial, temporal, and/or dietary shifts to safer but potentially less optimal resources (Swanson et al., 2014; Vanak et al., 2013). These can result in a range of often multifaceted partitioning mechanisms (Creel, 2001; Hayward et al., 2009; Périquet et al., 2015)

In this context, African large carnivore guilds are unique in that they can feature particularly large and diverse assemblages of species, all of which are increasingly threatened by rising anthropogenic pressures. In eastern Africa, complete large carnivore communities include lion (*Panthera leo*, extirpated from approximately 94% of historical range; Wolf & Ripple, 2017), leopard (*Panthera pardus*, 48-67%; Jacobson et al., 2016), cheetah (*Acinonyx jubatus*, 91%; Durant et al., 2015), spotted hyaena (*Crocuta crocuta*, 24%), striped hyaena (*Hyaena hyaena*, 15%), and African wild dog (*Lycaon pictus*, 93%; Wolf & Ripple, 2017). Due to the range of potential interactions, sympatric relationships can play an important role in shaping the habitat use of these species, and thus have important implications for their management and conservation (Balme et al., 2017; Swanson et al., 2014). As large carnivores are especially vulnerable to local extinction (Woodroffe & Ginsberg, 1998), and their loss can induce fundamental changes in community structure and functioning (Ripple et al., 2014), understanding these interaction dynamics is therefore important for conserving intact ecosystems (Cardillo et al., 2004; Di Minin et al., 2016; Marshall et al., 2016).

Furthermore, large carnivore guilds evolved within large, ecologically heterogeneous ecosystems (Creel, 2001). However, rising demand for land is increasingly restricting many populations to smaller tracts of habitat (Kiffner et al., 2015; Ray et al., 2005), which can force increased levels of overlap between competitors, and potentially preclude naturally evolved partitioning mechanisms. This is compounded by the fact that interspecific interactions are expected to be strongest under conditions of

resource limitation (Donadio & Buskirk, 2006; Wiens, 1989), and can be altered by human presence (Carter et al., 2012; Lewis, Bailey, et al., 2015). As a result, understanding interactions in human-impacted systems, and how these vary across disturbance gradients, will be crucial for the successful conservation of large carnivore communities in modern conservation landscapes (Karanth et al., 2017).

A range of mechanisms have been identified facilitating co-existence between sympatric African carnivores, including partitioning of prey resources (Mbizah et al., 2012), space (Creel & Creel, 1996; Durant, 1998) and activity patterns (Hayward et al., 2009). Some dominant-subordinate dynamics have become increasingly clear; both cheetah and African wild dog (hereafter: wild dog) densities and distributions have been found to vary with lion and spotted hyaena densities (Creel & Creel, 1996, 1998; Mills & Gorman, 1997), with these suggested as potential threats to cheetah (Chauvenet et al., 2011; Kelly & Durant, 2000; but see Broekhuis et al. (2013), Swanson et al. (2014), and Vanak et al. (2013) for recent evidence of the contrary) and especially wild dog population viability (Creel & Creel, 1996, 1998; Dröge et al., 2016). Competitive pressure from lions on wild dogs is exerted through a combination of kleptoparasitism (Speakman et al., 2016) and direct morality of both adults and young (Groom et al., 2016; Woodroffe & Ginsberg, 1999), and it has led wild dogs to develop a range of behavioural and demographic adaptions to lion presence (Courchamp & Macdonald, 2001; Creel & Creel, 2002). In particular, there is evidence that wild dogs are excluded from areas heavily used by lions – typically areas with higher prey densities – and that they employ coarser-scale habitat partitioning to coexist with lions (Creel, 2001; Mills & Gorman, 1997; Swanson et al., 2014). Nevertheless, most studies have been carried out at small spatial scales, rarely investigating population-level avoidance dynamics, and the nature of these displacement mechanisms over large scales therefore remains uncertain, particularly across habitat types and anthropogenic pressure gradients. With wild dogs classified as 'Endangered' by the IUCN, and with only four populations numbering over 400 individuals believed to remain (Woodroffe & Sillero-Zubiri, 2020), a more in-depth understanding of these relationships is paramount to help ensure their persistence in modern African landscapes.

Research similarly suggests that activity and distribution patterns of leopard can be affected by interspecific competition (Carter et al., 2015; Vanak et al., 2013), due to risk of kleptoparasitism, injury,

and direct mortality from lions, spotted hyaena, and potentially wild dogs (Bailey, 2005). Nevertheless, although there is some evidence of interspecific exclusion of leopard by lion (Maputla et al., 2015), most studies have found little evidence of avoidance at coarser spatial scales (Balme et al., 2017; Miller et al., 2018; Rafiq et al., 2020). This suggests that avoidance dynamics are likely taking place at finer scales (Rafiq et al., 2019) and depend on site-specific variables (Maputla et al., 2015; Vanak et al., 2013). Nevertheless, studies examining the relationship between lion and leopard at a population level are limited (but see Miller et al. (2018)), as are those taking place in human-shaped areas. As leopards share approximately 91% of lion range (Balme et al., 2017), there is a need to improve our understanding of these dynamics.

Finally, interactions between wild dog and leopard have received little research attention, despite the high potential for interspecific competition due to substantial dietary overlap (Hayward & Kerley, 2008). Although leopards are larger and have been known to kill wild dogs, the social structure of wild dogs generally places them in a dominant position (Estes, 1991). Nevertheless, co-existence mechanics between these species remain ambiguous (Swanson et al., 2014; Vanak et al., 2013), and population-level competitive interactions are yet to be studied.

To address these knowledge gaps, we apply two-species conditional occupancy models that account for habitat covariates and imperfect detection (Mackenzie et al., 2002; Richmond et al., 2010) to large-scale detection/non-detection large carnivore sign survey data. We employ these to investigate co-occurrence and co-detection patterns between three threatened sympatric large carnivores (lion, leopard, and wild dog) across Tanzania's ~50,000 km^2 Ruaha-Rungwa landscape, which features a complete African large carnivore guild, and what is believed to be one of the continent's most important remaining wild dog populations (Woodroffe & Sillero-Zubiri, 2020). Two-species occupancy models provide an opportunity to evaluate competitive interactions at a landscape scale (Mackenzie et al., 2004; MacKenzie et al., 2017; Steinmetz et al., 2013), investigating population-level spatial avoidance mechanisms that cannot be identified through finer scale methods, such as GPS collar studies or dietary analyses (Dröge et al., 2016; Hayward & Kerley, 2008; Swanson et al., 2016; Vanak et al., 2013). Nevertheless, this method has only been employed to investigate partitioning between sympatric

African carnivores on a handful of occasions (Miller et al., 2018; Ramesh et al., 2017), and never for wild dogs. Because intraguild interactions are likely to vary with resource availability (Karanth et al., 2017), habitat structure (Janssen et al., 2007), and human disturbance (Lewis, Logan, et al., 2015), as well as with scale (Broekhuis et al., 2017), we carry out a set of analyses across habitats, land management strategies, and anthropogenic impact levels, and at two biologically relevant spatial scales. Finally, we compare the relative influence of top-down interference competition pressures with that of bottom-up resources and anthropogenic impacts in determining large carnivore habitat use.

We predicted that wild dog occurrence would be lower at sites used by lions, and that these effects would be particularly evident at the finer scale investigated. We predicted that leopard occurrence would not be impacted by lion or wild dog occurrence at the coarser scale, due to leopard instead employing finer-scale spatiotemporal avoidance (Rafiq et al., 2020). We predicted that detection of subordinate species would be lower at co-occupied sites, as these may be less abundant and/or minimise movements to avoid encounters (Atwood et al., 2011). As intraguild predation theory predicts that subordinate predators should select habitats based on both food and safety from predation (Creel, 2001; Gompper et al., 2016; Heithaus, 2001), we expect interspecific effects to have a similar importance to biotic resources in driving wild dog habitat use, and possibly that of leopard at the finer scale investigated. Finally, intraguild predation theory suggests stronger impacts as resources decline, due to dominant predators having to search more widely for prey, and thus increasing interference interactions (Polis et al., 1989), and because species might be forced to share space due to anthropogenic pressures (Strampelli et al., 2018). We therefore also predicted that spatial partitioning would be less pronounced, and interspecific impacts felt more strongly, in more disturbed areas of the landscape.

Overall, our study provides one of the first population-level, multi-scale investigations into large carnivore intraguild competition in a human-impacted, multiple-use African landscape. In doing so, we provide novel insights that can help inform conservation decisions in modern settings. We also show that conditional two-species occupancy models can be applied to sign survey datasets to successfully investigate interspecific effects between large carnivores, albeit with some species-specific limitations.

4.2. METHODS

4.2.1. Study area

The Ruaha-Rungwa conservation complex is a ~50,000 km^2 mosaic of protected and non-protected areas, located in south-central Tanzania (Fig. 4.1). The largest protected area (PA) in the system is Ruaha National Park (NP; 20,226 km^2), reserved for photographic tourism. The complex also comprises three additional strict PAs which are instead reserved for trophy (sport) hunting (Rungwa, Kizigo and Muhesi Game Reserves (GRs) – 9,175 km^2, 5,140 km^2, and 2,720 km^2, respectively), as well as a number of less-strictly protected areas. These include Lunda-Mkwambi Game Controlled Area (GCA; 1,720 km^2) and Rungwa South Open Area (OA; 3,870 km^2), where both trophy hunting and additional resource extraction by local communities are permitted, and two community-managed Wildlife Management Areas (WMAs), MBOMIPA and Waga (947 and 344 km^2, respectively), where both photographic and hunting tourism are permitted (although neither was taking place at the time of study).

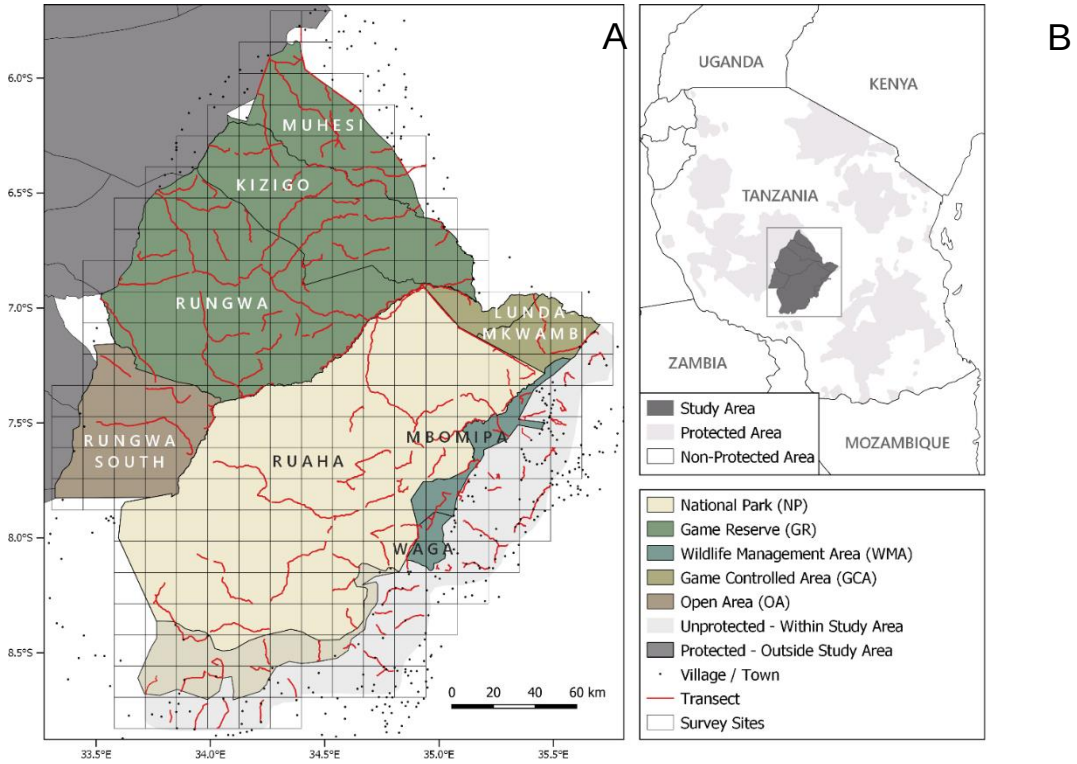


Figure 4.1. The Ruaha-Rungwa conservation landscape (A), including survey transects employed to study co-occurrence of large carnivores in the ecosystem, within the wider context of Tanzania's protected area system (B).

The complex in unfenced, and is surrounded by unprotected village lands to the south and east, and by additional OAs and GCAs to the west and north. On-the-ground law enforcement is generally highest in Ruaha NP and in certain sections of the GRs, and lower in the GCA, OA, and WMAs. The landscape experiences a range of anthropogenic impacts, including: land clearing for subsistence agriculture (both in unprotected lands and within some PAs); illegal natural resources extraction, particularly bushmeat poaching, fishing, logging, and burning for honey gathering; and legal natural resource extraction, in the form of trophy hunting and logging. Although impacts vary in severity across the complex's extent, most are stronger in the less-strictly protected areas (GCA, OA, WMAs; TAWIRI, 2019; Chapter 3).

Ruaha-Rungwa exhibits a mixed mosaic of *Acacia-Commiphora* open savannah/bushland and central Zambezian and Eastern *Brachystegia*-dominated miombo woodlands (Olson et al., 2001). Altitude ranges from 696 m to 2,171 m (ESA, 2009), and the complex is semi-arid, with annual rainfall being highly seasonal (December-April) and varying between 450 and 900 mm across its extent (Fick & Hijmans, 2017). The landscape harbours a complete eastern African large carnivore guild, including regionally and globally important populations of lion (IUCN Red List Status: Vulnerable), leopard (Vulnerable), cheetah (Vulnerable), wild dog (Endangered), spotted hyaena (Least Concern), and striped hyaena (Near Threatened) (IUCN, 2020; TAWIRI, 2009). Nevertheless, the area is relatively understudied, and to date little research has been carried out on the ecology of these populations.

4.2.2. Data collection

Vehicle-based sign surveys were employed to collect detection/non-detection presence/absence data on large carnivores across the Ruaha-Rungwa landscape. Large carnivores perform extensive movements along road networks (Mckenzie et al., 2012) and spoor (track)-based surveys have been shown to be a particularly efficient and effective method to collect data on African large carnivores over vast landscapes (Barea-Azcón et al., 2007; Thorn et al., 2010), including for all of our study species (Everatt et al., 2014, 2019; Henschel et al., 2016, 2020; Petracca et al., 2019; Searle et al., 2020).

Surveys were carried out over two dry seasons, between 7 July and 29 November 2017, and 29 June and 21 November 2018. The survey team consisted of a driver and two experienced trackers seated on

custom-made seats on the bull-bar of the vehicle. The vehicle was driven at a maximum speed of 10 km/h, and surveying took place between dawn and approximately 10:00 am, before a high-standing sun made detection difficult. If another vehicle travelled on the road during surveying, the transect was ended. Spoor of five large carnivores (lion, leopard, cheetah, wild dog, and spotted hyaena) were recorded. For all species, data were recorded in the form of detection/non-detection (1 or 0) at the species level within individual 500 m segments. Transects varied in length based on the amount of roads present within each site (see: '4.2.3. Study Design').

4.2.3. Study design

Our goal was to test interspecific spatial partitioning between sympatric large carnivores in Ruaha-Rungwa, and whether effects varied across management strategies and gradients of anthropogenic disturbance, as well as with spatial scale. As a result, our study design employed five different sampling grids: a first, comprising the complete landscape, including non-protected areas (Fig. 4.2A); a second, comprising only PAs (Fig. 4.2B); a third, comprising only PAs receiving regular on-the-ground law enforcement (Fig. 4.2C); and a fourth, comprising only trophy hunting PAs (Fig. 4.2D). Across these, co-occurrence was investigated at a scale representative of home range selection by large carnivores, equivalent to Johnson (1980)'s second order scale of habitat selection (hereafter: 'home range selection' (HRS) scale; Everatt et al., 2015, 2019; Chapter 3). This nested design allowed us to investigate how effects changed across anthropogenic impact levels and management strategies. In addition, because evaluating competitive interactions at a single scale may lead to misleading inferences (Richmond et al., 2010), and scale-dependency has been hypothesised to explain contrasting patterns of predator suppression in African carnivores (Broekhuis et al., 2013; Swanson et al., 2016), a fifth analysis was carried out, to investigate co-occurrence patterns at a finer scale, equivalent to that of habitat use within the home range (i.e. Johnson (1980)'s third order of habitat selection; hereafter 'temporary use selection within the home range' (TUS) scale; Davidson et al., 2012; Everatt et al., 2015; Chapter 3). The two spatial scales employed can also be considered equivalent to investigating long-term (pre-emptive) and short-term (reactive) spatial avoidance, respectively (Dröge et al., 2016; Swanson et al., 2016).

Sampling sites consisted of 225 km^2 grid cells at the HRS scale, and of ~1 km^2 areas at the TUS scale, obtained by placing a 250 m buffer around 2 km transect segments (these being located within HRS scale sites; Fig. 4.2E; Everatt et al., 2015, Chapter 3). Only TUS sites located within HRS sites where both species of interest had been detected were included in the TUS analysis; this ensured that areas with no presence at a coarser scale were not erroneously interpreted as being avoided at this finer scale. We were able to survey the majority of sampling sites in the landscape, ensuring representative coverage (Fig. 4.1 & 4.2). A minimum of 6 km and a maximum of 20 km were surveyed within each HRS site (differences in sampling effort are accounted for in the modelling process; Mackenzie et al., 2002).

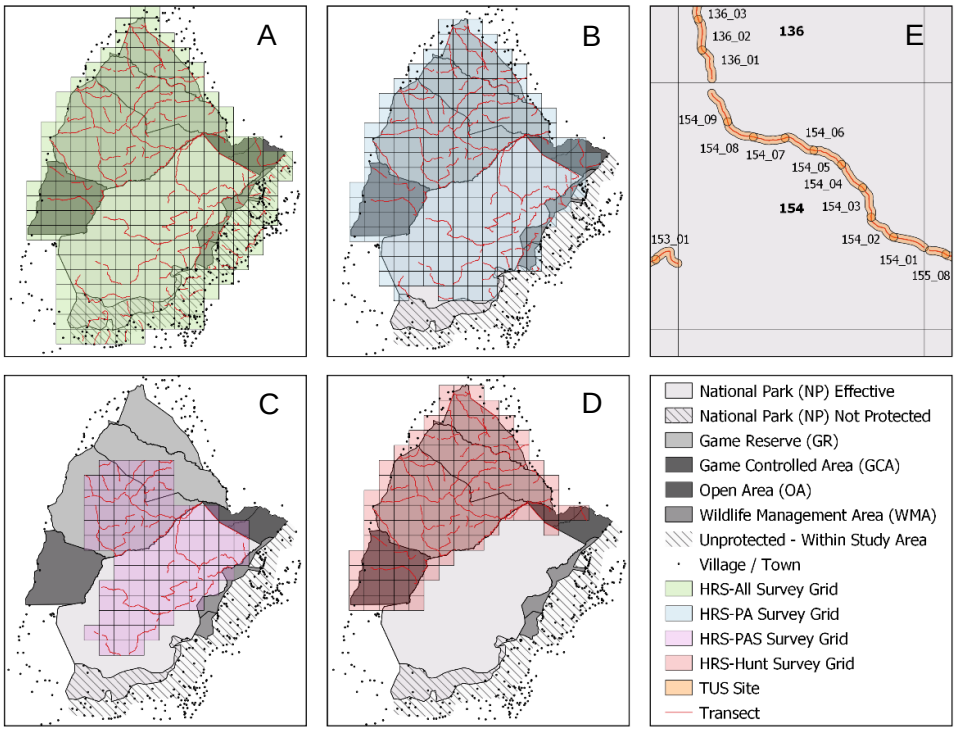


Figure 4.2. The five sampling grids employed to investigate co-occurrence patterns of three sympatric large carnivores in Ruaha-Rungwa. A = HRS-ALL, investigating co-occurrence at the home range selection (HRS) scale, and including all data, including from non-protected areas; B = HRS-PA, investigating co-occurrence at the HRS scale, and including only data from protected areas; C = HRS-PAS, investigating co-occurrence at the HRS scale, and including only data from protected areas with regular law-enforcement; D = HRS-HUNT, investigating co-occurrence at the HRS scale, and including only data from trophy hunting areas; and E = TUS, investigating co-occurrence at the finer temporary use within the home range (TUS) scale. Sampling sites consist of 225 km^2 systematic grid cells in sampling arrays at the HRS scale, and of an area of ~1 km^2 around 2 km survey transect segments at the TUS scale. The coloured area in each HRS-scale map shows the respective portion of the landscape included in each sampling grid.

4.2.4. Co-occurrence modelling

We fitted conditional single-season two-species occupancy models (Mackenzie et al., 2004; Richmond et al., 2010) in Program PRESENCE 2.12.37 (Hines, 2006) to the sign-based detection/non-detection data. Conditional two-species occupancy models allow the probability of occupancy and detection of one species (subordinate; species B) to be modelled as a function of the occupancy and detection status of the other (dominant; species A), while controlling for habitat effects (Richmond et al., 2010). This parametrisation was chosen due to its stability when incorporating covariates (MacKenzie et al., 2017).

We tested several hypotheses regarding interspecific spatial interactions of three sympatric large carnivores in the study area: lion, leopard, and wild dog. Co-occurrence dynamics between spotted hyaena and cheetah and other large carnivores could not be modelled due to insufficient heterogeneity in detection (spotted hyaena) or detections (cheetah). Throughout this study, lion were considered dominant to wild dog and leopard, and wild dog were considered dominant to leopard (Estes, 1991).

To test our hypotheses on co-occurrence, we estimated the following occupancy parameters at each scale, and within each sampling grid: Ψ^{A} (occupancy probability of the dominant species), Ψ^{BA} (occupancy probability of the subordinate, when the dominant is present), and Ψ^{Ba} (occupancy probability of the subordinate, when the dominant is absent; Table 4.1). We fitted a set of *a priori* models which assumed that the presence of the dominant species influenced the subordinate (i.e. $\Psi^{BA} \neq \Psi^{Ba}$; 'conditional' models), as well as models where the occupancy of the subordinate was independent of presence of the dominant species ($\Psi^{BA} = \Psi^{Ba}$; 'unconditional' models). To determine whether there was evidence of interspecific effects, competing conditional and unconditional models were compared by model ranking based on their Akaike Information Criterion, adjusted for small sample size (AICc). AICc values and model weights acted as a measure of the relative amount of evidence for each model. For each analysis, the conditional model ($\Psi^{BA} \neq \Psi^{Ba}$) receiving the most support would suggest either avoidance ($\Psi^{BA} < \Psi^{Ba}$) or aggregation ($\Psi^{BA} > \Psi^{Ba}$), while the unconditional model ($\Psi^{BA} = \Psi^{Ba}$) receiving the most support would instead suggest that occurrence is independent.

Table 4.1. Parameters in the conditional two-species occupancy model (adapted from Richmond et al., 2010).

Parameter	Definition
Ψ^{A}	Probability of occupancy of species A
Ψ^{BA}	Probability of occupancy of species B, with species A present
Ψ^{Ba}	Probability of occupancy of species B, with species A absent
p^{A}	Probability of detection of species A, with species B absent
r^{A}	Probability of detection of species A, with species B present
p^{B}	Probability of detection of species B, with species A absent
r^{BA}	Probability of detection of species B, with both species present and species A detected during sampling interval
r^{Ba}	Probability of detection of species B, with both species present and species A not detected during sampling interval

Note: Species A is assumed to be dominant, and species B subordinate

To control for habitat effects, and ensure that any identified interspecific effect was not a result of different habitat preferences or detection patterns, we incorporated habitat (site use) and detection covariates from the best ranked model from single-species analyses. These employed the same data, and were carried out at the same spatial scales and employing the same sampling designs (see Chapter 3 for complete single-species methodology and model rankings, and Appendix 3.1 for descriptions, rationale, and sampling methodologies of covariates employed). All site covariate data were normalized to facilitate model convergence (Hines, 2006), and variables that were highly correlated (i.e. $r > 0.6$) were not included in the same model. See Appendix 4.1 for all input data, for all analyses. By fitting models with and without interspecific, habitat, and detection covariates (Table 4.2), and ranking them against each other, we compared the role of interspecific and habitat effects in shaping occurrence. A general model was employed for detection (p), containing as many parameters as possible (i.e. $pA \neq rA \neq pB \neq rBA \neq rBa$, and the best-ranked detection covariates identified in single-species model).

Table 4.2. Ranked competing conditional and unconditional co-occurrence models, to evaluate the relative role of interspecific interactions and habitat partitioning on site use of lion, leopard, and wild dog in Ruaha-Rungwa. Models are presented in order of increasing complexity (number of parameters)

Model[1]	Type	Model Notation[2]	Interspecific effects	Habitat covariates	Detection covariates
1	Unconditional	$\Psi^{BA} = \Psi^{Ba}$	No	No	No
2	Conditional	$\Psi^{BA} \neq \Psi^{Ba}$	Yes	No	No
3	Unconditional	$\Psi^{BA} = \Psi^{Ba}$	No	No	Yes
4	Conditional	$\Psi^{BA} \neq \Psi^{Ba}$	Yes	No	Yes
5	Unconditional	$\Psi^{BA} = \Psi^{Ba}$	No	Yes	Yes
6	Conditional	$\Psi^{BA} \neq \Psi^{Ba}$	Yes	Yes	Yes

[1] All models include a general model for *p (*$pA \neq rA \neq pB \neq rBA \neq rBa$, and the best-ranked detection covariates from single-species model)

[2] Unconditional models estimate a single ΨB (i.e. ΨBA = ΨBa) and assume that the probability of site use of species B is not affected by the presence of species A, whereas conditional models estimate ΨBA and ΨBa separately (i.e. ΨBA≠ΨBa) and assume that the probability of site use of species B is affected by the probability of site use of species A.

To also test for interspecific effects on detection, we estimated the following parameters in each analysis: p^A (probability of detecting the dominant species, given the absence of the subordinate), p^B (probability of detecting the subordinate, given the absence of the dominant), r^A (probability of detecting the dominant, given both are present), r^{BA} (probability of detecting the subordinate, given both are present and the dominant is detected), r^{Ba} (probability of detecting the subordinate, given both are present and the dominant is not detected; Table 4.1). We compared a set of *a priori models*, based on AICc model rankings, to test whether the detection probability of the subordinate species was either conditional on the occurrence ($p^B \neq r^{BA}$, $p^B \neq r^{Ba}$) or the detection ($r^{Ba} \neq r^{BA}$) of the dominant species, or independent and thus unconditional on the dominant species ($p^B = r^{Ba} = r^{BA}$). In addition, we tested whether the detection of the dominant species was conditional on the detection of the subordinate species ($p^A \neq r^A$) or unconditional ($p^A = r^A$). To control for other effects on detection, we incorporated the best-ranked detection covariates from single-species models (Chapter 3). When testing for detection effects, all models employed the top-ranked model for occupancy, as identified in the previous step (as per Estevo et al., 2017).

Finally, we also calculated the species interaction factor ('SIF') for occupancy (φ) and detection (δ; Richmond et al., 2010) from the top-ranked model for each species pair, in each analysis. The SIF represents a likelihood ratio of co-occurrence and co-detection for the two species, estimating how likely the two species are to co-occur compared to what would be expected under a hypothesis of independence (Richmond et al., 2010), and is calculated for conditional models as:

$$\phi = \frac{\Psi^A \Psi^{BA}}{\Psi^A(\Psi^A \Psi^{BA} + (1-\Psi^A)\Psi^{Ba})} \qquad \delta = \frac{r^A r^{BA}}{r^A(r^A r^{BA} + (1-r^A)\, r^{Ba})}$$

If the SIF = 1, or if the estimate of the SIF ± SE includes 1, the two species occur independently. SIF > 1 suggests that the two species are more likely to co-occur than would be expected under the null hypothesis of independence (aggregation), whereas SIF < 1 indicates spatial avoidance of the dominant species by the subordinate.

Overall, to draw inferences about co-occurrence and co-detection, for each species pairing at the different scales of interest, we considered: the estimated parameters (Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, r^{a}, p^{a}, p^{B}, r^{Ba}, r^{BA}) of models with strong support ($\Delta AIC < 2$), the relationships between them, model rankings, and SIFs (Estevo et al., 2017; Gutiérrez-González & López-González, 2017; Nagy-Reis et al., 2017).

For all analyses, sampling occasions were defined as spatially replicated transect segments within each surveyed site. Segment length was set to account for spatial autocorrelation (Markovian dependence) in detection; this was achieved by testing for this in Program PRESENCE 2.12.37, increasing sampling occasion length until there was no more evidence of spatial autocorrelation (Henschel et al., 2016; Hines, 2006). As this was achieved at a length equal to or shorter than 5 km for all species (see Chapter 3 for additional details), sampling occasions consisted of 5 km transect segments in all analyses at the HRS scale. At the TUS scale, sampling occasions comprised 2 – 4 continuous 500 m segments. Models that explicitly address the issue of spatial autocorrelation (Hines et al., 2010) cannot be implemented in two-species analyses. Although a removal sampling design was attempted as an alternative way to account for spatial correlation in detections, the naturally low detectability of large carnivores meant we could not achieve convergence once the necessary data were removed. As a result, it was not possible to account for spatial autocorrelation in detection at the TUS scale.

In all analyses, the occupancy estimator (Ψ) was interpreted as the probability of site use, rather than that of occupancy, in order to relax the closure assumption and thus minimise potential assumption violations (Mackenzie et al., 2017).

4.3. RESULTS

We surveyed a total of 2,789 km of transects across eight PAs and completely non-protected lands (Fig. 4.1). A total of 185 sites were sampled at the HRS scale (average survey effort per site = 15.1 km), while 1484 sites were sampled at the TUS scale. Overall, we recorded 40 independent detections of wild dog, 162 of lion, and 234 of leopard. We also recorded 13 independent detections of cheetah and 447 of spotted hyaena.

4.3.1. Large carnivore co-occurrence & co-detection

In all analyses, models which incorporated the effects of habitat covariates on site use fitted better than models without any habitat covariates ($\sum w = 0.99$ vs $\sum w < 0.01$). In addition, models which included habitat covariates, but not interspecific effects, almost always received significantly stronger support than models which included interspecific effects, but not habitat effects (see Appendix 4.2 for full model rankings). This indicates that in most cases, and even when significant interspecific effects were identified (see below), habitat use was driven more strongly by habitat effects than interspecific ones.

4.3.1.1. *Lion & wild dog interspecific associations*

After accounting for habitat and detection effects, we found some evidence of wild dog avoidance of lion at the HRS scale; however, these effects were not significant. Although the conditional model ($\Psi BA \neq \Psi Ba$) ranked higher than the unconditional ($\Psi BA = \Psi Ba$) in all analyses at this scale, the latter also always received strong support ($\Delta AICc < 2$; Table 4.3). Nevertheless, while not significantly different due to relatively wide standard errors, probability of wild dog use at sites where lion were absent was consistently greater than where lion were present (i.e. $\Psi Ba > \Psi BA$; Table 4.4, Fig. 4.3). Similarly, the SIF for occurrence consistently suggested non-significant avoidance ($\varphi < 1$) at all HRS scale analyses, with the effect being strongest when sampling across the wider landscape (i.e. HRS-ALL; Table 4.4, Fig. 4.4A).

On the other hand, there was statistically significant evidence for wild dog avoidance of lion at the TUS scale. Although the unconditional model also received strong support (Table 4.3), the statistically

significant difference between wild dog site use when lion is present or absent ($\Psi BA = 0.16 \pm 0.11$ S.E. and $\Psi Ba = 0.42 \pm 0.14$, respectively; Table 4.4, Fig. 4.3), indicates that wild dog use of areas within the home range with lion presence was greatly reduced. The SIF also suggested a significant avoidance effect ($\varphi = 0.55 \pm 0.31$; Table 4.5, Fig. 4.4A), strongly supporting the hypothesis of wild dog avoidance of lion at this scale. Furthermore, this was the only analysis, of all species pairs and at both spatial scales, in which a model including interspecific effects, but not habitat covariates, received strong support (Appendix 4.2). This suggests that avoidance of lion has a particularly strong impact on space use by wild dog within the home range.

With regards to detection, in all analyses at the HRS scale the SIF (δ) suggested a negative association between detection of wild dog and lion, although effects were not significant (Table 4.4, Fig. 4.4B). In addition, although results across the different analyses suggested wild dog detection to be lower when lion are present and detected than when they are present but not detected ($rBA < rBa$), these effects were also not significant. Model rankings in all the analyses at the HRS scale (with the exception of within hunting areas only, HRS-HUNT) similarly provided only marginal evidence for wild dog detection being different when lions were also present and detected ($pB=/=rBA$) or present and not detected ($pB=/= rBa$) compared to when lion were absent, based on the alternative ($pB=rBa=rBa$) also receiving strong support (Table 4.5). There was, however, strong support for lion detection being greater when wild dog were absent, based on both parameter estimates (i.e. $pA>rA$; Table 4.4) and model rankings (i.e. only models where $pA \neq rA$ receiving strong support in all HRS analyses; Table 4.5).

Within the home range (TUS), the SIF provided strong evidence for wild dog detection being negatively associated with that of lion ($\delta = 0.33 \pm 0.25$; Table 4.4, Fig. 4.4B). Moreover, detection of wild dog was greater when lion were absent ($pB>rBA/rBa$; Table 4.4), and, at sites used by lion, was greater when lion were not detected than when they were ($rBa>rBA$). This was also indicated by model rankings ($pB=rBA=rBa$ not receiving strong support; Table 4.5). On the other hand, there was little support for detection of lion within the home range differing when wild dog were also detected (based on models where $pA \neq rA$ and $pA=rA$ ranking similarly; Table 4.5).

Table 4.3. Summary of co-occurrence model rankings used to evaluate the role of interspecific interactions on occurrence of three sympatric large carnivores (lion, leopard, and wild dog) in Ruaha-Rungwa, at two spatial scales (equivalent to the home range selection (HRS) and the temporary use selection within the home range (TUS) scales). Interspecific interactions at the HRS scale were investigated across different levels of anthropogenic impacts, including across the whole landscape (HRS-ALL), within protected areas only (HRS-PA), within protected areas with regular law-enforcement only (HRS-PAS), and within trophy hunting areas only (HRS-HUNT). For each analysis, models in which site use of the subordinate species depends on the presence (ΨBA) or the absence (ΨBa) of the dominant species (conditional models, denoted as ψBa ≠ ψBA) were compared against models in which site use of the subordinate species is independent of the presence of the dominant species (unconditional models, denoted as ψBa = ψBA). Only the best-supported conditional and unconditional models from each analysis are presented; see Appendix 4.2 for full model rankings.

Model	AICc	ΔAICc	W_i	Npars	-2loglike
Lion-Wild Dog					
HRS-All					
ΨBA≠ΨBa	823.28	0.00	0.55	17	789.28
ΨBA=ΨBa	823.69	0.41	0.45	17	789.69
HRS-PA					
ΨBA≠ΨBa	796.12	0.00	0.56	17	762.12
ΨBA=ΨBa	796.65	0.53	0.44	17	762.65
HRS-PAS					
ΨBA≠ΨBa	380.44	0.00	0.52	13	354.44
ΨBA=ΨBa	380.59	0.15	0.48	13	354.59
HRS-Hunt					
ΨBA≠ΨBa	495.40	0.00	0.53	13	469.40
ΨBA=ΨBa	495.61	0.21	0.47	13	469.61
TUS					
ΨBA≠ΨBa	593.39	0.00	0.45	11	571.39
ΨBA=ΨBa	594.68	1.29	0.23	11	572.68
Lion-Leopard					
HRS-All					
ΨBA≠ΨBa	1284.63	0.00	0.77	16	1252.63
ΨBA=ΨBa	1287.01	2.38	0.23	16	1255.01
HRS-PA					
ΨBA≠ΨBa	1187.94	0.00	0.51	16	1155.94
ΨBA=ΨBa	1188.01	0.07	0.49	16	1156.01
TUS					
ΨBA≠ΨBa	3993.13	0.00	0.55	16	3961.13
ΨBA=ΨBa	3993.55	0.42	0.45	16	3961.55
Wild Dog-leopard					
TUS					
ΨBA≠ΨBa	936.79	0.00	0.4872	15	906.79
ΨBA=ΨBa	936.85	0.06	0.4728	15	906.85

A general model for detection (pA≠rA≠pB≠rBA≠rBa) was employed to model co-occurrence. ΨA = site use of the dominant species; ΨBA = site use of the subordinate species, when the dominant species is present; ΨBa = site use of the subordinate species, when the dominant species is absent. AICc = Akaike Information Criteria, adjusted for small sample size; nPars = number of parameters in the model; W_i = model weight; -2LogLike = twice the negative likelihood of the model.

Table 4.4. Site use (ψ), detection probability (p and r), and species interaction factors (SIF – phi and delta) parameter estimates and associated standard errors from the top-ranked model investigating co-occurrence between lion, leopard, and wild dog in Ruaha-Rungwa, at the different spatial scales and anthropogenic impact levels investigated.

	ΨA	**ΨBA**	**ΨBa**	***p*A**	***r*A**	***p*B**	***r*BA**	***r*Ba**	**φ**	**δ**
Lion-Wild Dog										
HRS-ALL	0.59	0.25	0.43	0.45	0.27	0.11	0.18	0.26	0.69	0.78
	(0.07)	(0.08)	(0.26)	(0.05)	(0.06)	(0.09)	(0.08)	(0.08)	(0.34)	(0.24)
HRS-PA	0.72	0.33	0.58	0.54	0.32	0.10	0.18	0.25	0.77	0.78
	(0.09)	(0.11)	(0.34)	(0.06)	(0.07)	(0.09)	(0.08)	(0.09)	(0.28)	(0.25)
HRS-PAS	0.86	0.55	0.72	0.76	0.30	0.22	0.17	0.21	0.95	0.86
	(0.08)	(0.17)	(0.43)	(0.09)	(0.08)	(0.13)	(0.09)	(0.07)	(0.12)	(0.30)
HRS-HUNT	0.65	0.34	0.50	0.50	0.31	0.14	0.21	0.29	0.77	0.75
	(0.12)	(0.14)	(0.23)	(0.07)	(0.10)	(0.10)	(0.10)	(0.10)	(0.37)	(0.31)
TUS	0.51	0.16	0.42	0.22	0.44	0.30	0.05	0.29	0.55	0.33
	(0.12)	(0.11)	(0.14)	(0.09)	(0.15)	(0.07)	(0.07)	(0.19)	(0.31)	(0.25)
Lion-Leopard										
HRS-ALL	0.53	0.77	0.65	0.26	0.47	0.44	0.52	0.50	1.46	1.02
	(0.07)	(0.06)	(0.06)	(0.11)	(0.04)	(0.06)	(0.05)	(0.06)	(0.45)	(0.06)
HRS- PA	0.73	0.89	0.86	0.19	0.48	0.46	0.51	0.44	1.02	1.08
	(0.10)	(0.05)	(0.09)	(0.11)	(0.05)	(0.06	(0.05)	(0.04)	(0.08)	(0.07)
TUS	0.47	0.50	0.45	0.19	0.49	0.42	0.23	0.33	1.06	0.81
	(0.06)	(0.06)	(0.06)	(0.05)	(0.03)	(0.03)	(0.03)	(0.04)	(0.09)	(0.07)
Wild Dog-Leopard										
TUS	0.26	0.38	0.42	0.38	0.36	0.38	0.41	0.21	0.92	1.46
	(0.07)	(0.14)	(0.09)	(0.08)	(0.09)	(0.05)	(0.11)	(0.08)	(0.29)	(0.34)

ψA = site use of dominant species; ψBA = site use of subordinate species, when the dominant species is present; ψBa = site use of subordinate species, when the dominant species is absent; ; pA = probability of dominant species being detected, when the subordinate species is absent; rA = probability of dominant species being detected, when the subordinate species is present; pB = probability of subordinate species being detected, when the dominant species is not present; rBA = probability of subordinate species being detected, when the dominant species is present and detected; rBa = probability of subordinate species being detected, when the dominant species is present but not detected; φ = SIF for occupancy: ratio of how much more (>1) or less (<1) likely the species are to co-occur at a site compared to what would be expected if the species occurred independently of each other; δ = SIF for detection: ratio of how much more (>1) or less (<1) likely the species are to be detected together in a survey compared to what would be expected if they were detected independently

Table 4.5. Summary of co-occurrence model rankings used to evaluate the role of interspecific interactions on detection of three sympatric large carnivores (lion, leopard, and wild dog) in Ruaha-Rungwa, at two spatial scales and at different levels of anthropogenic impacts (see main text and Table 4.3 for additional details). Only models with strong support (i.e. ΔAICc<2) are presented; for full model rankings see Appendix 4.2.

Model	AICc	ΔAICc	W_i	Npars	-2loglike
Lion-Wild dog					
HRS-All					
pA≠rA≠pB≠rBA≠rBa	823.28	0.00	0.41	17	789.28
pA≠rA≠pB≠rBA=rBa	823.98	0.70	0.29	17	789.98
pA≠rA≠pB=rBA=rBa	824.54	1.26	0.22	17	790.54
HRS-PA					
pA≠rA≠pB≠rBA≠rBa	796.12	0.00	0.43	17	762.12
pA≠rA≠pB≠rBA=rBa	796.77	0.65	0.31	17	762.77
pA≠rA≠pB=rBA=rBa	797.5	1.38	0.22	17	763.50
HRS-PAS					
pA≠rA≠pB≠rBA≠rBa	380.44	0.00	0.36	13	354.44
pA≠rA≠pB≠rBA=rBa	380.63	0.19	0.32	13	354.63
pA≠rA≠pB=rBA=rBa	380.64	0.20	0.32	13	354.64
HRS-Hunt					
pA≠rA≠pB=rBA=rBa	491.98	0.00	0.69	13	465.98
TUS					
pA≠rA≠pB≠rBA≠rBa	593.39	0.00	0.30	11	571.39
pA=rA≠pB≠rBA≠rBa	593.66	0.27	0.26	11	571.66
pA≠rA≠pB≠rBA=rBa	595.23	1.84	0.12	11	573.23
Lion-Leopard					
HRS-All					
pA≠rA≠pB≠rBA≠rBa	1284.63	0.00	0.31	16	1252.63
pA≠rA≠pB≠rBA=rBa	1284.73	0.10	0.30	16	1252.73
pA≠rA≠pB=rBA=rBa	1285.91	1.28	0.16	16	1253.91
HRS-PA					
pA≠rA≠pB≠rBA≠rBa	1187.94	0.00	0.49	16	1155.94
pA≠rA≠pB≠rBA=rBa	1189.57	1.63	0.22	16	1157.57
pA≠rA≠pB=rBA=rBa	1189.72	1.78	0.20	16	1157.72
TUS					
pA≠rA≠pB≠rBA≠rBa	3993.13	0.00	0.94	16	3961.13
Wild Dog-Leopard					
TUS					
pA≠rA≠pB≠rBA≠rBa	936.79	0.00	0.35	15	906.79
pA=rA≠pB≠rBA≠rBa	936.82	0.03	0.34	15	906.82

All detection models included the top-ranked model for site use (see Table 4.3). pA = probability of dominant species being detected, when the subordinate species is absent; rA = probability of dominant species being detected, when the subordinate species is present' pB = probability of subordinate species being detected, when the dominant species is not present; rBA = probability of subordinate species being detected, when the dominant species is present and detected; rBa = probability of subordinate species being detected, when the dominant species is present but not detected. AICc = Akaike Information Criteria, adjusted for small sample size; nPars = number of parameters in the model; W_i = model weight; -2LogLike = twice the negative likelihood of the model. In all analyses, "=" was used to designate parameters set as equal, while we used "≠" to designate parameters set as different

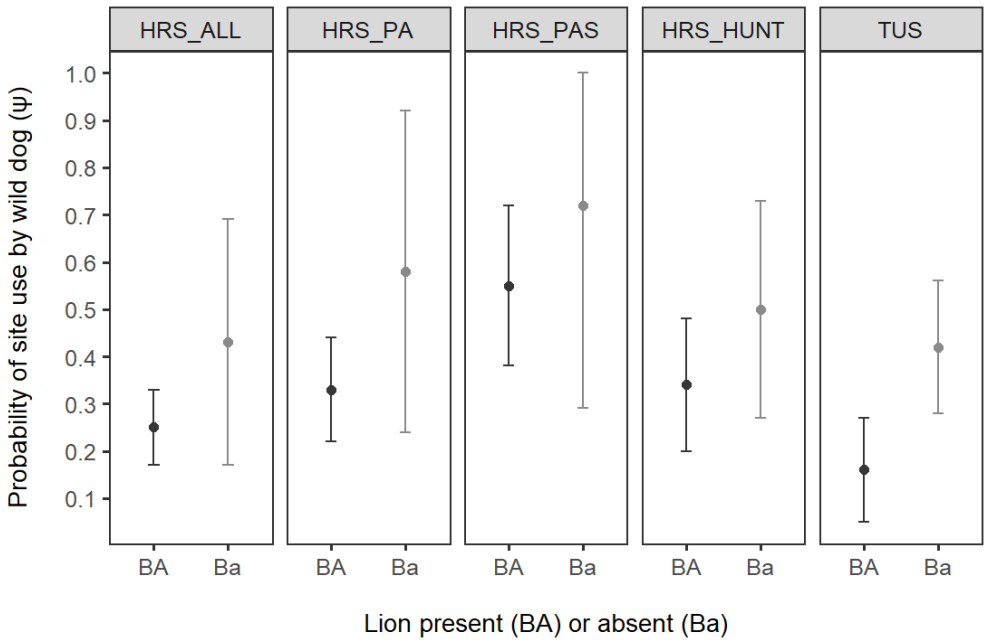


Figure 4.3. Mean probability of wild dog site use (with associated standard error) given the presence (BA) or absence (Ba) of lion, from the top-ranked model in the different analyses carried out across the Ruaha-Rungwa landscape (see text for details).

4.3.1.2. *Lion & leopard interspecific associations*

Due to leopard being detected at almost all sites within strongly-protected (HRS-PAS) and hunting (HRS-HUNT) areas, it was not possible to carry out single-species occupancy analyses for leopard in these sampling grids; as a result, co-occurrence between lion and leopard could also not be investigated within these sampling grids.

In the remaining analyses at the HRS scale, we found no evidence of interspecific exclusion of leopard by lion. On the other hand, both model rankings ($\Psi BA \neq \Psi Ba$; Table 4.3) and parameter estimates ($\Psi BA > \Psi Ba$, $\varphi > 1$; Table 4.4) indicated a positive association, with these effects being significant in one analysis (HRS-ALL: $\Psi BA = 0.77 \pm 0.06$ and $\Psi Ba = 0.65 \pm 0.06$, $\varphi = 1.46 \pm 0.45$; Table 4.4, Fig. 4.4A). Similar association effects were also observed at the TUS scale, although these were not significant (Tables 4.3 & 4.4, Fig. 4.4A).

The SIF for detection (δ) suggested positive associations in the detection of leopard and lion at the HRS scale, with this effect being significant in one of the two analyses (HRS-PA: $\delta = 1.08 \pm 0.07$; Table 4.4,

Fig. 4.4B). Parameter estimates and model rankings instead provided little evidence of leopard detection being affected by the presence of lion at the HRS scale (estimates of pBa, rBA, rBa are similar, Table 4.4; models where pB=rBA=rBa also receive strong support; Table 4.5). On the other hand, detection of lion was significantly greater when leopard were present (rA>pA; Table 4.4), as also supported by model rankings (pA≠rA, with no models where pA=rA receiving strong support; Table 4.5).

Within the home range (TUS), on the other hand, results revealed a negative association between detection of lion and leopard ($\delta = 0.81 \pm 0.07$; Table 4.4, Fig. 4.4B), and that detection of leopard was significantly lower when lion were present (pB≠rBA≠rBa being the only model with strong support, Table 4.5; pB>rBA/rBa; Table 4.4). Furthermore, leopard detection was greater at sites where lion were present, but not detected, than at sites where lion were present, and also detected (rBa>rBA; Table 4.4). Finally, detection of lion was greater when leopard were present (pA≠rA, Table 4.5; rA>pA, Table 4.4).

4.3.1.3. *Wild dog & leopard interspecific associations*

Due to the widespread detection of leopard and the relatively low number of detections of wild dog at the HRS scale, it was not possible to model co-occurrence between these species at this spatial scale.

Within the home range (TUS scale), there was little evidence of leopard habitat use being affected by wild dog presence, based on both model rankings (strong support for the unconditional model; Table 4.3) and parameter estimates (ΨBa similar to ΨBA, φ close to and overlapping 1; Table 4.4, Fig. 4.4A). Regarding co-detection, the SIF (δ) suggested a significant positive association between the two species ($\delta = 1.46 \pm 0.34$; Table 4.4, Fig. 4.4B). The effect of wild dog presence on leopard detection was, on the other hand, inconclusive: although model rankings suggested an effect (pB≠rBA≠rBa; Table 4.3), leopard detection when wild dog were not present (pB) was similar to that when wild dog were present and detected (rBA; Table 4.4). Finally, there was also little evidence of wild dog detection differing with leopard occurrence, based on models where pA=rA receiving strong support (Table 4.3), and on similar parameter estimates (pA and rA) in the unconditional model (Table 4.4).

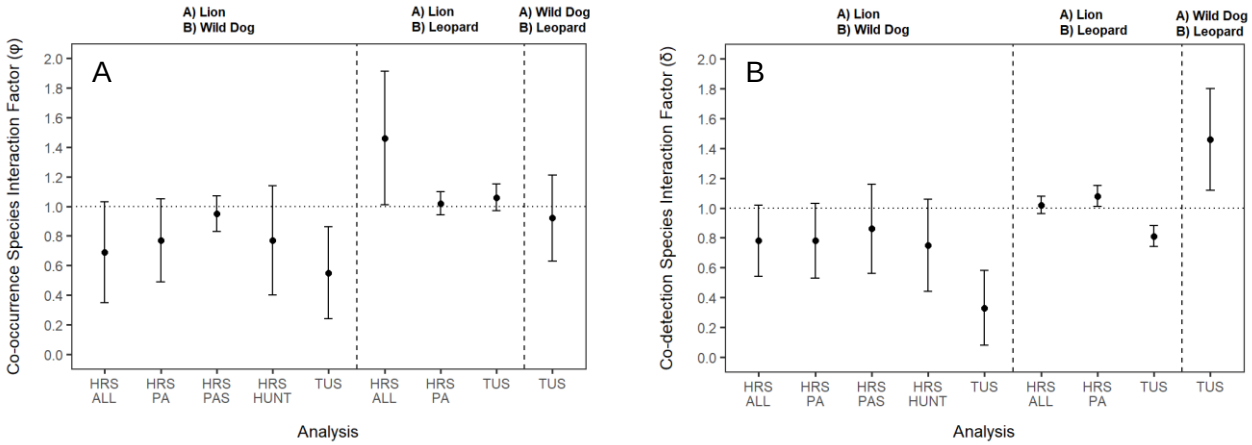


Figure 4.4. Species interaction factors (SIFs; with respective standard errors) representing the level of co-occurrence (φ; A) and co-detection (δ; B) between lion, leopard, and wild dog in Ruaha-Rungwa, for the top-ranked model for the different analyses carried out (see text for details). An SIF value exceeding 1 (dotted line) indicates that the species co-occur more often than expected; a value of less than 1 indicates that the species co-occur less often than expected; and a value of 1 indicates that the species are co-occurring randomly.

4.4. DISCUSSION

Intraguild interactions among large carnivores can have important impacts on the habitat use of subordinate species (Arim & Marquet, 2004). Nevertheless, although avoidance is often assumed to lead to costly displacement from preferred habitats or resources (e.g. Durant, 1998, 2000), recent evidence suggests that this may not always be the case (Balme et al., 2017; Miller et al., 2018; Swanson et al., 2016). Here, we employed two-species occupancy models to examine patterns of co-occurrence and co-detection between three sympatric large carnivores in a modern, mixed-use African conservation landscape, at two biologically relevant spatial scales, and assess the relative influence of interspecific interactions and habitat covariates in shaping their habitat use. Overall, our findings help shed light on an assemblage that has rarely been examined using statistical modelling approaches at this scale, and provide further evidence that intraguild effects are complex and species-specific (Swanson et al., 2016).

4.4.1. Interspecific effects between sympatric carnivores in Ruaha-Rungwa

4.4.1.1. *Lion & wild dog*

We found some evidence of interspecific exclusion of wild dog by lion at the coarser HRS scale. Although these effects were not statistically significant (Table 4.4), this may, at least in part, be due to the relatively low number of wild dog detections (a consequence of the species' wide ranging nature; Creel & Creel, 2002), which likely contributed to the relatively wide standard errors observed. The same issue was noted when modelling large carnivore co-occurrence in Asia (Steinmetz et al., 2013). Given this, and the evidence of spatial avoidance at all four analyses at this scale (Fig. 4.3; Table 4.2), including the SIF and associated SEs having a consistent effect and barely overlapping 1 (Fig. 4.4), it is unlikely that distributions of both species at this scale are independent of each other.

In addition, wild dog detection was lower at sites used by lion, and was negatively associated with that of lion. As detection of free-moving animals is influenced by movement rate, use intensity, and local abundance (Efford & Dawson, 2012; Ladle et al., 2018), these results suggest that wild dogs are either found at lower abundance in areas used by lions, that they use these areas more rarely (Robinson et al., 2014), or that they decrease their movements within them. Furthermore, as occupancy modelling does

not account for intensity of use or variations in species density (Hayward et al., 2009), it is possible that wild dog disproportionately avoid only areas with high densities of lion, contributing to the observed lack of significance at this scale. This is supported by single species analysis of the same data (Chapter 3), and by the fact that, where wild dog were absent, lion detection was significantly greater. Taken together, these results suggest that lion are influencing wild dog spatial patterns, and potentially population dynamics, at a landscape scale.

Our findings thus add to the growing body of literature suggesting spatial displacement of wild dog from areas of high lion density (Creel & Creel, 2002; Marneweck et al., 2019; Mills & Gorman, 1997; Vanak et al., 2013). Indeed, wild dog have been found to avoid optimal areas with high prey availability when these were also favoured by lions, which likely carries heavy demographic costs (Webster et al., 2012). However, because the models employed cannot directly infer the mechanisms of the underlying ecological interactions (MacKenzie et al., 2017), the observed effects could, at least in part, be a result of wild dog being unable to persist in areas of high lion use due to increased mortality, rather than solely avoidance (Creel & Creel, 1996; Groom et al., 2016; Speakman et al., 2016). Additional research is therefore recommended to disentangle these effects, and determine the relative role of each mechanism.

Furthermore, there was more evidence of landscape-scale avoidance of lion by wild dog when sampling across broader areas (HRS-ALL, HRS-PA), which included more impacted habitats, than when analyses were restricted to the better protected areas of the landscape (HRS-PAS). This supports hypotheses that intraguild interactions between predators increase with resource scarcity (Caro & Stoner, 2003; Donadio & Buskirk, 2006; Palomares & Caro, 1999). On the other hand, these findings could also be a result of wild dog avoiding some of the best protected areas of the landscape altogether, due to these exhibiting higher prey (TAWIRI, 2019) and therefore lion (Chapter 5) densities. Indeed, wild dog occurrence in Ruaha-Rungwa was greatest in miombo woodlands (Chapter 3), which exhibit intermediate prey and lion densities (Frost, 1996; TAWIRI, 2019; Chapter 5), and where wild dog are also likely subject to reduced rates of lion-inflicted mortality and kleptoparasitism, due to reduced visibility (Creel, 2001; Dröge et al., 2016; Mills & Gorman, 1997). Taken together, these findings

suggest that the observed preference for miombo woodlands by wild dog in Ruaha-Rungwa is likely due to this habitat acting as a refuge from high lion densities.

Our modelling also revealed strong evidence of wild dog avoidance of lion within the home range (TUS), with wild dog being more than twice as likely to use an area of their home range if this was not also used by lion. The fact that wild dog are less likely to be detected when lions are present or detected is further evidence of this, and suggests that, where they do share home ranges, wild dog exhibit strong fine-scale avoidance of lion, likely through olfactory cues and other fine-scale detection mechanisms (Webster et al., 2010, 2012). These finer-scale avoidance effects appear to be particularly strong, with this being the only analysis, for all species pairings and scales, where interspecific effects had a stronger influence than other resources or pressures on habitat use (Appendix 4.2).

Overall, our findings indicate multi-scale interspecific avoidance effects, with wild dog appearing to avoid areas of high lion density at a coarser scale, while also strongly avoiding lions at a finer scale in areas of lower lion density, where they do co-occur. Such evidence of spatial partitioning at multiple spatial scales reveal a particularly strong impact of lion on wild dog space use. Thus, our findings contribute to the increasing body of evidence supporting landscape-level impacts of lion on wild dog (Groom et al., 2016; Swanson et al., 2014), and showing that niche partitioning effects can occur across multiple spatial dimensions (Vanak et al., 2013). Our results also suggest that such effects are likely to be density dependent, and we recommend further research across gradients of densities of both species.

4.4.1.2. *Lion & leopard*

Contrary to our hypothesis, leopard appeared to act independently of lion, with no evidence of interspecific exclusion at either scale investigated. Instead, we observed positive spatial associations between the two species, at both scales. This aligns with increasing evidence that leopard do not spatially segregate from lions (Balme et al., 2017; Miller et al., 2018), with co-existence instead promoted through a combination of dietary partitioning (du Preez et al., 2017), behavioural adaptations (e.g. arboreal caching of prey; Bailey, 2005), and spatiotemporal avoidance at even finer scales than those assessed in our analysis (e.g. Balme et al. (2017) and Vanak et al (2013), who found that radio-

collared leopards vacated areas when within 50-100 m of lions). Indeed, the lower detection of leopard at the TUS scale when lion were also present reveals avoidance at a very fine spatial scale, likely through a combination of olfactory, acoustic, and visual cues (du Preez et al., 2015; Rafiq et al., 2020). Our findings thus further suggest that, while leopards do react to lions, they do not do so at a spatial scale that would result in broad-scale displacement or prevent leopard from accessing key resources (Miller et al., 2018). By responding reactively, and only avoiding preferred habitats immediately following lion presence, leopards likely minimise risk of encountering lions while still maintaining access to key resources (Vanak et al., 2013).

On the other hand, the positive co-occurrence patterns observed are likely a consequence of imperfectly modelled shared habitat preferences, with leopard and lion both independently selecting for similar areas of higher prey availability (at the HRS scale) and catchability (at the TUS scale; Chapter 3; Hopcraft et al., 2005). The positive associations in detections (at the HRS scale), the fact that lion detection was greater when leopard was present or detected (at both scales), and detection of leopard not being affected by lion presence (at the HRS scale), are all similarly probably consequences of both species selecting for similar areas within their home range, and/or of positively correlated abundances (Balme et al., 2017; Miller et al., 2018). This mirrors findings in impacted areas of Mozambique (Strampelli et al., 2018), suggesting that interspecific exclusion effects from lion are not strong enough to prevent leopards from sharing less disturbed areas of human-impacted landscapes with lions. Indeed, association between the two species was stronger when including more degraded areas (HRS_ALL), providing further support for intraguild interactions being more evident with habitat degradation and resource limitation (Harihar et al., 2011; Karanth et al., 2017; Odden et al., 2010).

Overall, it is likely that lion-inflicted leopard mortality resulting from sharing habitats is compensated by processes that reduce other causes of mortality (Balme et al., 2017; Boyce et al., 1999), increase reproductive success (Crooks et al., 1998), and/or decrease emigration (Karki et al., 2007), and our results suggest that pressure by lion is likely to only possibly exclude leopard at very high densities of the former (Caro & Stoner, 2003; Holt & Polis, 1997; Palomares & Caro, 1999), or in particularly unfavourable habitat conditions (Caro & Stoner, 2003; Heithaus, 2001; Karanth et al., 2017).

4.4.1.3. *Wild dog & leopard*

Although it was not possible to model wild dog and leopard co-occurrence at a landscape scale, there is little evidence of leopard habitat use within the home range being impacted by wild dog presence. Conversely, wild dog detection not varying with leopard presence suggests that wild dog occurrence is not impacted by leopard. Although interspecific competition is most prevalent where similarly sized species share similar prey species (Palomares & Caro, 1999), as is the case for leopard and wild dog (Hayward & Kerley, 2008), the observed effect is likely a result of leopard employing similar adaptations to those employed to coexist with lions (Rafiq et al., 2020). Furthermore, while leopards are mostly nocturnal, wild dog exhibit crepuscular hunting habits (Creel & Creel, 2002). This temporal segregation likely aids co-occurrence, as does the less consistent dominance relationship between these two species, with leopards having been known to kill adult wild dogs (Hayward et al., 2006).

4.4.1.4. *Relative effect of interspecific competition and other habitat factors in driving habitat use*

Results suggest that, in most cases, other habitat and anthropogenic effects play a more important role than interspecific pressures in driving habitat use of large African carnivores. The exception was the impact of lion on wild dog at the finer (within the home range) scale, which exhibited the single strongest association observed at this scale, thus revealing a particularly strong interaction. This is in line with studies elsewhere, which have found that other habitat requirements are generally more important than interspecific competition in structuring carnivore communities, even when evidence of such effects is present (Cruz et al., 2015; Estevo et al., 2017; Gompper et al., 2016; Gutiérrez-González & López-González, 2017; Nagy-Reis et al., 2017).

4.4.2. Conservation implications

The structure of carnivore communities has far-reaching impacts in terrestrial ecosystem, with intraguild interactions among predators and the resulting pressures on prey species having the potential to lead to cascading effects on vegetation structure and composition (Estes et al., 2011; Ripple et al., 2014; Roemer et al., 2009).

Our results indicate that the successful conservation of wild dog in modern African systems will require sufficient space and habitat heterogeneity to ensure the availability of competition refuges (Groom et al., 2016). By revealing that interspecific exclusion by lion is likely driving wild dog avoidance of the most prey-rich and well-protected areas of the landscape, our findings highlight the need for areas that are still strongly-protected, and host important prey bases, but which do not exhibit very high densities of lion (e.g. as is the case for miombo woodlands in Ruaha NP and in parts of Rungwa GR). This is especially the case since wild dog exhibit very low tolerances to habitat conversion (Chapter 3), thus precluding avoidance through the increased use of more anthropogenically-disturbed areas, a strategy employed by some subordinate predators (e.g. leopard with tiger; Kafley et al., 2019). As anthropogenic pressures increase across wild dog range, it will be critical that vulnerable populations are able to minimise detrimental effects of intraguild interference and predation. Conservation managers must therefore identify and ensure the effective protection of habitats (including beyond protected areas) which may be less rich in prey and in other charismatic large carnivores, but which can serve as key competition refuges for wild dog.

Our findings thus highlight the critical importance of landscape-scale conservation planning (Trombulak & Baldwin, 2010) for wild dog, and the need to include interspecific effects as part of a holistic approach to conservation planning, PA management, and species recovery programmes (Groom et al., 2016; Ritchie et al., 2012). By better understanding species interactions, particularly in light of anthropogenic disturbance, conservation managers will also be able to better predict how system changes may impact carnivore communities in modern systems (Rich et al., 2017); such predictions will be particularly relevant in response to global climate change, with rates of range expansion and contraction of species likely to be influenced by co-occurring species (Svenning et al., 2014).

Finally, our findings include some encouraging implications for large carnivore management, in that lion and leopard appear to be able to use the same areas without population-level repercussions, even in relatively impacted habitats. Knowledge of this should help align management strategies for both species, and streamline conservation interventions (Miller et al., 2018).

4.4.3. Methodological considerations & main study limitations

Our study highlights the importance of considering biological scale in habitat use investigations (Everatt et al., 2015; Hearn et al., 2018; Klaassen & Broekhuis, 2018), as the true extent of the impact of lion occurrence on wild dog would not have been evident from analyses restricted to a single spatial scale.

In addition, we show that conditional co-occurrence modelling can be successfully employed to study interspecific interactions from detection/non-detection sign survey data. Although individual-level interspecific interactions have been extensively studied at finer spatial and temporal scales through radio or GPS-based telemetry (Dröge et al., 2016; du Preez et al., 2015; Klaassen & Broekhuis, 2018; Swanson et al., 2016; Vanak et al., 2013), direct observation (Balme et al., 2017; Broekhuis et al., 2017; Creel & Creel, 1996), and co-occurrence modelling applied to camera trap data (Cusack et al., 2016; Miller et al., 2018), these methodologies must often rely on small sample sizes, and are typically not suitable or cost-effective enough to provide the population level insights that are necessary to inform landscape-scale management (Karanth et al., 2017). While co-occurrence models have been applied to investigate sympatric carnivore co-occurrence in Asia (e.g. Steinmetz et al., 2013; Sunarto et al., 2015) and the Americas (e.g. Gutiérrez-González & López-González, 2017; Sollmann et al., 2012), applications to large African carnivores have until now been few (Cusack et al., 2016; Miller et al., 2018), and, as far as we are aware, never using sign-based data. We believe that our study shows that the method holds significant promise to improve understanding of population-level mechanisms in African conservation landscapes, and we encourage similar studies elsewhere, particularly given the existing availability of sign-based detection/non-detection datasets (e.g. Crosmary et al., 2018; Everatt et al., 2019; Petracca et al., 2019; Henschel et al., 2016, 2020). We therefore encourage similar research elsewhere, across habitats, density gradients, and land use types, to ensure that the potential role of intraguild interactions is fully appreciated in conservation planning. Ideally, these should be complemented by intensive, finer-scale studies (such as through GPS collar data; e.g. Dröge et al., 2016), as we acknowledge the temporal scale of studies such as ours may be too broad to discern finer-scale interspecific dynamics. As a result of this, and because two-species occupancy models only show patterns in spatial distributions, and not information on the causality of observed patterns, we believe

both methods can provide complementary insights to help inform management. Finally, our study emphasizes the importance of also accounting for interspecific effects on detection when investigating co-occurrence, as recently highlighted by others (Barros et al., 2020).

The main limitation of the employed methodology, on the other hand, was our inability to model spotted hyaena and cheetah interspecific interactions. This was due to either low detections (cheetah) or high naïve occupancy and low heterogeneity in use (spotted hyaena). This is a shortfall of this investigation, particularly given the evidence of interactions between spotted hyaena and lion in the study area (Cusack et al., 2016). We nonetheless believe the method could be applied to these species in other settings (e.g. areas with higher densities of cheetah, or where spotted hyaena distribution is limited more heavily by anthropogenic or biotic factors). We also encourage the development of conditional co-occurrence models that can account for the lack of independence between spatially replicated sampling occasions, as done for single species models (Hines et al., 2010). This would allow future studies to be able to account for this potential source of bias, which we were not able to do, and which we acknowledge as being a limitation of our study.

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4.6. APPENDICES

Appendix 4.1. Co-occurrence modelling input data

Appendix 4.2. Co-occurrence model rankings

APPENDIX 4.1 – CO-OCCURRENCE MODELLING INPUT DATA

All input files (including detection matrices, site covariates, and detection covariates) for all species, at all scales, can be accessed at:

https://github.com/pstrampelli/Co-occurrence-Analyses-Input-Files

APPENDIX 4.2 – CO-OCCURRENCE MODEL RANKINGS

Outputs of the co-occurrence modelling, for all species and at all scales, can be accessed at:

https://github.com/pstrampelli/Co-occurence-Model-Rankings

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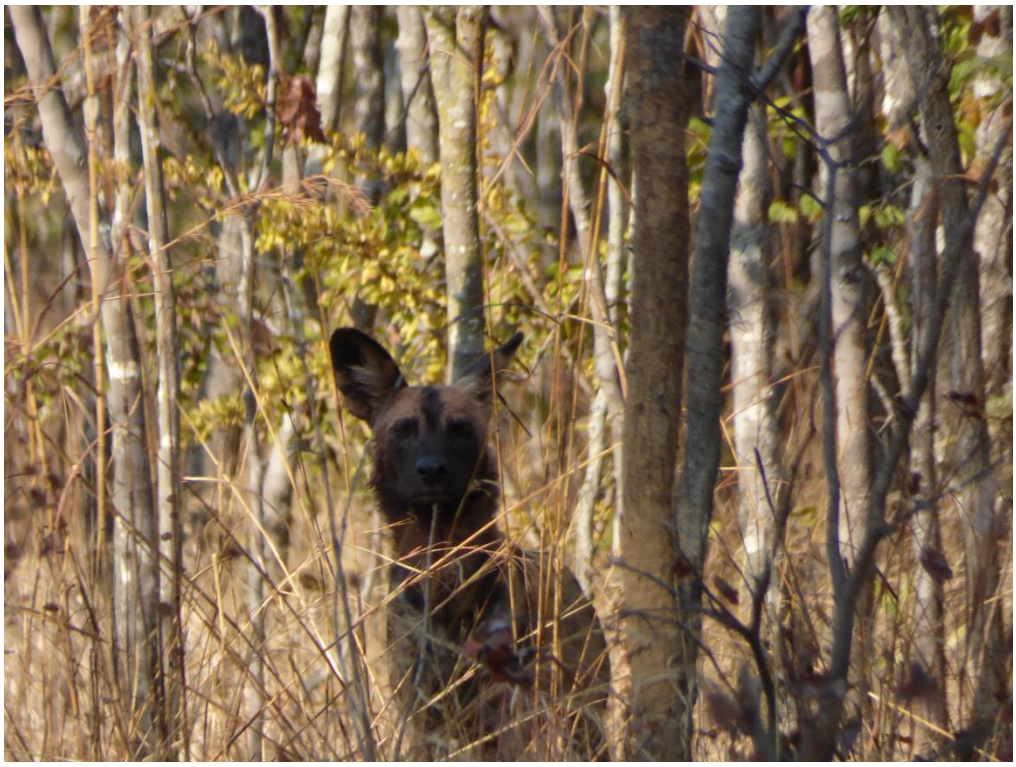
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Miombo woodlands cover approximately half of Ruaha-Rungwa (~25,000 km^2). Here, lion and spotted hyaena exist at intermediate densities, and the woodlands act as critical habitats for African wild dog and, surprisingly, cheetah.

Miombo areas also hold more dry season surface water than most habitats in the landscape, thus being of key importance for a range of herbivores in the drier months, including elephant, buffalo, zebra, giraffe, and sable & roan antelope.

CHAPTER 5

Spatially explicit density estimates from a globally important lion population in southern Tanzania: Implications for monitoring and conservation management



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Spatially explicit density estimates from a globally important lion population in southern Tanzania: Implications for monitoring and conservation management

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ABSTRACT

Accurate and precise estimates of population status are required to inform and evaluate conservation management and 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 landscape, a global lion stronghold for which no empirical estimates of status are available. In doing so, 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 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 management types. Finally, we discuss implications of our findings for the study area and for broader lion conservation management.

5.1. INTRODUCTION

The African lion (*Panthera leo*) is classified as Vulnerable by the IUCN (Bauer et al., 2016). As a result of its naturally low densities, large spatial requirements, and potential for conflict with humans, the species is particularly susceptible to extinction in anthropogenically impacted landscapes (Bauer et al., 2016), with lions currently estimated to occupy only 8% of their historical sub-Saharan range (Riggio et al., 2013; Wolf & Ripple, 2017).

Due to rising anthropogenic threats and the species' strong ecological, economic and cultural value, lions have received increased conservation attention in recent years (Bauer et al., 2020; Macdonald et al., 2016). However, although an accurate understanding of population status is fundamental for the management of threatened species (Campbell et al., 2002), most lion populations across Africa still lack reliable population status estimates, particularly outside of southern Africa (Bauer et al., 2016). Although Tanzania, particularly southern and western Tanzania, supports crucial lion strongholds (Bauer et al., 2016; MNRT, 2016), most of its lion populations lack published baseline status assessments. Furthermore, there is a strong geographical bias, with most research having focused on populations in well-protected photographic tourism areas in the north of the country (Belant et al., 2016, 2019; Kissui & Packer, 2004; Packer et al., 2005). This lack of population assessments hinders effective conservation management of populations, by impeding activities such as population monitoring, the evaluation of management interventions, and the setting of sustainable use quotas (Mills, 1991).

This is particularly relevant to Tanzania's conservation landscape, where the majority of protected areas (PAs) permit trophy hunting. State-owned trophy hunting PAs cover about 234,000 km^2, compared to ~104,000 km^2 of National Parks (photographic tourism areas; MNRT, 2018); these therefore form a crucial component of Tanzania's conservation framework, and comprise an important proportion of the lion's geographical range in the country (MNRT, 2016). Partly as a result of the vast number and size of PAs dedicated to trophy hunting, Tanzania is Africa's most popular destination for hunting of wild lions (Lindsey et al., 2013). Trophy hunting has been argued to have substantial potential to foster conservation of wildlife, particularly large carnivores, by creating incentives for the retention of land

under wildlife-based uses, with a relatively low ecological footprint (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2012). If poorly managed, however, it can negatively impact large carnivore populations, potentially to such an extent that they are no longer viable in the long term (Creel et al., 2016; Packer et al., 2010). Although offtake quotas in Tanzania are set and reviewed annually (MNRT, 2016), the paucity of empirical information on the status of hunted lion populations leads these to be based on generalised estimates of sustainable offtake (MNRT, 2016; Packer et al., 2010), rather than on reliable population estimates, as recommended by sustainable use guidelines (IUCN, 2012). Addressing these knowledge gaps is therefore considered a conservation priority in the country (TAWIRI, 2009).

In recent years, advances in spatially explicit capture-recapture (SECR) modelling have facilitated the estimation of the status of populations, by allowing density to be estimated directly as a state parameter (Borchers & Efford, 2008; Royle & Young, 2008). SECR models have since been employed to estimate lion population density based on unstructured search-encounter surveys relying on direct observation (Braczkowski, Gopalaswamy, Nsubuga, et al., 2020; Elliot et al., 2020; Elliot & Gopalaswamy, 2016; Gogoi et al., 2020); however, collecting such data can challenging in areas where populations exist at low densities, or where individuals are elusive due to human persecution (Henschel et al., 2020). For many readily individually-identifiable large carnivores, this issue has been circumvented by applying SECR models to remotely-triggered camera trap data, with this becoming the standard monitoring protocol for a range of species (Green et al., 2020), including leopard (e.g. Strampelli et al., 2018), tiger (e.g. Karki et al., 2013), and jaguar (e.g. Boron et al., 2016). However, the lack of easily identifiable pelage patterns on lions has resulted in this methodology being applied to the species only a handful of times, and only at single sites within a landscape (Kane et al., 2015; Rich et al., 2019), preventing comparisons across habitats and land management types.

Here, we estimate lion population density through SECR modelling of modern white-flash camera trap data for the first time, using a double-blind observer identification process to also assess the reliability of the method. Our study area is the Ruaha-Rungwa landscape, a vast, mixed-use conservation complex in south-central Tanzania; although considered one of only four lion strongholds in East Africa (Riggio et al., 2013), no published empirical lion population density estimates are available for this area, which

includes the region's second largest National Park and some of Tanzania's most important trophy hunting areas. We modelled lion density at four sites in Ruaha-Rungwa: two within different habitats in Ruaha National Park (a well-protected photographic tourism area), one in Rungwa Game Reserve (a well-protected trophy hunting area), and one site in a less-strictly protected community-managed buffer area (MBOMIPA Wildlife Management Area). We provide the first spatially explicit density estimates for a lion population in Tanzania, and explore the implications of our findings for lion conservation management and monitoring both in the study area and across Africa.

5.2. METHODS

5.2.1. Study area

The Ruaha-Rungwa ecosystem is a ~50,000 km^2, unfenced multiple-use conservation complex in south-central Tanzania, and is a globally valuable ecoregion and a Key Landscape for Conservation (European Commission, 2016; Olson et al., 2001). The largest PA in the complex is Ruaha National Park (NP), which at 20,226 km^2 is the second largest in East Africa. Only photographic tourism is permitted within the NP, and the area receives relatively high levels of on-the-ground law enforcement. To the north of the NP are Rungwa (9,175 km^2), Kizigo (5,140 km^2), and Muhesi Game Reserves (2,720 km^2; GRs). These are also strict PAs, but with consumptive use of wildlife through trophy hunting as their primary revenue generation mechanism. To the east of Ruaha NP are MBOMIPA (947 km^2) and Waga Wildlife Management Areas (344 km^2; WMAs), less-strictly protected community-managed PAs, which form a buffer between Ruaha NP and unprotected village lands. MBOMIPA experiences moderate levels of on-the ground law enforcement, and although both photographic tourism and trophy hunting are permitted, neither were taking place at the time of study. A less-strictly protected Game Controlled Area (GCA) and Open Area (OA) complete the PA complex (Fig. 5.1).

Ruaha-Rungwa is located at the intersection between three ecoregions: southern *Acacia-Commiphora* bushland and grasslands, and both Central Zambezian and Eastern miombo woodlands and grasslands (Olson et al., 2001). The climate of the region is semi-arid to arid, with an average annual precipitation of 600 mm (Fick & Hijmans, 2017). The Great Ruaha River, forming the boundary between Ruaha NP and MBOMIPA WMA, is a key dry season water source for wildlife in the system. The complex is home to all of eastern Africa's large carnivore species, and has been identified by the Tanzania Wildlife Research Institute (TAWIRI) as a priority for large carnivore research and conservation in the country (TAWIRI, 2009).

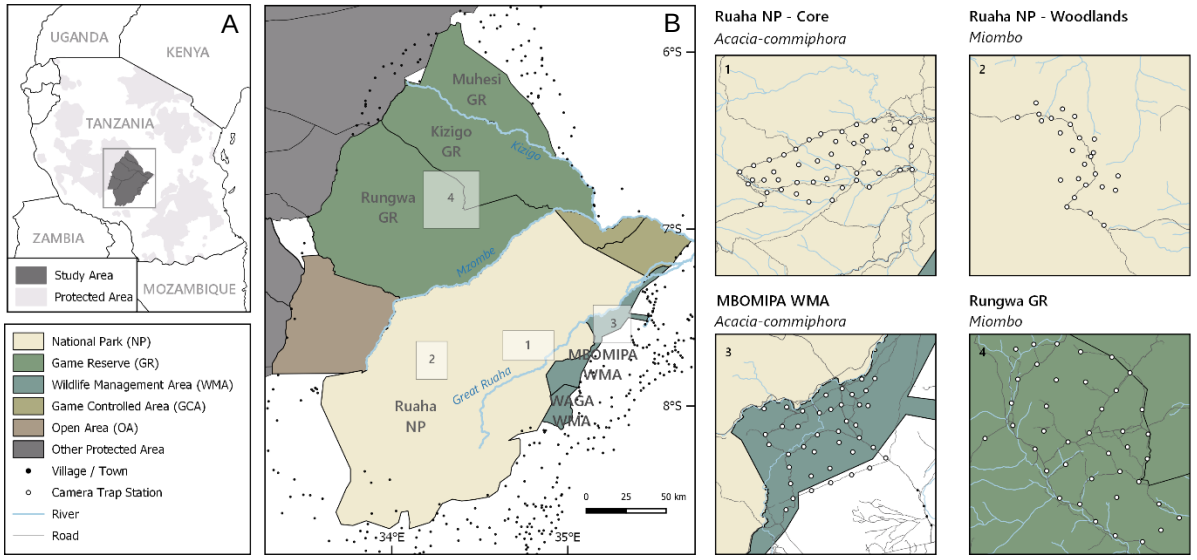


Figure 5.1. The Ruaha-Rungwa conservation landscape (B), located within the geographical context of Tanzania's protected area network (A). Protected areas not typically considered part of the Ruaha-Rungwa conservation complex are shaded in grey in (B). Map includes the largest rivers in the region. Only villages in close proximity of the PA complex are shown. Insets 1 – 4: camera traps survey grids carried out in 2018 and 2019.

5.2.2. Camera trap survey design

We carried out four systematic camera trap surveys at different sites in Ruaha-Rungwa, between June and November 2018 and July and October 2019. All surveys took place in the dry season. Survey grids consisted of paired camera trap stations (Cuddeback Professional Color Model 1347, Non Typical Inc., Wisconsin, USA). Spacing between stations was based on estimated female lion dry season home range size in the study area (~170 km^2, based on satellite collar data; RCP, unpublished data), to ensure that all individuals in the survey area had a non-zero capture probability (Noss et al., 2013). Survey grids were designed so that the sampled area exceeded male dry season home range size (~290 km^2; RCP, unpublished data), whenever logistical constraints allowed for this. Survey duration for each grid was restricted to three months; this is generally considered appropriate for minimising demographic closure violations, and is consistent with previous studies of large felids (Alexander et al., 2015; Karanth, 1995).

Between June and September 2018, forty-four stations (88 cameras) were deployed in the core tourist area of Ruaha NP, a well-protected and prey-rich (TAWIRI, 2019) *Acacia-Commiphora* habitat near the Great Ruaha River, a key source of surface water in the dry season (Fig. 5.1; Table 5.2). Between August and November 2018, twenty-six stations (52 cameras) were set out in an area of miombo

woodland habitat in the north-west of Ruaha NP. The area also receives regular on-the-ground law enforcement, and relatively few anthropogenic impacts. Forty stations (80 cameras) were deployed in MBOMIPA WMA between September and November 2018, in primarily A*cacia-Commiphora* habitat, also near the Great Ruaha River and relatively prey-rich. Due to its proximity to unprotected village lands, however, the area experiences greater levels of human disturbance. Finally, between July and October 2019, forty stations (80 cameras) were deployed in central Rungwa GR, within the actively hunted Rungwa Ikiri block, in an area of miombo woodlands and seasonal floodplains. The area experiences relatively high levels of law enforcement, and intermediate levels of illegal human impacts.

Camera stations were set out along roads, game trails, and near water points, to maximise captures of large carnivores (Tobler et al., 2013). At each station, cameras were mounted on trees at a height of 30 – 40 cm, on opposite sides of the road or trail, facing inwards, in order to attempt to photograph both flanks of animals. Cameras were camouflaged and placed within metal protective cases secured with binding wire, to prevent damage by animals or people.

5.2.3. Density estimation

Population density was modelled within a maximum-likelihood spatially explicit capture-recapture (SECR) framework, using the package *secr 4.2.0* (Efford, 2020) in *R v. 3.6.3* (R Core Team, 2019). SECR models estimate density explicitly while accounting for imperfect detection (Royle et al., 2009), and simulations have shown that the method provides accurate results for social animals, such as lions, even when their ranging patterns may violate assumptions of independence between activity centres and individuals' movements (López-Bao et al., 2018). A SECR approach was chosen over spatial mark-resight (SMR), which has been employed for lions elsewhere (Kane et al., 2015; Rich et al., 2019) because: a) current SMR models do not permit the modelling of sex as a covariate, and preliminary analyses revealed significant differences in model parameters for males and females; and b) the use of white-flash cameras resulted in a relatively high proportion of captures being suitable for individual identification, permitting the application of SECR models without the risk of biasing estimates.

For each of the four survey grids, we used captures of the flank with the greater number of photographs, to avoid biasing capture probabilities for individuals whose flanks could not be matched (Augustine et al., 2018). Lions were identified and sexed from a combination of whisker spots, scars and marks, pelage patterns (for younger individuals), mane size and shape (for males), and nose shape. Only individuals estimated to be > 1 year of age (i.e. considered adults or sub-adults; Miller et al., 2016) were considered. Due to the relative novelty of this method for lion, we used a double-blind observer identification process to determine how differences in photo identification between individual researchers might influence density estimation, as previously done for other species (e.g. puma, *Puma concolor*; Kelly et al., 2008; Rich et al., 2014). For two of the four sites (MBOMIPA WMA & Rungwa GR), we had two investigators independently identify and classify photographs of lion, with each kept unaware of how the other had identified and categorised captures. This approach was only implemented at two sites (randomly selected) as this was deemed sufficient to assess the extent of consensus in identifications.

Individual capture and trap effort histories were developed following recommended procedures (Efford, 2020), with each night (24 hours – 12:00 pm to 12:00 pm) treated as a separate sampling occasion (Goldberg et al., 2015). For the two sites with two investigators carrying out identifications, three capture histories were created: two from the classification of each investigator, and one employing only the captures for which both had independently agreed on the identification (the final 'consensus' input data; Rich et al., 2014). To ensure that the identifications were completely independent, no comparisons were carried out post-identification, so that the consensus capture history consisted only of captures for which the consensus had been reached independently. All input files can be accessed in Appendix 5.1.

Buffer size was increased around each grid until density estimates stabilised, to ensure that no individual outside the buffer area could be captured (Noss et al., 2013). As camera traps do not physically capture animals, stations were classified as proximity detectors, acting independently of one another (Efford, 2020). A half-normal detection function was fitted to model the distance between home range centre and camera stations (Boron et al., 2016; Efford, 2004). This describes the probability of capture (P) of an individual *i* at a trap *j* as a function of distance *d* from the activity centre of the individual to the trap, as follows: $Pij = g0 \exp(-dij^2/(2\sigma^2))$, where *g0* is the capture probability at the home range centre, and σ

is a spatial parameter related to home range size (Efford, 2004). A Bernoulli or binomial encounter model was fitted to the data, as this is most relevant to camera trap studies (Royle et al., 2009).

As lions exhibit sex-specific traits in their ranging behaviours (Loveridge et al., 2009), sex was modelled as a covariate by fitting a hybrid mixture model (Efford, 2020). In addition, as large carnivores often use roads to travel (Mckenzie et al., 2012), whether a station was located on- or off-road might impact the capture parameter (*g0*). The impact of sex on both the capture (*g0*) and movement (σ) parameters, and of road placement on *g0*, were therefore tested by comparing eight alternative models: secr.0 (null model), secr.sex.g (*g0* varies between males and females), secr.sex.s (σ varies between males and females), secr.sex (both *g0* and σ vary between males and females), secr.road (*g0* varies between on and off road stations), secr.road.sex.g (*g0* varies between sex and between on and off road stations), secr.road.sex.s (*g0* varies between on and off road stations, and σ varies between males and females), and secr.road.sex (*g0* varies between on and off road stations and between males and females, and σ varies between males and females; Boron et al., 2016; Efford, 2020; Table 5.1). In the Rungwa GR grid, cameras were moved on- and off-road a few times during the survey, following requests from management. As a result, the covariate 'road' was not included, meaning only four models were tested (secr.0, secr.sex. secr.sex.s, secr.sex.g). Models were ranked using the Akaike Information Criterion, adjusted for small sample size (AICc; Burnham & Anderson, 2004), and the top-ranked model was employed to derive density and other parameter estimates.

Table 5.1. Candidate models of population density fitted to lion camera trap data, testing the influence of sex and camera location (on- or off-road) on model parameters. Models containing the covariate 'road' were not tested in the Rungwa GR grid.

Model	g0[1]~	σ[2]~
secr.0	1	1
secr.sex.g	sex	1
secr.sex.s	1	sex
secr.sex	sex	sex
secr.road	road	1
secr.road.sex.g	road + sex	1
secr.road.sex.s	road	sex
secr.road.sex	road + sex	sex

[1] g0 = capture probability at home-range centre

[2] σ = spatial movement parameter

[3] 1 = parameter modelled as constant

5.3. RESULTS

5.3.1. Survey effort

Across the four survey sites, a total sampling effort of 11,447 camera trap nights across 150 camera stations yielded 1,491 images of lion.

Including only images of the flank with the greatest number of captures for each survey grid resulted in 590 unique capture events of lion (Table 5.2). Proportions of identifiable photographs varied between surveys (Table 5.2), but were always above the recommended 70% threshold for SECR modelling (Rich et al., 2019).

Table 5.2. Survey design details and summary results for the four camera trap grids in Ruaha-Rungwa

	Ruaha NP (Core)	**Ruaha NP (Woodlands)**	**MBOMIPA WMA**	**Rungwa GR**
Primary habitat type	*Acacia-Commiphora*	Miombo	*Acacia-Commiphora*	Miombo
Survey duration (nights)	83	90	70	91
Stations	45	26	40	40
Trap nights	3,380	2,172	2,689	3,206
Mean trap nights per camera	80	84	67	80
Average station spacing	1.96 km	1.88 km	2.08 km	3.46 km
Survey area[1]	223 km^2	152 km^2	270 km^2	555 km^2
Buffer width	15 km	18 km	15 km	18 km
Flank with most captures	Right	Left	Right	Left
Independent lion captures[2]	390	67	53	80
Proportion of identifiable captures[2,3]	90%	79%	95%	83%
Individuals recorded[2,3]	48	14	18	21
Female	30	9	9	11
Male	18	5	9	10
Recapture rate[2,3,4]	74%	71%	67%	61%

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

[2] Based on the flank with most captures for each grid. Includes both identifiable and non-identifiable captures

[3] For sites with two investigators (MBOMIPA WMA & Rungwa GR) figures from the consensus capture histories are presented

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

5.3.2. Inter-observer variability in identification

In the MBOMIPA WMA survey grid, of the 37 right-side photographs of males, observers agreed on 36 (i.e. both independently categorised the picture as the same individual (n=35), or as unidentifiable and to be discarded (n=1)), equal to 97% agreement. Of the 23 right-side photographs of females, observers agreed on all 23 (100%), both categorising all pictures as the same individuals. Overall agreement was therefore 98% (59/60). Both observers identified 9 males and 9 females from the dataset.

In the Rungwa GR survey grid, of the 46 left-side photographs of males, observers agreed on 40 (same individual (n=36) and unidentifiable and to be discarded (n=4)), equal to 87% agreement. Of the 47 right-side photographs of females, observers agreed on 42 (same individual (n=30) and unidentifiable and to be discarded (n=12)), equal to 89% agreement. Overall agreement was therefore ~88% (82/93). The consensus capture history comprised 10 males and 11 females.

Overall agreement for both sides and sexes was therefore 92% (141/153 captures).

5.3.3. Population density

Buffer width stabilised at between 15 – 18 km for the different grids (Table 5.2). The top ranked model was secr.road.sex.g for the Ruaha NP core grid, secr.0 for the Ruaha NP miombo grid, secr.sex.s for the MBOMIPA WMA grid, and secr.road.sex.s for the Rungwa GR grid (Table 5.3; see Appendix 5.3 for full model outputs). Sex was therefore found to have a significant impact on movement in two of the four grids, and on capture probability in two, while camera location (on- or off-road) affected capture probability in one grid.

Population density was highest in the Ruaha NP core grid, at 6.12 ± 0.94 lions per 100 km^2. The next highest density of 4.05 ± 1.02 (Investigator 1) / 4.06 ± 1.03 (Investigator 2 & consensus) per 100 km^2 was estimated for the MBOMIPA WMA grid. This was followed by 2.44 ± 0.55 (Investigator 1), 2.30 ± 0.53 (Investigator 2) and 2.25 ± 0.52 (consensus) per 100 km^2 in Rungwa GR, and 1.75 ± 0.62 per 100 km^2 in the miombo of Ruaha NP (Table 5.4, Fig. 5.2).

Table 5.3. Model rankings of models describing lion population density for four survey grids in Ruaha-Rungwa, based on AIC corrected for small sample size (AICc). Top-ranked model shaded in grey.

Model[1]	nPar[2]	LogLik[3]	AICc[4]	ΔAICc[5]	AICc Wt[6]
Ruaha NP – Core (*Acacia-Commiphora*)					
secr.road.sex.g	6	-709.4524	1432.954	0.000	0.5366
secr.road.sex	7	-708.2932	1433.386	0.432	0.4324
Secr.road.sex.s	6	-712.3028	1438.654	5.700	0.0310
secr.road	5	-717.3033	1446.035	13.081	0.0000
secr.sex	6	-716.2892	1446.627	13.673	0.0000
secr.sex.g	5	-717.8330	1447.095	14.141	0.0000
secr.sex.s	5	-720.9387	1453.306	20.352	0.0000
secr.0	4	-726.1470	1461.224	28.270	0.0000
Ruaha NP – Woodlands (miombo)					
secr.0	4	-143.5402	299.525	0.000	0.7961
secr.road	5	-143.3846	304.269	4.744	0.0743
secr.sex.s	5	-143.5010	304.502	4.977	0.0661
secr.sex.g	5	-143.5402	304.580	5.055	0.0636
secr.road.sex.s	6	-143.3487	310.697	11.172	0.0000
secr.road.sex.g	6	-143.3841	310.768	11.243	0.0000
secr.sex	6	-143.4991	310.998	11.473	0.0000
secr.road.sex	7	-143.3482	319.363	19.838	0.0000
MBOMIPA WMA (*Acacia-Commiphora*)[7]					
secr.sex.s	5	-134.4441	283.888	0.000	0.6828
secr.road.sex.s	6	-134.0510	287.738	3.850	0.0996
secr.sex.g	5	-136.4340	287.868	3.980	0.0933
secr.sex	6	-134.1178	287.872	3.984	0.0932
secr.road.sex.g	6	-136.1072	291.851	7.963	0.0127
secr.0	4	-140.5996	292.276	8.388	0.0103
secr.road.sex	7	-133.7871	292.774	8.886	0.0080
secr.road	5	-139.9246	294.849	10.961	0.0000
Rungwa GR (miombo)[7]					
secr.sex	6	-177.3467	372.693	0.000	0.6794
secr.sex.s	5	-180.0976	374.195	1.502	0.3206
secr.sex.g	5	-188.9111	391.922	19.129	0.0000
secr.0	4	-191.3137	393.127	20.434	0.0000

[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

[2] Number of model parameters

[3] Log-likelihood

[4] Akaike Information Criterion, adjusted for small sample size

[5] Difference from best ranking (lowest AIC) model

[6] AICc model weights

[7] For sites with two investigators (MBOMIPA WMA & Rungwa GR), results from the consensus capture histories are presented; see Appendix 5.3 for the complete model rankings

Table 5.4. Population density parameter estimates for the four survey grids, based on the top-ranked model

secr Model Parameter[1]	Estimate ± SE	95% CI
Ruaha NP (core)		
g0 (F, on-road)	0.014 ± 0.002	0.012 – 0.017
g0 (M, on-road)	0.024 ± 0.003	0.019 – 0.030
g0 (F, off-road)	0.006 ± 0.001	0.004 – 0.010
g0 (M, off-road)	0.011 ± 0.003	0.007 – 0.017
σ	3584 ± 174	3259 - 3941
D	**6.12 ± 0.94**	4.54 – 8.26
Ruaha NP (woodlands)		
g0	0.009 ± 0.003	0.005 – 0.016
σ	4926 ± 828	3551 – 6833
D	**1.75 ± 0.62**	0.88 – 3.45
MBOMIPA WMA		
Investigator 1		
g0	0.018 ± 0.004	0.014 – 0.028
σ_F	1670 ± 206	1313 – 2125
σ_M	2963 ± 379	2308 – 3804
D	**4.05 ± 1.02**	2.49 – 6.60
Investigator 2 & Consensus		
g0	0.017 ± 0.004	0.011 – 0.028
σ_F	1691 ± 212	1325 – 2159
σ_M	2995 ± 394	2317 – 3871
D	**4.06 ± 1.03**	2.49 – 6.62
Rungwa GR		
Investigator 1		
g0 (F)	0.019 ± 0.006	0.009 – 0.037
g0 (M)	0.006 ± 0.002	0.004 – 0.011
σ_F	2107 ± 255	1663 – 2670
σ_M	5816 ± 909	4289 – 7887
D	**2.44 ± 0.55**	1.58 – 3.78
Investigator 2		
g0	0.007 ± 0.001	0.004 – 0.010
σ_F	3294 ± 408	2586 – 4196
σ_M	5395 ± 698	4191 – 6945
D	**2.30 ± 0.53**	1.47 – 3.59
Consensus		
g0 (F)	0.020 ± 0.007	0.009 – 0.041
g0 (M)	0.006 ± 0.002	0.04 – 0.011
σ_F	2023 ± 264	1569 – 2610
σ_M	5816 ± 909	4289 – 7887
D	**2.25 ± 0.52**	1.40 – 3.48

[1] D = Population density, defined as the number of adult and sub-adult lions per 100 km^2; g0 = capture probability at home range centre; σ = spatial movement parameter related to home range size; F = female; M = male

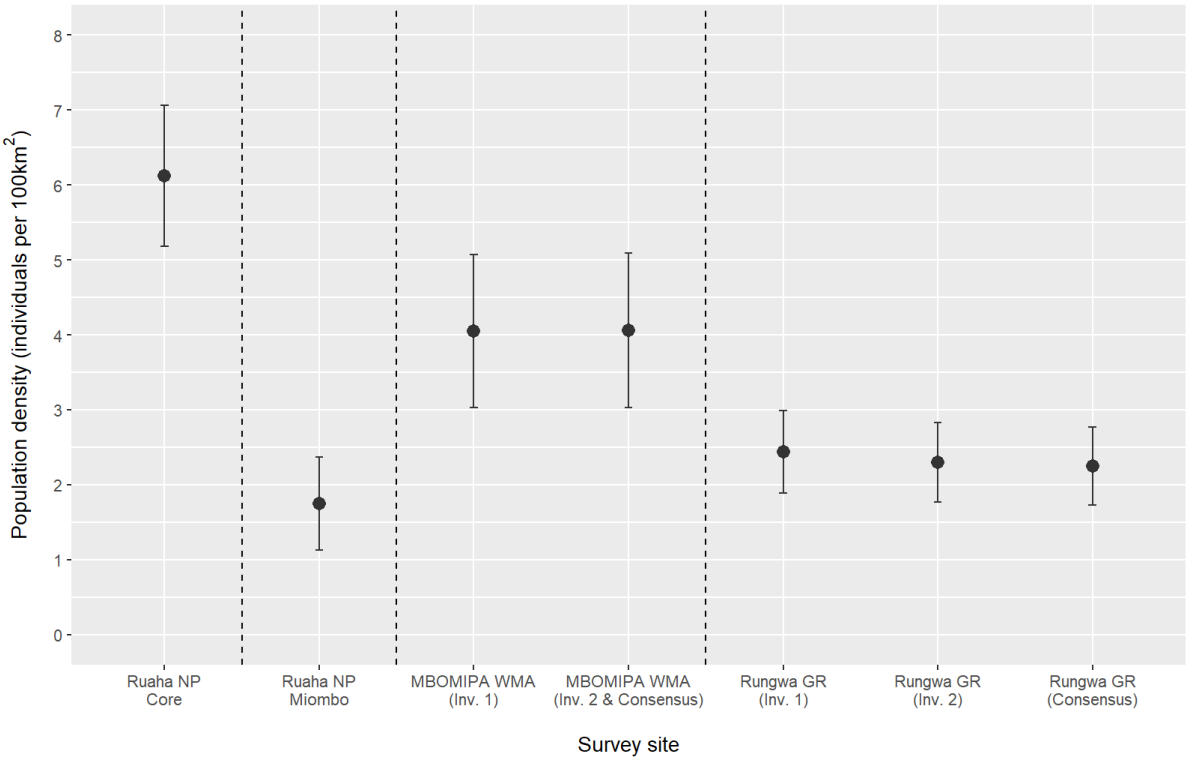


Figure 5.2. Lion population density estimates (and associated standard errors) for the four surveyed sites in Ruaha-Rungwa. For sites where a double-blind multiple investigator approach was employed (MBOMIPA WMA and Rungwa GR), density estimates from individual capture histories, as well as from an independently-reached consensus capture history, are presented.

5.4. DISCUSSION

Reliable population estimates are critical for conservation planning, and to develop sustainable management strategies for large carnivores (Campbell et al., 2002). Here, we showcase the applicability of a relatively novel approach, providing robust baseline lion population density estimates across different habitat and land management types in the Ruaha-Rungwa landscape, a globally important yet understudied conservation stronghold for the species (Bauer et al., 2016). These are the first spatially explicit lion population density estimates from Tanzania, and include some of the first published densities from a trophy hunting area. Our findings also provide some of the first insights into a lion population in a Central Zambezian miombo habitat.

5.4.1. SECR and camera traps to assess and monitor lion populations

Understanding how habitats, land management strategies, or interventions affect lion densities is critical for their conservation, and accurate population estimates are required to avoid misinformed management decisions (Hayward et al., 2015). However, few estimates with sufficient levels of precision are currently available for lion populations (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Dröge et al., 2020), resulting in decisions often being based on non-empirical methods and data (Bauer et al., 2016; Elliot & Gopalaswamy, 2016).

We show that, provided certain conditions are met (see below), camera trap surveys combined with SECR modelling can be an effective way to obtain robust and relatively precise density estimates for a lion population, across a variety of habitats and land management regimes. Inter-observer differences in photo identification did not lead to significant differences in density estimates (Fig. 5.2; Table 5.4). Inter-observer agreement was particularly high in the survey grid with higher road density (WMA dataset; 98%), highlighting the value of placing cameras on roads. Nevertheless, even in the dataset with lower levels of agreement (88%; Rungwa GR), density estimates from the two independent investigators and their consensus were similar. Inter-observer agreement in identification was also higher than reported in similar investigations with pumas (Kelly et al., 2008; Rich et al., 2014), possibly due to being facilitated by variation in manes of male lions. This indicates that it is possible to reliably

identify lions from high quality, white-flash camera trap pictures, and we therefore encourage practitioners to further explore applications of this method to help guide science-based conservation management of lion populations. We recommend this approach (including double-blind identification, where possible) be used instead of, or as a complement to, SECR modelling through direct observation (Elliot & Gopalaswamy, 2016) in areas where direct observation is challenging (due to low densities, closed habitat, or lions being particularly elusive), or where status assessments are also required for other large carnivore species (leopard, spotted hyaena). Either method could also be supplemented with non-invasive DNA-based analysis of scats, also within a SECR framework, to increase precision of estimates (Gopalaswamy et al., 2012) and provide insights into connectivity between populations (Burton et al., 2018). Integrating telemetry data from GPS collars to improve the precision of parameter estimates also warrants further exploration (Murphy et al., 2019). Regardless of the type of data employed, density estimates based on SECR modelling will be comparable across areas and over time. Thus, because all these data collection methods hold promise, we recommend studies comparing their relative suitability and effectiveness across sites, as well as their integration into single frameworks.

At the same time, our study revealed some limitations of the methodology, which should be taken into account if implementing similar surveys elsewhere. Firstly, camera traps must use white (xenon) flash, as pilot studies revealed that most night-time photographs from infrared variants are not suitable to effectively distinguish individual lions. In addition, both capture and identification are aided by stations being located on roads or large trails, as is the case for other large carnivores (e.g. jaguars; Tobler et al., 2013). Nevertheless, a good road network is not a strict requirement: although our study grid in the miombo woodlands of Ruaha NP had a single road traversing the grid area (Fig. 5.1), capture and identification rates were still within acceptable margins for SECR modelling (Table 5.2; Hedges et al., 2015; Rich et al., 2019).

In addition, SECR methodologies are likely to be challenging and/or costly to implement at the scales required to obtain overall estimates of density over vast, heterogeneous landscapes. Thus, although precise estimates from well-chosen representative areas can inform the management of wider landscapes (Dröge et al., 2020), as shown by our study, we encourage efforts to further develop

improved stratification protocols for SECR-based methodologies, to obtain mean densities across wider areas from representative sites (Efford & Fewster, 2013; Royle & Converse, 2014). Until then, and in areas where SECR methodologies are not viable, we recommend supplementing these targeted surveys with alternative, coarser-level efforts, such as sign-based occupancy surveys (Everatt et al., 2019; Henschel et al., 2020), to provide complementary landscape-scale status indicators.

Finally, we echo Elliot & Gopalaswamy (2016) in cautioning against the comparison of density estimates obtained through different methods (e.g. spatial versus non-spatial techniques), even from the same area. Doing so may identify trends in population status that are instead a result of the contrasting interpretation of the state variable of interest (population density) by different methods, and thus lead to misleading conservation inferences.

5.4.2. Lion densities across habitats and land management types in Ruaha-Rungwa

Lion population density was highest in the core tourist area of Ruaha NP, at 6.12 ± SE 0.94 adult and sub-adult lions per 100km^2. In addition to receiving strong formal protection and relatively high levels of law enforcement, the area also holds some of the highest dry season prey densities in the landscape, due to the presence of the Great Ruaha River and other important surface water refuges, and to the grassland habitat being able to support high grazer biomass year-round (TAWIRI, 2019). The high observed densities are therefore in line with our knowledge of the species' ecology: both legal protection and on-the-ground law enforcement have been found to have a strong positive effect on lion persistence and occurrence (Everatt et al., 2015; Henschel et al., 2016; Chapter 3), and lion densities generally increase with greater availability of prey (Ferreira & Funston, 2010).

Although lions have been found to reach population densities as high as 17 per 100 km^2 in the Maasai Mara (Elliot & Gopalaswamy, 2016), most populations exhibit densities of 0.5 – 4 individuals per 100 km^2 (Bauer et al., 2016; although note that most densities have been estimated through index methods, making direct comparisons difficult). Our results therefore identify the area in Ruaha NP near the Great Ruaha River as supporting one of the highest lion densities reliably recorded in Africa. Furthermore, although the survey grid was located relatively near the river (grid centre point distance = 13.9 km),

and incorporated other important dry season surface water sources, it was not located along the river itself, suggesting that lions may exist at even greater local densities in the landscape.

Lion population density in MBOMIPA WMA was estimated at 4.06 ± SE 1.03 individuals per 100 km^2 (consensus estimate). Although slightly lower than in the core area of Ruaha NP, this is still high for the species (Bauer et al., 2016). The survey grid was located in similarly highly productive habitat, even closer to the Great Ruaha River (grid centre point distance = 6.3 km), with relatively high dry-season prey densities (TAWIRI, 2019). However, the area is more anthropogenically impacted, with probability of occurrence of illegal human activity approximately nine times greater in the MBOMIPA study grid area than in the core area of Ruaha NP at the time of study (Chapter 3). Although Tanzania's WMAs are geared towards revenue generation for local communities through photographic tourism or trophy hunting (Moyo et al., 2016), neither of these were taking place in MBOMIPA at the time of the study, resulting in little revenue being generated from the PA. Consequently, although funding support from conservation organisations enabled the start of anti-poaching patrols just prior to data collection (in March 2018; STEP, 2019), law enforcement in previous years had been considerably lower than in adjacent Ruaha NP (STEP, pers. comm.), which likely affected lion densities both directly (e.g. through snaring – Lindsey et al., 2011) and indirectly (e.g. through prey depletion from bushmeat poaching – Rosenblatt et al., 2016). Impacts may further be exacerbated by the area's lack of tourist presence, which has been shown to act as a deterrent to illegal activities (Jachmann et al., 2011; Saikim et al., 2016), and vulnerability to edge effects (Woodroffe & Ginsberg, 1998), as a result of MBOMIPA's elongated shape and position as a buffer zone between Ruaha NP and unprotected village lands. This is likely to particularly be the case due to adjacent village lands experiencing very high levels of human-lion conflict, with at least 17 lions killed in retaliation for livestock predation in MBOMIPA and adjacent community lands between 2017 and 2020 (RCP, unpublished data).

There also appears to be a strong gradient in density within MBOMIPA itself, as 90% of lion detections occurred near the Great Ruaha River, further from the boundary with village lands (Appendix 5.2). Although this is likely partly a consequence of anthropogenic impact gradients, there are also few alternative sources of dry season surface water in the area, suggesting that the observed density gradient

is likely driven by a combination of both biotic and anthropogenic factors. Further evidence is provided by lions moving shorter distances in MBOMIPA than in the core area of Ruaha NP (σ; Table 5.4), yet existing at lower population densities, due to individuals being concentrated near the river rather than using the available habitat evenly (as was instead more the case in the NP). These patterns are likely a consequence of prey being concentrated along the river due to the lack of alternative water sources, and highlight the indirect importance of dry season surface water for lions (Davidson et al., 2013).

Although lower than densities observed near the Great Ruaha River, the lion density estimated in the Ikiri block of Rungwa GR (2.25 ± SE 0.52 lions per 100 km^2; consensus estimate) is still higher than, or similar to, densities obtained using SECR methods elsewhere (Braczkowski, Gopalaswamy, Nsubuga, et al., 2020; Rich et al., 2019). Thus, even though miombo woodlands are a low-productivity habitat (Campbell et al., 2007; Frost, 1996), supporting relatively low ungulate biomass (estimated at only 20-30% of that expected with comparable rainfalls in other savannah habitats; Frost, 1996), our findings indicate that lions can nevertheless exist at intermediate densities in miombo habitat. It is also likely that mortality from trophy hunting is having an impact on lion population density in Rungwa GR, as shown to be the case in hunted populations elsewhere (Mweetwa et al., 2018; Rosenblatt et al., 2014), including in Tanzania (Brink et al., 2016; Packer et al., 2009, 2010). On the other hand, trophy hunting operators in Tanzania are required to carry out supplementary protection and law-enforcement activities, and these are often not replaced once hunting operators vacate an area (MNRT, 2016; TAWA, pers. comm.). Patrol staff numbers have been shown to play a key role in lion persistence (Henschel et al., 2016), and low illegal human activity was the strongest predictor of lion occurrence across PAs in Ruaha-Rungwa (Chapter 3). Thus, while mortality from hunting will negatively impact lion densities in the Ikiri block of Rungwa GR, the active management and investments associated with the presence of hunting operators are likely also mitigating other potential sources of mortality for lions. Furthermore, since 2015 Rungwa Ikiri has been a priority in the landscape for increased law-enforcement interventions, in the form of concerted investments in protection and support to the Tanzania Wildlife Management Authority (TAWA)'s operations, including by the Southern Tanzania Elephant Project (STEP, 2019), the Wildlife Conservation Society (WCS; WCS, 2020), and the U.S.

Department of State (U.S. Embassy in Tanzania, 2016). Thus, while it is difficult to ascertain the exact impact of each individual law-enforcement support measure, it is likely they all play a part in improving the conservation outlook of lions in the area.

Finally, the lowest lion population density was estimated in the miombo woodlands in Ruaha NP (1.75 ± SE 0.62 individuals per 100 km^2), with a density lower (albeit not significantly) than in similar habitat in Rungwa GR. Aerial surveys and relative abundance indices from camera trap data suggest that densities of most herbivores are higher in the Rungwa Ikiri area than in the miombo woodlands area surveyed in the NP (TAWIRI, 2019; Appendix I), likely as a result of the greater availability of dry season surface water and lower precipitation in Rungwa Ikiri (herbivore biomass in miombo has been found to decline as precipitation increases, contrary to the general trend in African savannahs; Coe et al., 1976; Frost, 1996). These are likely to be the primary drivers of the observed differences between the two miombo sites surveyed, particularly since anthropogenic disturbance was found to be moderate at both sites, and slightly greater in Rungwa Ikiri (Chapter 3).

Conversely to densities, the movement parameters (σ) were greatest in the two miombo woodland grids (Table 5.4), indicating that lions are moving greater distances than in the higher prey density riverine habitats of the Great Ruaha river valley. This further suggests that differences in densities between miombo and *Acacia-Commiphora* habitats are likely primarily driven by biotic rather than anthropogenic drivers. Although an alternative explanation could be increased poaching of prey, causing lions to have to travel farther to forage, the relatively low levels of poaching pressures observed at both sites (Chapter 3; this study) make this unlikely. The fact that incorporating the effect of sex on movement (σ) improved density estimation in two of the four grids (Table 5.3), with males exhibiting wider ranging patterns than females, is in line with the literature (Loveridge et al., 2009).

5.4.3. Implications for conservation policy and management

Our results suggest that lion populations can exist at intermediate densities even in trophy hunting areas, provided strong protection and sustainable practices are in place, and that on-the-ground investments such as law enforcement, rather than overarching management strategy (i.e. photographic or trophy

hunting tourism), are more important for lion conservation. Lion offtake quotas across Tanzania, including in Rungwa GR, were historically greater than the recommended threshold of sustainable harvest for lions of 0.5 per 1,000 km^2 (MNRT, 2016; Packer et al., 2010). However, following the implementation of the 2010 Tourist Hunting Regulations, offtakes declined considerably, with offtake in Rungwa GR falling below the recommended threshold, to 0.41 ± 0.19 lions per 1,000 km^2, between 2011 and 2016 (MNRT, 2016). The proportion of hunted lions below the commonly recommended minimum age (6 years; Begg et al., 2018; Whitman et al., 2007), the hunting of which has been shown to lead to high probabilities of local extirpation (Creel et al., 2016), also decreased considerably following the implementation of the new regulations (MNRT, 2016). These policy changes have likely improved densities of hunted lion populations in the landscape, including in Rungwa Ikiri (although lion ageing has been argued to not always be easily achievable by hunting operators in Tanzania, which may affect compliance; Gayo et al., 2020). However, while the surveyed hunting block exhibited relatively high levels of law enforcement, there is evidence that not all blocks in the landscape receive comparable conservation investments (Chapter 3; TAWA, pers. comm.). Thus, while we encourage our findings to be employed to guide management in Rungwa Ikiri, including quota setting, we caution against extrapolation to other areas, and instead recommend similar surveys in other blocks, to ensure management is guided by site-specific insights. We recommend camera trap based SECR or alternative robust methodologies as scale-appropriate monitoring tools in hunting areas, ideally through a multi-stakeholder collaborative initiative. Such efforts would improve the long-term sustainability of quotas, and promote long-term persistence of populations (IUCN, 2012).

The high density of lions estimated in a community-run WMA highlights the potentially important role of community lands for large carnivores, and their importance in minimising edge effects for core PAs (Woodroffe & Ginsberg, 1998). Although WMAs in Tanzania have been shown to have the potential to secure high densities of herbivores (Kiffner et al., 2019), our study is one of the first to assess the efficacy of a WMA at protecting a large carnivore population (see also Appendix I). The fact that MBOMIPA appears relatively effective at this is encouraging, particularly since 38 WMAs have been gazetted or are planned across the country (Bluwstein & Lund, 2018; Kicheleri et al., 2018).

Nevertheless, the lack of conservation-based revenue in MBOMIPA, and in WMAs elsewhere in the country (USAID, 2013), risks jeopardising long-term community participation, which is essential for their success (Keane et al., 2020; Moyo et al., 2016). Promoting revenue generation through conservation-oriented activities, and thus helping overcome the high opportunity costs faced by communities committing their land to conservation, should therefore be seen as a conservation priority in the country (Lindsey et al., 2014; USAID, 2013). This is particularly the case for WMAs such as MBOMIPA, located in highly productive areas, whose contribution to the ecosystem is likely considerably greater than their relatively small size may indicate. Furthermore, while findings of ecological success should be seen in a positive light, the proliferation of wildlife populations may have negative repercussions for people adjacent to wildlife areas (Salerno et al., 2016). Indeed, the high levels of lion retaliatory killings in and around MBOMIPA (Dickman et al., 2014) suggest that this is the case in the study area, and we therefore recommend the continued prioritisation of human-carnivore conflict mitigation efforts in adjacent unprotected lands (RCP, 2020)

The confirmation that lions can exist in Tanzanian miombo woodlands at intermediate densities also has important conservation significance. Although almost two thirds of lion range in Tanzania is in primarily miombo habitat (Bauer et al., 2016; Olson et al., 2001), with this also being an important habitat for lion strongholds in Mozambique and Zambia (Bauer et al., 2016; Riggio et al., 2013), lion populations in miombo woodlands have until now received comparatively lower research attention, particularly in central and western Tanzania (Bauer et al., 2016; TAWIRI, 2009; but see Kiffner et al., 2009). We therefore encourage additional studies on the ecology and conservation status of lions in miombo areas, particularly due to most such areas in Tanzania being trophy hunting and/or less-strictly protected areas (e.g. GCAs, OAs WMAs; MNRT, 2016).

Finally, by revealing significant heterogeneity in lion densities across the landscape, our results bring attention to the importance of sampling across habitats and land management types within a landscape, and not only in the areas likely to host the highest densities, which can lead to erroneous population inferences (Smallwood & Schonewald, 1996; Suryawanshi et al., 2019). Our analyses also suggest that high density pockets, such as the Great Ruaha river valley in Ruaha-Rungwa, are likely to be

particularly important for lion populations, and act as population sources for the wider area. As heterogeneous densities are common in large carnivore populations occupying diverse landscapes (Sarmento & Carrapato, 2019; Silver et al., 2004), the identification of such areas should be seen as a priority for threatened lion populations. Much like the availability of reliable population assessments, understanding such density gradients will be essential for the effective management of lion populations, by enabling the prioritisation of areas of key conservation importance.

5.4.4. Additional methodological considerations & main study limitations

Although consensus between investigators was high, no communication or comparisons between investigators took place, to ensure independence in identification. It is therefore likely that consensus would be even greater if this had been instead permitted, and this should be explored in future efforts.

The two sampling grids in miombo habitat exhibited the greatest proportion of captures which had to be discarded (21% in Ruaha NP, and 17% in the consensus history of Rungwa GR). While such proportions of unusable captures are still acceptable for SECR modelling (Rich et al., 2019), it is possible that density estimates from these two sites may as a result exhibit a slight negative bias.

In addition, although we discuss the importance of ensuring representative surveying, we were not able to deploy a grid in *Acacia-commiphora* areas of the landscape that are not located near an important dry season surface water source. These areas, which are more arid and include the escarpment of Ruaha NP, comprise a significant portion of the landscape, and, based on prey and sign surveys (TAWIRI, 2019; Chapter 3), may exhibit the lowest natural densities of lion within Ruaha NP. Thus, it is likely that heterogeneity within the landscape is even greater than results indicate, and future surveys should target this habitat, to ensure that efforts are representative of the study population.

5.4.4.1. *Potential violations of model assumptions*

The assumption of SECR models that all individuals are uniformly and independently distributed over the state space (in our case, the survey grid) are inherently violated by social species such as lions. However, simulation have shown that SECR models can nevertheless be reliably applied to species violating these assumptions, with minimum impact on density estimates (Efford et al., 2009; López-

Bao et al., 2018). This has led SECR models to be considered appropriate and commonly employed for a range of social species, from primates (Arandjelovic & Vigilant, 2018) to wolves (Roffler et al., 2019).

Survey grids are recommended to be larger than the estimated average male home range size (Noss et al., 2013; Tobler & Powell, 2013). Based on preliminary lion home range size from satellite collar data (RCP, unpublished data), this was potentially achieved for three of the four camera trap grids; on the other hand, it is likely that the survey grid in the miombo woodlands of Ruaha NP (152 km^2) does not fully meet this assumption. This reduced grid size was a result of lack of accessibility in the area, and may have resulted in artificially lowered movement parameters (σ), which in turn would lead to density estimates exhibiting a positive bias (Foster & Harmsen, 2012). Nevertheless, simulations suggest that even assuming particularly large home ranges (400 km^2) and low detection probabilities at home range centre ($g0 = 0.01$), the resulting density bias would be less than 10% (Tobler & Powell, 2013). Additionally, simulations indicate that reduced grid size is not as much of an issue as only surveying high density 'hotspots' (Suryawanshi et al., 2019), which we made efforts to avoid. Nonetheless, we recommend future studies attempt to avoid violating this assumption, whenever possible.

Considering the estimates for σ (Table 5.4), and the general recommendation that maximum trap spacing should be around 2σ (Sollmann et al., 2013; Sun et al., 2014), the spacing employed in all grids was more than adequate, and is very unlikely to have left 'holes' in the grid.

Capture-recapture models assume there is no misidentification of individuals (Efford, 2004), and the fact that identifications varied slightly between the two investigators suggests this assumption was likely violated to some extent. Nevertheless, results of the double-blind approach employed, as well as the density estimates being very similar, indicate that misidentification was very low.

Finally, the fact that our estimates were obtained over a relatively short survey period (3 months) reduced concerns over population closure (Karanth & Nichols, 1998).

5.5. ACKNOWLEDGEMENTS

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5.6. APPENDICES

Appendix 5.1. SECR Input Files

Appendix 5.2. Detection Maps

Appendix 5.3. Full SECR Model Outputs

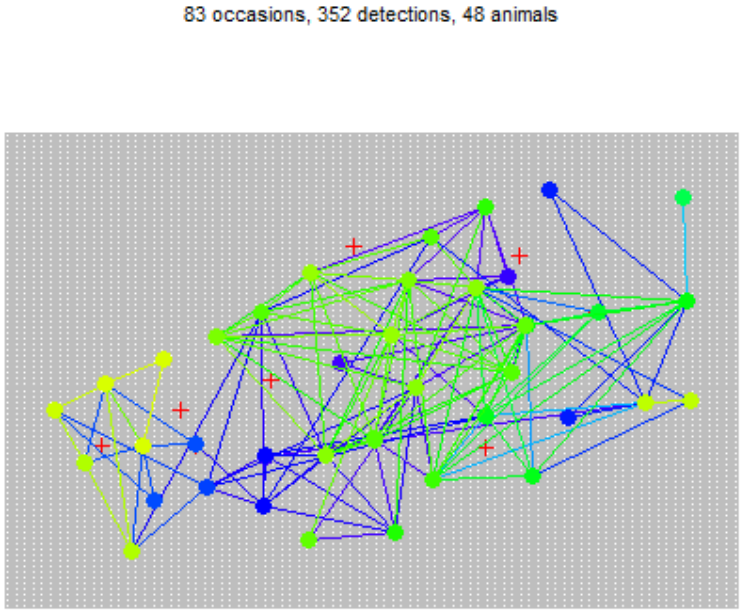
APPENDIX 5.1 – SECR INPUT FILES

All SECR input files, for all analyses, can be accessed at:

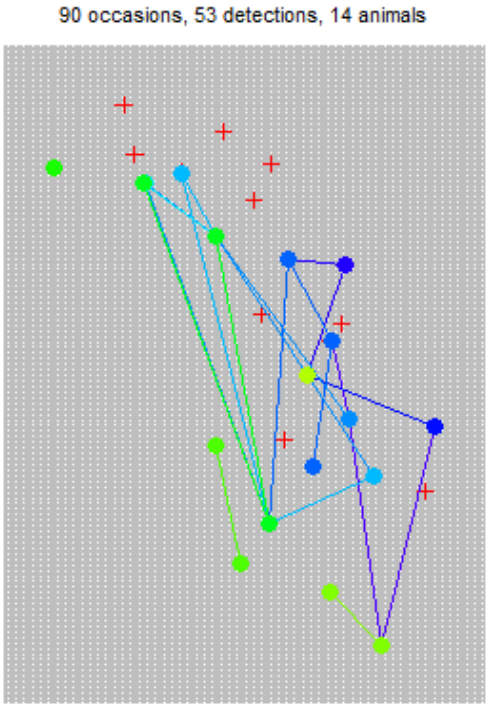
https://github.com/pstrampelli/SECR-Input-Files

APPENDIX 5.2 – DETECTION MAPS

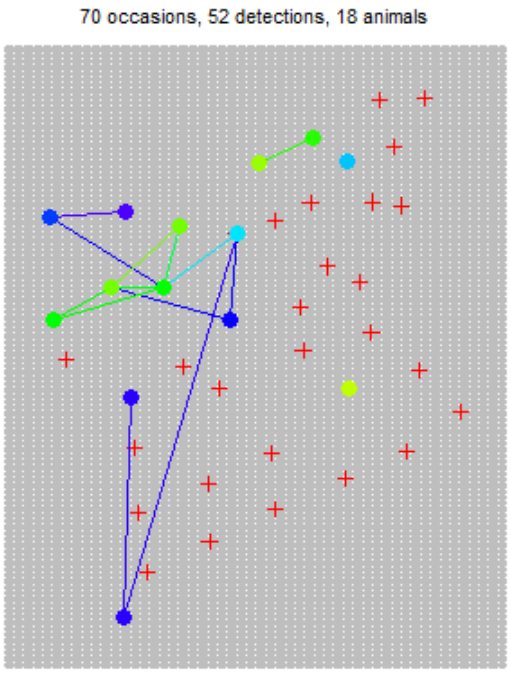
Ruaha NP (Core)



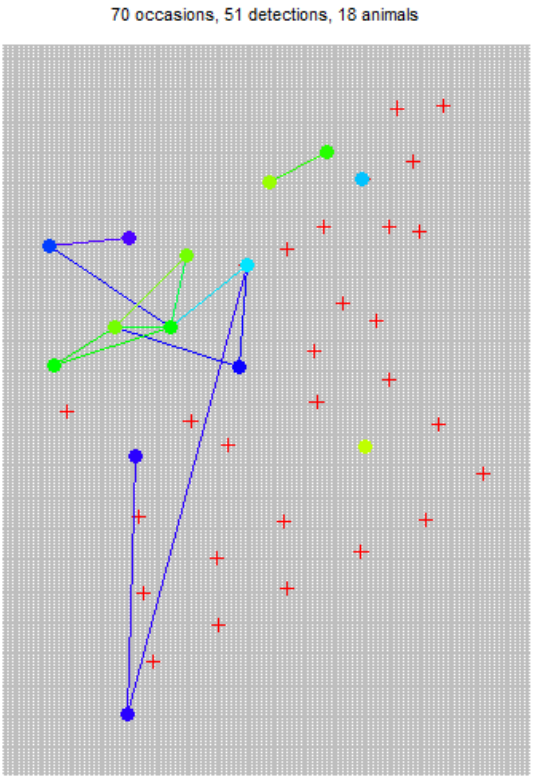
Ruaha NP (Woodlands)



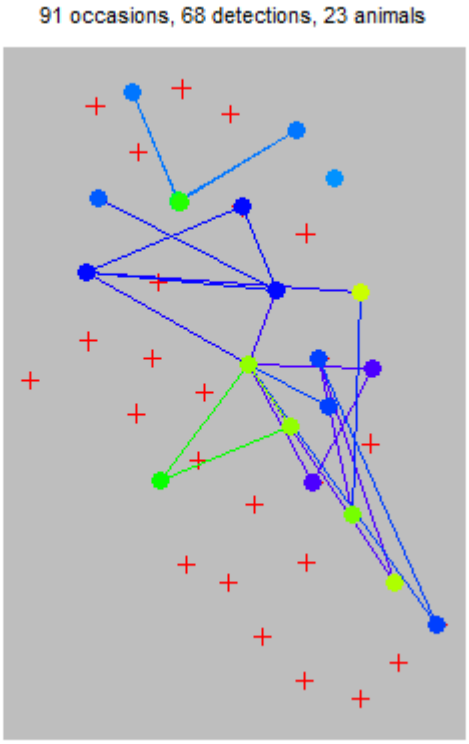
MBOMIPA WMA (Investigator 1)



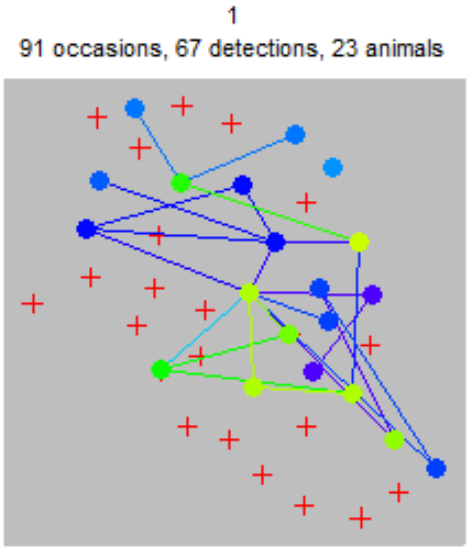
MBOMIPA WMA (Investigator 2 & Consensus)



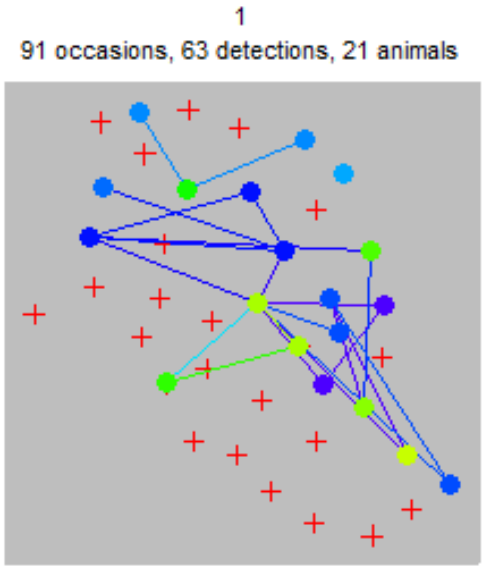
Rungwa GR (Investigator 1)



Rungwa GR (Investigator 2)



Rungwa GR (Consensus)



APPENDIX 5.3 – FULL SECR MODEL OUTPUTS

Full SECR model outputs, from all analyses, can be accessed at:

https://github.com/pstrampelli/Full-SECR-Modelling-Outputs

5.7. REFERENCES

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The Ruaha escarpment. Comprising approximately one fifth of the NP (~4,000 km^2), the area is very dry between June and November, and wildlife densities are low.

However, this portion of the PA complex is believed to be important for African wild dog and cheetah, and possibly for striped hyaena. Understanding the relative seasonal importance of different landscape components is essential for successful conservation planning.

CHAPTER 6

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



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Insights into the status and distribution of cheetah (Acinonyx jubatus) in an understudied potential stronghold in southern Tanzania

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ABSTRACT

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 south-central Tanzania. We employed data from four methods (systematic camera trap surveys, sign surveys, community camera trapping, and observations by photo-tourism guides) to improve knowledge of this understudied 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 provide some of the first evidence that miombo woodlands 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 revealed that cheetah are using unprotected areas, although rarely. Finally, we show that collaborations with tourism operators can be employed to monitor cheetah populations within tourism areas, although we also identify 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 Tanzania and elsewhere across its African range.

6.1. INTRODUCTION

The cheetah (*Acinonyx jubatus*) is classified as 'Vulnerable' to extinction by the IUCN (Durant et al., 2015), having disappeared from 20 countries and occupying only 9% of its historic range (Durant et al., 2017). The species is also relatively understudied compared to other large carnivores, with a paucity of information on the distribution and status of many populations, particularly across its eastern African range (Durant et al., 2015). Furthermore, geographical bias in research efforts is evident also within individual range countries: for example, although Tanzania is believed to harbour several globally important populations of cheetah (Durant et al., 2015), research to date has focused almost exclusively on the Serengeti-Mara transboundary population in northern Tanzania (e.g. Durant et al., 2007; Schaller, 1968).

The Ruaha-Rungwa conservation landscape, in south-central Tanzania, is a 50,000 km^2 multiple-use complex of protected and unprotected areas. Ruaha-Rungwa is thought to host Tanzania's second largest cheetah population, believed to potentially be one of only four populations in eastern Africa to number over 200 adult and adolescent individuals, and is therefore considered a regional stronghold for the species (Durant et al., 2015). Nevertheless, no empirical studies exist on cheetah in this landscape, and published records of presence in much of the protected area (PA) complex are anecdotal and >10 years old (Gros, 2000, 2002; TAWIRI, 2009). As a result, obtaining additional knowledge on the status and distribution of this population is considered a national conservation priority for the species (TAWIRI, 2016).

We begin to address this knowledge gap by providing some of the first insights into Ruaha-Rungwa's cheetah population, drawing on a variety of data sources. Systematic camera trap surveys were used to confirm presence and attempt to estimate population density at four sites within different PAs and habitats in the landscape; sign surveys were employed to obtain landscape-scale insights on distribution, across habitats and management strategies; camera traps employed for a community-engagement project were used to determine occurrence in unprotected village lands; and direct observational sightings by photographic tourism guides were used to assess and monitor the population within a core

area of the complex, and determine whether the method would be suitable for long-term monitoring of protected cheetah populations.

We combine these data to provide the first insights on the distribution and population status of this globally important cheetah population, examining the importance of different habitats and land management types for the species. In addition, we discuss the potential benefits of using data from tourism operators as a monitoring tool for cheetah populations, and employ findings to identify further research and conservation priorities for the species in the region.

6.2. METHODS

6.2.1. Study area

The Ruaha-Rungwa ecosystem is a ~50,000 km^2 multiple-use conservation complex in south-central Tanzania, comprising a mosaic of unfenced protected and non-protected areas (Fig. 6.1). The eight component PAs (Ruaha National Park (NP); Rungwa, Kizigo, and Muhesi Game Reserves (GRs); Lunda-Mkwambi Game Controlled Area (GCA); Rungwa South Open Area (OA); and MBOMIPA and Waga Wildlife Management Areas (WMAs)) experience a range of management strategies and revenue generation mechanisms (including photographic and trophy hunting tourism), and are subject to varying levels of law enforcement and anthropogenic pressures (see Appendix 6.1 for a detailed description of each component PA).

The landscape is located at the intersection of three ecoregions: the Southern *Acacia-Commiphora* bushland and grasslands, consisting of semi-arid savannah vegetation, and both the Central Zambezian and the Eastern miombo woodlands, comprising mixed woodland and open floodplain grassland habitats (Olson et al., 2001). The climate is semi-arid to arid, with an average annual precipitation of 600 mm (Fick & Hijmans, 2017). Ruaha-Rungwa has been identified by the Tanzania Wildlife Research Institute (TAWIRI) as a priority for large carnivore research and conservation (TAWIRI, 2009).

6.2.2. Systematic camera trap surveys

Four camera trap arrays were set out in the dry seasons of 2018 and 2019, within different habitat and PA types: (1) *Acacia-Commiphora* bushland and grasslands in the core tourist area of Ruaha NP (2018); (2) miombo woodlands in a more remote area of Ruaha NP (2018); (3) A*cacia-Commiphora* habitat in MBOMIPA WMA (2018); and (4) mixed miombo woodland and grasslands in Rungwa GR (2019; Fig. 6.1). Camera traps were deployed systematically: each array consisted of 26 – 45 paired camera stations, spaced approximately 2 – 4 km apart, and sampled an area of between 150 – 550 km^2 (see Appendix 6.2 for additional details on the survey protocol).

All cheetahs photographed in these four arrays were identified to an individual level, based on their unique pelage patterns. These data were then employed to attempt to estimate cheetah population density at each of the four survey sites, within a maximum-likelihood spatially explicit capture-recapture (SECR) framework (Brassine & Parker, 2015; Efford, 2004; see Appendix 6.2 for additional methodological details).

6.2.3. Sign surveys

Sign surveys were implemented across the wider Ruaha-Rungwa landscape, including in all eight PAs and in unprotected village lands to the south and east, over two dry seasons (July-November 2017 and June-November 2018; Fig. 6.1). Vehicle-based transects were carried out once along most roads and tracks present in the landscape, and relied on expert trackers to record signs of cheetah presence in the form of spoor (tracks; see Appendix 6.2 for additional details on the protocol employed). The different components of the landscape were sampled with similar levels of effort (Fig. 6.1), to obtain a baseline understanding of cheetah distribution within the different components of the landscape.

6.2.4. Community camera trapping

Additional data on cheetah presence in unprotected village lands to the east of the PA complex were obtained from camera traps deployed by the Ruaha Carnivore Project (RCP) as part of a community-engagement programme ('community camera trapping'; RCP, 2019). A total of 43 camera traps were deployed non-systematically over an area of circa 650 km^2 (Fig. 6.1) by 13 participating communities, between the 1st of January 2018 and the 31st of December 2019, prioritising areas in village land thought to be most used by wildlife (not all cameras were always active; mean active cameras per month = 29, maximum = 35. See Appendix 6.2 for additional details). As per the systematic camera trap surveys, cheetah were identified from photographs at an individual level.

6.2.5. Direct sightings from photographic tourism guides

Direct observations of cheetah were recorded by photo-tourism guides operating in Ruaha NP, through a collaboration between photographic tourism operators and the RCP (RCP, 2019). Data were collected across two distinct portions of the NP (Fig. 6.1), by 24 guides from 8 photo-tourism lodges over most

of 2018 (276 days; see Appendix 6.2 for additional details). For any sighting of cheetah, guides used a digital camera to attempt to photograph all individuals present, and recorded the GPS location of the sighting. Cheetah were subsequently identified at an individual level from these photographs.

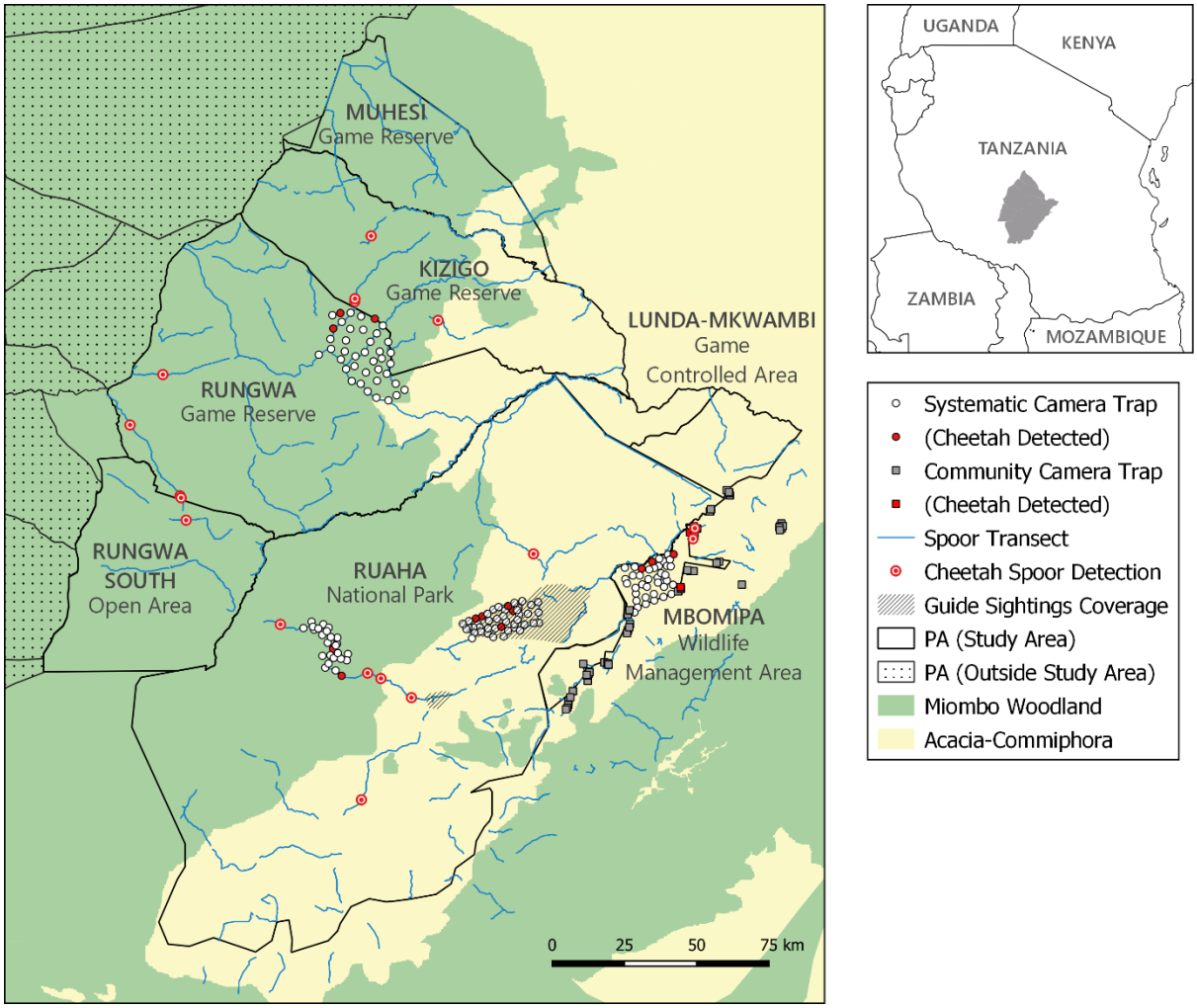


Figure 6.1. The study area, including the different component PAs, main habitat types, and survey methods employed to obtain insights into the status of cheetah in Ruaha-Rungwa. All cheetah detections, from all survey methods except direct sightings from photo-tourism guides (for which an area of operation is instead shown), are depicted. Note that while the boundary between the two component blocks of Lunda-Mkwambi GCA is shown, the Rungwa South Open Area and Rungwa Mzombe Open Area hunting blocks are presented under a single nomenclature ('Rungwa South Open Area').

6.3. RESULTS

A total of 11,668 camera trap nights from the four systematic camera trap surveys resulted in 30 photographs of cheetah, from 17 independent capture events (Table 6.1). One individual (male) was recorded in both arrays in Ruaha NP. Due to insufficient numbers of captures and recaptures, we were unable to estimate cheetah population density through SECR modelling at any of the four survey sites.

A total of 2,789 km of sign surveys were carried out across the landscape (2,376 km within PAs and 413 km in unprotected lands; Table 6.1). These resulted in 17 independent cheetah detections; all were of single individuals, except in two cases where two individuals were recorded together. Cheetah were confirmed to be present in at least 5 of the 8 PAs surveyed (Fig. 6.1).

Cheetah were detected twice by community camera traps over the study period, at two of the 43 camera traps deployed (Appendix 6.2, Table S6.2). Three individuals were identified from these two detections; two had been already been detected in the nearby MBOMIPA WMA systematic camera trap survey, while one was a newly identified individual.

Finally, we obtained a total of 782 pictures of cheetah from 59 independent sightings with photographs by photo-tourism guides in 2018. An additional 32 sightings were recorded without photographs, resulting in a total of 91 cheetah detection events. Photographs from 57 of these events (97%) were employed to identify 11 individual cheetahs, from 4 independent groups, while photographs from 2 sightings (3%) were not of sufficient quality to allow identification, and were discarded. There was no overlap between individuals identified from direct sightings and those detected in the camera trap surveys. See Appendix 6.3 for a list of identified individuals, from all methods.

Table 6.1. Summary of the data employed to investigate cheetah distribution and status in Ruaha-Rungwa.

Method	Approximate area sampled (km^2)	Survey effort (days/CT nights/km)[1]	Cheetah detection events[2]	Individual cheetahs identified
Systematic camera trap survey				
Ruaha NP *(Acacia-Commiphora)*	223	83 (3,601)	8	3
Ruaha NP *(*miombo*)*	152	90 (2,187)	2	2
MBOMIPA WMA	270	70 (2,689)	4	3
Rungwa GR	555	91 (3,191)	3	2
Total	1,200	334 (11,668)	17	9
Sign survey				
Ruaha NP	20,152	1,122	6	N/A
Rungwa GR	9,056	689	4	N/A
Kizigo GR	5,104	385	4	N/A
Muhesi GR	2,688	336	0	N/A
MBOMIPA & Waga WMAs	1,138	131	2	N/A
Lunda-Mkwambi GCA	1,839	161	0	N/A
Rungwa South OA	3,751	146	1	N/A
Village lands (unprotected)	7,350	413	0	N/A
Total	51,078	2,789[3]	17	N/A
Community camera traps	650	730 (20,957)	2	3[4]
Guide sightings programme	600	276	59	11

[1] Survey duration is presented in days for guide sightings efforts, in both days and camera trap nights (in brackets) for camera trapping efforts, and in km surveyed for sign surveys

[2] Multiple individuals recorded together are counted as a single event

[3] Surveys carried out along the boundaries between two PAs were included in effort calculations for both

[4] Two of these individuals were also captured in the systematic camera trap survey in MBOMIPA WMA

6.4. DISCUSSION

By combining data from a range of sources, we provide some of the first insights into the distribution and status of cheetah in the Ruaha-Rungwa landscape, considered a stronghold for the species in eastern Africa (Durant et al., 2015). The records of cheetah in western Ruaha NP and Rungwa South OA are the first in these areas, and constitute a range extension of known presence for the species into areas where it is currently recorded as 'Possible' (i.e. possibly resident; TAWIRI, 2016; Durant et al., 2015).

Our results suggest that cheetah are distributed widely across Ruaha-Rungwa. Cheetah were recorded in all four systematic camera trap surveys, and sign surveys confirmed that the species is likely to be present across most of the landscape: although only 17 independent cheetah signs were recorded, these were widespread rather than localised, coming from 5 different PAs (Fig. 6.1). Overall, cheetah were detected across a range of management strategies (photographic and hunting tourism, state and community-run), protection levels (strictly and less-strictly protected areas), and habitats (A*cacia-Commiphora* bushland and miombo woodlands). Our results thus echo findings elsewhere suggesting that cheetah can adapt to a wider range of environmental and management conditions than previously thought (Bissett and Bernard, 2007; Broomhall, 2006).

On the other hand, our surveys also revealed that, while widespread, cheetah likely exist at relatively low densities across Ruaha-Rungwa. The low number of spoor detections (Table 6.1) may be at least in part due to low detectability, possibly as a result of cheetah avoiding roads to minimise encounters with sympatric predators or humans (Brassine & Parker, 2015). However, similar surveys elsewhere have yielded significantly higher rates of detection (e.g. Henschel et al., 2020), suggesting that the species is likely occurring at relatively low densities in the landscape. The relatively low number of individual cheetahs identified over one year in the core tourist area of Ruaha NP (11 belonging to 4 separate groups), based on photo-tourism guide sightings, indicates that this may be the case even in the core tourist area of Ruaha NP, which exhibits particularly high prey densities (TAWIRI, 2019). The fact that we were unable to model population density in any of the four systematic camera trap surveys provides further evidence for this. Nevertheless, ours is not the first study that was unable to estimate cheetah

density from cameras placed mostly on roads (Boast et al., 2015; Brassine & Parker, 2015), and adds to the growing evidence indicating that camera trap survey protocols employed to estimate population density of other individually-marked large African carnivores (e.g. leopard, Strampelli et al., 2018; spotted hyaena, Rich et al., 2019) may be unsuitable to estimate population densities of cheetah. Instead, a cheetah-specific array targeting cheetah scent-marking posts is likely to be required (Boast et al., 2015; Brassine & Parker, 2015; Edwards et al., 2018), and we therefore encourage the use and further development of such study designs.

Although cheetah are particularly vulnerable to population suppression through edge effects, due to the wide-ranging nature of the species (Durant et al., 2015; Woodroffe & Ginsberg, 1998), the apparent low cheetah densities in Ruaha-Rungwa are likely a result of biotic factors. Cheetah are a naturally low-density species, particularly in arid habitats and less-productive areas (Durant et al., 2017). Approximately half of Ruaha-Rungwa is relatively arid (<600 mm mean annual precipitation), and the wetter portion of the landscape consists of miombo woodlands, a relatively low-productivity habitat which supports ungulate biomasses at only 20 – 30% of other savannah habitats with comparable rainfall (Frost, 1996). Thus, although we recommend further research to assess whether anthropogenic pressures and edge effects are having a detrimental effect on cheetah in the landscape, we believe the Ruaha-Rungwa population is likely to exist at naturally low densities.

Our results also reveal the importance of miombo woodlands for cheetah in the landscape, providing some of the first evidence for this habitat (not generally considered an important habitat for the species; *cf*. IUCN/SSC, 2007) being important for an African cheetah population. Systematic camera trap surveys confirmed cheetah presence in both miombo sites surveyed, and eleven of the seventeen independent sign detections of cheetah were from miombo habitats (Fig. 6.1), even though survey effort was slightly greater in *Acacia-Commiphora*. Although historically associated with open grasslands (e.g. Caro, 1994), it is now recognised that woodlands and other thicker habitats may play a key role for the species across its range (e.g. Bissett & Bernard, 2007; Broomhall, 2006; Mills et al., 2004). Miombo habitats consist of woodlands interspersed with seasonally flooded open patches (‘mbugas’ or ‘dambos’), and there is increasing evidence that cheetah preferentially select for mixed habitats of this

kind, as they provide both stalking cover and open areas to give chase, increasing hunting success (e.g Klaassen and Broekhuis, 2018; Mills et al., 2004). Indeed, when reintroduced in Matusadona NP (Zimbabwe), cheetah were found to use the woodland areas (including miombo) for resting and travelling, and the open grasslands for hunting (Purchase & du Toit, 2000). Woody cover is also likely to reduce kleptoparasitism and both adult and juvenile mortality from sympatric large carnivores, by providing concealment opportunities (Broekhuis et al., 2013; Caro, 1994; Mills et al., 2004). Thus, although most studies of cheetah in woodland are from primarily mopane habitat in Southern Africa (Weise et al., 2017), our study suggests that woodlands may be an important habitat for the species more widely across its range, and that miombo habitat may be more important than previously believed for cheetah in Tanzania. We therefore call for additional studies on cheetah population ecology in woodland habitats, both miombo and others, to complement the wider body of knowledge for the species in more open habitats.

In particular, our findings highlight the urgent need for additional surveys on the status of the species elsewhere in Tanzania, particularly to the west of our study area, between the Ruaha-Rungwa and Katavi-Ugalla conservation landscapes. The species' presence is currently considered 'Possible' (i.e. possibly resident) within the ~50,000 km^2 of partially protected and unprotected areas between these key landscapes for cheetah, as it is unknown whether cheetah occur here, or whether there is connectivity between the populations (TAWIRI, 2016; Durant et al., 2015). The majority of these areas consist of mixed miombo woodlands and grasslands, similar to the habitats found to be important for cheetah in Ruaha-Rungwa. Given that the majority of cheetah's 'Possible' range in Tanzania is primarily miombo habitat (~115,000 km^2 out of ~220,000 km^2; Olson et al., 2001; Durant et al., 2015), we recommend such surveys be considered a national priority for the species, particularly due to the increasingly rapid rates of loss observed in these habitats (Lobora et al., 2017). Questionnaire surveys of PA managers, hunting operators, and community members are a reliable and cost-effective method to obtain baseline distribution data on cheetah and other species over large scales and heterogeneous landscapes, and identify potential connectivity corridors to prioritise for conservation (Farhadinia et al., 2018; Madsen et al., 2020). Alternatively, using detection dogs to locate cheetah scats, and employing

genetic analysis to obtain insights on distribution, population size, and connectivity, also holds potential (Becker et al., 2017; although precursor presence/absence questionnaire surveys would likely still be required, given the vast size of the area). On the whole, further research into understudied cheetah populations in central and western Tanzania is urgently needed to identify the conservation actions required to ensure long-term persistence of these potentially globally important populations.

In this context, collaboration between researchers and tourism operators has been identified as an under-appreciated source of data for monitoring African carnivore populations (Rafiq et al., 2019), and our study confirms this is a suitable method to monitor cheetah within tourism areas. The method was also relatively cost effective: one year of continuous monitoring of ~600 km^2 cost approximately US$3,400 (Appendix 6.2), less than the cost of a similarly long-term camera trapping or direct observation study (RCP, unpublished data). Furthermore, the method allowed for the identification of more individuals than the different systematic camera trap surveys (Table 6.1), despite the latter covering an overall larger area (~1,200 km^2 through systematic camera trap surveys; ~600 km^2 through direct sightings). The technique could also be further improved by obtaining survey effort data (e.g. through GPS tracklogs) from guides, to allow the estimation of population density through SECR modelling (Broekhuis et al., 2020; Broekhuis & Gopalaswamy, 2016; Linden et al., 2020; Rafiq et al., 2019). Nevertheless, employing data from a range of sources also allowed us to identify limitations of relying solely on direct observation methods for population monitoring. None of the three individuals recorded by camera traps set out in the core tourist area, within the same area where direct sightings data were collected (Fig. 6.1), were recorded by photo-tourism guides during the same period. Furthermore, the vast majority (91%) of identified cheetah sightings by guides were of members of the same group of related individuals (Appendix 6.3), suggesting that direct observation studies may risk under-reporting individuals that are more shy and/or less habituated to vehicles. This is likely to particularly be an issue in vast, heterogeneous landscapes such as Ruaha-Rungwa, where individuals may migrate into the study area from areas with less human presence, or where they are persecuted. Thus, while we promote the use of this and similar citizen scientist-based methods as a cost-effective monitoring tool for cheetah in tourism areas, we also encourage supplementing this with data from additional sources (e.g. camera

traps) for shorter periods. It is also worth noting that none of the individuals identified through direct sightings were detected by camera traps, although this is likely to be a result of the group sighted most often by guides appearing to not often use the area where the systematic camera trap array was set out.

Although community camera trapping revealed that cheetah were occasionally using unprotected village lands to the east of Ruaha NP and MBOMIPA WMA, the number of captures was relatively low, particularly compared to those of other sympatric predators (RCP, unpublished data). This suggests that cheetah are rarely using unprotected lands in the area, as also indicated by the comparatively lower rates of livestock predation by the species (Dickman, 2008). Furthermore, all three cheetahs identified were captured by camera traps located particularly near the WMA boundary, with two of the three individuals having already been identified in the WMA systematic camera trap survey. This suggests individuals occasionally carrying out forays from the WMA into unprotected land, rather than a stable population persisting solely in unprotected lands. Overall, we encourage the use of similar bycatch data from non-ecological sources to help monitor elusive and cryptic species in unprotected areas, where more conventional techniques may be less suitable.

Finally, we note that one individual was recorded in two different systematic camera trap surveys (the *Acacia-Commiphora* and miombo arrays in Ruaha NP), having travelled a minimum distance of 64 km in two months. This evidence of wide-ranging movement, combined with the observed low density and widespread distribution, highlights the importance of landscape-scale conservation planning (IUCN/SSC 2007; Trombulak and Baldwin, 2010) for the species, both in Ruaha-Rungwa and elsewhere in Africa. We therefore encourage conservation efforts to reflect these characteristics of the species, by ensuring efforts are implemented at appropriate and meaningful biological scales.

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6.6. APPENDICES

Appendix 6.1. Additional Details on the Study Area

Appendix 6.2. Detailed Survey Protocols

Appendix 6.3. Ruaha-Rungwa Cheetah Records & Identification Data

APPENDIX 6.1 – ADDITIONAL DETAILS ON THE STUDY AREA

In the manuscript version of this Chapter, we included additional details on the Ruaha-Rungwa landscape as an Appendix. As this is for the most part repetition of information already introduced in pervious Chapters, it is not included here. However, for completion, it can be accessed at:

https://github.com/pstrampelli/Additional-Details-on-the-Study-Area-Appendix-6.1-

APPENDIX 6.2 – DETAILED SURVEY PROTOCOLS

Systematic camera trap surveys

Systematic camera trap survey arrays consisted of 26 – 45 paired stations, and were set out for between 70 – 101 days (Table S6.1). This is generally considered adequate for assuming demographic closure, and is consistent with previous studies of large felids (Alexander et al., 2015; Karanth, 1995). Stations were set out at semi-regular intervals, between 2 – 4 km apart, surveying areas of varying sizes (Table S6.1). We used cameras of model Cuddeback Professional Color Model 1347, Non Typical Inc., Wisconsin, USA. Stations were set out along roads, game trails, and at water points, to maximise captures of large carnivores, as these often employ roads and trails to travel (Mckenzie et al., 2012). At each station, two cameras were mounted on trees at a height of 30 – 40 cm, on opposite sides of the road or trail, facing inwards, to photograph both flanks of animals and help with individual identification.

Table S6.1. Systematic camera trap surveys carried out across the Ruaha-Rungwa landscape.

Survey Array	Stations	Area sampled (km^2)	Survey length (days)	Total camera trap nights
1. Ruaha NP (*Acacia-Commiphora*)	45	223	83	3,601
2. Ruaha NP (miombo)	26	152	90	2,187
3. MBOMIPA WMA	40	270	70	2,689
4. Rungwa GR	40	555	91	3,191

Following individual identification of cheetahs based on their pelage patterns, spatially explicit capture-recapture (SECR) analyses were attempted for each survey array using the package *secr 4.2.0* (Efford, 2020) in *R v. 3.6.3* (R Core Team, 2019). SECR models estimate density explicitly, while accounting for imperfect detection (Royle et al., 2009), and have been successfully employed to estimate cheetah density from camera trap data (Belbachir et al., 2015; Brassine & Parker, 2015). However, models failed to converge in all four study sites due to insufficient recaptures.

Sign Surveys

Sign-based surveys were carried out over two dry seasons, between 7 July and 29 November 2017, and 29 June and 21 November 2018. Standard protocols for vehicle-based large carnivore surveys were followed (Henschel et al., 2016; Chapter 3). The survey team consisted of a driver and two experienced trackers seated on custom-made seats on the bull-bar of the vehicle. The vehicle was driven at a maximum speed of 10 km/h, and surveying was carried out between dawn and approximately 10:00 am, before a high-standing sun made detection difficult. If another vehicle travelled on the road during surveying, surveying was ended. Whenever a cheetah track was detected, information was recorded on number of individuals, age of sign, and direction of travel. All attempts were made to survey the different components of the landscape with similar levels of effort.

Community camera trapping

Cameras were located opportunistically to maximise captures of large carnivores and other wildlife, mostly along trails or water points. Cameras of the same models described above were employed, as well as cameras of model HC500 HyperFire, Reconyx, Wisconsin, USA.

Table S6.2 includes a list of participating villages, as well as the duration of their involvement and number of cameras deployed.

Table S6.2. Villages participating in the community camera trapping (CCT) programme.

Village	Location	Active cameras (by month)																							
		01/18	02/18	03/18	04/18	05/18	06/18	07/18	08/18	09/18	10/18	11/18	12/18	01/19	02/19	03/19	04/19	05/19	06/19	07/19	08/19	09/19	10/19	11/19	12/19
Idodi	-7.777, 35.198	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Isele	-7.359 35.430	2	3	3	3	3	3	3	3	3	3	2	2	2	2	1	1	0	0	0	0	2	2	2	2
Kinyika	-7.345 35.442	1	2	1	1	1	2	2	2	2	2	1	2	2	3	2	1	1	1	1	0	2	2	1	1
Kisanga	-7.304 35.459	3	2	1	1	2	2	2	3	3	2	2	2	2	3	2	2	2	3	3	3	3	3	3	3
Kisilwa	-7.521 35.443	0	0	0	0	0	0	0	3	3	3	3	3	3	3	0	2	3	3	3	3	3	3	3	3
Kitisi	-7.750 35.124	3	2	3	2	3	2	2	1	1	1	2	2	2	3	3	2	3	3	3	3	3	3	3	3
Mafuluto	-7.521 35.443	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	2	2	2	1	1	1	2	2	2
Magombwe	-7.438 35.459	2	2	2	2	2	2	2	3	3	3	3	3	3	2	2	0	1	1	2	3	2	2	2	2
Mahuninga	-7.930 35.067	2	3	2	2	2	2	2	3	1	1	1	1	1	2	1	1	2	2	2	2	2	2	2	2
Makifu	-7.869 35.069	2	3	3	2	2	2	2	4	3	3	3	3	3	3	3	4	3	3	3	3	3	3	3	2
Malinzanga	-7.643 35.365	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Mapogoro	-7.813 35.122	2	2	2	2	2	2	3	1	0	2	2	2	2	2	2	3	1	1	1	1	1	2	2	2
Tungamalenga	-7.833 35.095	1	2	2	2	2	2	2	3	2	2	2	2	1	2	2	2	2	2	2	2	1	1	1	1
Total		26	29	27	25	27	27	28	35	30	31	30	31	30	34	27	26	26	27	27	27	29	31	30	29

Direct sightings from ecotourism guides

The collaboration between ecotourism guides and the Ruaha Carnivore Project (RCP) began in 2014, with the involvement of the first tourist lodges and photographic tourism guides. Since then, the number of lodges and guides participating in the programme has increased considerably; the following lodges collaborated with RCP for the guide sightings programme in 2018, for a total of 24 participating guides:

Table S6.3. Tourist lodges participating in ecotourism guides sightings programme.

Lodge	Location (X, Y)	Number of participating guides in 2018	Period active[1]
Ruaha River Lodge	34.8718, -7.7676	6	January-February May-December
Mdonya Old River Lodge	34.6514, -7.7686	5	January-February June-December
Mwagusi Safari Camp	34.9285, -7.6074	3	January-February May-December
Kigelia Ruaha	34.9592, -7.5585	3	January June-December
Asilia Jabali	34.8391, -7.6154	1	July-December
Asilia Kwihala	34.8372, -7.5912	1	July-December
Jongomero	34.5700, -7.9068	2	January-February July-December
Tandala	35.005675, -7.770316	3	January-February June-December

[1] The period active include times when data was received from lodge guides, not necessarily when the lodge itself was operational

Participating guides recorded their movements whenever on game drives with clients, through the Cybertracker (https://www.cybertracker.org/) application on a tablet (Google Nexus 7, Asus, Taipei, Taiwan) provided by the RCP. Whenever a large carnivore was sighted, information on the location, species, number of individuals, and activity was recorded through Cybertracker. Pictures of the animal(s) were taken with a digital camera (Nikon COOLPIX B500/B700, Nikon, Tokyo, Japan), also provided by the RCP.

Costs for one year of monitoring, for 24 participating guides, were estimated at $3400, as detailed in Table S6.4.

Table S6.4. Cost for one year of monitoring of cheetah through direct sightings from tourist lodge guides.

Item	Quantity	Unit price (USD, total)	Unit Price (USD, per year) [1]	Total annual price (USD)
Bridge digital camera (Nikon Coolpix B500/B700)	24	150	50	1200
Android tablet (Asus Google Nexus 7)	24	100	50	1200
Fuel (for data collection from guides)	NA	NA	NA	1000
TOTAL				**3400**

[1] Cameras were replaced on average every three years, and tablets every two years with the annual estimated cost amortised based on this

APPENDIX 6.3 – RUAHA-RUNGWA CHEETAH RECORDS & IDENTIFICATION DATA

A detailed list of all recorded cheetah detections and sightings (with coordinates and additional information), from all methods, can be accessed at:

https://github.com/pstrampelli/Ruaha-Rungwa-Cheetah-Records-Identification-Data

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Grasslands along the boundary between Ruaha NP (right) and Lunda-Mkwambi GCA (left).

The black cotton soil, while very fertile, becomes almost impassable with the first rains of the season. This impacts accessibility in the landscape, and, combined with the area's vast size, precludes the use of some of the survey techniques employed in this study in the wet season.

CHAPTER 7

Trends and biases in African large carnivore population assessments: Identifying priorities and opportunities from two decades of research



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Trends and biases in African large carnivore population assessments

- TITLE -

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ABSTRACT

Conservation planning and management of threatened species requires accurate assessments of population status and monitoring of trends. However, there is evidence that large carnivore population assessments, and biodiversity monitoring in general, may not be evenly distributed, or targeted where most needed. Here, we provide the first review of African large carnivore population assessment studies published in peer-reviewed literature over the last two decades (2000-2020), with the goal of investigating trends in research effort and identifying gaps in knowledge. We used generalised linear models (GLMs) and generalised linear mixed models (GLMMs) to identify taxonomic and geographical biases, as well as potential socio-economic drivers. We found population assessments to be biased towards southern and eastern Africa, particularly South Africa and Kenya. Northern, western and central Africa were generally under-represented, with DRC, Angola, South Sudan, and Chad being identified as particular priorities for further research. Research focus was significantly biased towards lion, and significantly against striped hyaena, despite the latter being the species with the widest continental range. African wild dog also exhibited a negative bias in research attention, although this was partly explained by its relatively restricted distribution. The number of country assessments for a species was significantly positively associated with its geographic range in that country, while there was little evidence of research effort being associated with a country's socio-economic status, or with the conservation status of species. The majority of studies were carried out in photographic tourism protected areas under government management, while non-protected and trophy hunting areas received comparatively little attention. Outside of South Africa, more than half of studies were led by researchers not affiliated with an institution in the study country, suggesting that significant opportunities exist for capacity building in range states. Overall, large parts of Africa remain under-represented in the literature, and opportunities exist for further research on most species and in most countries. We develop recommendations for actions aimed at overcoming the identified biases, and provide researchers, practitioners and policy makers with priorities to help inform future research and monitoring agendas.

7.1. INTRODUCTION

Africa is host to a unique diversity of extant large carnivore species, including the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*), spotted hyaena (*Crocuta crocuta)*, striped hyaena (*Hyaena hyaena*), and brown hyaena (*Parahyaena brunnea*). Nevertheless, large carnivore populations across Africa have undergone rapid declines in recent decades, primarily as a result of habitat loss and fragmentation, loss of prey, and conflict with humans (Brodie et al., 2021; Wolf & Ripple, 2017). As a result, there is an urgent need to ensure that remaining populations are effectively studied and monitored. In addition to being fundamental for understanding ecological processes and population dynamics (Elliot & Gopalaswamy, 2016), knowledge of the status and trends of populations is essential for their conservation management, as it allows practitioners to identify threats to their viability, evaluate the effectiveness of interventions, implement adaptive monitoring programmes, and inform policy decisions (Suryawanshi et al., 2019; Witmer, 2005).

Indeed, in recent years, such data have been used to inform a wide range of both local and international management and policy decisions affecting large African carnivores, including national action plans and regional conservation strategies (IUCN, 2007; TAWIRI, 2016), range wide meta-analyses (Weise et al., 2017), international policies (USFWS, 2015), conservation status and extinction risk assessments (IUCN, 2020), and trophy hunting management and quota setting (Mweetwa et al., 2018; Packer et al., 2010). They have also been employed to identify conservation units and population strongholds (Riggio et al., 2013) and range wide priorities (Bauer et al., 2015), and to inform action around controversial management practices (Miller & Funston, 2014; Packer et al., 2013).

In this context, population density is often considered the golden standard for population assessment and monitoring (Boitani & Powell, 2012). Unlike abundance, densities allow for comparisons over time and between sites, enabling researchers and managers to understand how population status varies with biotic factors (e.g. Chapter 5), anthropogenic disturbances (Balme et al., 2010; Henschel et al., 2011), or land management strategies (Swanepoel et al., 2015). Without such data, knowledge gaps are often filled in by expert opinion (Weise et al., 2017); this, however, has been shown to promote the use of

biased management approaches, by potentially hindering the implementation of ecologically-meaningful planning (Artelle et al., 2013; Popescu et al., 2016) and science-based prioritisation of conservation actions (Darimont et al., 2018; Moqanaki et al., 2018). Successful large carnivore conservation will therefore require reliable population assessments (Braczkowski et al., 2020), ideally from a wide range of geographical and management contexts.

However, as a result of their naturally low densities, nocturnal and secretive nature, and wide ranging habits, estimating population parameters for large carnivores can be logistically challenging and financially costly (Karanth & Nichols, 2017). Indeed, robust African carnivore population measures have been argued to be severely lacking (Riggio et al., 2013), and there is evidence that biodiversity monitoring and research as a whole is under-represented in Africa (Di Marco et al., 2017; Martin et al., 2012; Stocks et al., 2008; Velasco et al., 2015). Conservation research also suffers from both taxonomical and geographical sampling biases, with research not always occurring where it most needed (Velasco et al., 2015; Wilson et al., 2016), including for large African carnivores (Balme et al., 2014). Knowledge gaps can compromise conservation efforts (Trimble & van Aarde, 2012), and biases might translate into policies, potentially impacting the achievement of biodiversity conservation targets (Velasco et al., 2015). It is therefore important to understand and monitor such biases, in order to track progress made and re-align efforts where needed (Di Marco et al., 2017; Donaldson et al., 2016).

Here, we carry out the first systematic review of all published, peer-review studies estimating population density or abundance of large African carnivore populations over the last 20 years (2000 – 2020). We determine research patterns and the geographical and taxonomic representativeness of these studies, and identify biases and data gaps in population assessments and monitoring. Finally, we use this information to identify future research priorities and opportunities.

7.2. METHODS

7.2.1. Literature review

We conducted a review of published, peer-reviewed literature using Google Scholar (17 July – 31 October 2020), compiling all studies where population density of one or more African large carnivore species (lion, leopard, cheetah, African wild dog, spotted hyaena, striped hyaena, brown hyaena) was either explicitly estimated, or derived from an empirically measured parameter (e.g. home ranges). Literature was searched for by entering, in quotation marks, full scientific and vernacular species names, as well as "density", "abundance", "population", "assessment", or "survey". As our intention was to review trends and biases in peer-reviewed literature from the last two decades, only studies published between 1st January 2000 and 31st October 2020 were considered. The resulting records were screened, and all papers that did not include density or abundance estimation as an output were excluded. If more than one species was included in a single study, a separate record was produced for each.

Although it was not necessary for population density to be the primary parameter of interest in the study, studies were only included if the methodology employed to obtain density estimates was described in detail, thus providing the opportunity for this to be subjected to peer review. Studies estimating population abundance were included only if the size of the sampled area was explicitly defined and measured. Only estimates published in peer-reviewed literature were considered; this was done to ensure data and information quality (Suryawanshi et al., 2019), and because, as a result of many unpublished reports not being publicly available, studies published in the scientific literature are those most readily available to most policy makers, conservation managers, and researchers, and therefore most likely to influence international conservation policy and the disbursement of conservation funding (Giam & Wilcove, 2012). Estimates reported in a peer-reviewed study from non-peer reviewed sources (e.g. Weise et al., 2017), where the methodology employed was not described (e.g. Balme et al., 2017), or where estimates were obtained indirectly by extrapolating from the sampled area to a wider area (e.g. Trinkel, 2009) were not included. We also did not include density estimates from intensively managed populations (e.g. Buk et al., 2018), as the exact number of individuals being known prior to the study

precluded the type of exploratory studies of interest in this review. This was only relevant to some populations of lion, cheetah, and African wild dog in South Africa.

For each study that fitted the above criteria, we extracted information on: year of publication, year(s) of data collection, authors' institutional affiliations (as listed in the publication) and nationality (local or foreigner, based on a web search), study area, ecosystem, country, region, land use and ownership type (as described in the publication; if multiple uses occurred – e.g. photographic tourism and trophy hunting – both were listed), density estimate and estimation method, and other additional details.

Finally, we are aware of recent discussions regarding the reliability of some large carnivore population assessment methods (e.g. Braczkowski et al., 2020; Dröge et al., 2020), and of common issues in large carnivore density estimation studies, such as that of under-sampling the study area (Suryawanshi et al., 2019). However, given that our goal was to assess research effort, we did not make distinctions based on methods employed, or on other features of the studies themselves.

7.2.2. Analyses

Findings of the literature review were employed to identify taxonomic trends in research effort, including the total number of studies and the study density (i.e. studies per km^2 of geographical range) per species. Geographic range maps and data for each species were obtained as polygons from the IUCN Red List (https://www.iucnredlist.org/). We also determined spatial patterns in research, through the total number of studies and the study density per country and per region, both by species and overall. Finally, we investigated patterns in land tenure of the areas where research was carried out, and the affiliation and nationality (local versus foreigner) of the authors of the research.

7.2.2.1. *Generalised Linear Mixed Models (GLMMs) and Generalised Linear Models (GLMs)*

We employed Generalised Linear Mixed Models (GLMMs) and Generalised Linear Models (GLMs) to investigate taxonomic and spatial biases in large carnivore population assessments. We also tested the effect of potential explanatory variables on research effort, while also obtaining a more nuanced understanding of the identified biases by controlling for these variables.

GLMMs

Models that combined species were fitted by Poisson GLMMs, with the number of studies coded as the explanatory variable. Country and Species were included as random effects (random intercepts) to control for multiple observations (i.e. data points for multiple species in each country, and for multiple range countries for each species); positive values for the random effects indicate more surveys than would be expected for that species or in that country based on the explanatory variables included in the model, while negative values indicate fewer, with the magnitude of the value signifying the strength of the effect. Larger values for the random effect variance (for both species and countries) indicate larger variation between the individual species' or countries' random intercepts, while smaller values suggest that variation between individual countries or species is lower.

To first determine biases in research effort by species and countries, without controlling for potential drivers, a model was built with only Species and Country as random effects (Model 1; Table 7.1). Next, a model was fitted controlling for differences in species' geographical range (Range) between countries, with Range modelled as a fixed effect (Model 2). This allowed us to (a) determine how country biases changed after controlling for differences in geographical range; and (b) test whether large carnivore range in a country was a good predictor of research effort. To then investigate whether research effort was associated with the socio-economic status of a country, three socio-economic variables were selected for inclusion: economic development (measured through GDP per capita; World Bank, 2020); societal development (measured through the Human Development Index (HDI); UNDP, 2020); and country fragility, risk, and vulnerability (measured through the Fragile States Index; FFP, 2020). These were chosen due to having been previously included in similar studies (Fisher et al., 2011; Giam & Wilcove, 2012; Stocks et al., 2008). However, GDP per capita and HDI were highly correlated (R^2 = -0.8), resulting in high variance inflation factors; as a result, only GDP and Fragility were retained for use in the analyses. A Poisson GLMM was thus built with socio-economic variables (GDP per capita and Fragility) modelled as fixed effects, to determine whether research was associated with socio-economic development, and identify which countries exhibited more or less research than expected based on their socio-economic status (Model 3). To then test which countries exhibited the most and

least research effort after accounting for differences in both geographical range and socio-economic status, an additional model was developed, with both modelled as fixed effects (Model 4). Finally, to test whether the number of published population assessments was related to the conservation status of a species, a model was built with Conservation Status included as a categorical variable (using Least Concern as the baseline variable), with GDP, Fragility, and Range included as fixed effects (Model 5). Conservation status was extracted from the IUCN Red List of Threatened Species (IUCN, 2020). Different models were fitted, instead of just a full model (i.e. Model 5), in order to determine which countries received the most and least research attention based on multiple possible definitions of interest (overall, and when accounting for differences in geographical range, socio-economic development, or both). As socio-economic data were not available for two countries (Eritrea and Somalia), to simplify the modelling process these were not included in any analysis. All models were validated by posterior predictive checks, dispersion parameters, and model residuals (see Appendix 7.4 for additional details and results of these).

All analyses followed a Bayesian approach to parameter estimation using JAGS (Plummer, 2003) in R (version 3.6.1; R Core Team, 2019) with the package *runjags* (Denwood, 2020). Explanatory variables were standardised to improve MCMC chain convergence and aid interpretation of results. Prior to analyses, variable collinearity was assessed using variance inflation factors and pairwise correlations, which found no issues. All models used three MCMC chains, diffuse priors, and ran for enough iterations to produce an effective sample size >10,000 (Kruschke & Liddell, 2018). MCMC chain convergence was confirmed with trace-plots and the Gelman-Rubrin statistic. Variables (both fixed and random effects) were considered to have a significant effect if they exhibited a credible non-zero effect (i.e. zero not contained within the 95% highest density interval (HDI) of the posterior distribution).

Table 7.1. All-species Poisson GLMMs built to identify biases in research effort and test the effect of explanatory variables (geographical range, GDP, fragility, conservation status of species) on population assessments.

Model Number	Model Name	Fixed Effects			Random Effects		Description
		Range	*GDP, Fragility*	*Conservation Status*	*Country*	*Species*	
1	Species & Country Only	No	No	No	Yes	Yes	Differences in survey effort by species & country
2	Range	Yes	No	No	Yes	Yes	Differences in survey effort by species & country, accounting for differences in large carnivore geographical range between countries
3	Socio-economic	No	Yes	No	Yes	Yes	Differences in survey effort by species & country, controlling for socio-economic differences between countries
4	Range + Socio-economic	Yes	Yes	No	Yes	Yes	Differences in survey effort by species & country, accounting for differences in large carnivore geographical range and socio-economic status between countries
5	Range + Socio-economic + Status	Yes	Yes	Yes	Yes	Yes	Differences in survey effort by species & country, accounting for differences in large carnivore geographical range and socio-economic status between countries, and testing the effect of conservation status

Legend: Range = Geographical range, based on IUCN Red List range maps (IUCN, 2020); GDP = Gross Domestic Product per capita (World Bank, 2020); Fragility = country fragility, risk and vulnerability (FFP, 2020); Conservation Status = IUCN Red List status of species (IUCN, 2020).

GLMs

In addition to the all-species GLMMs, GLMs were employed to investigate species-specific research geographical biases, and test the effect of geographical range and country socio-economic indicators (GDP per capita, Fragility) on research effort on individual species. GLMs were used over GLMMs as, unlike the all-species models, datasets for individual species did not have multiple observations per country, therefore allowing their applicability.

Models were first fitted with a Poisson distribution and validated by posterior predictive checks, dispersion parameters, and model residuals. If a Poisson model was not suitable for the data, zero-inflated Poisson, negative binomial, or zero-inflated negative binomial models were used, validated by the same methods employed for the GLMMs (Appendix 7.4). Country residuals were employed to determine the effect at a country level: a positive residual signified a country had more studies than expected based on the employed model variables, while a negative residual signified fewer. Residuals were deemed to represent a significant effect if the 95% highest density interval (HDI) of the posterior distribution did not contain zero. For each species, two models were developed: one testing the effect of, and accounting for, differences in geographical range (equivalent to Model 2 in Table 7.1); and one

testing the effect of, and accounting for, differences in both geographical range and a socio-economic indicators (equivalent to Model 4 in Table 7.1).

Leopard, spotted hyaena, and cheetah data were fitted with Poisson GLMs with one outlier removed to reduce overdispersion; lion data was fitted with a Negative Binomial GLM (NBGLM) when controlling for range only, and with a Poisson GLM when controlling for both range and socio-economic indicators. There was some evidence of overdispersion for some species; see Appendix 7.4 for additional details. African wild dog, striped hyaena, and brown hyaena could not be modelled individually due to too few data points (range countries) and/or insufficient variance (i.e. most range countries had zero studies).

7.3. RESULTS

7.3.1. Literature review & research trends

Our search of the published literature revealed 106 peer-reviewed articles (studies) which estimated population density of one or more large carnivore species in Africa. Overall, these provided a total of 283 estimates of large carnivore population density, across all species (Fig. 7.1, 7.2). The number of studies appears to be on the increase, with the four years exhibiting the greatest number of studies all falling between 2014 and 2020.

Studies were predominantly carried out on protected land managed by the government (63%), followed by private reserves (17%), land under community-based management (16%), and unprotected areas (11%). Land tenure was unclear for 2% of studies. 82% of studies took place in areas where non-consumptive (photographic) tourism occurred, 33% in an area with livestock ranching, game ranching, and/or farming, 15% in an area with trophy hunting, and 3% in a logging or mining concession. 54% of studies were led (first-authored) by researchers affiliated with an organisation based in the study country, 70% of studies had a national of the study country as an author, and 84% of studies had at least one author affiliated with an organisation based in the study country. However, when looking only at studies outside of South Africa, lead researchers were affiliated with a local organisation on only 43% of publications, only 59% of studies included a national of the study country as an author, and 79% of studies included an author based in the study country. See Appendix 7.1 for a complete list of all studies and associated information, and Appendix 7.2 for additional details on the presentation of the data.

7.3.2. Taxonomic trends in research

Lion was the species with the most population density assessments in peer-reviewed literature (56 independent studies which fitted the described criteria, leading to 89 independent estimates of population density), followed by spotted hyaena (34 studies, 78 estimates), leopard (31 studies, 64 estimates), cheetah (17 studies, 19 estimates), brown hyaena (10 studies, 24 estimates), African wild dog (6 studies, 7 estimates), and finally striped hyaena (2 studies, 2 estimates; Table 7.2; Fig. 7.1).

Lion was also the species with the greatest study density (studies per 100,000 km^2 of range), with this being an order of magnitude greater than for all other species. The species with largest continental range, striped hyaena, was that subject to the lowest research attention. Although spotted hyaena ranked second in number of studies, due to its vast geographical range study density was lower than for all other large carnivore species, except striped hyaena (Table 7.2; Fig. 7.1).

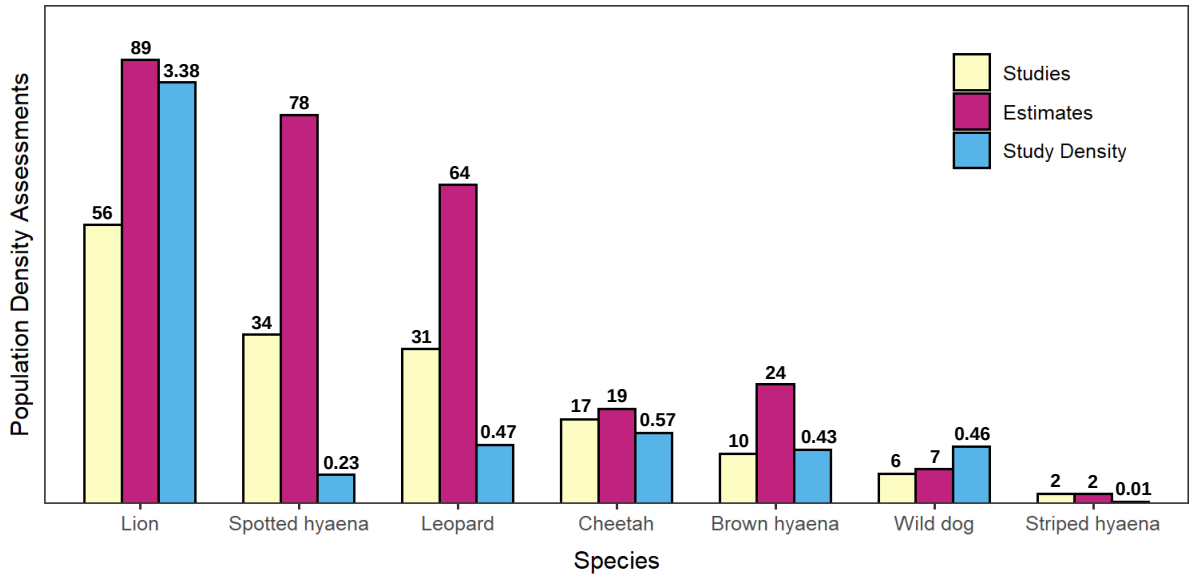


Figure 7.1. Number of peer-reviewed population density assessments (studies), number of individual population density estimates, and density of peer-reviewed studies (studies per 100,000 km^2 of geographical range) for large African carnivores (2000 – 2020).

Table 7.2. Summary of literature review and species-specific trends in peer-reviewed large African carnivore population assessments (2000-2020).

Species	Studies	Density Estimates	Geographical Range (km^2)*	Studies / 100,000 km^2	Estimates / 100,000 km^2
Lion	56	89	1,654,375	3.38	5.38
Spotted Hyaena	34	78	14,498,078	0.23	0.54
Leopard	31	64	6,613,000	0.47	0.97
Cheetah	17	19	2,976,963	0.57	0.64
Brown Hyaena	10	24	2,304,325	0.43	1.04
African Wild Dog	6	7	1,303,469	0.46	0.54
Striped Hyaena	2	2	15,244,137	0.01	0.01

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

7.3.3. Geographical trends in research

7.3.3.1. *Regional trends*

Across all species, southern Africa was the region with the greatest number and density of large carnivore population assessments, followed by eastern Africa (Table 7.3).

Table 7.3. Regional geographical trends in large carnivore research in Africa (2000 – 2020), all species combined. All figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. See Table S7.1 for species-specific insights.

Region	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 100,000 km^2	Estimates / 100,000 km^2
Southern	12,114,919	60	155	0.50	1.28
Eastern	12,587,456	35	80	0.28	0.64
Central	6,116,580	7	40	0.11	0.65
Western	4,832,540	4	7	0.08	0.14
Northern	8,145,160	1	1	0.01	0.01

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

The greatest number of published lion population assessments came from eastern Africa, followed by southern, central, and finally western Africa (Table S7.1). Nevertheless, although it counted only three studies, western Africa exhibited the highest density of lion population assessments, due to the species' limited range in the region. The vast majority of leopard population assessments were carried out in southern Africa, with more than twice the amount of studies here than in all other regions combined. Northern Africa, on the other hand, was last in terms of both overall studies and study density. Cheetah population assessments also focused primarily in southern Africa, followed by eastern and northern Africa, with no population assessments in western or central Africa. Eastern Africa, however, exhibited the greatest density of cheetah studies. African wild dog population assessments were relatively evenly spread across the continent (with the exception of western Africa, with no population estimates); overall research effort was, however, considerably lower than for the felids. The majority of spotted hyaena population estimates came from southern Africa (which also exhibited the greatest study density), followed by eastern and central Africa; no studies took place in western or northern Africa. Both of the only two published striped hyaena population assessments took place in eastern Africa. Finally, brown hyaena population assessments were only carried out in Southern Africa, the only region where the species is present (Table S7.1).

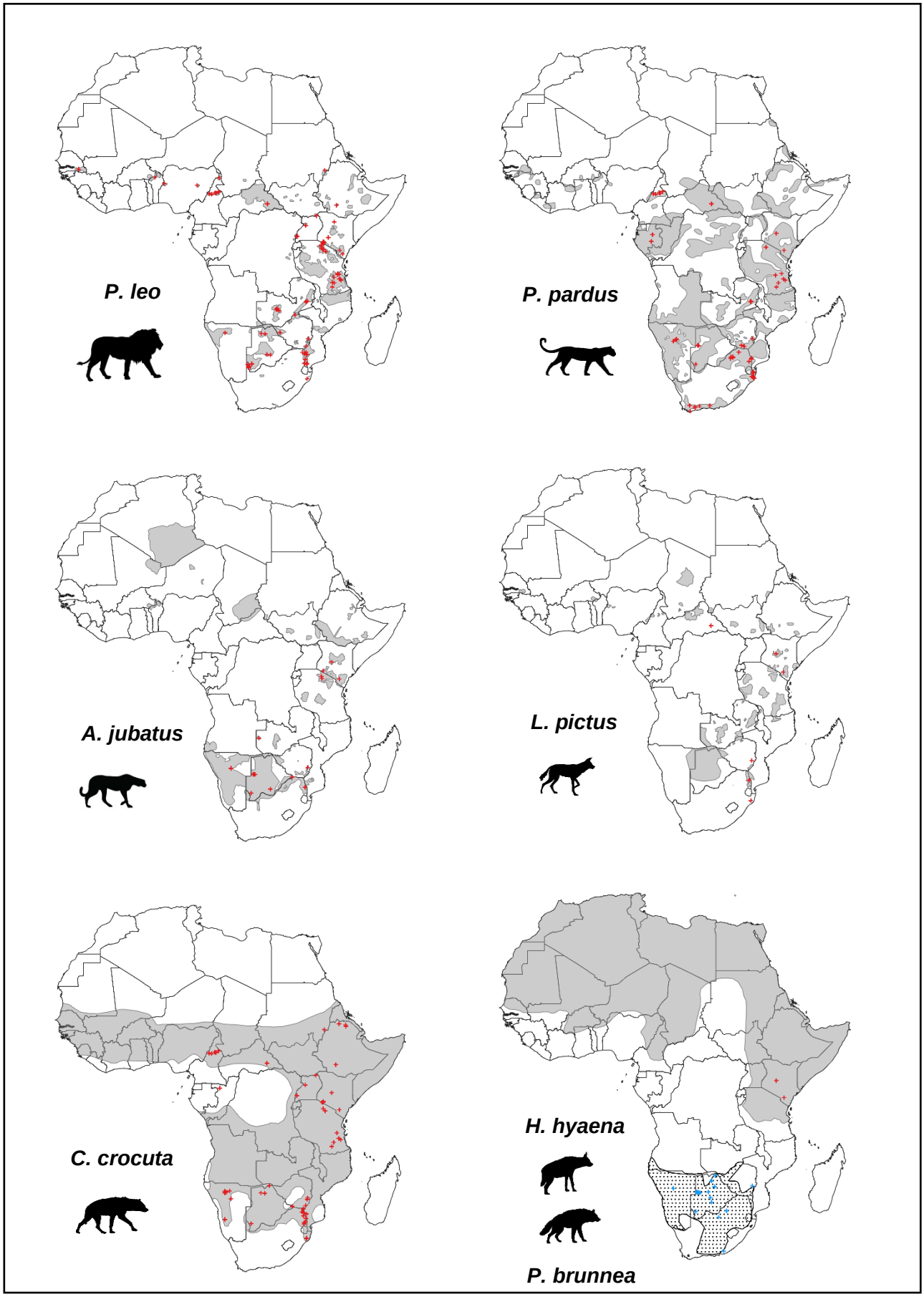


Figure 7.2. Location of peer-reviewed African large carnivore population assessment studies (2000 – 2020). Red crosses show estimates of population density, except in the case of brown hyaena, where blue crosses are used instead. When a study estimated multiple population densities, these are shown as separate points. Grey areas represent current geographical ranges (IUCN, 2020), except in the case of brown hyaena, where a dotted pattern is used instead.

7.3.3.2. *Country trends*

South Africa was the country with the greatest number of large carnivore population assessments, followed by Tanzania, Kenya and Botswana. Study density, on the other hand, was highest in Niger, followed by South Africa, Cameroon, and Kenya. Twenty-seven countries with at least one large carnivore species (57%) had no published density estimation studies (Table 7.4; Fig. 7.5).

For lion, Tanzania was the country with the greatest number of studies, followed by Kenya and South Africa. Uganda was the country with the highest density of assessments, followed by Cameroon and South Africa; if we only consider countries with >40,000 km^2 of lion range, however, South Africa exhibited the greatest study density, followed by Kenya, Zimbabwe, and Zambia. CAR, Ethiopia, Namibia, and Mozambique all exhibited large species range, but few (two or fewer) studies. Six countries (24%) had no published lion population assessment studies (Table S7.2). For leopard, South Africa was the country with the most population assessment by a wide margin, with more studies than in all other range countries combined. Only 26% of leopard range states had a published density estimate, and the two countries with the greatest leopard range in Africa, Angola and the DRC, had none (Table S7.3). Botswana was the country with the most cheetah population assessments, followed by Kenya, Namibia, and Tanzania. Zambia had the highest density of cheetah studies; if we only consider countries with > 40,000 km^2 of range, however, Kenya was first, followed by Zimbabwe and Tanzania. 60% of cheetah range states had no published population assessments, including some with large tracts of range (Chad, Ethiopia; Table S7.4).

Peer-reviewed African wild dog population assessments were only carried out in four countries over the last two decades: South Africa, Kenya, Zimbabwe, and CAR. Study density was highest in South Africa, partly due to the species' relatively small range in the country. Overall, 78% of range countries had no published African wild dog population assessments, including the five countries with the largest geographical range (Table S7.5). For spotted hyaena, South Africa, Cameroon, Ethiopia, Kenya, and Namibia exhibited the most studies (although South Africa was the country with the most estimates by a wide margin; Table S7.6). Cameroon had the highest density of assessments, followed by South Africa and Congo. The countries with the first and third greatest spotted hyaena range, Angola and DRC, had

no estimates; in total, 25 range countries (64%) had no studies (Table S7.6). For striped hyaena, peer-reviewed assessments have only taken place in Kenya (two studies), with 96% of range states having no published density estimates (Table S7.7). Finally, Botswana and South Africa were the countries with the most brown hyaena population assessments, and Botswana, Zimbabwe, and South Africa were those with the highest study density. Four range countries (50%) had no studies (Table S7.8).

Table 7.4. Large carnivore population assessments in Africa (2000-2020) by country, all species combined. Figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. Refer to Tables S7.2 – 7.8 for species-specific insights.

Country	Studies	Estimates	Geographical Range (km^2) *	Studies / 100,000 km^2	Estimates / 100,000 km^2
South Africa	26	73	1,601,900	1.62	4.56
Tanzania	15	37	2,871,700	0.52	1.29
Kenya	12	28	1,735,300	0.69	1.61
Botswana	11	38	2,469,150	0.45	1.54
Namibia	10	16	2,388,600	0.42	0.67
Zambia	7	12	1,305,900	0.54	0.92
Cameroon	5	29	600,740	0.83	4.83
Zimbabwe	4	13	752,800	0.53	1.73
Ethiopia	4	5	2,884,486	0.14	0.17
Mozambique	3	4	1,413,300	0.21	0.28
Uganda	2	7	468,900	0.43	1.49
Niger	1	1	17,190	5.82	5.82
Gabon	1	3	255,600	0.39	1.17
Benin	1	1	300,400	0.33	0.33
Senegal	1	1	349,800	0.29	0.29
Congo	1	1	386,000	0.26	0.26
Burkina Faso	1	1	572,550	0.17	0.17
Nigeria	1	2	1,012,000	0.10	0.20
CAR	1	10	1,147,040	0.09	0.87
Sudan	1	2	1,729,400	0.06	0.12
Algeria	1	1	3,089,900	0.03	0.03
Angola	0	0	2,009,200	0.00	0.00
Burundi	0	0	28,700	0.00	0.00
Chad	0	0	1,940,300	0.00	0.00
Cote d'Ivoire	0	0	273,400	0.00	0.00
Djibouti	0	0	24,800	0.00	0.00
DRC	0	0	1,751,000	0.00	0.00
Egypt	0	0	1,015,800	0.00	0.00
Equatorial Guinea	0	0	12,800	0.00	0.00
Eritrea	0	0	257,798	0.00	0.00
Eswatini	0	0	38,369	0.00	0.00
Ghana	0	0	209,100	0.00	0.00
Guinea	0	0	277,100	0.00	0.00
Guinea-Bissau	0	0	43,000	0.00	0.00
Lesotho	0	0	100	0.00	0.00
Liberia	0	0	41,200	0.00	0.00
Libya	0	0	1,758,000	0.00	0.00
Malawi	0	0	135,600	0.00	0.00
Mali	0	0	1,602,600	0.00	0.00

Mauritania	0	0	1,140,960	0.00	0.00
Morocco	0	0	976,900	0.00	0.00
Rwanda	0	0	28,500	0.00	0.00
Sierra Leone	0	0	62,700	0.00	0.00
Somalia	0	0	1,314,700	0.00	0.00
South Sudan	0	0	1,271,872	0.00	0.00
The Gambia	0	0	11,300	0.00	0.00
Togo	0	0	54,600	0.00	0.00
Tunisia	0	0	163,600	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

7.3.4. Model results

7.3.4.1. *GLMMs (all species)*

There were significantly more studies than expected on lion, and significantly fewer than expected on striped hyaena (the species exhibiting the strongest effect), both when including only species and countries as variables (Model 1; Table S7.9), and when also controlling for differences in geographical range (Model 2; Table 7.5). In addition, African wild dog exhibited a relatively strong negative research bias, and spotted hyaena and leopard a moderate positive bias (although for spotted hyaena this decreased once accounting for its vast geographical range). Brown hyaena and cheetah exhibited relatively weak, inconclusive effects (Fig. 7.3).

Geographical range had a significant positive effect in all models where it was included (Model 2, Table 7.5; Model 4, Table S7.11; Model 5, Table S7.12; Fig. 7.4), indicating that having more species range in a country was associated with more studies, even when accounting for additional variables. On the other hand, there was little evidence of the socio-economic status of a country, or of the conservation status of a species, being strong predictors of the number of studies in a country or for that species, respectively. This was the case both when not controlling for any additional explanatory variable (Model 3, Table S7.10), and when also controlling for geographical range (Model 4, Table S7.11; Model 5, Table S7.12; Fig. 7.4).

As expected, the values of the random intercepts showed that South Africa, Kenya, and Tanzania exhibited the strongest positive biases in research (Model 1, Table S7.9; Fig. S7.1). When controlling for geographical range in each country (Model 2, Table 7.5), South Africa then Kenya still ranked

highest, while Tanzania dropped to fifth, with Cameroon and Botswana ranking higher. This suggests that part of the positive bias in research observed for Tanzania was due to its vast large carnivore national range. Chad, South Sudan, DRC, and Angola ranked lowest, due to the large amount of range and the lack of studies (Table 7.5; Fig. 7.5).

When controlling for socio-economic indicators, but not geographical range (Model 3), Kenya and Cameroon exhibited the largest values of the random intercepts, indicating greater research effort than would be expected based on their socio-economic indicators. South Africa fell to fifth, suggesting that part of the country's positive research bias can be explained by its higher socio-economic status. Angola still exhibited the lowest random intercept value; however, Eswatini, Malawi and Ghana now exhibited considerably lower values, due to the combination of lack of studies and relatively high socio-economic status (Table S7.10; Fig. S7.2). When controlling for both socio-economic indicators and geographical range, both with (Model 5) and without (Model 4) conservation status modelled as a variable, Kenya, Cameroon and Zimbabwe had more studies than expected, while Angola again ranked last, with Ghana, Malawi and DRC also ranking very low (Table S7.11, S7.12; Fig. S7.3).

Table 7.5. Results of the Poisson GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries (Model 2). Species and countries are modelled as random effects. Significant (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) values are highlighted in bold. For countries, a positive value indicates more assessments than expected based on large carnivore geographical range within that country, while a negative fewer.

Name	Mean	HDI low	HDI high	SD
Intercept	-2.18	-3.66	-0.73	0.74
Range *	**0.61**	**0.26**	**0.95**	**0.18**
Country Random Effect Variance	1.77	1.08	2.55	0.39
Species Random Effect Variance	1.44	0.51	2.74	0.68
Brown Hyaena	-0.26	-1.60	1.08	0.67
Cheetah	0.33	-0.92	1.69	0.65
Leopard	0.49	-0.73	1.78	0.62
Lion *	**1.55**	**0.30**	**2.85**	**0.63**
Spotted Hyaena	0.38	-0.87	1.64	0.62
Striped Hyaena †	**-1.90**	**-3.71**	**-0.38**	**0.86**
African Wild Dog	-0.55	-1.94	0.85	0.69
South Africa *	**3.20**	**2.27**	**4.19**	**0.50**
Kenya *	**2.91**	**1.96**	**3.92**	**0.50**
Cameroon *	**2.55**	**1.49**	**3.68**	**0.56**
Botswana *	**2.48**	**1.50**	**3.52**	**0.52**
Tanzania *	**2.21**	**1.21**	**3.31**	**0.54**

Zimbabwe *	**2.20**	**1.10**	**3.32**	**0.57**
Namibia *	**1.79**	**0.70**	**2.93**	**0.57**
Zambia *	**1.57**	**0.39**	**2.76**	**0.60**
Mozambique	1.13	-0.16	2.38	0.64
Uganda	1.06	-0.42	2.53	0.75
CAR	1.00	-0.36	2.32	0.68
Ethiopia	0.94	-0.36	2.19	0.65
Gabon	0.57	-1.54	2.65	1.08
Congo	0.51	-1.57	2.56	1.06
Nigeria	0.46	-1.63	2.48	1.05
Sudan	0.33	-1.29	1.91	0.81
Senegal	-0.01	-2.00	1.88	0.99
Benin	-0.11	-2.11	1.72	0.98
Burkina Faso	-0.13	-2.11	1.74	0.98
Tunisia	-0.17	-3.53	3.18	1.70
Morocco	-0.39	-3.52	2.71	1.59
Algeria	-0.40	-2.47	1.63	1.05
The Gambia	-0.54	-3.62	2.33	1.54
Lesotho	-0.56	-3.65	2.25	1.52
Equatorial Guinea	-0.57	-3.66	2.29	1.53
Djibouti	-0.60	-3.70	2.21	1.52
Egypt	-0.71	-3.65	2.04	1.48
Mauritania	-0.72	-3.73	1.99	1.47
Liberia	-0.79	-3.73	1.89	1.45
Rwanda	-0.79	-3.64	1.96	1.45
Guinea-Bissau	-0.79	-3.71	1.85	1.44
Libya	-0.79	-3.74	2.04	1.48
Burundi	-0.79	-3.74	1.89	1.46
Sierra Leone	-0.79	-3.66	1.93	1.45
Togo	-0.81	-3.75	1.83	1.44
Ghana	-0.85	-3.74	1.80	1.43
Eswatini	-0.86	-3.80	1.71	1.43
Guinea	-0.87	-3.74	1.76	1.44
Cote d'Ivoire	-0.88	-3.78	1.72	1.41
Niger	-1.16	-3.88	1.29	1.34
Mali	-1.16	-3.93	1.28	1.35
Nigeria	-1.17	-3.89	1.29	1.35
Malawi	-1.18	-3.88	1.29	1.34
Chad	-1.43	-4.01	0.95	1.29
South Sudan	-1.45	-4.06	0.90	1.29
DRC	-1.60	-4.22	0.67	1.27
Angola	-1.74	-4.25	0.51	1.23

Legend: HDI = Highest Density Interval; SD = standard deviation; Range = country range, based on IUCN Red List polygons (IUCN, 2020); * = value suggests significant positive effect; † = value suggests significant negative effect.

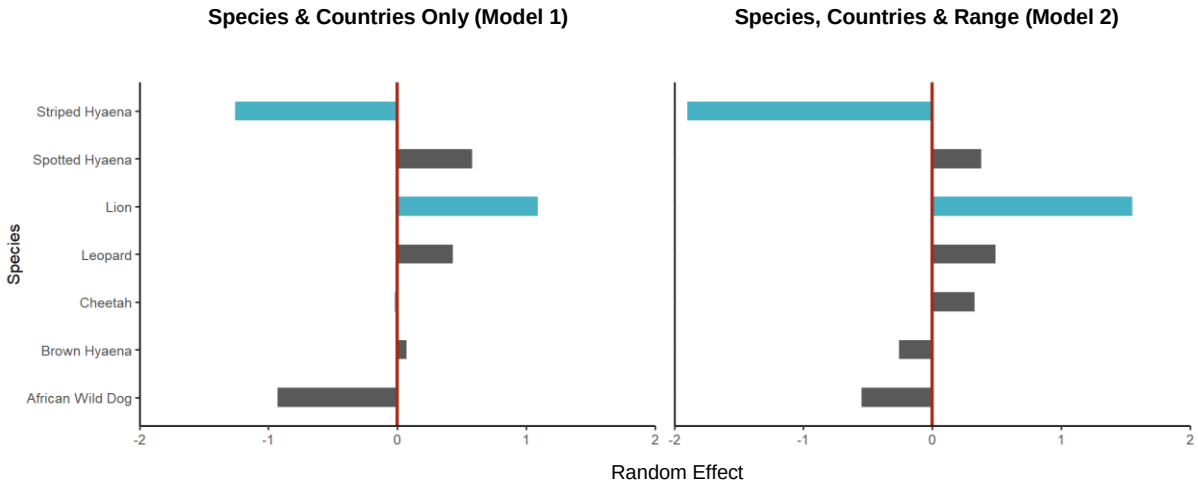


Figure 7.3. Random intercept values for species from the Poisson GLMM without explanatory variables (Model 1, Table S7.9) and for that accounting for geographical range (Model 2, Table 7.5). In both cases, values for lion and striped hyaena indicate a significant effect (i.e. zero not contained within the 95% HDI of the posterior distribution), with this being strongest when accounting for geographical range of species. The moderate negative effect for African wild dog, and positive effect for spotted hyaena, on the other hand, were partly explained by their restricted and very large geographical ranges, respectively.

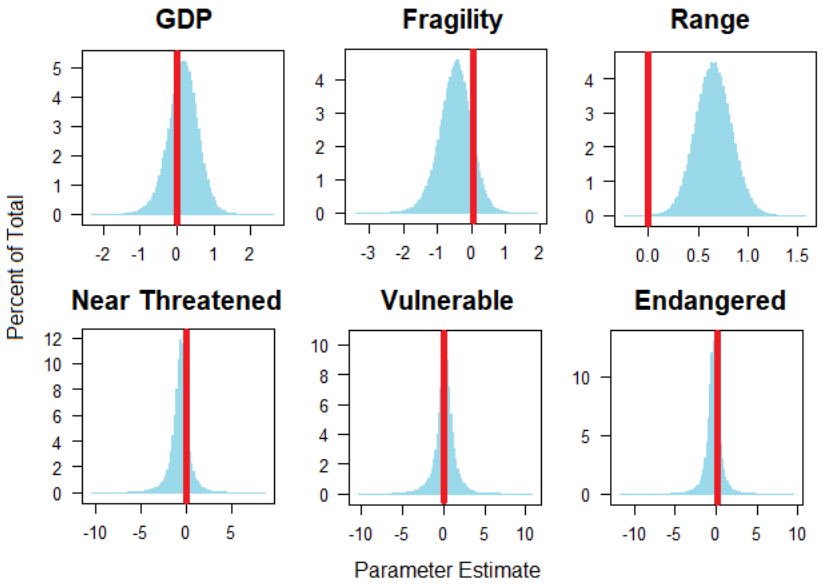


Figure 7.4. Posterior distributions for effects of geographic range, socio-economic indicators (GDP per capita, fragility), and conservation status on large carnivore population assessments (all species), from the most parametrised GLMM (Model 5; Table S7.12). Red line signifies zero effect. Range was the only variable with a credible effect (positive). While it was not possible to rule out that fragility had zero effect, the posterior distribution leaned towards a negative effect for fragility (i.e. more studies in less fragile countries). There was little evidence for GDP per capita or conservation status of a species affecting the number of population assessments.

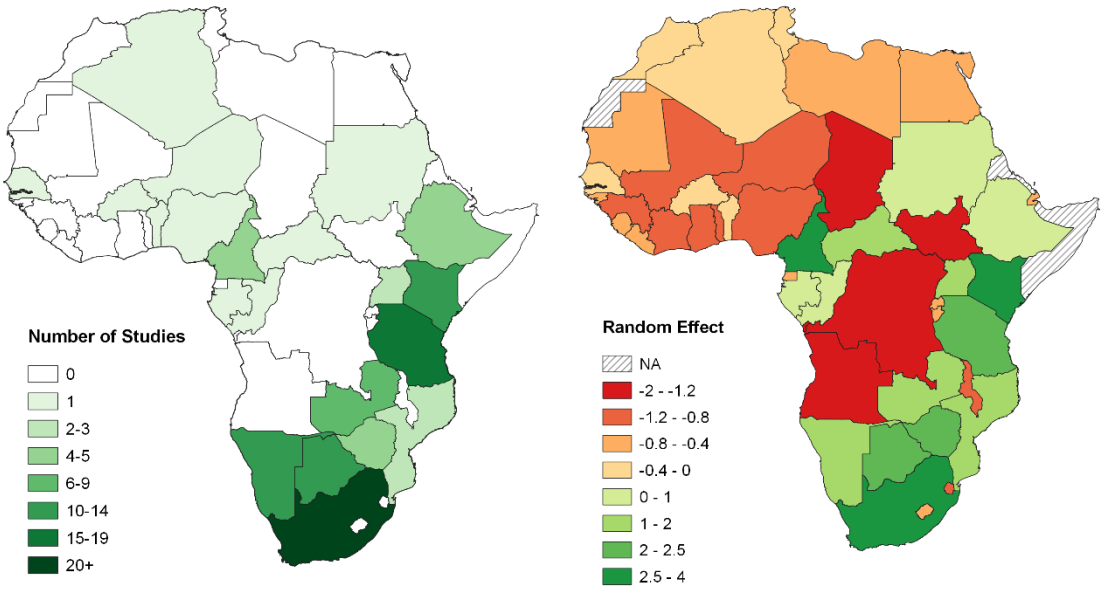


Figure 7.5. Left: Number of large carnivore population assessment studies in Africa, by country. Right: Random effects for individual countries from the Poisson GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries (Model 2). A positive value (green) indicates more population assessments than expected based on large carnivore geographical range within the country (all species), while a negative value (red) fewer. See Tables 7.4 & 7.5 for country specific values. For all figures in this study, country boundaries are based on the definitions of the African Union (https://web.archive.org/web/20130927110741/http://www.afrimap.org/english/images/report/AfriMAP-AU-Guide-EN.pdf)

7.3.4.2. *GLMs (individual species)*

Geographical range was the only variable tested that had a significant positive effect on the number of lion, leopard, and spotted hyaena population assessments within a country. Cheetah population assessments were not strongly predicted by any of the variables tested. Greater country fragility exhibited relatively strong (but not significant) negative associations for all species. Greater GDP per capita was a moderate positive predictor only of spotted hyaena assessments (Fig. 7.6).

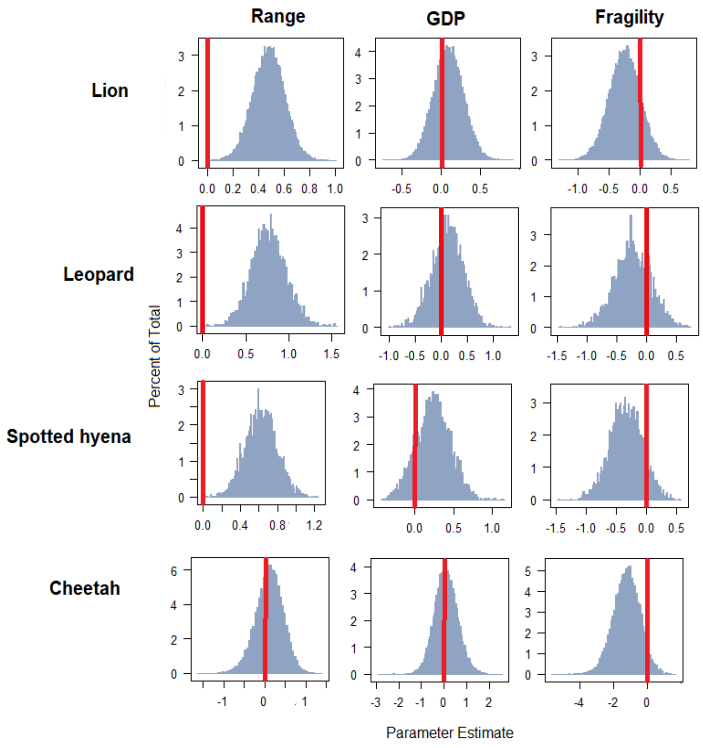


Fig. 7.6. Posterior distributions for effects of geographic range and socio-economic indicators on population assessments of lion, leopard, spotted hyaena, and cheetah (other species could not be modelled due to insufficient data). Red line signifies zero effect. Range had a positive, significant impact for lion, leopard, and spotted hyaena.

For lion, Kenya, South Africa, and Cameroon had significantly more population assessments than would be expected based on geographical country range, while a number of countries exhibited significant negative biases, with CAR and South Sudan having the smallest values of random intercepts (Table 7.6). Kenya (outlier), Cameroon, South Africa, Zimbabwe, and Zambia had significantly more assessments than would be expected based on countries' lion geographical range, GDP, and fragility, while Angola, CAR, and Namibia significantly fewer, as did six other countries (Table 7.6; due to the small amount of data points model fit was not ideal – see Appendix 7.4 for additional details). For leopard, South Africa was an outlier, exhibiting the largest positive bias in studies, and Zimbabwe, Cameroon and Kenya also had significantly more population assessments than would be expected based on geographical range, while Angola, DRC and Ethiopia were the most understudied. All of these effects held true when accounting for GDP and fragility (Table S7.13). In the case of cheetah, Kenya, Botswana, and Tanzania were the countries with the most population assessments when controlling for geographical range, while Algeria, Chad, and Ethiopia had the fewest. Controlling also for GDP and

fragility, Kenya (outlier), Zimbabwe, Tanzania, and Zambia had more studies than expected, while Benin, Angola, and Burkina Faso had the least (Table S7.14). For spotted hyaena, Cameroon, South Africa, and Namibia exhibited the largest values of the random intercepts when accounting for geographical range, and Angola, DRC, and Nigeria the smallest. Finally, Cameroon (outlier), Kenya, Zimbabwe, and South Africa had the most spotted hyaena population assessments when also controlling for countries' GDP and fragility, while Angola, Gabon, Nigeria, and DRC had the fewest (Table S7.15).

Table 7.6. Results of the models investigating biases in lion population assessments in Africa, accounting for geographical range (A; Negative Binomial GLM), and for geographical range and socio-economic differences between countries (B; Poisson GLM). One outlier (Kenya) was removed from analysis A (strong positive effect). Significant (i.e. credible non-zero) fixed effect values are highlighted in bold. For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant effect in analysis A.

	A – RANGE			**B - RANGE & SOCIO-ECONOMIC**		
Name	**Mean**	**HDI low**	**HDI high**	**Mean**	**HDI low**	**HDI high**
(Intercept)	0.73	0.29	1.17	0.43	0.08	0.79
Range *	**0.51**	**0.08**	**0.95**	**0.48**	**0.23**	**0.72**
GDP	NA	NA	NA	0.10	-0.26	0.48
Frag	NA	NA	NA	-0.25	-0.75	0.24
Kenya *	**3.46**	**1.59**	**5.36**	NA	NA	NA
South Africa *	**2.35**	**0.94**	**3.73**	**2.53**	**1.12**	**4.09**
Cameroon *	**2.05**	**0.78**	**3.36**	**3.85**	**2.47**	**5.24**
Zimbabwe	0.66	-0.01	1.34	**1.76**	**0.86**	**2.77**
Zambia	0.62	-0.08	1.33	**1.46**	**0.70**	**2.26**
Uganda	0.36	-0.25	0.98	**1.05**	**0.35**	**1.81**
Botswana	0.35	-0.50	1.21	-0.54	-2.03	1.00
Tanzania	0.28	-1.09	2.12	1.01	-0.98	3.18
Nigeria	-0.29	-0.67	0.10	-0.01	-0.57	0.53
Sudan	-0.3	-0.67	0.10	0.23	-0.38	0.89
Burkina Faso	-0.31	-0.68	0.08	-0.20	-0.80	0.40
Benin	-0.31	-0.68	0.07	-0.41	-1.22	0.39
Senegal	-0.33	-0.69	0.04	-0.38	-1.04	0.27
Mozambique †	**-0.52**	**-0.96**	**-0.08**	-0.37	-0.93	0.23
Ethiopia †	**-0.63**	**-0.95**	**-0.31**	**-0.50**	**-0.89**	**-0.12**
Namibia †	**-0.68**	**-1.02**	**-0.35**	**-1.34**	**-1.87**	**-0.80**
Niger †	**-0.91**	**-1.21**	**-0.63**	**-0.98**	**-1.22**	**-0.75**
Chad †	**-0.91**	**-1.21**	**-0.62**	**-0.9**	**-1.19**	**-0.62**
Malawi †	**-0.92**	**-1.22**	**-0.63**	**-1.10**	**-1.46**	**-0.75**
Angola †	**-0.92**	**-1.23**	**-0.63**	**-1.13**	**-1.38**	**-0.89**
DRC †	**-0.92**	**-1.23**	**-0.64**	**-0.90**	**-1.20**	**-0.61**
South Sudan †	**-0.93**	**-1.24**	**-0.64**	**-0.91**	**-1.27**	**-0.58**
CAR †	**-0.99**	**-1.57**	**-0.49**	**-1.01**	**-1.91**	**-0.14**

Legend: HDI = Highest Density Interval; Range = Geographical range of species, based on IUCN Red List range maps (IUCN, 2020); GDP = Gross Domestic Product per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect

7.4. DISCUSSION

While studies have examined general biases in conservation research (Di Marco et al., 2017; Velasco et al., 2015; Wilson et al., 2016), here, for the first time, we discuss research trends, biases, and knowledge gaps in peer-reviewed population assessments of large carnivores in Africa. Our review highlights the progress that has been made, while identifying significant shortcomings in the availability of published population assessments. Lion, followed by spotted hyaena, were the target of most research, while striped hyaena, followed by African wild dog, were the most understudied. Southern and eastern Africa were the better studied regions, although due to country and ecosystem biases significant gaps remain even there. The number of published assessments for a species in a country was related to country range for most species, while a country's GDP or stability did not have a significant effect on research. Extinction risk of a species (measured through conservation status) was not a good predictor of research attention. Overall, considerable scope for future work exists for all species and for most countries, and researchers, funding agencies, and governments should consider the identified data gaps when planning future research or making decisions that affect research output. Below, we expand on these findings and use them to identify opportunities and priorities for further work.

7.4.1. Taxonomic representativeness & biases

Our analyses found that, over the past two decades, lion was the species subject to the greatest number of population assessments, both overall and by study density (Fig. 7.2, Table 7.2), and relative to species' geographical range (Table 7.5).

While the reasons for this positive bias will vary across the species' range, it is likely that its highly charismatic nature (Macdonald et al., 2015), role as a keystone and flagship species (Bauer & Henschel, 2015; Leader-Williams & Dublin, 2000), and ability to attract conservation funding and generate revenue through tourism (Maciejewski & Kerley, 2014) all play a role. In addition, particularly when compared to species such as wild dog and cheetah, a relatively large number of methodologies have been employed to survey lion populations, including call-ins, spoor counts, and capture-recapture techniques (Braczkowski et al., 2020). This relatively wide breadth of available methodologies, and the

relative ease of implementing some of them (e.g. call-ins, spoor counts), likely also played a part in the species receiving greater research attention. On the other hand, the large number of studies for spotted hyaena, the second most studied species, are likely partly driven by its vast distribution (as indicated by our model findings; Fig. 7.3), as well as by the relatively large number of survey methods applicable to the species, including call-ins (Ferreira & Funston, 2016), spoor surveys (Bauer & Henschel, 2015), and capture-recapture applied to camera trap data (Fouché et al., 2020). In addition, assessments primarily targeting lions often employed the data collected to also estimate spotted hyaena density (e.g. Ferreira & Funston, 2016). Nevertheless, due to the species' wide distribution, study density was lower than for all other species except striped hyaena (Table 7.2), suggesting that considerable knowledge gaps remain across its range.

Striped hyaena had the lowest number of population assessments, and the strongest negative research bias. This is in line with previous work suggesting that knowledge of the species is particularly low (AbiSaid & Dloniak, 2015), and is likely due to a combination of factors, including: populations often existing outside of formally protected areas (PAs; AbiSaid & Dloniak, 2015); the species being more secretive and less well-known (Macdonald et al., 2015), and thus less apt at raising conservation and tourism revenue (Di Minin et al., 2013; Okello et al., 2008); and the fact much of its range is in northern Africa, a region exhibiting low levels of conservation research (Agha et al., 2018; Hickisch et al., 2019; Trimble & van Aarde, 2012). Finally, the fact that some methods employed to survey other species, such as call-ins, cannot be applied to striped hyaena is likely to also have played a part.

The other large carnivore which exhibited a negative bias in research was wild dog (although this was not significant; Table 7.5). This is of particular concern due to the species being the most threatened of the African large carnivores (Woodroffe & Sillero-Zubiri, 2020), and supports suggestions that conservation research can be poorly aligned with conservation priorities, especially in relation to threatened species (Di Marco et al., 2017; Wilson et al., 2016). Further evidence for this is also provided by our finding that conservation status did not affect number of studies on a species (Table S7.12). The observed paucity of estimates for wild dog is likely a result of the species being less well-known compared to the felids (Macdonald et al., 2015), and a combination of ecological and methodological

factors. Wild dogs are social, low density species, with very large home ranges which often range outside of PA boundaries (Creel & Creel, 2002); as a result, some survey methods (e.g. camera trapping) can be difficult to apply to the species, while others are not suitable due to behavioural characteristics (e.g. call-ins). Indeed, although relatively low-cost methods such as spoor counts have occasionally been employed to survey wild dog populations (Henschel et al., 2020), approximately half of published density estimates were obtained through resource-intensive long-term studies or citizen-science approaches, highlighting the difficulty associated with surveying the species rapidly. Finally, several important populations were the subject of long-term studies prior to the period considered (e.g. Selous Game Reserve, Creel & Creel, 1998; Kruger National Park, Mills & Gorman, 1997), and most wild dog populations in South Africa are part of an intensively managed metapopulation (Davies-Mostert et al., 2015), where the exact number of individuals is known (and were therefore not eligible for our review, even though they are actively monitored). These factors are also partly responsible for the observed negative research bias.

Leopard exhibited a slight positive bias in research, and there was little evidence of brown hyaena or cheetah experiencing strong biases in either direction. In the case of leopard and brown hyaena, their suitability to camera trap based methods and to spoor counts has likely had a positive role in promoting assessments of both species, as has the leopard's wide range and charismatic nature (Maciejewski & Kerley, 2014). While the cheetah is highly charismatic (Di Minin et al., 2013; Macdonald et al., 2015), listed as vulnerable to extinction (Durant et al., 2015), and has high potential to generate conservation revenue through tourism (Maciejewski & Kerley, 2014; Okello et al., 2008), a lack of standardised survey techniques for the species is likely to have played a role in survey efforts not being greater. Additionally, the fact that, like for wild dog, numerous populations in South Africa inhabit small, intensively managed reserves (Buk et al., 2018) also played a part in the number of available estimates being relatively low.

For all species, both when combined and when analysed individually, greater geographical range in a country was found to correspond to greater research effort in that country (with the exception of cheetah), while conservation status did not affect the number of population assessments of a species.

Our results thus echo others in indicating that conservation research does not necessarily follow a pattern of threat among species (Mamo et al., 2020). Instead, our findings suggest that a range of factors, in addition to species' geographical range, all play a role in driving the number of large carnivore population assessments, including the species' ecology, charisma, ability to generate conservation funding and tourism revenues, and the applicability of survey methods.

7.4.2. Geographical representativeness & biases

7.4.2.1. *Regional and intra-regional trends & biases*

The observed greater research effort in southern Africa is likely a result of greater conservation research investments the region (Brockington & Scholfield, 2010; Wilson et al., 2016), as well as the favourable socio-economic characteristics of some countries (UNDP, 2020). For most species, eastern Africa was the second most studied region; this is likely due to the region still harbouring numerous important large carnivore populations, as well as the long history of conservation investments and research in some countries (e.g. Kenya and Tanzania; Brockington & Scholfield, 2010). Nevertheless, approximately half (48%) of lion, 60% of cheetah, and 31% of spotted hyaena assessments in the region were from a single population, in the Serengeti-Mara (Appendix 7.1), even though the ecosystem comprises only ~7% of lion's, ~8% of cheetah's, and ~1% of spotted hyaena's eastern African range. Thus, despite the relatively high level of research overall, many of the region's populations are still understudied.

Low research effort in northern Africa is likely due to most large carnivore populations in the region existing at low density and outside of PAs (Belbachir et al., 2015), to conservation research investments (including technical capacity building) being comparatively low in the region, and to the instability of some countries (Di Marco et al., 2017; Wilson et al., 2016). Similarly, the low level of research in western and central Africa for most species (Table 7.2, Table S7.1) mirrors the region's under-representation across wider conservation research (Hickisch et al., 2019; Trimble & van Aarde, 2012; Wilson et al., 2016). For central Africa, this negative bias is likely to primarily be a consequence of high volatility and low conservation investments in the region (Brockington & Scholfield, 2010; FFP, 2020). In western Africa, the fact that conservation investments and wildlife-oriented tourism have

historically been lower than in southern and eastern Africa (Brockington & Scholfield, 2010; UNWTO, 2018) has likely had an impact on research effort in the region.

Overall, our findings therefore largely agree with claims of biases towards carnivore research and conservation activities in eastern and southern Africa (Ray et al., 2005). Nevertheless, when accounting for the fact that, for many species, their geographical range is much greater in these regions, the density of population assessments was actually lower than in central and western Africa for a number of species (Table S7.1). In addition, for several species, many assessments in eastern Africa are from a small number of populations, with the majority of the species' other populations in the region having received little attention. Without the aforementioned studies on the Serengeti-Mara population, for example, eastern African would exhibit the lowest lion study density of any range region. These findings suggest that, when accounting for differences in geographical range and the repeated sampling of a few populations, the observed biases in population assessments towards certain regions are less clear-cut than they may initially appear.

7.4.2.2. *Country trends & biases*

As lack of research attention can impede the achievement of biodiversity conservation objectives (Di Marco et al., 2017), the fact that 57% of African countries with large carnivore range did not have a single published, peer-reviewed population assessment is of particular concern. When accounting for differences in geographical range between countries, Angola, South Sudan, DRC, and Chad stood out as those exhibiting the strongest negative bias in research (Table 7.5), likely primarily as a consequence years of unrest and insecurity in these countries (FFP, 2020).

South Africa showed the strongest positive bias in published research (Table 7.5), with the greatest number of population assessments for several species (Tables S7.2-S7.8). Although analyses suggest that, at a continental scale, socio-economic indicators are not a good predictor of research, the fact that South Africa dropped from first to fifth strongest positive bias in research when accounting for these (Table S7.10) suggests that greater economic development and/or stability are likely playing some role in the positive bias in research effort for the country (Fisher et al., 2011; Stocks et al., 2008). Indeed,

conservation investments are particularly high in South Africa (Brockington & Scholfield, 2010). Similarly, for most other countries in southern Africa positive biases diminished when including socio-economic indicators, suggesting that better socio-economic conditions likely play a part in the greater research in the region.

Although Tanzania was the country with the second highest total number of peer-reviewed large carnivore assessments, accounting for geographical range caused the country to exhibit only the fifth strongest positive bias in research (Table 7.5), indicating that part of the high effort is due to the country being home to considerable large carnivore range. Similarly, although it was the country with the largest number of lion studies, when controlling for both socio-economic indicators and range the country fell to sixth (Table 7.6). Furthermore, 60% of all published lion population assessments were carried out in a single ecosystem (Serengeti), with only four assessments instead carried out in the remaining ~350,000 km^2 (92%) of lion country range; here, the density of studies was comparable to the most understudied countries on the continent. Similarly, all cheetah assessments were from a single population, also that of the Serengeti, even though the majority of cheetah country range is elsewhere (Fig. 7.2). A similar in-country bias was also observed in Kenya, with 50% of all studies and 45% of lion studies being from the Mara system, even though this covered only ~3% of national lion range. These in-country biases towards a small number of well-studied-populations suggest that the overall number of studies should not be the sole metric of research effort in a country.

Finally, our findings suggest there are no strong associations between socio-economic indicators and research effort, in contrast to previous research (Stocks et al., 2008). This is likely, at least in part, to be a consequence of the continental scale investigated; indeed, the strength of the positive bias for certain countries (e.g. South Africa) was reduced when accounting for socio-economic differences, suggesting an impact. Nevertheless, our results lead us to agree with studies suggesting that the extent of published research in a country is dependent on a range of additional factors, including research history and interests of individuals and organisations, priorities of funding agencies and governments, in-country support and capacity for science, and language barriers to publication (Griffiths & Dos Santos, 2012; Trimble & van Aarde, 2012). Our results also indicate that, for all large carnivores combined and for

most individual species, country fragility exhibited a negative association with research (although not significantly; Table 7.5, Fig. 7.4, 7.6). As lack of stability has been shown to be associated with greater conservation threats (Jha & Bawa, 2006), our findings thus suggest that efforts may be lower in countries where such research is most needed, likely due to greater political instability and poor governance hindering conservation researchers and practitioners (Agha et al., 2018; Dickman et al., 2015; Garland, 2008).

7.4.3. Opportunities & recommendations

Reducing the identified geographical and taxonomic biases in population assessments would help ensure that all species and areas of conservation importance have an adequate knowledge base available, thus improving their conservation outlook (Wilson et al., 2016). We argue that addressing the identified geographical biases should be the most pressing priority: while a focus towards certain species, such as lion, may indirectly lead to conservation benefits for other species (e.g. by identifying areas requiring additional conservation investments), research from well-studied areas is unlikely to be able to support conservation decisions in poorly-studied regions (Di Marco et al., 2017). Thus, much like for the wider conservation research field (Trimble & van Aarde, 2012), geographical biases in research and assessments are more immediate hurdles for science-based conservation management of African large carnivores. As a result, northern, western, and central Africa should be considered priority regions for future research. Increased attention should in particular be given to the twenty-eight countries which currently do not have any published estimates (Table 7.4), especially Angola, DRC, South Sudan, and Chad, given their considerable large carnivore geographical country ranges (Table 7.4, 7.5) and their potential importance for the conservation of these species (Dickman et al., 2015). Within southern and eastern Africa, we encourage prioritising additional research outside of South Africa and the Serengeti-Mara ecosystem, respectively, to complement the extensive efforts there.

Shortfalls in conservation research in countries with high levels of biodiversity but low income can be due to a lack of trained and/or funded biologists (Gaston, 2000), research infrastructure (Wilson et al., 2016), or dedicated finances (Githiru et al., 2015). As a result, building capacity of researchers and practitioners in large carnivore survey and monitoring techniques in under-represented areas should be

a priority. Outside of South Africa, the fact that only 59% of studies included a co-author from the study country reinforces findings suggesting that research in developing and tropical countries is disproportionately led by scientists from more developed areas (Stocks et al., 2008), and shows there is considerable need for such capacity building efforts. Breaking down structural racism and discrimination in academia and conservation practice will also play a key role in addressing the observed biases (Chaudhury & Colla, 2020). For these reasons, we recommend that both donors and foreign researchers maximise the involvement of local scientists and practitioners in future assessments, including through capacity building efforts such as training workshops and the provision of funds and equipment, which is likely to be necessary for long-term reduction in research biases.

In addition, conservation donors and funders should encourage efforts in understudied regions, as well as for understudied species, to ensure that conservation research occurs where it is most needed, and avoid the observed ecosystem biases (Di Marco et al., 2017; Wilson et al., 2016). This being said, we also urge funders, practitioners, and researchers to recognise the importance of scale dependency in such recommendations, as even within more studied countries gaps remain: in Tanzania, the country with the greatest lion range and the most lion studies, due to in-country biases most populations have yet to be subject to peer-reviewed assessments. We therefore emphasize the importance of decision and investment processes being multi-scale, and of appreciating the intricacies of the identified biases.

On a species level, we echo calls for further population assessments of striped hyaena across its range (AbiSaid & Dloniak, 2015). We also strongly recommend prioritising further population assessments of wild dog, particularly due to the species' classification as 'Endangered' (Woodroffe & Sillero-Zubiri, 2020). Such efforts are especially required in countries that have been identified as crucial to the species, but where no recent assessments have been carried out (e.g. Tanzania and Botswana; Kuiper et al., 2018). Since the lack of well-established methods to survey wild dog populations is a key reason for these knowledge gaps (Woodroffe & Sillero-Zubiri, 2020), longer-term intensive monitoring studies such as those carried out for some populations prior to this review's considered period (e.g. in Selous; Creel & Creel, 1996), alongside further development of novel, cost-effective methodologies (e.g. citizen-science based techniques; Marnewick et al., 2014), are strongly recommended. The possibility

of instead monitoring populations through alternative status parameters, such as species' occupancy (Henschel et al., 2020; Chapter 3), should also be explored.

Our findings also highlight the need for additional cheetah population assessments, particularly in northern, western, and central Africa, and in eastern Africa outside of the Serengeti-Mara ecosystem. Studies in Chad and Ethiopia should be considered a priority, due to the lack of assessments and large country ranges. As for wild dog, we also recommend further development and standardisation of cheetah population monitoring techniques, including the exploration of novel citizen-science based approaches (Marnewick et al., 2014; Weise et al., 2017). For brown hyaena, we recommend the prioritisation of assessments across different habitats and land-use types (Kent & Hill, 2013), and in countries where the species is yet to be surveyed (Angola, Mozambique, Eswatini; Table S7.8).

In the case of leopard, surveys are urgently required in the 74% of range states without any published estimates, particularly those with especially large geographical range (Angola, DRC, Ethiopia, and South Sudan; Table S7.3). Although considered a highly adaptable species, leopard populations are increasingly under threat (Stein et al., 2020), and the fact that study density was low everywhere outside of southern Africa is of concern. Due to the wide range of habitats and land use types the species inhabits (Hunter, 2015), and to allow for the timely identification and mitigation of threats at a range wide scale, it is crucial that research and monitoring be carried out across the species' range, rather than in localised 'hubs', as is currently the case (South Africa; Table S7.3).

For spotted hyaena, future efforts should prioritise populations in northern and western Africa, as no assessments are available from these regions, as well as in countries with extensive range but no surveys (Angola, DRC, Nigeria, Somalia, and South Sudan). Studies should also be encouraged for the many populations in central Africa, and even in southern and eastern Africa, which have received little research attention do date. Overall, the relatively low study density (Table 7.2), combined with the species' wide adaptability (Bohm & Höner, 2015), indicate that considerable knowledge gaps still exist for the species.

Study density for lion was lowest in central Africa, which should therefore be considered a priority region for further assessments. Nevertheless, considerable opportunity for further work exists in most range countries; even in Tanzania and Kenya, the two with the greatest number of assessments, the majority of populations have not been assessed (including what are believed to be some of the continent's most significant remaining populations; Bauer et al., 2016). Overall, the fact that even for lion, the species with the strongest positive bias in research, considerable data gaps still exist highlights the extent to which African large carnivore populations are presently understudied and under-monitored.

Across the continent, efforts should be made to address the observed sampling bias towards photographic tourism areas, and against trophy hunting areas. Trophy hunting areas in Africa cover a greater area than National Parks (Lindsey et al., 2007), and, given that accurate estimates of population size are crucial to ensure the sustainability of trophy hunting (Mweetwa et al., 2018; Packer et al., 2010), we recommend that future efforts provide attempt to bridge this gap. Similarly, although working on public and/or unprotected land can be logistically challenging (Agha et al., 2018; Martin et al., 2012), efforts should also be made to address the negative sampling bias associated with these areas, as our findings support the global pattern of biodiversity monitoring largely taking place within PA networks (Martin et al., 2012). While some large carnivores species are increasingly restricted to PAs (e.g. lion; Riggio et al., 2013), meaning that such a bias is to be expected, the fact that some species still heavily occupy areas outside PAs (e.g. spotted hyaena, Bohm & Höner, 2015; cheetah in southern Africa; Weise et al., 2017), and that non-protected areas encompass the majority of wildlife habitat across the continent (Agha et al., 2018), highlights the need for future efforts to include boundary and non-protected areas.

Finally, we conclude by recommending better accounting for species' extinction risks when directing research attention and funds. Currently, conservation status appears to have little influence on the amount of research received by different large carnivore species in Africa (at least with regards to population assessments), and efforts should therefore be made to ensure that limited conservation funds are directed to species and populations that require them the most.

7.4.4. Methodological considerations & main study limitations

Our review identified a number of density estimation efforts which were not published in peer-reviewed literature and/or were not publicly available. It is therefore important to acknowledge that the status of some populations has been assessed, and may be actively monitored, even though research findings are not available. In addition, in South Africa, several smaller protected areas hold populations of lion, cheetah and wild dog that are intensively monitored (Buk et al., 2018; Davies-Mostert et al., 2015), meaning they do not qualify for explorative studies such as those treated in this review, even though their status is known.

Thus, while our goal was to specifically identify biases and opportunities with regards to where exploratory peer-reviewed research is being carried out, it is clear that our review is an underestimate of the overall number of populations for which data on status and trends exists (particularly in southern Africa), and it is likely that consideration of grey literature would have influenced some of the conclusions of this study. Nonetheless, while we appreciate that subjecting estimates to peer-review may not be considered necessary if the sole goal is management of a population, for wider meta-analyses and policy, and to assess the response of different populations to different resources and threats, and thus inform their management, estimates would benefit from undergoing scientific peer-review, to ensure their reliability and accordance with developed methodologies (Suryawanshi et al., 2019). We therefore encourage researchers, managers, and practitioners to publish findings of population assessments whenever possible, to confirm their reliability and make insights available to the wider scientific research and conservation management communities.

7.5. APPENDICES

Appendix 7.1. African Large Carnivore Density Studies & Estimates

Appendix 7.2. Additional Reporting Details

Appendix 7.3. Supplementary Tables & Figures

Appendix 7.4. Additional Model Fitting Details

APPENDIX 7.1 – AFRICAN LARGE CARNIVORE DENSITY STUDIES & ESTIMATES

A list of all peer-reviewed density estimation studies from the literature review, as well as individual density estimates and additional information extracted during the review process, can be accessed at:

https://github.com/pstrampelli/African-Large-Carnivore-Density-Studies-Estimates

APPENDIX 7.2 – ADDITIONAL REPORTING DETAILS

The details below are relevant to the data presented in Appendix 7.1.

In situations where a survey spanned multiple PAs and the overall combined size of the PAs sampled was unclear (e.g. Rich et al., 2019), the size of the largest of the PAs surveyed is reported.

When not explicitly presented, the area sampled by a study was calculated differently depending on the methodology employed: for studies employing camera trap grids, this was calculated as the area formed by the minimum convex polygon (MCP) between the different camera traps; for call-in studies, it consisted of the number of call-in stations multiplied by the area sampled by each (calculated as π multiplied by the square of the response radius (in km) employed by the authors); and for spoor counts, distance sampling, and intensive monitoring studies it consisted of the area provided by the authors. If the sampled area was not provided by the authors, or it was not possible to calculate it through the above methodology based on information provided by the authors, it was recorded as 'Unclear'.

Where a single study provided two results for different years for the same exact study area (e.g. Rosenblatt et al., 2014) the most recent is provided. Similarly, for long-term intensive studies presenting in a single study a range of density estimates for the same area, the most recent being presented.

Where a minimum and a maximum density was provided for the study period, but no single average density or additional information was (e.g. M'soka et al., 2016), the estimate presented consists of the arithmetic mean of the minimum and maximum.

Note that, throughout this study, geographical regions and country boundaries are based on definitions by the African Union, as provided and accessed here: https://web.archive.org/web/20130927110741/http://www.afrimap.org/english/images/report/AfriMAP-AU-Guide-EN.pdf

APPENDIX 7.3 – SUPPLEMENTARY TABLES & FIGURES

Table S7.1. Geographical trends in large African carnivore population assessments, by region (2000 – 2020).

Region	Geographical Range (km²)*	Studies	Density Estimates	Studies / 10,000 km² **	Estimates / 10,000 km² **
LION (*Panthera leo*)					
Eastern	585,600	23	37	0.39	0.63
Southern	737,450	20	34	0.27	0.46
Western	52,300	3	4	0.57	0.76
Central	299,140	6	14	0.20	0.47
Northern	0	0	0	NA	NA
LEOPARD (*Panthera pardus*)					
Southern	2,908,700	22	41	0.076	0.141
Eastern	1,754,700	5	10	0.028	0.057
Central	1,901,600	3	10	0.016	0.053
Western	317,100	1	3	0.032	0.095
Northern	9,400	0	0	0	0
CHEETAH (*Acinonyx jubatus)*					
Southern	1,233,400	11	12	0.089	0.097
Eastern	484,732	5	6	0.103	0.124
Northern	704,300	1	1	0.014	0.014
Western	99,440	0	0	0.000	0.000
Central	238,300	0	0	0	0
AFRICAN WILD DOG (*Lycaon pictus*)					
Southern	693,400	3	3	0.043	0.043
Eastern	369,526	2	2	0.054	0.054
Central	156,740	1	2	0.064	0.128
Western	29,200	0	0	0	0
Northern	0	0	0	NA	NA
SPOTTED HYAENA (*Crocuta crocuta*)					
Southern	4,247,200	15	42	0.035	0.099
Eastern	4,988,600	13	22	0.026	0.044
Central	2,200,500	6	14	0.027	0.064
Western	2,697,100	0	0	0	0
Northern	110,960	0	0	0	0
STRIPED HYAENA (*Hyaena hyaena*)					
Eastern	4,404,298	2	2	0.0045	0.0045
Western	1,637,400	0	0	0	0
Central	1,320,300	0	0	0	0
Northern	7,320,500	0	0	0	0
Southern	0	0	0	NA	NA
BROWN HYAENA (*Hyaena brunnea*)					
Southern	2,294,769	11	24	0.048	0.105
Eastern	0	0	0	NA	NA
Western	0	0	0	NA	NA
Central	0	0	0	NA	NA
Northern	0	0	0	NA	NA

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km² of geographical range

Table S7.2. Peer-reviewed lion population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 10,000 km^2 **	Estimates / 10,000 km^2 **
Tanzania	377,300	10	19	0.27	0.50
Kenya	69,500	9	12	1.29	1.73
South Africa	40,600	6	14	1.48	3.45
Botswana	201,450	5	6	0.25	0.30
Cameroon	19,740	5	11	2.53	5.57
Zambia	113,800	4	8	0.35	0.70
Zimbabwe	44,400	3	3	0.68	0.68
Mozambique	192,300	2	2	0.10	0.10
Uganda	2,500	2	4	8.00	16.00
Benin	13,000	1	1	0.77	0.77
Burkina Faso	10,600	1	1	0.94	0.94
CAR	264,100	1	3	0.04	0.11
Ethiopia	109,600	1	1	0.09	0.09
Namibia	128,700	1	1	0.08	0.08
Nigeria	7,400	1	2	1.35	2.70
Senegal	18,300	1	1	0.55	0.55
Sudan	8,500	1	1	1.18	1.18
Angola	10,100	0	0	0.00	0.00
Chad	3,100	0	0	0.00	0.00
DRC	12,200	0	0	0.00	0.00
Malawi	6,100	0	0	0.00	0.00
Niger	3,000	0	0	0.00	0.00
South Sudan	18,200	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km^2 of geographical range

Table S7.3. Peer-reviewed leopard population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 10,000 km^2 **	Estimates / 10,000 km^2 **
South Africa	401,300	14	28	0.35	0.70
Tanzania	672,100	3	8	0.04	0.12
Zimbabwe	160,000	2	3	0.13	0.19
Cameroon	184,300	2	8	0.11	0.43
Kenya	312,900	2	2	0.06	0.06
Botswana	367,200	2	4	0.05	0.11
Namibia	568,900	2	3	0.04	0.05
Zambia	236,100	1	2	0.04	0.08
Gabon	250,000	1	3	0.04	0.12
CAR	375,500	1	2	0.03	0.05
Mozambique	457,000	1	1	0.02	0.02
Angola	696,900	0	0	0.00	0.00
DRC	696,600	0	0	0.00	0.00
Ethiopia	346,900	0	0	0.00	0.00
Congo	310,300	0	0	0.00	0.00
South Sudan	249,800	0	0	0.00	0.00
Benin	132,300	0	0	0.00	0.00
Chad	71,200	0	0	0.00	0.00
Uganda	65,100	0	0	0.00	0.00
Sudan	42,200	0	0	0.00	0.00
Somalia	39,300	0	0	0.00	0.00
Cote d'Ivoire	39,200	0	0	0.00	0.00
Guinea	31,200	0	0	0.00	0.00
Senegal	29,400	0	0	0.00	0.00
Liberia	23,000	0	0	0.00	0.00
Eritrea	22,600	0	0	0.00	0.00
Burkina Faso	19,000	0	0	0.00	0.00
Ghana	14,700	0	0	0.00	0.00
Equatorial Guinea	12,800	0	0	0.00	0.00
Nigeria	11,500	0	0	0.00	0.00
Malawi	11,100	0	0	0.00	0.00
Eswatini	10,100	0	0	0.00	0.00
Guinea-Bissau	7,000	0	0	0.00	0.00
Mali	6,000	0	0	0.00	0.00
Egypt	5,800	0	0	0.00	0.00
Algeria	3,600	0	0	0.00	0.00
Sierra Leone	3,000	0	0	0.00	0.00
Rwanda	2,200	0	0	0.00	0.00
Djibouti	1,600	0	0	0.00	0.00
Burundi	900	0	0	0.00	0.00
Niger	500	0	0	0.00	0.00
Togo	300	0	0	0.00	0.00
Lesotho	100	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km^2 of geographical range

Table S7.4. Peer-reviewed cheetah population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km²)*	Studies	Density Estimates	Studies / 10,000 km² **	Estimates / 10,000 km² **
Botswana	453,000	5	7	0.11	0.15
Kenya	123,800	3	3	0.24	0.24
Namibia	510,000	2	2	0.04	0.04
Tanzania	119,000	2	3	0.17	0.25
Algeria	704,300	1	1	0.01	0.01
South Africa	140,300	1	1	0.07	0.07
Zimbabwe	48,100	1	1	0.21	0.21
Zambia	29,400	1	1	0.34	0.34
Chad	204,200	0	0	0.00	0.00
Ethiopia	193,392	0	0	0.00	0.00
Mali	63,300	0	0	0.00	0.00
South Sudan	44,740	0	0	0.00	0.00
Angola	44,700	0	0	0.00	0.00
CAR	34,100	0	0	0.00	0.00
Niger	13,690	0	0	0.00	0.00
Benin	13,100	0	0	0.00	0.00
Burkina Faso	9,350	0	0	0.00	0.00
Mozambique	7,900	0	0	0.00	0.00
Uganda	2,600	0	0	0.00	0.00
Sudan	1,200	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km² of geographical range

Table S7.5. Peer-reviewed African wild dog population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km²)*	Studies	Density Estimates	Studies / 10,000 km² **	Estimates / 10,000 km² **
Kenya	68,300	2	2	0.29	0.29
South Africa	22,900	2	2	0.87	0.87
CAR	60,740	1	2	0.16	0.33
Zimbabwe	38,000	1	1	0.26	0.26
Botswana	352,400	0	0	0.00	0.00
Tanzania	213,300	0	0	0.00	0.00
Zambia	173,100	0	0	0.00	0.00
Chad	88,800	0	0	0.00	0.00
Namibia	84,100	0	0	0.00	0.00
South Sudan	41,732	0	0	0.00	0.00
Ethiopia	30,594	0	0	0.00	0.00
Mozambique	22,900	0	0	0.00	0.00
Sudan	15,600	0	0	0.00	0.00
Nigeria	11,600	0	0	0.00	0.00
Senegal	8,400	0	0	0.00	0.00
Cameroon	7,200	0	0	0.00	0.00
Burkina Faso	6,400	0	0	0.00	0.00
Benin	2,800	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km² of geographical range

Table S7.6. Peer-reviewed spotted hyaena population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 10,000 km^2 **	Estimates / 10,000 km^2 **
Cameroon	172,100	4	10	0.23	0.58
South Africa	220,100	4	24	0.18	1.09
Namibia	368,500	4	9	0.11	0.24
Kenya	580,400	4	7	0.07	0.12
Ethiopia	1,104,000	4	4	0.04	0.04
Botswana	552,100	3	3	0.05	0.05
Tanzania	945,100	3	7	0.03	0.07
Zimbabwe	297,400	2	4	0.07	0.13
Mozambique	711,100	2	2	0.03	0.03
Congo	75,700	1	1	0.13	0.13
Uganda	241,000	1	3	0.04	0.12
CAR	405,900	1	3	0.02	0.07
Sudan	716,800	1	1	0.01	0.01
Zambia	752,600	1	1	0.01	0.01
Angola	1,214,600	0	0	0.00	0.00
DRC	1,042,200	0	0	0.00	0.00
Nigeria	770,500	0	0	0.00	0.00
Somalia	637,700	0	0	0.00	0.00
South Sudan	619,700	0	0	0.00	0.00
Mali	513,700	0	0	0.00	0.00
Chad	476,800	0	0	0.00	0.00
Burkina Faso	274,200	0	0	0.00	0.00
Guinea	245,900	0	0	0.00	0.00
Cote d'Ivoire	231,200	0	0	0.00	0.00
Senegal	196,700	0	0	0.00	0.00
Ghana	166,800	0	0	0.00	0.00
Malawi	118,400	0	0	0.00	0.00
Eritrea	117,600	0	0	0.00	0.00
Benin	115,100	0	0	0.00	0.00
Mauritania	110,960	0	0	0.00	0.00
Sierra Leone	59,700	0	0	0.00	0.00
Togo	52,200	0	0	0.00	0.00
Guinea-Bissau	36,000	0	0	0.00	0.00
Burundi	27,800	0	0	0.00	0.00
Rwanda	26,300	0	0	0.00	0.00
Liberia	18,200	0	0	0.00	0.00
Eswatini	12,400	0	0	0.00	0.00
The Gambia	11,300	0	0	0.00	0.00
Gabon	5,600	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km^2 of geographical range

Table S7.7. Peer-reviewed striped hyaena population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 10,000 km^2 **	Estimates / 10,000 km^2 **
Kenya	580,400	2	2	0.03	0.03
Cameroon	217,400	0	0	0	0
Chad	1,096,200	0	0	0	0
CAR	6,700	0	0	0	0
Eritrea	117,598	0	0	0	0
Djibouti	23,200	0	0	0	0
Somalia	637,700	0	0	0	0
Sudan	945,100	0	0	0	0
South Sudan	297,700	0	0	0	0
Uganda	157,700	0	0	0	0
Tanzania	544,900	0	0	0	0
Ethiopia	1,100,000	0	0	0	0
Morocco	976,900	0	0	0	0
Algeria	2,382,000	0	0	0	0
Tunisia	163,600	0	0	0	0
Libya	1,758,000	0	0	0	0
Egypt	1,010,000	0	0	0	0
Mauritania	1,030,000	0	0	0	0
Senegal	97,000	0	0	0	0
Mali	1,019,600	0	0	0	0
Burkina Faso	253,000	0	0	0	0
Ghana	27,600	0	0	0	0
Togo	2,100	0	0	0	0
Benin	24,100	0	0	0	0
Nigeria	211,000	0	0	0	0
Cote d'Ivoire	3,000	0	0	0	0

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km^2 of geographical range

Table S7.8. Peer-reviewed brown hyaena population assessments in Africa (2000-2020), by country.

Country	Geographical Range (km^2)*	Studies	Density Estimates	Studies / 10,000 km^2 **	Estimates / 10,000 km^2 **
South Africa	776,700	4	4	0.05	0.05
Botswana	543,000	4	18	0.07	0.33
Namibia	728,400	1	1	0.01	0.01
Zimbabwe	164,900	1	1	0.06	0.06
Angola	42,900	0	0	0.00	0.00
Mozambique	22,100	0	0	0.00	0.00
Eswatini	15,869	0	0	0.00	0.00
Zambia	900	0	0	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

** Density of studies and estimates per 10,000 km^2 of geographical range

Table S7.9. Results of the GLMM investigating biases in large carnivore population assessments in Africa, by species, not adjusting for geographical range or other variables (Model 1). Species and countries are modelled as random effects. Significant (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) values are highlighted in bold. For both species and countries, a positive value indicates more assessments than expected, and a negative fewer.

Name	Mean	HDI low	HDI high	SD
Intercept	-2.23	-3.60	-0.93	0.68
Country Random Effect Variance	1.97	1.22	2.85	0.43
Species Random Effect Variance	1.14	0.40	2.15	0.54
Brown Hyaena	0.07	-1.02	1.19	0.56
Cheetah	-0.02	-1.07	1.03	0.53
Leopard	0.43	-0.61	1.44	0.51
Lion *	1.09	0.11	2.12	0.51
Spotted Hyaena	0.58	-0.43	1.61	0.51
Striped Hyaena †	-1.26	-2.69	0.04	0.70
African Wild Dog	-0.93	-2.08	0.22	0.58
South Africa *	**3.43**	**2.45**	**4.48**	**0.52**
Kenya *	**3.16**	**2.17**	**4.25**	**0.53**
Tanzania *	**2.95**	**1.93**	**4.06**	**0.55**
Botswana *	**2.91**	**1.88**	**3.99**	**0.55**
Cameroon *	**2.55**	**1.45**	**3.72**	**0.58**
Zimbabwe *	**2.23**	**1.10**	**3.40**	**0.59**
Namibia *	**2.22**	**1.11**	**3.44**	**0.59**
Zambia *	**1.84**	**0.62**	**3.10**	**0.63**
Ethiopia *	**1.55**	**0.20**	**2.86**	**0.68**
Mozambique *	**1.46**	**0.15**	**2.80**	**0.67**
CAR	1.30	-0.10	2.69	0.71
Uganda	1.02	-0.48	2.56	0.77
Algeria	0.57	-1.62	2.71	1.11
Nigeria	0.54	-1.64	2.71	1.11
Sudan	0.52	-1.20	2.17	0.85
Congo	0.46	-1.69	2.56	1.09
Gabon	0.46	-1.76	2.56	1.10
Senegal	-0.08	-2.10	1.91	1.03
Burkina Faso	-0.18	-2.22	1.77	1.02
Benin	-0.19	-2.25	1.75	1.02
Morocco	-0.35	-3.90	3.13	1.81
Libya	-0.35	-3.94	3.13	1.81
Tunisia	-0.37	-3.97	3.07	1.80
Lesotho	-0.80	-4.07	2.14	1.62
Equatorial Guinea	-0.80	-4.01	2.21	1.61
The Gambia	-0.84	-4.07	2.11	1.60
Djibouti	-0.86	-4.08	2.11	1.60
Egypt	-0.86	-4.10	2.08	1.61
Mauritania	-0.92	-4.05	2.02	1.58
Guinea-Bissau	-1.10	-4.17	1.68	1.52
Rwanda	-1.10	-4.16	1.72	1.54
Liberia	-1.11	-4.18	1.65	1.52

Burundi	-1.11	-4.18	1.71	1.53
Guinea	-1.11	-4.13	1.73	1.53
Sierra Leone	-1.11	-4.31	1.59	1.53
Cote d'Ivoire	-1.15	-4.21	1.63	1.53
Togo	-1.15	-4.18	1.65	1.52
Ghana	-1.15	-4.12	1.68	1.52
Nigeria	-1.20	-4.13	1.59	1.50
Eswatini	-1.24	-4.23	1.52	1.50
Mali	-1.25	-4.24	1.45	1.48
Niger	-1.35	-4.32	1.30	1.47
DRC	-1.40	-4.36	1.20	1.45
Malawi	-1.42	-4.30	1.27	1.45
Chad	-1.53	-4.39	1.06	1.42
South Sudan	-1.53	-4.39	1.06	1.42
Angola	-1.56	-4.46	1.02	1.43

Legend: HDI = Highest Density Interval; SD = standard deviation; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.10. Results of the GLMM investigating biases in large carnivore population assessments in Africa, by species, controlling for socio-economic differences, not adjusting for geographical range (Model 3). Species and countries are modelled as random effects. Significant (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) values are highlighted in bold. For countries, a positive value indicates more assessments than expected based on their socio-economic indicators, and a negative fewer.

Name	Mean	HDI low	HDI high	SD
Intercept	-2.32	-3.74	-0.98	0.71
GDP	0.26	-0.63	1.14	0.44
Frag	-0.47	-1.50	0.52	0.51
Country Random Effect Variance	1.97	1.15	2.90	0.47
Species Random Effect Variance	1.16	0.40	2.20	0.55
Brown Hyaena	0.09	-1.00	1.24	0.57
Cheetah	-0.04	-1.13	1.02	0.55
Leopard	0.45	-0.56	1.51	0.53
Lion *	**1.13**	**0.15**	**2.19**	**0.52**
Spotted Hyaena	0.61	-0.37	1.71	0.53
Striped Hyaena †	**-1.27**	**-2.73**	**0.04**	**0.71**
African Wild Dog	-0.90	-2.08	0.23	0.59
Kenya *	**3.40**	**2.28**	**4.60**	**0.60**
Cameroon *	**2.95**	**1.62**	**4.30**	**0.69**
Tanzania *	**2.82**	**1.46**	**4.24**	**0.71**
Zimbabwe *	**2.72**	**1.30**	**4.21**	**0.75**
South Africa *	**2.38**	**0.85**	**4.02**	**0.81**
CAR *	**2.18**	**0.22**	**4.17**	**1.01**
Ethiopia *	**1.93**	**0.45**	**3.41**	**0.75**
Zambia *	**1.88**	**0.54**	**3.22**	**0.68**
Mozambique *	**1.72**	**0.25**	**3.27**	**0.77**
Uganda	1.42	-0.25	3.10	0.84
Sudan	1.30	-0.79	3.49	1.08
Botswana	1.22	-0.94	3.43	1.11
Namibia	1.17	-0.42	2.76	0.81
Nigeria	0.81	-1.57	3.16	1.20
Congo	0.60	-1.64	2.81	1.13
Algeria	0.11	-2.02	2.21	1.08
Burkina Faso	-0.13	-2.30	1.94	1.07
Senegal	-0.29	-2.49	1.78	1.08
Benin	-0.47	-2.73	1.70	1.12
Morocco	-0.50	-4.04	2.77	1.76
Gabon	-0.51	-3.03	1.91	1.24
Libya	-0.52	-4.10	3.01	1.80
Tunisia	-0.52	-4.09	2.70	1.74
The Gambia	-0.84	-4.10	2.21	1.63
Mauritania	-0.85	-4.02	2.11	1.59
Burundi	-0.86	-4.06	2.19	1.61
Lesotho	-0.86	-4.08	2.23	1.62
Egypt	-0.88	-4.21	1.95	1.59
Guinea	-0.88	-4.05	2.12	1.60

Guinea-Bissau	-0.90	-4.18	1.97	1.59
Djibouti	-0.94	-4.13	1.91	1.58
DRC	-0.97	-4.17	2.11	1.60
Liberia	-0.98	-4.13	1.97	1.58
Nigeria	-1.03	-4.23	1.82	1.56
Rwanda	-1.03	-4.20	1.84	1.57
Sierra Leone	-1.03	-4.19	1.82	1.57
Mali	-1.06	-4.12	1.84	1.55
Togo	-1.06	-4.22	1.77	1.55
Cote d'Ivoire	-1.07	-4.17	1.75	1.54
South Sudan	-1.07	-4.23	1.94	1.58
Chad	-1.09	-4.31	1.79	1.56
Niger	-1.10	-4.23	1.70	1.54
Equatorial Guinea	-1.22	-4.58	1.79	1.62
Eswatini	-1.37	-4.38	1.29	1.47
Malawi	-1.37	-4.37	1.36	1.49
Ghana	-1.54	-4.65	1.24	1.52
Angola	-1.59	-4.46	0.96	1.41

Legend: HDI = Highest Density Interval; SD = standard deviation; GDP = Gross Domestic Product, per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.11. Results of the GLMM investigating biases in large carnivore population assessments in Africa, controlling for socio-economic differences, and accounting for differences in geographical range between countries (Model 4). Species and countries are modelled as random effects. Significant (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) values are highlighted in bold. For countries, a positive value indicates more assessments than expected based on their socio-economic indicators and large carnivore range, and a negative fewer.

Name	Mean	HDI low	HDI high	SD
(Intercept)	-2.23	-3.82	-0.84	0.76
GDP	0.15	-0.68	0.95	0.41
Frag	-0.50	-1.46	0.43	0.48
Range *	**0.59**	**0.25**	**0.93**	**0.18**
Country Random Effect Variance	1.78	1.04	2.64	0.43
Species Random Effect Variance	1.46	0.53	2.78	0.69
Brown Hyaena	-0.26	-1.59	1.11	0.68
Cheetah	0.26	-1.02	1.62	0.66
Leopard	0.48	-0.75	1.78	0.63
Lion *	**1.55**	**0.36**	**2.92**	**0.64**
Spotted Hyaena	0.40	-0.84	1.69	0.63
Striped Hyaena †	**-1.95**	**-3.75**	**-0.28**	**0.90**
African Wild Dog	-0.55	-1.95	0.86	0.71
Kenya *	**3.14**	**2.08**	**4.26**	**0.56**
Cameroon *	**2.93**	**1.67**	**4.24**	**0.66**
Zimbabwe *	**2.68**	**1.31**	**4.08**	**0.71**
South Africa *	**2.32**	**0.87**	**3.83**	**0.76**
Tanzania *	**2.02**	**0.70**	**3.41**	**0.69**
CAR *	**1.84**	**0.01**	**3.71**	**0.94**
Zambia *	**1.56**	**0.29**	**2.84**	**0.65**
Uganda	1.38	-0.21	3.00	0.81
Mozambique	1.29	-0.12	2.73	0.73
Ethiopia	1.27	-0.11	2.73	0.72
Sudan	1.05	-0.91	3.11	1.02
Botswana	1.03	-0.96	3.08	1.03
Namibia	0.84	-0.62	2.36	0.76
Nigeria	0.72	-1.53	2.97	1.15
Congo	0.62	-1.59	2.69	1.09
Burkina Faso	-0.15	-2.19	1.80	1.01
Gabon	-0.16	-2.53	2.12	1.17
Senegal	-0.26	-2.29	1.71	1.02
Tunisia	-0.29	-3.60	2.92	1.66
Benin	-0.46	-2.59	1.58	1.06
Morocco	-0.55	-3.70	2.40	1.56
The Gambia	-0.56	-3.60	2.40	1.54
Burundi	-0.62	-3.73	2.18	1.52
Lesotho	-0.66	-3.72	2.18	1.52
Guinea-Bissau	-0.66	-3.69	2.15	1.51
Djibouti	-0.67	-3.64	2.18	1.50
Mauritania	-0.69	-3.69	2.09	1.49
Guinea	-0.69	-3.71	2.07	1.49

Egypt	-0.72	-3.70	2.07	1.49
Liberia	-0.73	-3.71	2.10	1.50
Rwanda	-0.76	-3.68	2.02	1.47
Algeria	-0.76	-2.84	1.25	1.04
Sierra Leone	-0.77	-3.83	1.92	1.48
Togo	-0.79	-3.78	1.94	1.48
Cote d'Ivoire	-0.82	-3.73	1.95	1.46
Equatorial Guinea	-0.84	-3.95	2.12	1.53
Libya	-0.89	-4.07	2.08	1.55
Niger	-0.97	-3.80	1.66	1.42
Eswatini	-0.97	-3.88	1.63	1.43
Mali	-0.98	-3.84	1.58	1.41
Nigeria	-0.99	-3.84	1.64	1.41
South Sudan	-0.99	-3.93	1.71	1.44
Chad	-1.02	-3.95	1.60	1.41
DRC	-1.13	-4.02	1.47	1.40
Malawi	-1.22	-4.05	1.30	1.38
Ghana	-1.24	-4.14	1.35	1.42
Angola	-1.77	-4.29	0.50	1.25

Legend: HDI = Highest Density Interval; SD = standard deviation; Range = country range, based on IUCN Red List geographical range polygons GDP = Gross Domestic Product, per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.12. Results of the GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries and testing the effect of potential socio-economic predictors and species conservation status (Model 5). Species and countries are modelled as random effects. Significant (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) values are highlighted in bold. For countries, a positive value indicates more assessments than expected based on their socio-economic indicators and large carnivore range, and a negative fewer.

Name	Mean	HDI low	HDI high	SD
Intercept	-2.04	-4.35	0.14	1.12
GDP	0.16	-0.66	0.96	0.41
Frag	-0.49	-1.44	0.42	0.47
Range *	**0.65**	**0.30**	**1.01**	**0.18**
NT	-0.67	-3.28	1.87	1.25
VU	0.26	-2.92	3.26	1.53
EN	-0.29	-2.56	2.00	1.14
Country Random Effect Variance	1.76	1.03	2.61	0.42
Species Random Effect Variance	1.98	0.31	5.32	1.55
Brown Hyaena	0.97	-2.46	4.89	1.84
Lion	0.75	-2.12	3.98	1.49
Spotted Hyaena	0.04	-5.14	5.76	2.63
African Wild Dog	0.00	-4.98	5.20	2.48
Leopard	-0.35	-3.30	2.81	1.49
Cheetah	-0.53	-3.57	2.55	1.50
Striped Hyaena	-1.02	-4.94	2.47	1.85
Kenya *	**3.10**	**2.05**	**4.22**	**0.56**
Cameroon *	**2.92**	**1.66**	**4.23**	**0.66**
Zimbabwe *	**2.65**	**1.33**	**4.06**	**0.70**
South Africa *	**2.30**	**0.86**	**3.79**	**0.75**
Tanzania *	**1.95**	**0.66**	**3.35**	**0.69**
CAR *	**1.78**	**0.01**	**3.66**	**0.93**
Zambia *	**1.53**	**0.28**	**2.81**	**0.65**
Uganda	1.36	-0.27	2.93	0.81
Mozambique	1.26	-0.13	2.72	0.73
Ethiopia	1.20	-0.20	2.62	0.72
Sudan	1.02	-0.96	3.03	1.01
Botswana	0.98	-0.97	3.03	1.02
Namibia	0.80	-0.65	2.30	0.75
Nigeria	0.69	-1.55	2.93	1.14
Congo	0.61	-1.49	2.74	1.08
Burkina Faso	-0.14	-2.17	1.83	1.01
Gabon	-0.17	-2.44	2.18	1.17
Tunisia	-0.22	-3.53	3.01	1.67
Senegal	-0.25	-2.32	1.71	1.02
Benin	-0.44	-2.53	1.61	1.04
Morocco	-0.47	-3.64	2.53	1.57
The Gambia	-0.54	-3.59	2.35	1.52
Burundi	-0.61	-3.70	2.17	1.51
Lesotho	-0.62	-3.65	2.18	1.50
Djibouti	-0.63	-3.63	2.16	1.49

Guinea-Bissau	-0.63	-3.61	2.16	1.48
Mauritania	-0.64	-3.63	2.11	1.49
Guinea	-0.66	-3.65	2.11	1.48
Egypt	-0.69	-3.70	2.05	1.48
Liberia	-0.70	-3.69	2.05	1.48
Sierra Leone	-0.74	-3.59	2.06	1.46
Rwanda	-0.75	-3.70	1.96	1.47
Togo	-0.75	-3.63	2.02	1.46
Algeria	-0.78	-2.86	1.21	1.03
Cote d'Ivoire	-0.81	-3.75	1.79	1.44
Equatorial Guinea	-0.83	-3.88	2.09	1.51
Libya	-0.83	-3.94	2.17	1.55
Eswatini	-0.94	-3.80	1.67	1.41
Niger	-0.96	-3.79	1.59	1.39
Mali	-0.98	-3.80	1.62	1.40
Nigeria	-1.00	-3.84	1.56	1.39
South Sudan	-1.00	-3.95	1.65	1.43
Chad	-1.02	-3.78	1.67	1.40
DRC	-1.15	-3.94	1.47	1.37
Ghana	-1.19	-3.98	1.48	1.40
Malawi	-1.19	-3.92	1.37	1.36
Angola	-1.81	-4.28	0.42	1.22

Legend: HDI = Highest Density Interval; SD = standard deviation; Range = country range, based on IUCN Red List geographical range polygons GDP = Gross Domestic Product, per capita; Frag = country fragility index; NT = Near Threatened; VU = Vulnerable; EN = Endangered; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.13. Results of the models investigating biases in leopard population assessments in Africa, accounting for geographical range (A; Poisson GLM), and for geographical range and socio-economic differences between countries (B; Poisson GLM). One outlier (South Africa) was removed in both analyses (strong positive effect). Significant (i.e. credible non-zero) fixed effect values are highlighted in bold. For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant effect in analysis A.

	A – RANGE			B - RANGE & SOCIO-ECONOMIC		
Name	**Mean**	**HDI low**	**HDI high**	**Mean**	**HDI low**	**HDI high**
(Intercept)	-1.28	-1.94	-0.68	-1.42	-2.12	-0.77
Range *	**0.76**	**0.38**	**1.15**	**0.76**	**0.36**	**1.18**
GDP	NA	NA	NA	0.11	-0.48	0.71
Frag	NA	NA	NA	-0.23	-0.84	0.38
Zimbabwe *	**3.32**	**2.05**	**4.84**	**4.23**	**2.15**	**6.55**
Cameroon *	**3.13**	**1.93**	**4.51**	**3.87**	**2.14**	**5.88**
Kenya *	**2.23**	**1.36**	**3.20**	**2.67**	**1.49**	**3.90**
Botswana *	**1.89**	**1.07**	**2.75**	0.73	-0.92	2.55
Zambia *	**1.07**	**0.45**	**1.73**	**1.21**	**0.45**	**2.10**
Tanzania	1.02	-0.27	2.33	1.04	-0.71	2.92
Gabon *	**1.01**	**0.40**	**1.65**	0.46	-0.76	1.75
Namibia	0.77	-0.07	1.67	0.10	-1.06	1.37
CAR *	**0.53**	**0.04**	**1.06**	**1.22**	**0.08**	**2.50**
Mozambique	0.23	-0.28	0.75	0.45	-0.28	1.27
Lesotho †	**-0.41**	**-0.58**	**-0.24**	**-0.41**	**-0.63**	**-0.20**
Togo †	**-0.41**	**-0.58**	**-0.24**	**-0.37**	**-0.56**	**-0.20**
Niger †	**-0.41**	**-0.58**	**-0.24**	**-0.34**	**-0.51**	**-0.18**
Burundi †	**-0.41**	**-0.58**	**-0.24**	**-0.33**	**-0.51**	**-0.18**
Djibouti †	**-0.41**	**-0.58**	**-0.24**	**-0.41**	**-0.60**	**-0.23**
Rwanda †	**-0.41**	**-0.58**	**-0.24**	**-0.38**	**-0.56**	**-0.20**
Sierra Leone †	**-0.41**	**-0.58**	**-0.24**	**-0.38**	**-0.58**	**-0.19**
Algeria †	**-0.41**	**-0.58**	**-0.25**	**-0.46**	**-0.67**	**-0.26**
Egypt †	**-0.41**	**-0.58**	**-0.25**	**-0.40**	**-0.58**	**-0.23**
Mali †	**-0.41**	**-0.58**	**-0.25**	**-0.35**	**-0.52**	**-0.20**
Guinea-Bissau †	**-0.41**	**-0.58**	**-0.25**	**-0.35**	**-0.52**	**-0.19**
Eswatini †	**-0.41**	**-0.58**	**-0.25**	**-0.42**	**-0.62**	**-0.24**
Malawi †	**-0.41**	**-0.58**	**-0.25**	**-0.40**	**-0.62**	**-0.19**
Nigeria †	**-0.41**	**-0.58**	**-0.25**	**-0.36**	**-0.55**	**-0.19**
Equatorial Guinea †	**-0.41**	**-0.59**	**-0.25**	**-0.52**	**-0.97**	**-0.14**
Ghana †	**-0.42**	**-0.59**	**-0.25**	**-0.50**	**-0.85**	**-0.20**
Burkina Faso †	**-0.42**	**-0.59**	**-0.26**	**-0.40**	**-0.61**	**-0.21**
Liberia †	**-0.42**	**-0.59**	**-0.26**	**-0.38**	**-0.56**	**-0.20**
Senegal †	**-0.43**	**-0.60**	**-0.26**	**-0.45**	**-0.69**	**-0.22**
Guinea †	**-0.43**	**-0.60**	**-0.26**	**-0.36**	**-0.53**	**-0.19**
Cote d'Ivoire †	**-0.43**	**-0.60**	**-0.27**	**-0.40**	**-0.57**	**-0.24**
Sudan †	**-0.44**	**-0.61**	**-0.27**	**-0.33**	**-0.53**	**-0.16**
Uganda †	**-0.45**	**-0.62**	**-0.29**	**-0.39**	**-0.56**	**-0.23**
Chad †	**-0.46**	**-0.63**	**-0.29**	**-0.35**	**-0.55**	**-0.16**
Benin †	**-0.51**	**-0.68**	**-0.35**	**-0.55**	**-0.88**	**-0.27**
South Sudan †	**-0.62**	**-0.79**	**-0.45**	**-0.47**	**-0.76**	**-0.21**

Congo †	**-0.69**	**-0.87**	**-0.52**	**-0.63**	**-0.81**	**-0.44**
Ethiopia †	**-0.74**	**-0.92**	**-0.56**	**-0.64**	**-0.85**	**-0.44**
DRC †	**-1.39**	**-1.89**	**-0.89**	**-1.05**	**-1.69**	**-0.47**
Angola †	**-1.39**	**-1.89**	**-0.89**	**-1.36**	**-1.91**	**-0.85**

Legend: HDI = Highest Density Interval; Range = Geographical range of species, based on IUCN Red List range maps; GDP = Gross Domestic Product per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.14. Results of the models investigating biases in cheetah population assessments in Africa, accounting for geographical range (A; Poisson GLM), and for geographical range and socio-economic differences between countries (B; Poisson GLM). One outlier (Kenya) was removed in analysis B (strong positive effect). Significant (i.e. credible non-zero) fixed effect values are highlighted in bold. For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant effect in analysis A.

	A – RANGE			**B - RANGE & SOCIO-ECONOMIC**		
Name	**Mean**	**HDI low**	**HDI high**	**Mean**	**HDI low**	**HDI high**
(Intercept)	-0.49	-1.09	0.09	-1.51	-2.65	-0.46
Range *	**0.56**	**0.19**	**0.92**	0.10	-0.58	0.73
GDP	NA	NA	NA	0.10	-0.89	1.09
Frag	NA	NA	NA	-1.24	-2.79	0.25
Kenya *	**3.18**	**1.80**	**4.63**	NA	NA	NA
Botswana *	**2.86**	**1.35**	**4.44**	0.39	-1.52	2.34
Tanzania *	**1.89**	**0.87**	**2.94**	**2.33**	**0.24**	**4.90**
Zambia *	**0.84**	**0.06**	**1.63**	**1.45**	**0.18**	**2.92**
Zimbabwe *	**0.78**	**0.06**	**1.56**	**3.60**	**0.50**	**8.15**
South Africa	0.49	-0.09	1.13	-0.14	-1.23	1.01
Namibia	0.16	-0.76	1.08	0.02	-1.19	1.29
Sudan †	**-0.65**	**-0.90**	**-0.42**	**-0.25**	**-0.49**	**-0.05**
Uganda †	**-0.66**	**-0.90**	**-0.42**	**-0.39**	**-0.62**	**-0.16**
Mozambique †	**-0.66**	**-0.90**	**-0.42**	**-0.40**	**-0.64**	**-0.18**
Burkina Faso †	**-0.66**	**-0.90**	**-0.42**	**-0.51**	**-0.79**	**-0.24**
Benin †	**-0.67**	**-0.91**	**-0.43**	**-0.92**	**-1.65**	**-0.27**
Niger †	**-0.67**	**-0.90**	**-0.43**	**-0.35**	**-0.58**	**-0.13**
CAR †	**-0.68**	**-0.92**	**-0.45**	**-0.23**	**-0.48**	**-0.03**
Angola †	**-0.69**	**-0.93**	**-0.46**	**-0.51**	**-0.83**	**-0.21**
South Sudan †	**-0.69**	**-0.93**	**-0.46**	**-0.22**	**-0.51**	**-0.01**
Mali †	**-0.71**	**-0.95**	**-0.48**	**-0.35**	**-0.59**	**-0.13**
Ethiopia †	**-0.86**	**-1.09**	**-0.63**	**-0.38**	**-0.63**	**-0.14**
Chad †	**-0.87**	**-1.10**	**-0.64**	**-0.26**	**-0.53**	**-0.03**
Algeria †	**-1.23**	**-2.30**	**-0.15**	0.06	-1.57	1.70

Legend: HDI = Highest Density Interval; Range = Geographical range of species, based on IUCN Red List range maps; GDP = Gross Domestic Product per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect.

Table S7.15. Results of the models investigating biases in spotted hyaena population assessments in Africa, accounting for geographical range (A; Poisson GLM), and for geographical range and socio-economic differences between countries (B; Poisson GLM). One outlier (Cameroon) was removed in analysis B (strong positive effect). Significant (i.e. credible non-zero) fixed effect values are highlighted in bold. For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant effect in analysis A.

	A – RANGE			**B - RANGE & SOCIO-ECONOMIC**		
Name	**Mean**	**HDI low**	**HDI high**	**Mean**	**HDI low**	**HDI high**
(Intercept)	-0.18	-0.56	0.17	-0.52	-1.00	-0.08
Range *	**0.41**	**0.11**	**0.71**	**0.63**	**0.29**	**0.96**
GDP	NA	NA	NA	0.23	-0.21	0.68
Frag	NA	NA	NA	-0.35	-0.90	0.18
Cameroon *	**4.13**	**2.85**	**5.48**	NA	NA	NA
South Africa *	**3.96**	**2.83**	**5.26**	**2.57**	**1.13**	**4.13**
Namibia *	**3.47**	**2.50**	**4.44**	**1.94**	**0.75**	**3.28**
Kenya *	**2.81**	**2.02**	**3.69**	**3.71**	**2.55**	**5.00**
Botswana *	**1.92**	**1.28**	**2.62**	-0.42	-1.76	1.05
Zimbabwe *	**1.41**	**0.84**	**2.08**	**2.69**	**1.43**	**4.15**
Ethiopia *	**1.40**	**0.13**	**2.71**	**1.76**	**0.41**	**3.21**
Tanzania *	**1.03**	**0.15**	**1.95**	0.77	-0.61	2.16
Mozambique *	**0.65**	**0.11**	**1.21**	**1.10**	**0.25**	**1.95**
Congo	0.54	0.00	1.08	**1.20**	**0.39**	**2.04**
Uganda	0.33	-0.07	0.78	**1.11**	**0.41**	**1.84**
CAR	0.13	-0.23	0.48	**1.25**	**0.26**	**2.30**
Sudan	-0.24	-0.61	0.15	0.59	-0.16	1.41
Zambia	-0.29	-0.68	0.11	-0.19	-0.70	0.32
Gabon †	**-0.74**	**-0.95**	**-0.53**	**-1.04**	**-1.55**	**-0.58**
The Gambia †	**-0.75**	**-0.95**	**-0.54**	**-0.57**	**-0.79**	**-0.36**
Eswatini †	**-0.75**	**-0.95**	**-0.54**	**-0.67**	**-0.92**	**-0.44**
Liberia †	**-0.75**	**-0.96**	**-0.55**	**-0.52**	**-0.71**	**-0.33**
Rwanda †	**-0.75**	**-0.96**	**-0.55**	**-0.55**	**-0.75**	**-0.36**
Burundi †	**-0.75**	**-0.96**	**-0.55**	**-0.47**	**-0.66**	**-0.29**
Guinea-Bissau †	**-0.76**	**-0.96**	**-0.56**	**-0.50**	**-0.70**	**-0.32**
Togo †	**-0.76**	**-0.97**	**-0.56**	**-0.56**	**-0.77**	**-0.37**
Sierra Leone †	**-0.77**	**-0.97**	**-0.57**	**-0.56**	**-0.77**	**-0.36**
Mauritania †	**-0.79**	**-0.98**	**-0.60**	**-0.60**	**-0.79**	**-0.42**
Benin †	**-0.79**	**-0.99**	**-0.60**	**-0.74**	**-1.07**	**-0.43**
Malawi †	**-0.79**	**-0.99**	**-0.60**	**-0.62**	**-0.85**	**-0.38**
Ghana †	**-0.82**	**-1.00**	**-0.63**	**-0.92**	**-1.35**	**-0.52**
Senegal †	**-0.83**	**-1.01**	**-0.65**	**-0.77**	**-1.03**	**-0.50**
Cote d'Ivoire †	**-0.85**	**-1.02**	**-0.67**	**-0.68**	**-0.88**	**-0.48**
Guinea †	**-0.86**	**-1.03**	**-0.68**	**-0.58**	**-0.78**	**-0.38**
Burkina Faso †	**-0.87**	**-1.04**	**-0.70**	**-0.72**	**-0.95**	**-0.49**
Chad †	**-0.98**	**-1.14**	**-0.81**	**-0.62**	**-0.88**	**-0.38**
Mali †	**-1.00**	**-1.17**	**-0.84**	**-0.78**	**-0.96**	**-0.59**
South Sudan †	**-1.07**	**-1.26**	**-0.89**	**-0.70**	**-1.04**	**-0.38**
Nigeria †	**-1.17**	**-1.41**	**-0.94**	**-1.01**	**-1.33**	**-0.72**

DRC †	**-1.39**	**-1.78**	**-1.02**	**-1.01**	**-1.43**	**-0.60**
Angola †	**-1.55**	**-2.10**	**-1.06**	**-1.82**	**-2.45**	**-1.21**

Legend: HDI = Highest Density Interval; Range = Geographical range of species, based on IUCN Red List range maps; GDP = Gross Domestic Product per capita; Frag = country fragility index; * = value suggests significant positive effect; † = value suggests significant negative effect.

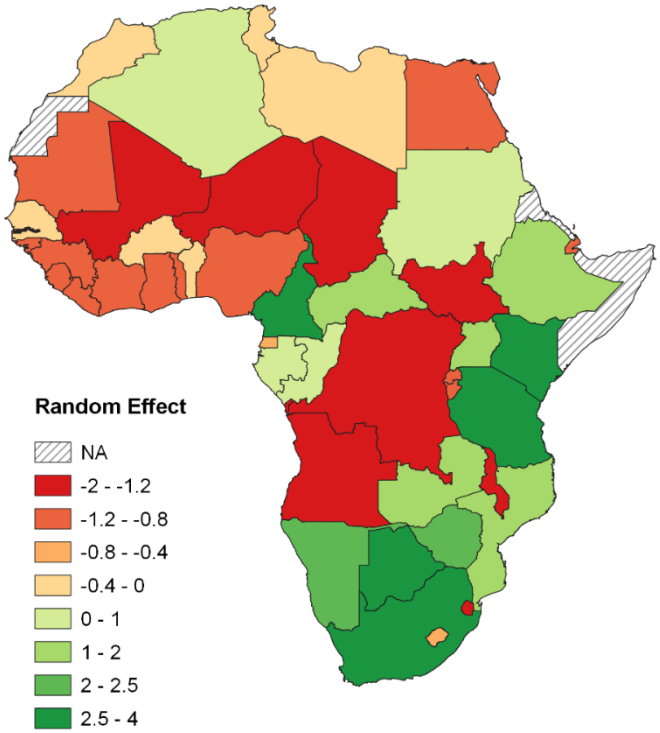


Figure S7.1. Random effects for individual countries from the Poisson GLMM investigating biases in large carnivore population assessments in Africa (species and countries only, not accounting for differences in large carnivore geographical range between countries or other variables; Model 1). A positive value (green) indicates more population assessments (all species) than expected, and a negative value (red) indicates fewer. See Table S7.9 for country specific values.

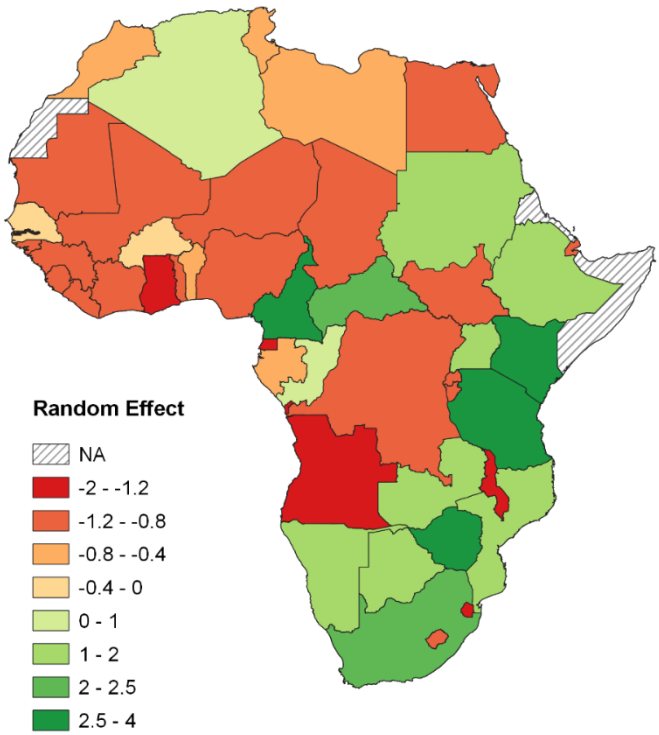


Figure S7.2. Random effects for individual countries from the Poisson GLMM investigating biases in large carnivore population assessments in Africa, controlling for socio-economic differences, not accounting for differences in large carnivore geographical range between countries (Model 3). A positive value (green) indicates more population assessments (all species) than expected based on the country's socio-economic indicators, a negative value (red) indicates fewer. See Table S7.10 for country specific values.

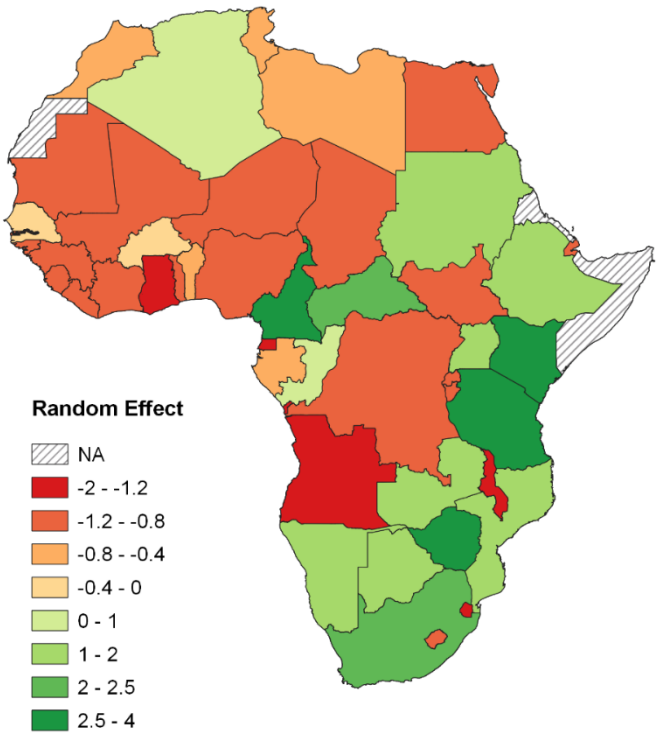


Figure S7.3. Random effects for individual countries from the Poisson GLMM investigating biases in large carnivore population assessments in Africa, controlling for socio-economic differences, and accounting for differences in large carnivore geographical range between countries (Model 4). A positive value (green) indicates more population assessments (all species) than expected based on their socio-economic indicators and large carnivore geographical range within that country, and a negative value (red) fewer. See Table S7.11 for country specific values.

APPENDIX 7.4 – ADDITIONAL MODEL FITTING DETAILS

All species Poisson GLMM

Model dispersion (0.70) was appropriate, and the posterior predictive check indicated good model fit (Fig. S7.4).

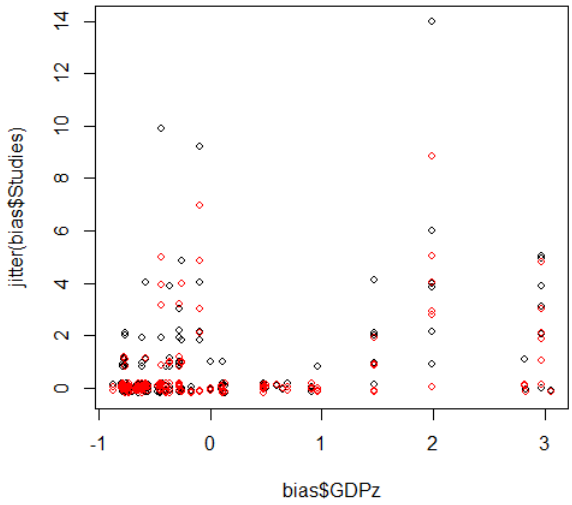


Figure S7.4. Posterior predictive check (PPC) for the most parametrised PGLMM (Range+GDP+Frag+Status), showing the actual data (black) and simulated data from the model (red). The check suggests a good fit.

Lion Poisson GLM

Lion data were fitted as a Poisson GLM (N=23) for the most parametrised model (Range+GDP+Frag). The model was over-dispersed (dispersion parameter = 3.12) and the posterior predictive check (PPC) showed that the model did not fit the observed data well. There was one residual outlier (Kenya). Removing Kenya reduced the dispersion parameter to 2.13 and improved the model fit (Fig. S7.5). The data were not better fitted by a negative binomial (NB) or zero-inflated Poisson (ZIP) GLM. Because of this, results from the Poisson GLM are presented in text. All models nonetheless reached the same conclusion – geographical range had a positive effect on the number of studies on lions, while GDP and Fragility did not.

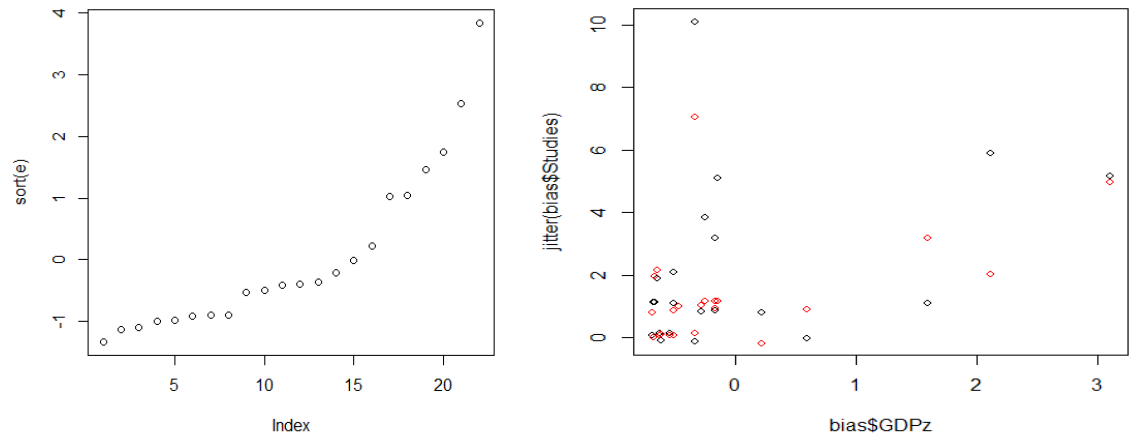


Figure S7.5. Model fit and posterior predictive check (PPC) for the most parametrised PGLM (Range+GDP+Frag) for lion, with one outlier removed (Kenya), showing the actual data (black) and simulated data from the model (red). The check indicates some overdispersion, likely due to small sample size (n=23; dispersion parameter = 2.13).

For the range only model, a Poisson GLM was first fitted to the data. This was overdispersed (dispersion parameter = 3.20 with no outliers removed, and 2.37 with one removed), and the posterior predictive check (PPC) showed that the model did not fit the observed data well. The data were not better fitted by a zero-inflated Poisson (ZIP) GLM. On the other hand, fitting a negative binomial (NB) GLM showed only little evidence of overdispersion (dispersion parameter = 1.52) and the PPC shows the model fitted the data well (Fig. S7.6); results from this are therefore presented in text.

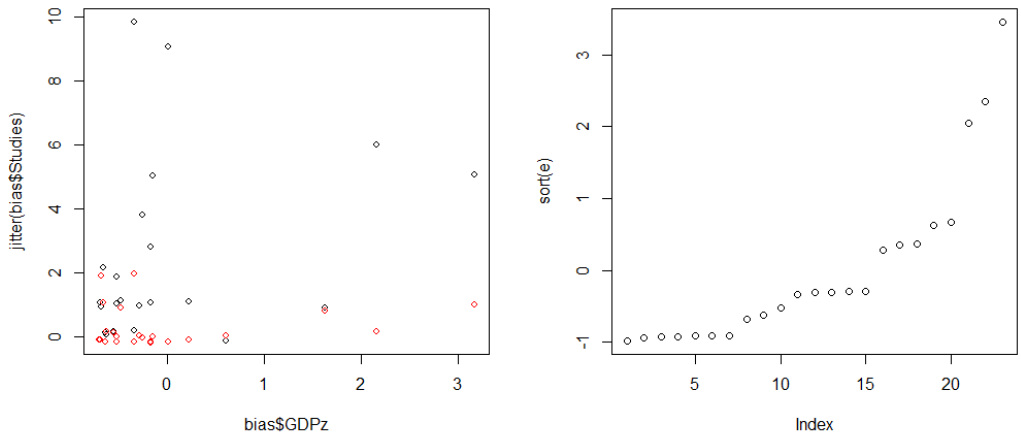


Figure S7.6. Model fit and posterior predictive check (PPC) for the NB GLM (Range) for lion, showing the actual data (black) and simulated data from the model (red). The check indicates slight overdispersion (dispersion parameter = 1.52), and the PPC suggests the model fitted the observed data well.

Leopard Poisson GLM

Leopard data were first fitted as a Poisson GLM (N=41) for the most parametrised model (Range+GDP+Frag). The model was over-dispersed (dispersion parameter = 2.56) and the posterior predictive check showed that the model fit was acceptable but not ideal. There was one residual outlier (South Africa). Removing this reduced the dispersion parameter to 1.47 and improved the model fit. The data were not better fitted by a zero-inflated negative binomial GLM or a zero-inflated Poisson GLM with additional outliers (Cameroon) removed. Results from the Poisson GLM with one outlier (South Africa) removed are therefore presented in text (N=41).

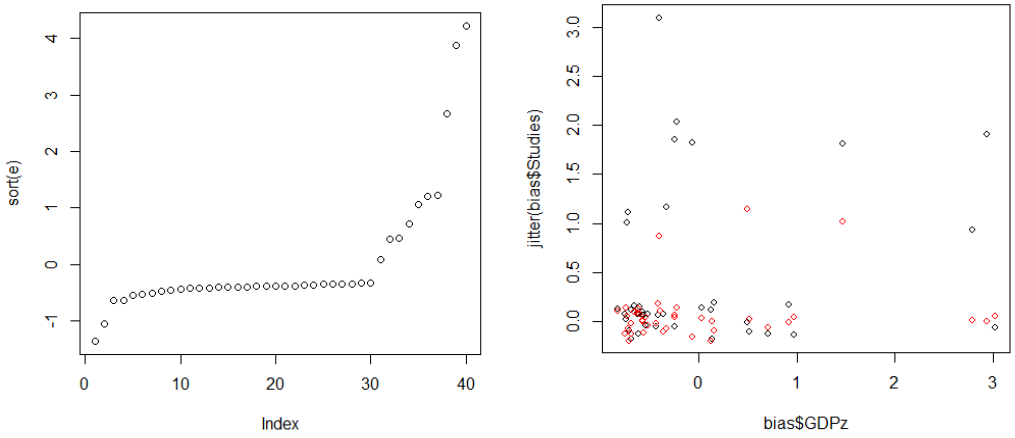


Figure S7.7. Model fit and posterior predictive check (PPC) for the most parametrised Possion GLM (Range+GDP+Frag) for leopard, with one outlier removed (South Africa), showing the actual data (black) and simulated data from the model (red). The check indicates slight overdispersion (n=41; dispersion parameter = 1.47).

For the range only model, a Poisson GLM was fitted to the data. This was overdispersed (dispersion parameter = 4.46). Once the outlier (South Africa) was removed, the model fitted the data well with little evidence of overdispersion (dispersion parameter = 1.13; Fig. S7.8); as a result, outputs from this model are presented.

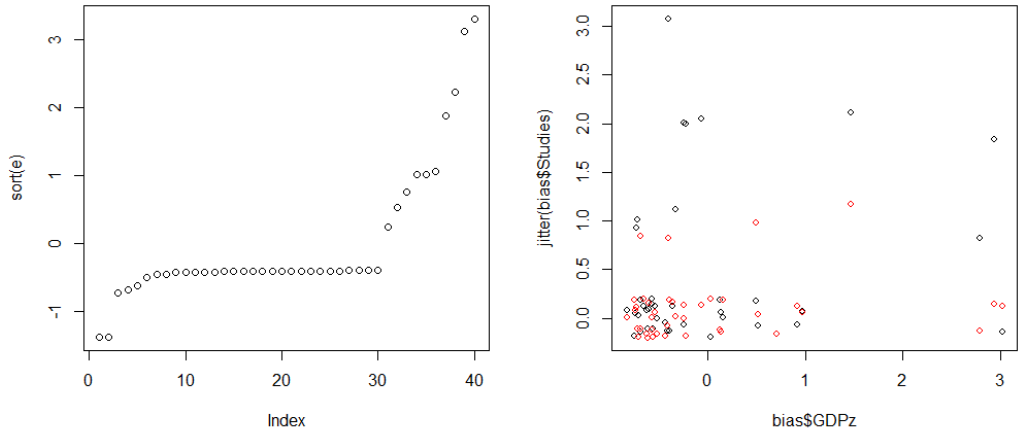


Figure S7.8. Model fit and posterior predictive check (PPC) for the Poisson GLM (range only) for leopard, with one outlier removed (South Africa), showing the actual data (black) and simulated data from the model (red). The check indicates almost no overdispersion (dispersion parameter = 1.13), and the PPC suggests the model fitted the observed data well.

Spotted Hyaena Poisson GLM

Spotted hyaena data were fitted as a Poisson GLM (N=40) for the most parametrised model (Range+GDP+Frag). The model was over-dispersed (dispersion parameter = 2.22), with one outlier (Cameroon). Removing the outlier reduced the dispersion parameter to 1.73 and improved the model fit (Fig. S7.9). The data were not better fitted by a negative binomial (NB) or zero-inflated Poisson (ZIP) GLM. The results from the Poisson GLM with the outlier (Cameroon) removed are therefore presented in text (N=40).

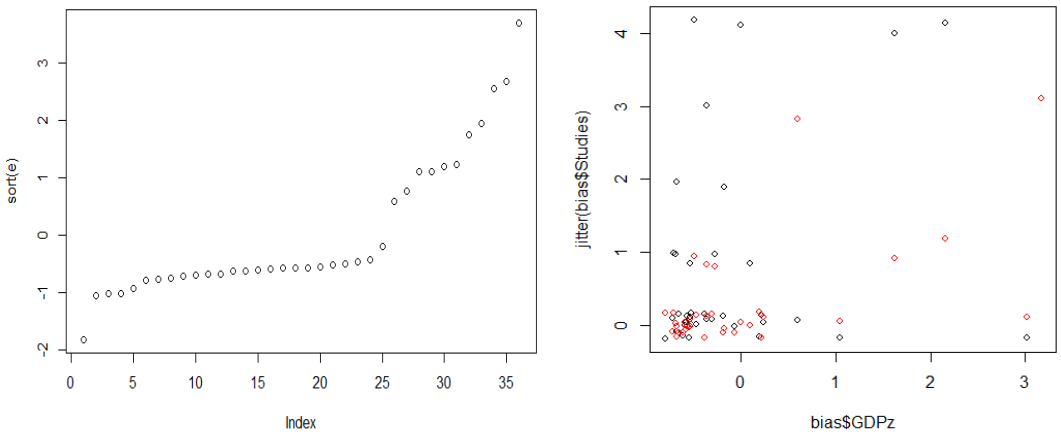


Figure S7.9. Model fit and posterior predictive check (PPC) for the most parametrised PGLM (Range+GDP+Frag) for spotted hyaena, with one outlier removed (Cameroon), showing the actual data (black) and simulated data from the model (red). The check indicates some overdispersion (n=40; dispersion parameter = 1.73).

For the range only model, a Poisson GLM was fitted to the data. There was some overdispersion (dispersion parameter = 2.33), but no outliers. The PPC revealed the model fitted the data relatively well (Fig. S7.10); as a result, outputs from this model are presented.

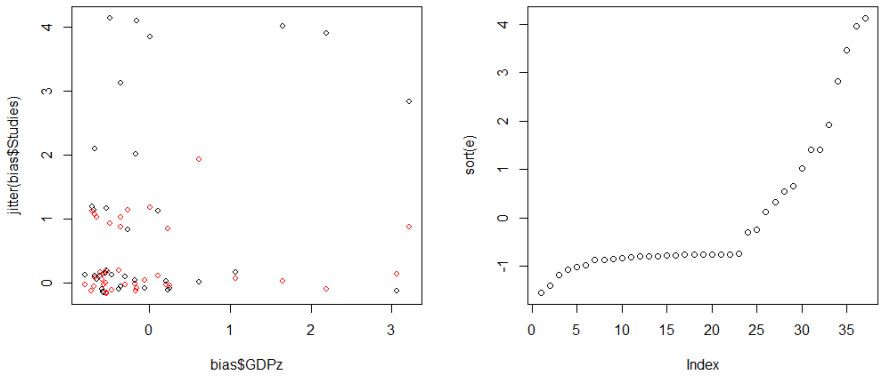


Figure S7.10. Model fit and posterior predictive check (PPC) for the Poisson GLM (range only) for spotted hyaena, showing the actual data (black) and simulated data from the model (red). The check indicates some overdispersion (dispersion parameter = 2.33), with the PPC suggesting the model fitted the observed data relatively well.

Cheetah Poisson GLM

Cheetah data were fitted as a Poisson GLM (N=20) for the most parametrised model (Range+GDP+Frag). The model was over-dispersed (dispersion parameter = 1.95), with one outlier (Kenya). Removing the outlier reduced the dispersion parameter to 1.58 and improved the model fit (Fig. S7.11). The data were not better fitted by a negative binomial (NB) or zero-inflated Poisson (ZIP) GLM. Results from the Poisson GLM with the outlier (Kenya) removed are therefore presented in text (N=20).

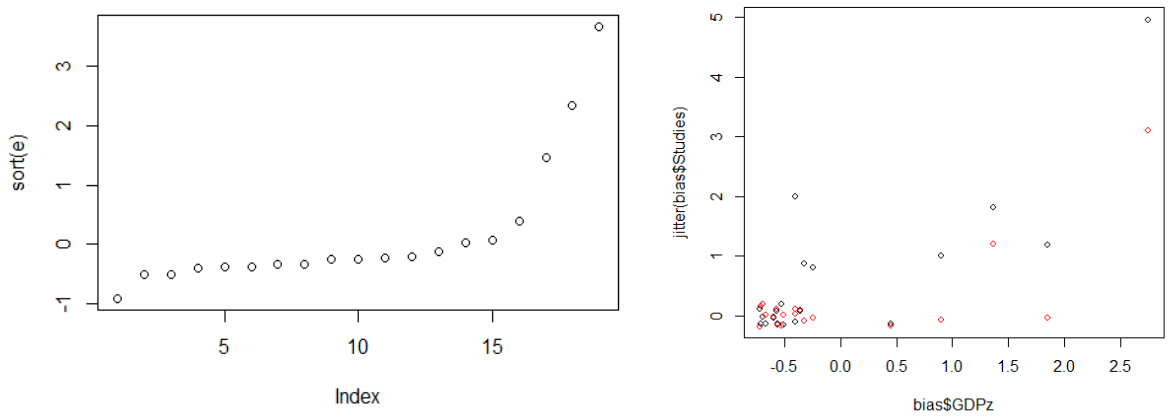


Figure S7.11. Model fit and posterior predictive check (PPC) for the most parametrised PGLM (Range+GDP+Frag) for cheetah, with one outlier removed (Kenya), showing the actual data (black) and simulated data from the model (red). The check indicates slight overdispersion, likely due to small sample size (n=20; dispersion parameter = 1.58).

For the range only model, a Poisson GLM was fitted to the data. There was slight overdispersion (dispersion parameter = 1.72), but no outliers. The PPC revealed the model fitted the data relatively well (Fig. S7.12); as a result, outputs from this model are presented.

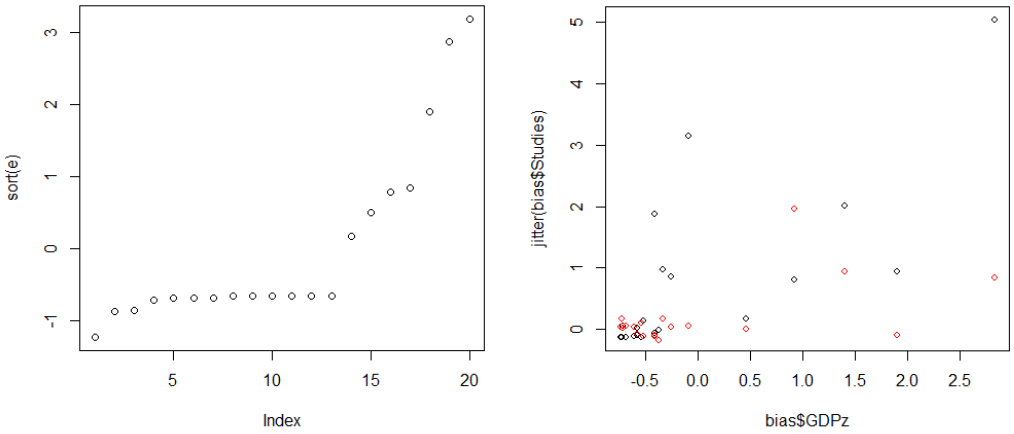


Figure S7.12. Model fit and Posterior predictive check (PPC) for the Poisson GLM (range only) for cheetah, showing the actual data (black) and simulated data from the model (red). The check indicates slight overdispersion (dispersion parameter = 1.72), with the PPC suggesting the model fitted the observed data relatively well.

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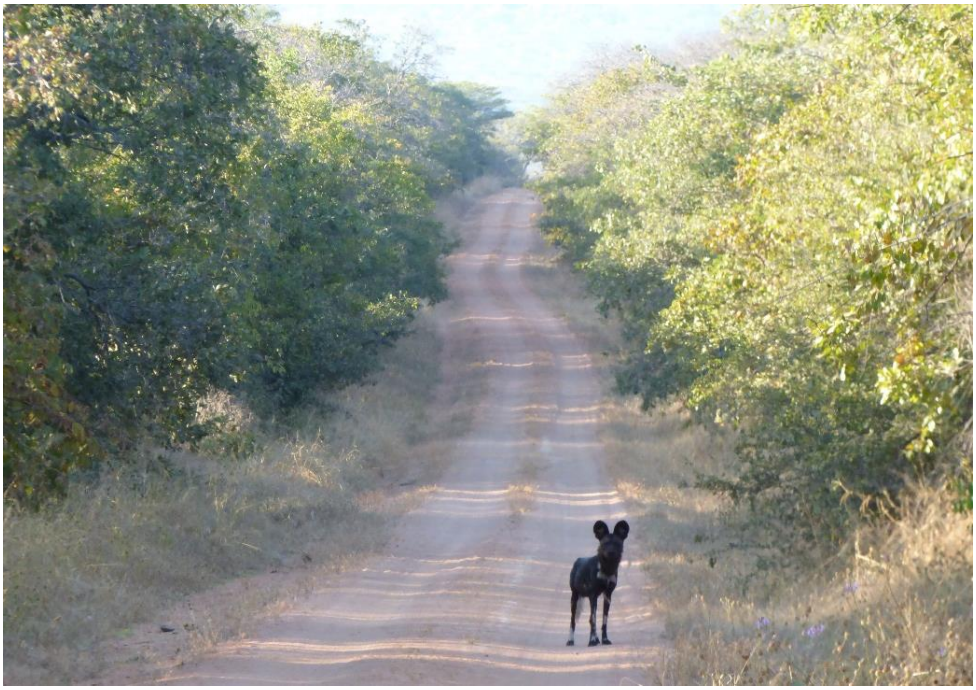


The easternmost regions of Ruaha NP. Parts of the ecosystem, such as this, are very arid in the late dry season, and become almost devoid of most wildlife.

Such areas, however, are particularly important for striped hyaena, with Ruaha-Rungwa forming the southernmost extension of the species' African range.

CHAPTER 8

Ruaha-Rungwa's large carnivores: Conservation status, threats, and future research priorities



To be circulated as a report to the Tanzania National Parks Authority (TANAPA), the Tanzania Wildlife Management Authority (TAWA), and the Tanzania Wildlife Research Institute (TAWIRI)

8.1. INTRODUCTION

This thesis comprises the first investigation of Ruaha-Rungwa's large carnivore guild at a landscape scale, and provides baseline ecological and conservation status data on one of Africa's most important remaining large carnivore assemblages (Wolf & Ripple, 2017). For most species, obtaining additional information on their distribution, habitat use, and conservation status in Ruaha-Rungwa was considered a national (TAWIRI, 2009, 2016) or even range wide priority (Woodroffe & Sillero-Zubiri, 2020). One of the goals of this thesis was therefore to help address these data and knowledge gaps.

In this summary Chapter, I synthesise insights from Chapters 3 – 6, and examine what they reveal about the conservation status of Ruaha-Rungwa's large carnivores. I also discuss threats and recommend possible mitigating actions, as well as future research requirements. Through this effort, I hope to provide conservation managers, practitioners, and researchers with a resource that can help guide large carnivore management and research agendas in the landscape, and in doing so improve the conservation outlook of these globally important populations.

8.1.1. Conservation status of large carnivores in Ruaha-Rungwa

The findings of this thesis (Chapters 3 – 6) confirm the hypotheses that Ruaha-Rungwa is home to important populations of lion (Bauer et al., 2016), leopard (Jacobson et al., 2016; Stein et al., 2020), cheetah (Durant et al., 2015, 2017), African wild dog (Woodroffe & Sillero-Zubiri, 2020), and spotted hyaena (Bohm & Höner, 2015). Similarly, although not part of this study, ancillary research suggests the landscape also hosts an important striped hyaena population (Appendix II).

8.1.1.1. *Lion*

Lion were found to be relatively widespread in Ruaha-Rungwa, using approximately 71% of sites surveyed within PAs in the landscape, and being present in all eight PAs and in non-protected areas around the complex. However, the species is not evenly distributed across the landscape: lion are significantly more likely to use (or persist in) areas with low illegal human activity, greater on-the-ground law enforcement, and greater availability of prey (particularly buffalo; Chapter 3). This is also

reflected in the very high densities of lion estimated in the Great Ruaha river valley, a well-protected area of high prey availability (Chapter 5). Miombo woodlands were found to be equally important for lion as more open savannah habitats, although here they do not appear to reach the same densities exhibited in the Great Ruaha valley, instead existing at intermediate densities even in relatively undisturbed patches (Chapter 5). The importance of miombo habitats for the species is probably a consequence of the greater availability of dry season surface water in these areas (Appendix 3.1), and thus of the greater seasonal availability of prey (e.g. buffalo, zebra). Lions are similarly distributed across photographic and trophy hunting tourism areas, but their occurrence is significantly greater in actively managed over vacant hunting blocks, due to the former receiving greater levels of law enforcement and lower incidences of human disturbance (Chapter 3).

Based on this thesis' findings, the main river valleys in the landscape – those of the Great Ruaha and Mzombe, and to a lesser extent of the Kizigo River – are the most important areas for lion in Ruaha-Rungwa in the dry season, and likely act as population sources for much of the rest of the landscape. These are followed by miombo woodlands, due to the availability of water and prey, particularly in Ruaha NP and Rungwa GR (due to the higher levels of both formal protection and on-the-ground law enforcement). On the other hand, the arid escarpment areas of Ruaha NP and of inner Lunda-Mkwambi GCA appear less important for the species in the dry season, due to lower availability of prey, and population densities are expected to be low here. Lion occurrence is also relatively low in south-west Ruaha NP (ex-Usangu GR), and in vacant blocks in the GRs, as a result of these areas exhibiting stronger anthropogenic impacts. Rungwa South OA also experienced lower lion site use for similar reasons, even though (like south-west Ruaha NP) it displays high dry season surface water availability, and therefore has the potential to be prime lion habitat. Nevertheless, as a result of the high levels of human pressures, these areas are likely currently acting as population sinks (Penteriani et al., 2018). Lion were found to be more common than wild dog or cheetah in unprotected areas, but less so than leopard, and especially than spotted hyaena (Chapter 3).

Overall, although data from the spoor surveys were not employed to estimate overall population density or abundance of lion in the landscape, due to recent concerns regarding the reliability of such methods

(Balme et al., 2009; Belant et al., 2019; Dröge et al., 2020; Elliot & Gopalaswamy, 2016; Gopalaswamy et al., 2015; Midlane, 2014; Rosenblatt et al., 2014), this thesis' findings suggest that Ruaha-Rungwa's lion population should be considered one of Africa's most important, due to its size, relative intactness, high observed population densities, and potential for connectivity with other populations (see '8.2. Threats & Recommendations, Takeaways, and Future Research').

At the same time, population density modelling in Chapter 5 suggests that some of the population estimates previously presented for the landscape may be overestimates. Chardonnet (2002) estimated a total population of 3,360 lions for the complex, based on a mean density of 8 lions per 100 km^2. Given that this is higher than the density in the core tourist area of Ruaha NP (Chapter 5), one of the most productive and best-protected areas in the landscape, this figure seems very unlikely. Instead, lion abundance in the complex is likely closer to that predicted by Mesochina et al. (2010), who estimated 1,485 lions in all PAs in the study area. However, given that densities in some of the best-protected miombo habitats were lower than the mean density of ~3.3 lions per 100 km^2 required for this, and that much of the landscape is more impacted than the areas sampled (the GCA and OA, Muhesi GR, and parts of the other PAs), it is probable that the true abundance of lion in the landscape is lower than this estimate as well. Applying index-based spoor count methodologies (Funston et al., 2010; Henschel et al., 2020; Winterbach et al., 2016) to the data collected for this thesis, while leading to estimates with wide confidence intervals (Dröge et al., 2020), could provide a way to indirectly estimate densities of lions (and other carnivores) at scales suitable to obtain landscape-wide population abundance estimates.

Finally, several publications (e.g. Abade et al., 2014), as well as official management sources (TANAPA, 2020) state that Ruaha hosts approximately 10% of the world's lions. This, however, appears to be a misrepresentation of previous population estimation efforts, arising from differences in terminology. Specifically, Riggio et al. (2013) cite figures from Mesochina et al. (2010) to estimate the Ruaha-Rungwa area to be home to 3,779 lions. While this does represent ~10% of their total continent-wide figure, the authors use the term 'Ruaha-Rungwa' to refer to the whole of central and western Tanzania, thus also including in this figure populations in Katavi-Rukwa-Lukwati, Ugalla, Moyowosi-Kigosi, Mahale, and areas in between. It is therefore likely that, as a result of this choice of

nomenclature, the 'Ruaha-Rungwa' population estimate presented by Riggio et al. (2013) was interpreted by other sources as referring to the more conventional definition of 'Ruaha-Rungwa', and eventually, through further misrepresentation, to Ruaha NP.

8.1.1.2. *Leopard*

Leopard are widespread across Ruaha-Rungwa, being estimated to use ~88% of sampled sites in PAs (Chapter 3). Unlike lion, they are relatively evenly distributed, occupying most habitats and levels of anthropogenic disturbance, thus confirming their greater adaptability (R. Estes, 1991). Indeed, although leopard densities are highest in the productive and well-protected Great Ruaha river valley (Appendix I), thus suggesting prey-rich areas are also disproportionately important for leopard, differences in densities between sites are lower than for lion (Appendix I). Occurrence is nevertheless greatest in areas which are well-protected, and/or which exhibit greater availability of water and prey (i.e. Great Ruaha and Mzombe river valleys, and miombo woodlands in Ruaha NP and Rungwa GR). Leopard are similarly widespread in both photographic and hunting tourism areas, but are more common in actively managed blocks compared to vacant ones. Leopard were found to be more common in unprotected areas than wild dog, cheetah, and lion, but less so than spotted hyaena (Chapter 3). For the same reasons as for lion, findings suggest that Ruaha-Rungwa should be considered a regional leopard stronghold.

8.1.1.3. *Cheetah*

Both spoor surveys and camera trapping suggest that cheetah are relatively widely distributed in the landscape (including in Rungwa South OA and south-west Ruaha NP, where their presence was previously unconfirmed); however, they likely exist at low population densities (Chapter 6). Although the paucity of cheetah detections did not allow for in-depth habitat use modelling (Chapter 3), the fact that none of these were in close proximity to major rivers suggests that priority areas for the species may be different than those for lion and leopard. Instead, cheetah in Ruaha-Rungwa may be faring best in areas of intermediate sympatric predator densities, as has been suggested to be the case elsewhere (Durant, 1998). Indeed, miombo woodlands, where lion and leopard densities were not as high as in the river valleys, were found to be important for the species. Similarly, spoor surveys suggest that the drier

escarpment of Ruaha NP and the eastern, drier part of MBOMIPA WMA may also be important cheetah areas. Additional research is required to better delineate priority areas for the species in the landscape (see '8.2. Threats & Recommendations, Takeaways, and Future Research'). Nevertheless, findings of this thesis suggest that photographic and trophy hunting areas are both important for cheetah in Ruaha-Rungwa, as are both miombo and *Acacia-Commiphora* habitats. As for the other felids, cheetah appear to fare better in actively managed than in vacant hunting blocks. Finally, cheetah were found to only rarely use village lands (Chapters 3, 6), particularly compared to most other large carnivores.

It was not possible to estimate cheetah population density, and thus determine whether Durant et al. (2017) are correct in estimating Ruaha-Rungwa's cheetah population at >200 individuals. However, the size and connectivity potential of the landscape, together with the species' wide distribution, suggests that this is one of the region's most important populations, and is thus of high conservation importance.

8.1.1.4. *African wild dog*

Wild dog were found to be relatively widespread across the landscape, albeit exhibiting a heterogeneous distribution, even within strongly protected areas (Chapter 3). Wild dogs in Ruaha-Rungwa are only rarely using areas with very high sympatric predator density, such as those adjacent to the main rivers in the landscape (Chapters 3, 4). Instead, areas of low or intermediate predator densities, with intermediate availability of prey, were found to be the most important for the species (as seen elsewhere in Tanzania – Selous GR, Creel, 2001). Likely for this reason, mean wild dog occurrence is significantly greater in miombo than in *Acacia-Commiphora* habitats, and the former should therefore be considered a key habitat for the species in Ruaha-Rungwa and across the wider region. This interspecific exclusion effect also probably explains why wild dogs are rarely sighted in the Great Ruaha river valley (TANAPA, pers. comm.), and why anecdotal records suggest that the species is instead more common in the adjoining MBOMIPA WMA (TAWIRI, 2009). Similarly to lion (and unlike leopard and spotted hyaena), wild dog are considerably less common in areas of high anthropogenic impacts (e.g. vacant hunting blocks, less-strictly protected areas; Chapter 3), suggesting that both biotic and anthropogenic factors are driving distribution in the landscape. Finally, mean wild dog occurrence is greater in the GRs than in Ruaha NP, likely due to the greater prevalence of woodlands in the former.

Thus, findings suggest that Rungwa GR and the areas of Ruaha NP with lower human disturbance and not along major rivers (i.e. miombo woodlands and the arid escarpment) are the most important dry season areas for wild dog in the complex. Nevertheless, additional finer-scale research is required to ascertain whether areas of critical importance may also be located within less-strictly protected areas (e.g. MBOMIPA WMA; see '8.2. Threats & Recommendations, Takeaways, and Future Research').

Finally, as we did not estimate wild dog population density from spoor (see '8.1.1.1. Lion'), it was not possible to determine whether the latest IUCN status assessment for the species is correct in suggesting that the area may support up to 500 individuals (Woodroffe & Sillero-Zubiri, 2020). Nevertheless, the species' relatively wide distribution in the landscape, combined with the presence of large packs (20+ individuals; pers. obs.), the vast size of the PA complex, and its connectivity potential, indicate that this is likely to be one of the most important remaining African wild dog populations.

8.1.1.5. *Spotted hyaena*

Spotted hyaena is the most widespread large carnivore in Ruaha-Rungwa, estimated to use ~98% of PA sites sampled. The species is ubiquitous across all PA designations, land management strategies, and habitats, and is the most common large carnivore in unprotected village lands (Chapter 3).

Nevertheless, it is probable that spotted hyaena exist at their highest densities in very prey-rich areas (e.g. the Great Ruaha and Mzombe river valleys), although additional research is required to confirm this. Similarly, the slightly lower occurrence observed in less-strictly protected areas and in vacant hunting blocks suggests that even this highly adaptable species is impacted by disturbance and habitat degradation, and likely exists at lower densities in these areas.

8.1.1.6. *Striped hyaena*

Although striped hyaena was not a focal study species of this thesis, the camera trap data employed for this research were also used in an ancillary study, which can be accessed in Appendix II, to estimate striped hyaena population density in Ruaha-Rungwa. The species exists at low densities in MBOMIPA WMA, and was not detected in any of the other systematic camera trap grids. Findings thus suggest that striped hyaena is likely restricted to the drier, easternmost areas of the landscape (i.e. eastern Ruaha

NP, MBOMIPA WMA, and possibly parts of Lunda-Mkwambi GCA, eastern Kizigo GR, and Muhesi GR). Further research into the distribution and habitat use of the species in Ruaha-Rungwa is strongly recommended (see '8.2. Threats & Recommendations, Takeaways, and Future Research').

8.1.1.7. *Ungulate species*

Greater kudu and giraffe are the most widespread of the ungulate species investigated, having been estimated to use 95% and 94% of the surveyed PAs in the landscape, respectively (Chapter 3). Impala and sable & roan, on the other hand, are common in one habitat type (*Acacia-Commiphora* for impala, and miombo woodlands for sable & roan), but almost completely absent from the other. Buffalo (estimated to use 61% of surveyed sites within PAs), and zebra (63%) are found in both habitats, but are less common in drier areas (due to their water dependence; Estes, 1991). Eland are widespread, but not common anywhere. Kudu and impala are the most common species in boundary and unprotected areas, and are likely to be key prey for large carnivores here.

Most species are similarly distributed across photographic and trophy hunting areas, except for impala (more common in Ruaha NP, due to more open habitat) and roan & sable (more common in hunting areas, due to the prevalence of preferred miombo habitat). Nevertheless, occurrence for most species is slightly higher in the NP, due to the overall slightly lower human impacts (Chapter 3). All species are more common in actively managed than vacant blocks, again probably due to differences in impacts.

Finally, species distribution maps developed in Chapter 3 are very similar to those from recent aerial surveys (TAWIRI, 2015, 2019). This suggests that both methods can be successfully employed to assess and monitor the distribution of ungulates over large scales. While maps developed from sign surveys are higher resolution (due to the greater number of data points employed), aerial surveys are more time-efficient, and thus will be the preferred choice for PA managers in most situations. Nevertheless, sign-based surveys revealed some areas to be important for species where these had not been recorded by aerial surveys (TAWIRI, 2019), suggesting that caution should be employed when associating a lack of detection in aerial censuses with absence (particularly in densely wooded miombo areas), much like is the case for sign surveys.

8.2. THREATS & RECOMMENDATIONS, TAKEAWAYS, AND FUTURE RESEARCH

In addition to the high levels of human-carnivore conflict in the landscape, which have been the subject of a number of studies in recent years (Abade et al., 2014; Dickman, 2008; Dickman et al., 2014; Dorward, 2018; Hariohay et al., 2017), this thesis also allowed the identification of a range of additional threats to Ruaha-Rungwa's large carnivores, as well as the definition of further research priorities.

Below, I explore these in more detail. Although the primary threat to long-term viability of the study populations is habitat conversion to agriculture (Chapter 3), here I focus primarily on pressures within PAs in the complex, as these are more nuanced and of more immediate interest to managers in the landscape. I also explore the main 'known unknowns' that warrant further attention, including general, species, and area-specific research priorities for large carnivores in the complex.

8.2.1. Usangu: boundary disputes, drying of the Great Ruaha, and illegal resource extraction

Improving the protection and intactness of the ~5,500 km^2 area annexed to Ruaha NP in 2008, previously gazetted as Usangu GR, should be a key conservation priority for the landscape.

About ~2,100 km^2 of this section – while officially part of Ruaha NP – is currently the source of boundary disputes, and hosts people, livestock, and large-scale cultivation efforts (Fig. 8.2; TAWIRI, 2019; this study). Finding a resolution to the ongoing dispute would likely be a highly impactful action for Ruaha-Rungwa's large carnivores, as it would add a considerable portion of very productive wildlife habitat to the ecosystem. This would also reduce illegal activity further inside the complex, and the diversion of water from the Great Ruaha River, which are both inflicting additional impacts on the landscape (see below). Nevertheless, there is evidence that previous resettlements from Ruaha NP have been carried out in unlawful and at times violent manners (Lankford et al., 2004; Sokile et al., 2003; Walsh, 2012); as a result, whichever solution is found should allow for the effective restoration of the ecosystem while appreciating the needs, rights, and requirements of neighbouring communities.

Addressing the high levels of illegal human activity in the non-contested ~3,400 km^2 gazetted in 2008 would also have strong beneficial effects for wildlife. Mean probability of illegal human activity was

approximately four times greater at sites in this area than in those already part of Ruaha NP before 2008 ($\bar{\bar{\psi}}$=0.83, SE = ± 0.05 versus $\bar{\bar{\psi}}$=0.21, SE = ± 0.06; Fig. 8.1; considering only sites in areas of Usangu whose status is not currently disputed). Conversely, occurrence of all prey and large carnivore species was significantly lower (Fig. 8.1). These differences likely stem from the area's vicinity to densely populated settlements in the contested section, the historically strong impacts in the area, and levels of law enforcement still being relatively low (although ranger posts are present, patrols were few at the time of study, and accessibility remains limited). Given the observed impact of illegal resource extraction within PAs on wildlife (Chapter 3; Loveridge et al., 2020), increasing law enforcement and minimising these impacts, both here and in other areas of the landscape exhibiting high human activity (Appendix 3.10), should be seen as a priority for PA managers. Additional studies aiming to better understand the drivers of individual illegal activities (Hariohay et al., 2019; Knapp et al., 2017), to enable the development of more tailored and nuanced interventions, are also recommended.

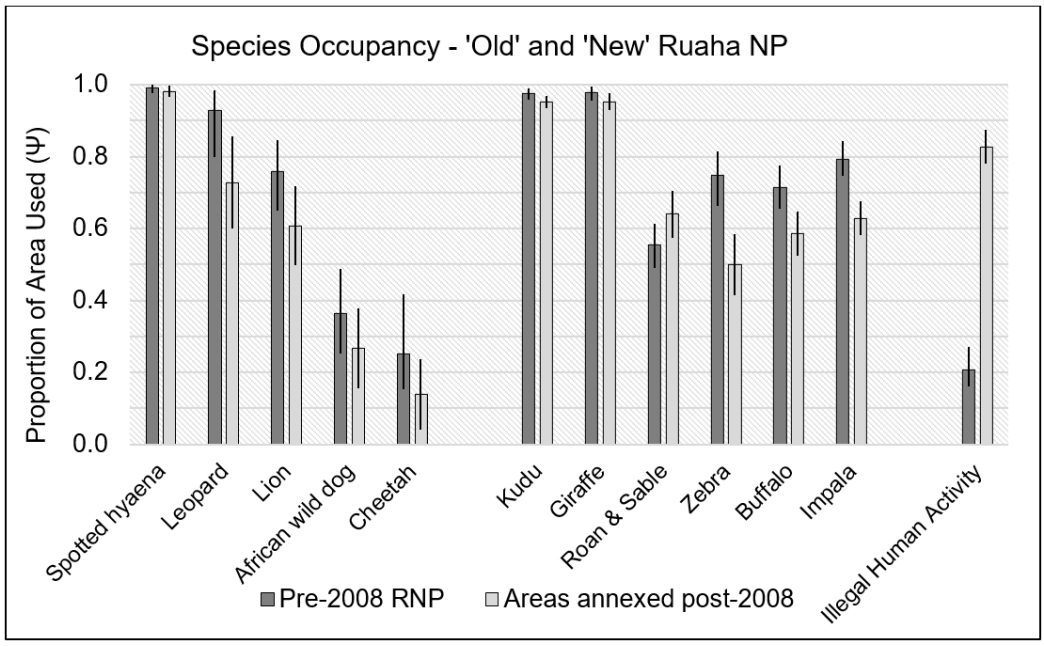


Figure 8.1. Mean probability of site use estimates for large carnivores, prey, and illegal human activity within the pre-2008 Ruaha NP, and in the area annexed in 2008 (i.e. the 'Usangu' area). Only sites in areas managed as NP by TANAPA are included, and not areas that are gazetted as part of the NP, but whose status is currently disputed.

Finally, it is also now well established that the large-scale cultivation projects in the contested Usangu area are the primary reason behind the gradual drying of the Great Ruaha River (Kashaigili, 2008;

Kashaigili et al., 2007), which has led to the loss of approximately 60% of Ruaha NP's dry season habitat (Coppolillo et al., 2008; Kashaigili et al., 2005, 2007). Given that areas adjacent to major rivers were found to be important dry season refuges for several ungulate species, including some which are particularly important for lion (e.g. buffalo), it is likely that these changes have had a significant impact on populations of lion and other large carnivores (particularly leopard and spotted hyaena). Implementing policies addressing this challenge would therefore have a strong positive impact on populations of prey and, consequently, large carnivores.

As a result of all the above, findings of this thesis suggest that constructively addressing the ongoing issues in Usangu, especially the drying of the Great Ruaha River, would be an extremely positive action to improve the conservation outlook of Ruaha-Rungwa's large carnivores. As a result, this should be seen as one of the priority conservation interventions in the landscape.

8.2.2. Hunting block vacancy & habitat degradation

Within trophy hunting areas, whether a hunting block was actively managed by hunting operators or vacant was a strong predictor of the status of large carnivores and their prey (Chapter 3); vacant blocks exhibited significantly greater levels of illegal human activity ($\bar{\hat{\psi}}$=0.77, SE = ± 0.07) than actively managed ones ($\bar{\hat{\psi}}$=0.34, SE = ± 0.07), and lower site use of all ungulate and carnivore species (particularly buffalo, zebra, lion, and wild dog).

As discussed in Chapter 3, the observed differences in human disturbance are likely primarily due to differences in law enforcement intensity, with vacant blocks exhibiting little evidence of regular protection activities. Indeed, once operators vacate a block, TAWA often lack the resources to carry out regular anti-poaching (MNRT, 2016; TAWA, pers. comm.), leading to these areas becoming more attractive for illegal activities. In addition, during the fieldwork for this thesis it became evident how block vacancy also impacted protection more indirectly: blocks being vacated led to lower revenue for TAWA, and the absence of graders or tractors – used by hunting operators to open roads at the start of each dry season – meant that accessibility in vacant blocks was compromised.

Thus, findings of this thesis highlight the need for solutions to improve protection in vacant hunting blocks in Ruaha-Rungwa. In the short term, reducing illegal activities that are common in these areas, particularly bushmeat hunting and snaring (this study), would positively impact large carnivores both directly, by minimising bycatch mortality, and indirectly, through greater availability of prey (Wolf & Ripple, 2016). In the longer term, however, alternative conservation-based revenue generation streams are likely to be required to promote continued profitability and community buy-in, and ultimately ensure the long-term securement of these areas (see Chapter 9).

8.2.3. Expanding human-carnivore conflict knowledge and mitigation efforts

The nature and drivers of the high levels of human-carnivore conflict to the east of MBOMIPA WMA and Ruaha NP have been studied in detail (Abade et al., 2014; Dickman, 2008; Dorward, 2018), and efforts aimed at mitigating these conflicts have been ongoing in the area since 2010 (RCP, 2020).

However, relatively little is known about human-carnivore conflict elsewhere in the landscape. Large carnivores were found to persist in boundary areas around much of the PA complex (Chapter 3), and high levels of conflict may therefore be present in most unprotected areas surrounding PAs in Ruaha-Rungwa. Indeed, the only other study to investigate human-carnivore conflicts in the landscape, to the west of Rungwa South OA, found high levels of conflict between pastoralists and carnivores, as a result of livestock depredations by spotted hyaena, lion, and leopard (Hariohay et al., 2017). Further research identifying additional conflict hotspots acting as ecological traps (Lamb et al., 2020), followed by the implementation of interventions reducing costs for both wildlife and affected communities (such as those developed for the landscape by the Ruaha Carnivore Project; RCP, 2019), and of conservation education programmes (Hariohay et al., 2018, 2019), should therefore be seen as priorities. This is especially the case since edge effects on large carnivore populations are especially severe where livestock farming is the primary land use bordering PAs (Schiess-Meier et al., 2010; van Bommel et al., 2007), as it the case for most of Ruaha-Rungwa. Such efforts would also allow an improved understanding of large carnivore space use in unprotected areas, which is essential to inform their conservation in mixed-used landscapes (Abade et al., 2014, 2020). In particular, collecting conflict data at a wider scale would help establish whether the observed low use of village lands by cheetah (Chapter

3, Chapter 6) and wild dog (Chapter 3) is due to behavioural differences, or to the species experiencing high levels of human-induced mortality in these areas. Improving existing compensation schemes, which were recently found to be relatively ineffective (Idd, 2020), would also be beneficial.

Finally, because kudu and impala are the most widespread prey species for large carnivores in boundary or unprotected areas (Chapter 3), safeguarding populations of these species should be seen as a priority in boundary areas and in village lands, in order to minimise the risk of large carnivores being driven to prey upon livestock as an alternative food source (Abade et al., 2014).

8.2.4. Maintaining a heterogeneous landscape and understanding seasonal dynamics

Findings of this thesis indicate that areas of lower primary productivity, which receive less tourism and conservation attention than the productive Great Ruaha and Mzombe river valleys, provide critical habitat for a number of large carnivore species, including wild dog (Chapter 3), cheetah (Chapter 6), and striped hyaena (Appendix II).

As already touched upon in Chapters 3, 4, and 6, the effective preservation of miombo woodlands and arid habitats will therefore be essential to successfully conserve Ruaha-Rungwa's large carnivore guild. Particularly for wild dog, given their low tolerance to habitat conversion (Chapter 3) and strong intraguild impacts from lions (Chapter 4), managers must ensure the availability of well-protected, intact habitats with sufficient prey availability but which do not exhibit high densities of lion (Creel, 2001; Winterbach et al., 2013). Care should also be taken to ensure that actions aiming to benefit other species (e.g. artificial provisioning of dry season water) does not lead to adverse effects for species using drier areas as refuges, as has been the case elsewhere (e.g. Kruger NP; Harrington et al., 2014).

Furthermore, while this thesis provides important first insights, more research is required into the role these habitats play for wild dog and cheetah. Given the remoteness and low accessibility of these areas, combined with both species' wide ranging behaviours, GPS collaring of individuals is recommended. Such finer scale efforts would allow a better understanding of both species' ranging and dispersal patterns (Cozzi et al., 2020), and thus help inform their conservation management. As findings suggest that wild dogs may be avoiding the best-protected areas as an indirect effect of competition with lion

(Chapter 4), such research would also allow the identification of potentially important refuges within less-strictly protected areas, which can then be prioritised for interventions.

Finally, habitat use insights obtained in this study are unlikely to be representative of wet-season mechanisms and patterns (see: '9.4. Limitations'). Supplementing these with wet season data, when both resource availability and anthropogenic pressures are bound to be different, should be a research priority. However, due to the inaccessibility of much of the landscape at this time, most data collection methods employed in this study would not to be applicable. As a result, GPS collaring (e.g. Loveridge et al., 2009) should be considered not only for wild dog and cheetah, but also for other large carnivores, to obtain wet season habitat use and ranging data which would otherwise be difficult to acquire. This would help develop recommendations that account for seasonal differences in spatial dynamics, and assist the conservation management of these populations.

8.2.5. Strictly protected photographic & trophy hunting PAs are similarly important

Strictly-protected photographic (Ruaha NP) and trophy hunting (Rungwa, Kizigo, Muhesi GRs) areas were found to be similarly important for large carnivores in the landscape (Chapter 3, 5, 6). Nevertheless, hunting areas are particularly important for wild dogs in Ruaha-Rungwa, likely due to the intermediate densities of lion and better concealment opportunities in miombo woodlands (Creel & Creel, 2002), which dominate much of the GRs. Hunting areas were also found to be particularly important for roan and sable antelope. Overall, results indicate that, in Ruaha-Rungwa, trophy hunting areas are as important for large carnivore conservation as the better-known Ruaha NP, and efforts should be made to bring similar conservation attention and investments to both.

8.2.6. The importance of securing MBOMIPA and other less-strictly protected areas

The findings of this thesis highlight the high conservation importance of the complex's less-strictly protected areas (MBOMIPA and Waga WMAs, Lunda-Mkwambi GCA, and Rungwa South OA).

MBOMIPA WMA, in particular, is considerably more important for the landscape's large carnivores than its relatively small size suggests; being adjacent to the Great Ruaha River, the area acts as a buffer zone between this key dry season refuge and unprotected village lands, thus playing an important role

in minimising edge effects for the population (Balme et al., 2010; Winterbach et al., 2013). Successful conservation within MBOMIPA will therefore be critical for Ruaha NP's large carnivore populations, some of which exist at some of their highest densities in these areas (lion, Chapter 5; leopard, Appendix I). In addition, the drier portions of MBOMIPA are important for cheetah (Chapter 6) and striped hyaena (Appendix II), and wild dogs also use these as denning sites (RCP, unpublished data). Thus, maintaining the integrity of MBOMIPA and its disproportionately beneficial role for Ruaha-Rungwa's large carnivores should be a population-level priority. Efforts should therefore be made to ensure both short-term protection (by promoting effective law enforcement; STEP, 2019) and long-term buy-in from communities, by attracting investments that promote conservation-oriented revenue generation. In particular, given the area's openness, potential for photographic tourism is considerable.

As a result of its high water availability, Waga WMA was also found to be an important dry season refuge for wildlife, and to play an important buffer role with villages to the south and east. Improving its prospects by facilitating the generation of conservation-based revenue is therefore also recommended; however, due to the thick miombo woodland habitat and presence of large numbers of tsetse flies (*Glossina*), sustainable trophy hunting tourism, and/or carbon sequestration payments (Jindal et al., 2008; Venter et al., 2009), would be better suited to the area.

Due to its location along the southern bank of the Mzombe River, Lunda-Mkwambi GCA also protects important dry season habitats. Indeed, large carnivore occurrence and ungulate density are high in this area (Chapter 3; TAWIRI, 2019), which likely acts as a source population for other areas of the complex. Furthermore, although few data are available, its drier interior, with lower densities of lion and spotted hyaena, may be important for wild dog, cheetah, and striped hyaena, based on findings in similar habitat elsewhere in the system. Ensuring the area receives regular law enforcement would thus have strong, beneficial effects on Ruaha-Rungwa's large carnivores. Further research in the area (e.g. through camera trapping) is also recommended.

Finally, Rungwa South OA experiences high levels of human disturbance and habitat loss (Chapter 3; TAWIRI, 2019). However, the area exhibits the greatest precipitation and primary productivity in the complex (Appendix 3.1), and thus has the potential to host important wildlife populations. It also forms

an important buffer between villages and north-west Ruaha NP, and is critical for connectivity with populations in western Tanzania (see below). Due to the area's densely wooded habitat, exploring carbon sequestration payment programmes (Jindal et al., 2008; Venter et al., 2009) and sustainable forestry management and utilisation solutions (Siry et al., 2005) should be particularly encouraged.

Thus, for different reasons, all less-strictly protected in Ruaha-Rungwa were found to be of high importance for the long-term success of the system. Nevertheless, due to all these areas experiencing high levels of human impacts, and presently generating little conservation-based revenue, if the status quo is maintained it is likely that over the next decade much of this key habitat will be lost. Indeed, our results confirmed mammal occurrence to already be lower in these areas, mirroring the trend noted elsewhere in Tanzania (Oberosler et al., 2019). As a result, identifying novel solutions that can bring direct conservation-linked benefits to communities, thus providing incentives to protect biodiversity and reduce detrimental activities, should be treated as a key conservation challenge to address in the landscape, as well as at a broader scale (see Chapter 9).

8.2.7. Long-term success: maintaining habitat connectivity

Some connectivity corridors between Ruaha-Rungwa and other conservation areas are believed to have been severed, and not be presently functional (Jones et al., 2009; Riggio & Caro, 2017; see Chapter 2). Nevertheless, although data are lacking, large carnivore populations in the complex are expected to still be contiguous with populations to the west, in Katavi NP and Rukwa-Lukwati-Piti GRs (through Piti East OA and Chunya-Lukwati OA), and to the north-west, in Ugalla GR (through a series of GCAs and OAs; Jones et al., 2009; Riggio & Caro, 2017). Connectivity to the east, to Udzungwa Mountains and Mikumi NPs, is possible but uncertain, as is that between the Usangu area of Ruaha NP and Mpanga-Kipengere GR (through the Igando-Igawa corridor; Jones et al., 2009; Riggio & Caro, 2017).

Indeed, although no functional connectivity assessments have been carried out, remote sensing imagery suggests that large tracts of intact habitat still exist within the GCAs and OAs linking Ruaha-Rungwa to complexes in the west and north-west (Fig. 8.2). Furthermore, findings of this thesis indicate that all large carnivores (with the possible exception of striped hyaena) are present in Rungwa South OA and

in southern Rungwa GR, two key corridor areas, and recently presence of lion, leopard, spotted hyaena, and wild dog was confirmed further west, in Rungwa River FR (Damien, 2019). Further evidence of ongoing genetic exchange between populations was provided by a recent study which found good levels of genetic diversity within lions in central and western Tanzania, with little evidence of inbreeding (Smitz et al., 2018). Combined, these insights suggest that maintaining these dispersal corridors should still be possible, if the appropriate actions are taken. This would considerably help improve large carnivore long-term prospects in the landscape, especially for particularly wide ranging species such as cheetah and wild dog (Cozzi et al., 2020). Nevertheless, there is evidence that habitat conversion in these areas is increasing at particularly rapid rates, and that their viability is at risk (Lobora et al., 2017; TAWIRI, 2019; Appendix III). Due to most of these corridors consisting of less-strictly protected areas, investments aimed at implementing solutions that can provide communities with conservation-oriented revenue (e.g. carbon credits, biodiversity payments, trophy hunting; Crossman et al., 2011; Lobora et al., 2017; Pringle, 2017; Venter et al., 2009), thus incentivising their long-term protection, should be urgently explored in these areas. As large carnivore genetic diversity in Africa is being impacted by rising habitat fragmentation (Curry et al., 2020), and these areas link multiple very large (>50,000 km^2) complexes, such measures would have a strong, impactful effect for the long-term viability of large carnivore populations in the region.

Such applied efforts should be preceded by research identifying the most important areas for connectivity, to allow for the informed prioritisation of investments. Ground surveys (either sign-based, camera trap based, or both), additional remote sensing analyses, and GPS collaring to map functional connectivity routes would all assist in this (Cushman et al., 2018; Hearn et al., 2018; Sarkar et al., 2018). If resources are limited, and given that the area between the complexes is vast, questionnaire presence/absence surveys targeting PA managers, professional hunters, village game scouts, and community members would be an effective and cost-efficient way to obtain insights into the distribution and movements of wildlife in these areas (Farhadinia et al., 2018; Madsen et al., 2020; Zeller et al., 2011). Similar research within the other corridors believed to possibly still be functional (to Udzungwa Mountains NP to the east, and to Mpanga-Kipengere GR to the south) is also recommended.

Table 8.1. Management & policy actions recommended to improve the conservation outlook of Ruaha-Rungwa's large carnivores, stemming from findings of this thesis.

Action	Area(s) targeted	Species most benefitting
Address settlements & large-scale cultivation in SW Ruaha NP (Usangu), and drying of the Great Ruaha	Southwest Ruaha NP (ex-Usangu)	Lion Leopard
Mitigate illegal activities within PAs	Highly impacted areas (vacant hunting blocks, SW Ruaha NP, less-strictly protected areas)	Lion Wild Dog
Ensure effective protection of lower prey density habitats in Ruaha NP (miombo woodlands, escarpment)	Ruaha NP	Wild Dog Cheetah
Mitigate human-carnivore conflict outside of PAs	Village lands surrounding Ruaha-Rungwa	All
Identify and implement novel conservation-based revenue generation solutions for MBOMIPA, other less-strictly PAs, and vacant hunting blocks in GRs	MBOMIPA WMA, Waga WMA, Lunda-Mkwambi GCA, Rungwa South OA, GRs	All
Maintain connectivity with other complexes	Areas to the west and north-west of Ruaha-Rungwa	Wild Dog Cheetah

Key:
Green = Can be led by local and international NGOs, in collaboration with local management authorities;
Blue = Under the sole responsibility of management authorities (TAWA, TANAPA);
Yellow = Will require high-level Government intervention;
Grey = Will likely require both high-level Government intervention and assistance from the international community

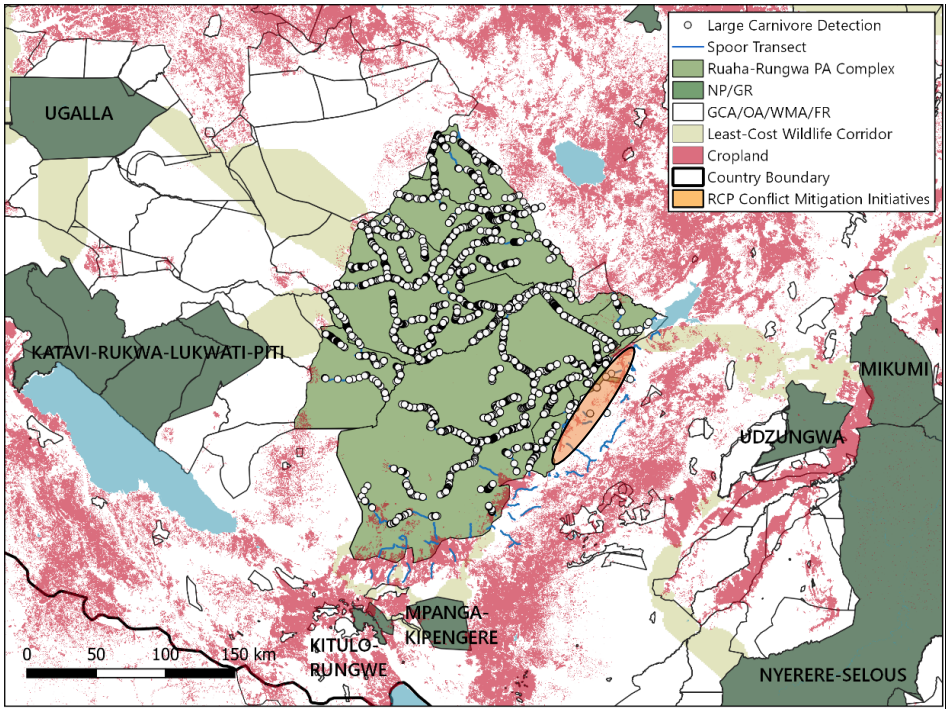


Figure 8.2. The Ruaha-Rungwa complex in the wider regional conservation context. Large carnivore detections from the spoor surveys are depicted, as are corridors believed to potentially still be viable (polygons from Riggio & Caro, 2017), and habitat conversion to agriculture (NASA, 2020). All depicted corridors are at risk, particularly those to the east (Udzungwa, Mikumi-Nyerere-Selous) and south (Mpanga-Kipengere, Kitulo-Rungwe). The approximate area of operation of the Ruaha Carnivore Project's (RCP) human-carnivore conflict mitigation programmes is depicted; as can be seen from detections, large carnivores are also widespread in boundary areas elsewhere in the landscape, and there are likely to be additional conflict hotspots which require identification and interventions.

8.3. CONCLUSION

Due to it hosting important populations of all of eastern Africa's large carnivores, its vast size, relative intactness, and potential for connectivity, Ruaha-Rungwa is of global importance for large carnivore conservation. Nevertheless, rising anthropogenic pressures, an evolving conservation landscape, and misguided past decisions place the area's long term viability under threat. Ensuring its effective long-term conservation will require a concerted, collaborative effort by wildlife authorities, local and international NGOs, researchers, the Government of Tanzania, the international donor community, and, most importantly, the people which inhabit it. The next decade will be critical for Ruaha-Rungwa and its large carnivores, and novel and bold solutions will need to be explored to ensure the area can retain its significant biodiversity conservation potential, while also contributing to the societal and economic development needs and goals of its human communities.

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The Usangu plains in south-west Ruaha NP, annexed to the NP in 2008.

Although wildlife densities are still low, due to the many years of human disturbance, effective protection and the area's fertile soil would allow this to become a key wildlife habitat, and potentially an important revenue earner for NP management.



Unprotected village lands to the east of Ruaha NP and MBOMIPA WMA. Due to the lack of physical barriers, large carnivores often range outside of PAs. Conflict between carnivores and local Barabaig and Maasai pastoralists is high, with carnivores speared or poisoned in both retaliatory and cultural killings.

Human-carnivore conflict mitigation efforts, such as those carried out by the Ruaha Carnivore Project in the landscape, are important, as is ensuring that wildlife brings direct benefit to communities, to incentivise its protection and thus minimise detrimental edge effects.



Ruaha NP rangers (TANAPA), and members of the Ruaha Carnivore Project, defusing a lion hunt by Barabaig warriors following a cattle depredation event.

In this particular instance, effective liaising by all stakeholders led to the hunt being abandoned, and the affected pastoralist receiving support for the development of a wire-fenced livestock enclosure. Further research is required to identify additional conflict hotspots elsewhere in the landscape.

CHAPTER 9

General Discussion & Conclusion



9.1. INTRODUCTION

Conserving African large carnivore populations through the 21st century will require a shift from existing pre-conceptions about what their conservation can, and should, entail, as well as a greater understanding of the role of anthropogenic influences within and around protected areas (PAs). The success of modern large carnivore conservation strategies will also depend on improved knowledge of numerous ecological and applied dynamics, including: the extent to which these species can persist across anthropogenic gradients and competing land management strategies (Chapters 3, 5, 6); the understanding and inclusion of interspecific interactions in conservation planning (Chapter 4); the availability and implementation of appropriate population monitoring protocols (Chapters 3, 5, 6, 7); and an understanding of how conservation can succeed within the wider contexts of local and national socio-economic development, by determining which strategies can achieve large carnivore conservation objectives while also promoting human societal improvements (Chapters 3, 5). Due to site-specific differences, it is important to understand the nuances of all the above at the individual PA or conservation landscape level (Chapters 3, 4, 5, 6, 8), and to also be able to compare such differences between systems (Chapter 7).

In this thesis, I attempted to provide insights that can help achieve the above through a study of the large carnivore population of Ruaha-Rungwa, a globally significant, multiple-use African landscape, characteristic of much of the continent's modern conservation areas. In this discussion, following a brief overview of the contribution to knowledge of my work, I evaluate the significance of my research for the wider large carnivore research and conservation communities. I focus in particular on the key themes treated in this thesis, including the surveying and monitoring of large African carnivore populations, trophy hunting and revenue generation in modern conservation landscapes, and the importance of conserving heterogeneous landscapes and of research being representative of the study systems. I also present additional questions of research interest which follow from my findings, and I explore the limitations of my work.

9.2. CONTRIBUTION TO KNOWLEDGE

In this thesis, I employed a series of ecological research methods to improve our understanding of the spatial ecology and conservation prospects of large carnivores in Tanzania's Rungwa-Ruaha ecosystem. I then contextualised my findings by carrying out a review of population density assessments of large African carnivores in the past twenty years.

9.2.1. Chapter 3

I show that availability of natural habitat is more critical for large carnivore persistence that legal protection, and that African wild dog exhibit the lowest threshold to habitat conversion, while spotted hyaena the highest. Lion are particularly vulnerable to human disturbances within PAs, while wild dogs are instead limited within PAs by biotic features, avoiding areas of high sympatric predator density. Leopard and spotted hyaena are very adaptable, but could not persist in fully human-dominated areas, unlike observed elsewhere. Whether an area is employed for photographic or trophy hunting tourism does not affect large carnivore occurrence, while greater legal protection and law enforcement does. Areas of intermediate prey availability (miombo woodlands and drier habitats) are critical for wild dog and possibly cheetah, and thus for conserving intact large carnivore guilds. Some ungulates (kudu, impala, and giraffe) are more successful in impacted habitats than others (buffalo, sable, zebra). Illegal activity within PAs is lower in areas with greater law enforcement. Vacant hunting blocks are more degraded, and experience lower occurrence of wildlife, than actively managed blocks. Overall, my results highlight the value of adopting an integrated approach to large carnivore conservation research in modern systems, and the need for landscape-scale conservation planning. I also identify and quantify the impact of a novel and pressing threat to Tanzania's biodiversity, in the form of the increased habitat degradation associated with the abandonment of trophy hunting areas.

9.2.2. Chapter 4

I find that wild dog are negatively associated with lion at both coarser and finer spatial scales, with effects being strongest in anthropogenically impacted areas. Leopard do not suffer from interspecific exclusion by lion at the scales investigated, and are instead positively associated with lion, particularly

in more impacted areas. Leopard habitat use is also not influenced by that of wild dog. Habitat use of large carnivores generally appears to be driven more strongly by other biotic or anthropogenic effects than by interspecific pressures, even when evidence of these is present. An exception is wild dog avoidance of lion within the home range, thus denoting a very strong interspecific effect. Overall, I provide further evidence that effects by dominant predators on subordinates are complex and species-specific. I also demonstrate the effectiveness of two-species occupancy models applied to sign data to investigate interspecific effects between large African carnivores over large scales, and how this can help inform their management.

9.2.3. Chapter 5

I provide the first spatially explicit density estimates for a lion population in Tanzania, including the first for a trophy hunting area and for a miombo ecosystem, generating insights valuable for lion management. I show that lions exist at highest densities in well-protected, prey-rich environments, and occur at intermediate densities in miombo woodlands, even when protection is high, and in well-protected trophy hunting areas. Prey-rich community-managed areas have the potential to sustain high densities of lion. I show that lions can be reliably identified at an individual level from white-flash camera trap pictures, and that the method employed is applicable across habitats and land management types, and has the potential to be an important tool for lion population management across Africa.

9.2.4. Chapter 6

I find that cheetah are widespread in Ruaha-Rungwa, but likely at low population densities, and that they only rarely use unprotected areas. I provide evidence of an extension of known geographical range of the species, and that miombo woodlands may be an important habitat for cheetah across its eastern African range. I show that collaborations with tourism operators can be employed to monitor cheetah populations, albeit with some limitations, and identify research priorities for the species in the region.

9.2.5. Chapter 7

I show that, over the last two decades, peer-reviewed large carnivore population assessments have been biased towards southern and eastern Africa, particularly South Africa and Kenya. Research focus is

significantly biased towards lion, and against striped hyaena. The number of published population assessments in a country is related to species' country range, but not to the country's socio-economic status. Research biases are present towards photographic tourism PAs under government management. Large areas are under-represented, and opportunities exist for further research on most species and in most countries. I provide recommendations to overcome identified biases, and map priorities for future research efforts. Finally, I show that significant opportunities exist for increased inclusion of local authors and capacity building in range countries, and provide recommendations on how to achieve this.

9.2.6. Chapter 8

Although not a data chapter, in Chapter 8 I employ findings of Chapters 3 – 6 to identify conservation priorities and recommend future research in Ruaha-Rungwa, as well as mitigation actions for the major threats identified for its large carnivore populations.

9.3. BROADER RELEVANCE & IMPLICATIONS OF FINDINGS

The work presented in this thesis has wider relevance to, and implications for, ecological research and biodiversity conservation beyond the study area. Here, I place my findings in the context of the wider research and conservation themes that are particularly relevant to my research, and expand on how they further our knowledge in these areas.

9.3.1. Complex systems and the need for integrated, anthropocentric research

With growing human development and associated demand for resources, African conservation systems are becoming progressively more heterogeneous and complex (Wilson & Primack, 2019). It is therefore essential that ecological and conservation research strive for similarly increasingly synthetic and integrated efforts (Everatt et al., 2019; Harris et al., 2019; Sévêque et al., 2020). In Ruaha-Rungwa, for example, without appreciating: the importance of dry-season surface water refuges for buffalo; the associations between buffalo and lion; the effect of high lion densities on wild dog occurrence and/or persistence; the importance of miombo woodlands for wild dog; the influence of human activity within PAs on lion; and the strong impact of hunting block vacancy on both species, it would be challenging to develop strategies that address the needs and improve the conservation outlook of the complete large carnivore guild, which should be the priority where these still exist (Woodroffe & Ginsberg, 2005).

However, many ecological studies still focus on single species, at single spatial scales, within small, non-representative well-protected areas (Balme et al., 2014; Suryawanshi et al., 2019). This hinders the appreciation of the complexities associated with modern systems, which will be critical to implement successful conservation actions in these novel landscapes. Research efforts should therefore aim to be multi-species, multi-scale, and, where possible, landscape-scale rather than localised to a single habitat or component (O'Neill et al., 2020; Suryawanshi et al., 2019), so that they can provide more in-depth insights than is possible from individual, smaller-scale efforts, even when summed together.

In addition, as shown by findings of Chapter 3, it is essential that the role of anthropogenic disturbances within PAs is appropriately taken into consideration. While carnivore-human interactions in boundary areas and conflict hotspots are relatively well studied (Lamb et al., 2020; Lozano et al., 2019), the effect

of disturbances within PAs is less so (but see Everatt et al., 2015, 2019; Henschel et al., 2011; Loveridge et al., 2020). The findings of this thesis, however, indicate that such effects can be strong, even within strictly-protected areas, and they must therefore be accounted for. Furthermore, responses to such pressures will vary across species' range, and depend on the relative intensities of individual disturbances (Everatt et al., 2019). As a result, further efforts investigating site and threat-specific variations in responses are recommended, as is research into the role such threats play in the creation of ecological traps (Penteriani et al., 2018). Moreover, as touched upon in Chapter 3, large carnivores have been found elsewhere to persist in completely converted, human-dominated habitats (Athreya et al., 2014; Yirga et al., 2013), which appeared to not be the case in Ruaha-Rungwa. Drivers behind these discrepancies in ecological persistence thresholds are likely complex, and will include different human societal attitudes, cultural norms, and traditions (Woodroffe, 2000). Additional research is therefore required into these thresholds and how such factors impact them, and into how human societal changes may affect the human-carnivore relationship (Western et al., 2019). This will be necessary to develop site-specific strategies (Winterbach et al., 2013), and help inform land use and species recovery planning (Foley et al., 2015). Better accounting for interspecific interactions will also be important (Chapter 4), particularly in response to climate change, as rates of range expansion and contraction will be influenced by co-occurring species (Svenning et al., 2014). More research into coexistence thresholds in impacted landscapes (Qi et al., 2020), especially between wild dog and lion, is therefore recommended.

Finally, it is critical that improved understanding of these novel, human-shaped systems by researchers does not take place in isolation. Rather, research must act as a key component of wider biodiversity conservation efforts, feeding directly into the management of study systems (Mulder et al., 2007). As complexity of biological systems increases, effective collaboration between researchers, PA managers, communities, and practitioners will become increasingly important, as will effective science communication (Bickford et al., 2012).Now more than ever, the study of ecology must be linked to the management insights required to secure biodiversity in a rapidly changing world.

9.3.2. Surveying & monitoring of large carnivore populations

As argued throughout this thesis, successful large carnivore conservation will also require effective population assessments and monitoring programmes (Elliot & Gopalaswamy, 2016). These will, in turn, rely on the availability of techniques that enable robust estimation of status parameters across habitats and land management types. This will be particularly important as landscapes become increasingly human-dominated, and the effects of anthropogenic pressures and competing management strategies on population status will need to be assessed (Welfelt et al., 2019).

The estimation of population density is considered the golden standard to assess and monitor mammal populations (O'Connell et al., 2011). Estimating density from intensive and continuous visual monitoring (e.g. Blackburn et al., 2016; Loveridge et al., 2016; Rosenblatt et al., 2014), however, is time and cost intensive, and only feasible in areas with suitable habitats and where populations are habituated. In Chapter 5, I show that spatially explicit capture-recapture (SECR) modelling applied to systematic white-flash camera trap data can be successfully employed to robustly estimate lion population densities over areas of 200-600 km^2. While this typology of models had occasionally been applied to camera trap data of lion before (Kane et al., 2015a; Rich et al., 2019), this was the first time that the methodology was employed over a range of habitats, land management strategies, and levels of anthropogenic impact, thus showcasing its applicability to a wide range of situations. The same camera trapping dataset was also employed, in accompanying research, to estimate population densities of two other large carnivores (leopard, Appendix I; striped hyaena, Appendix II), and should also be suitable to estimate spotted hyaena and wild dog densities, thus highlighting the technique's applicability for multi-species or guild-wide monitoring.

Furthermore, SECR models allow for the incorporation of a range of data sources (e.g. camera trap pictures, direct sightings, genetic identification of scat samples) in a single analysis (Elliot et al., 2020; Elliot & Gopalaswamy, 2016). As a result, the approach employed holds particular promise to estimate population densities in areas where individuals are shyer and/or exist at low densities, or where fewer data are available, and must be pooled from multiple sources. There also is considerable scope for further research and improvements of these models. For example, although the identification rate of

individuals was acceptable in this study, developments of spatial mark-resight (SMR) models that allow for the inclusion of hybrid mixture covariates (e.g. sex) would further increase the applicability of the technique, such as where only infra-red camera traps are available, or where photographs are of lower quality due to sub-optimal camera trap placement (e.g. due to lack of roads). Integrating telemetry data from GPS collars also holds promise to improve parameter estimation precision (Murphy et al., 2019).

Nevertheless, employing SECR methodologies to estimate mean population densities or overall abundances of large carnivores over particularly vast landscapes, such as Ruaha-Rungwa, is likely to remain challenging. In Chapter 3, I showed that occupancy modelling applied to sign surveys can be employed to estimate an alternative robust status parameter (proportion of area occupied, or used) in a relatively efficient and effective manner, over large areas. While the recommendation of employing occupancy and sign surveys to monitor large carnivore populations is not novel (Karanth et al., 2011; Thorn et al., 2010), and the methodology has already been applied over similarly large areas (Everatt, et al., 2019; Petracca et al., 2019), at multiple spatial scales (Everatt et al., 2015), and for multiple species (Henschel et al., 2020), this is the first time that all of the above is achieved simultaneously, while also modelling prey and human activity to improve large carnivore habitat use insights. In doing so, I hope to have further highlighted the potential of this technique as a tool to monitor large carnivore populations over large areas, and obtain insights into their habitat use and threats that can help improve their management.

Thus, for vast African conservation systems, monitoring programmes consisting of a combination of large scale, sign-based occupancy modelling and multiple camera trapping grids, stratified to cover a range of habitats, land management types, and anthropogenic impact gradients, would be a relatively efficient and effective way to provide conservation managers with both large-scale, population-level insights on large carnivore populations, their prey, and threats, and with higher-resolution, finer-scale population density estimates from representative and/or high importance areas. Where more appropriate, direct sightings or genetic data (where the capacity exists) can instead supplement or replace camera trap data, thus allowing the framework to be tailored to individual conservation areas. Whenever possible, these should involve multi-year or repeat surveys rather than one-off assessments,

to allow the estimation of trends and life history parameters (survival/mortality, recruitment, longevity, sex ratios) that drive changes in abundance (Karanth & Nichols, 2006).

While such an approach would provide more in-depth insights into the management requirements of a population than a single estimate of overall abundance, it will nevertheless require a shift from the necessity (whether perceived or real) of researchers and conservation managers to provide an estimate of overall population size, which remains the primary parameter of interests for many surveys and monitoring programmes (O'Connell et al., 2011). It would, instead, be necessary to accept that populations can still be effectively managed without the availability of such information, and that this may not be a question that should be asked, or that can be reliably answered, for populations spanning particularly large areas at this point in time. As pressure to provide overall estimates of population size often comes from policy makers, governmental officials, or donors (Braczkowski, Gopalaswamy, Elliot, et al., 2020), such a shift in approach will require successfully liaising with these stakeholders, as well as effective science communication.

At the same time, it is possible that further advancement of existing techniques may enable the reliable and accurate estimation of overall population size over large areas, and this should therefore also be encouraged. Improving the scalability of SECR-based methodologies should be investigated, including by pooling different data sources (Elliot & Gopalaswamy, 2016). In addition, the further development of index-based techniques that estimate density over large areas indirectly, such as spoor counts (Funston et al., 2010; Winterbach et al., 2016), should also be explored. Specifically, addressing recent concerns regarding the robustness and precision of this method (Dröge et al., 2020; Elliot & Gopalaswamy, 2016; Gopalaswamy et al., 2015) should be seen as a priority, in order to clarify for the scientific and conservation communities whether the technique, or a revised version of it, is indeed suitable for large-scale density estimation of large carnivore populations. Finally, methods integrating multiple modelling techniques also hold promise: Dey et al. (2017), for example, combined large-scale sign-based occupancy with systematic camera trapping within a subset of the landscape (a similar survey design to that employed in this thesis, and recommended above) to obtain landscape-wide estimates of mean population density for tigers over a 38,000 km^2 area in India. Investigating the

applicability of such methods to large carnivores in Africa is therefore recommended, as is, more broadly, further research into the relationship between occupancy and density (Linden et al., 2017; Rogan et al., 2019). Thus, while a shift away from absolute numbers is encouraged, continued innovation to attempt to address existing methodological capacity gaps should also be supported.

Finally, Chapter 6 shows that citizen science methods hold promise as complementary monitoring tools, contributing to the growing body of literature highlighting their potential (Dagorne, D., Kanté, A., & Rose, 2020; Marnewick et al., 2014; Rafiq et al., 2019). While these will not be universally applicable, such methods can provide cost-effective monitoring of large carnivore populations in certain contexts, such as within well-visited tourism areas. As a result, their further development and applicability to a wider range of situations should be explored, and, where possible, conservation managers should ensure an efficient use of limited resources by integrating these within established monitoring programmes.

9.3.2.1. *Avoiding pitfalls in density estimation*

The availability of novel methods to estimate large carnivore population densities will inevitably lead to comparisons with estimates obtained using different methods, particularly if populations are re-sampled over time. However, such comparisons are unlikely to be appropriate, due to the different ways in which the density parameter is calculated by different techniques. For instance, many estimates of density obtained through intensive monitoring are not spatially explicit, as they do not account for ranging outside of the study area, as SECR techniques instead do. Brink et al. (2012), for example, estimated lion population density in an intensive study area in the Selous GR by dividing the total number of individuals that used the study area over a certain period by the size of the area. While such estimates may be suitable to identify trends if consistent methodology is maintained over time, it would not be appropriate to compare these with density estimates obtained through spatial methods, as it is probable that applying SECR modelling to the same data would result in lower estimates (Noor et al., 2020; Rich et al., 2014). This is also likely why most SECR-based lion density estimates generally find themselves on the lower end of the range (Braczkowski et al., 2020; Elliot et al., 2020; Kane et al., 2015b; Rich et al., 2019; Chapter 5). Indeed, the estimate obtained from along the Great Ruaha River in this study, while higher than all SECR-based African lion estimates except that from the Maasai

Mara (Elliot & Gopalaswamy, 2016), is still less than half that obtained by Brink et al. (2012) for an area where lions are sighted less frequently, prides are smaller, and prey densities are lower (Essential Destinations, 2020; TAWIRI, 2018, 2019).

Thus, if population density estimated through spatially explicit approaches is to be considered the best interpretation of the parameter, most estimates from non-spatial methods would likely be considered overestimates. Comparing estimates from different methods may therefore lead to incorrect conclusions or to the identification of trends which are methodological artefacts, rather than reflecting underlying changes in population status. For these reasons, such comparisons should be discouraged, and it is important that researchers, conservation managers, and policy makers are aware of such methodological differences, to avoid interpreting apparent yet potentially unsubstantiated decreases in density as signs of population collapse. This will once again require research to be successfully integrated within wider conservation management and policy, as well as clear and effective science communication. A study which applies both spatial and non-spatial approaches to the same dataset would help elucidate the effect of these differences on density estimation, and is therefore recommended.

9.3.3. The unsung importance of miombo woodlands

Miombo areas are understudied across Africa (Abdallah & Monela, 2007), including with regards to large carnivores (Davis et al., 2020). However, the work presented in this thesis confirms that, although they exhibit low primary productivity (Frost, 1996), miombo woodlands can host important populations of mammals, including of species often associated with more open habitats (e.g. lion, cheetah, zebra, buffalo; Chapters 3, 6). As many miombo areas are threatened by rapid deforestation, including in Tanzania (Lobora et al., 2017), sustainable forest management practices (Campbell et al., 2007) would therefore have a positive effect on a range of threatened mammals. In particular, my findings suggest that providing effective protection to miombo habitats will be critical to secure several important populations of Africa's most threatened large carnivore, the wild dog (Woodroffe & Sillero-Zubiri, 2020). As many of Tanzania's less-strictly protected and more threatened PAs consist primarily of miombo (Lobora et al., 2017), particularly in the understudied western and southern regions, these insights should be used to catalyse increased conservation attention to these areas.

9.3.4. Trophy hunting and the need for innovative conservation solutions

Finally, my research found that vacant hunting areas in Ruaha-Rungwa, which had been abandoned by hunting operators and returned to the government for management, exhibited significantly greater levels of human impacts and environmental degradation, and lower occurrence of both large carnivores and their prey, than blocks receiving investments from operators. Furthermore, additional research performed alongside this thesis revealed that vacant blocks in Tanzania also suffer from significantly higher rates of habitat conversion to agriculture (Appendix III).

Given the large tracts of hunting PAs that have become vacant since 2015 (~113,000 km^2; FZS, 2018), block abandonment, and associated decrease in management investments, has the potential to be a novel, under-appreciated key threat to Tanzania's biodiversity, particularly if the environmental degradation observed in Ruaha-Rungwa is found to be common elsewhere. As discussed in greater detail in Chapter 3, the primary drivers of this degradation are believed to be the lack of management investments by hunting operators, and of funding for law enforcement by government management authorities (TAWA) due to these areas not generating revenue. It is also probable that disenchantment with the conservation process by surrounding communities is contributing to the observed high levels of illegal activities (Hariohay et al., 2018, 2019; Kicheleri et al., 2018; Moyo et al., 2016).

Similarly to vacant blocks, less-strictly protected areas (i.e. GCA, OA, WMAs) in Ruaha-Rungwa also experienced higher human disturbance and lower wildlife occurrence (Chapters 3, 5), as also noted elsewhere in Tanzania (Jones et al., 2019; Oberosler et al., 2019). These areas also experience high rates of habitat loss at a national scale (Appendix III), highlighting their generally lower capacity at conserving large mammal populations compared to NPs and GRs (Riggio et al., 2019; Stoner et al., 2006, 2007). As the majority of Tanzania's protected land is under such designations (MNRT, 2016), results thus indicate that most of the country's wildlife (at least by geographical extent) is located in areas at greater risk of environmental degradation, and more vulnerable to conversion to agriculture. Drivers of these patterns will be similar to those identified for vacant blocks, with lower community buy-in and minimal law enforcement (due to the lack of revenue generated) unable to achieve the levels of protection necessary to secure these habitats (Lobora et al., 2017; Pelkey et al., 2000; Stoner et al.,

2007). As many vacant blocks are located within less-strictly protected areas (FZS, 2018), anthropogenic impacts are likely to be particularly strongly felt in these.

Taken together, these findings are of particular conservation concern. Rapid human population growth, and associated increased in demand for land, are the primary drivers of the rising pressure on the continent's natural resources and wild spaces (Appendix III; Newmark, 2008; Watson et al., 2016). Even countries strongly committed to the preservation of their natural resources, such as Tanzania, will not be able to continue reserving large tracts of land for biodiversity conservation if this is not associated with significant economic or societal gains (Buscher & Fletcher, 2020). Indeed, although a considerable amount of the country's land, particularly in southern, central, and western Tanzania, is still under low human influence (Riggio et al., 2020), these areas are increasingly under threat (Appendix III; Jones et al., 2018; Lobora et al., 2017). It is therefore essential to identify conservation-oriented strategies that can help secure these areas while enabling economic value creation at both local (community) and national (government) levels (Buscher & Fletcher, 2020; Lindsey et al., 2014; Pringle, 2017). As the human population in the region keeps increasing, bottom-up, community buy-in will be especially critical, as incentives for people to coexist with large carnivores will depend on whether the benefits of coexistence offset the costs (Winterbach et al., 2013). Since less-strictly protected areas often play important seasonal roles (Jenkins et al., 2002) and act as dispersal corridors between core PA complexes (Jones et al., 2009), securing such areas will be key to ensure the long-term intactness of ecosystems.

In this context, findings of this thesis (Chapters 3, 5), as well as research carried out alongside it (Appendix III), suggest that, if managed correctly, trophy hunting – while undoubtedly having an impact on the target populations – can play a role in securing African wildlife habitats, while assisting in economic value creation for local communities (Lindsey et al., 2007). However, as shown by the consequences of block vacancy, results also identify a shortcoming in the system if demand for hunting tourism decreases, as happened at a global scale during the COVID-19 pandemic (Lindsey et al., 2020). Nonetheless, due to the role that trophy hunting currently plays in generating conservation revenue for large areas, and the fact that PAs in Africa are already severely underfunded (Lindsey et al., 2015, 2018), findings of this thesis align with others in cautioning against interventions that impact the

viability of the hunting industry before ensuring that alternative, conservation-based revenue generation mechanisms are identified and implemented (Di Minin et al., 2016; Dickman et al., 2019; Lindsey et al., 2012, 2013). Indeed, due to the observed consequences of decreases in management revenue, any action accelerating this (e.g. trophy hunting bans) should be matched with commitments to replace these funding streams, ideally before their enactment. At the same time, such conclusions do not detract from the proven detrimental effects of poorly-regulated and managed hunting (Creel et al., 2016; Loveridge et al., 2007; Naude et al., 2020; Packer et al., 2010), and continued efforts should be made to improve sustainability, transparency, and equality within the industry (Begg et al., 2018; Gayo et al., 2020).

It is nevertheless unlikely that trophy hunting alone will be sufficient to ensure long-term protection to all of Tanzania's PAs currently using this as their main revenue generation mechanism. In 2014, when revenues from trophy hunting where considerably greater than now, annual revenue from the industry in Tanzania was of US$16.7 million, or approximately US$54.9 per km^2 (based on 304,400 km^2 of land under hunting-based uses; MNRT, 2016, 2018). This is less than 6% of the estimated required funding per km^2 per year for effective conservation of lions (Lindsey et al., 2018). Thus, regardless of the future role of trophy hunting, novel, large-scale mechanisms are required to raise conservation funding for these areas, and provide incentives to maintain these under conservation-friendly land uses. As the international community benefits greatly from the preservation of biodiversity and ecosystem services (especially the sequestration of carbon; Fisher et al., 2011; Lobora et al., 2017), it should be encouraged to collaborate with Tanzania's conservation authorities to explore such solutions, and contribute towards the vast opportunity costs of conservation (Green et al., 2018; Lindsey et al., 2014, 2018; Waldron et al., 2017). Opportunities may include debt for nature swaps, payment for ecosystem services (of particular interest are carbon payments), a conservation basic income, private philanthropy, sustainable livestock-wildlife systems, and wildlife-friendly agriculture (Buscher & Fletcher, 2020; Crossman et al., 2011; Green et al., 2005; Keesing et al., 2018; Pringle, 2017; Venter et al., 2009; Western et al., 2020). Legislative changes encouraging public-private partnerships for the management of Tanzania's vacant hunting blocks and less-strictly protected areas (particularly WMAs) should also be supported, as these represent a promising tool to develop externally-funded, conservation-oriented

land use strategies while providing tangible economic value (Baghai et al., 2020; Lindsey et al., 2014, 2018). Given that most PAs, including those generating revenue from photographic tourism, already require further investment and subsidies to meet their management and opportunity costs (Green et al., 2018; Lindsey et al., 2018, 2020), these mechanisms should be explored in full regardless of the status.

At the same time, broader cross-sectoral land use planning is needed within a landscape theory framework (Arts et al., 2017; Githiru et al., 2015), to concomitantly prioritise both conservation and development interventions. Due to current rates of habitat loss and degradation (Chapter 3; Appendix III; Lobora et al., 2017; Riggio et al., 2019) and limited in-country conservation resources (Caro & Davenport, 2016), it is unlikely that all these many areas of Tanzania still hosting large mammal populations will be able to be retained for wildlife-based uses. As a result, pragmatic, multi-criteria conservation planning assessments that stretch beyond ecological considerations to also incorporate socio-economic, political, and administrative factors (e.g. Srivathsa et al., 2020) are urgently required for the country. Such initiatives should be employed to prioritise limited conservation investments based on a range of factors – including wildlife, carbon, water, climate change forecasts (e.g. John et al., 2020), and human needs – to conserve areas whose safeguarding can enable Tanzania to attain both its biodiversity targets and development goals. A spectrum of other effective area-based conservation measures (OECMs; Dudley et al., 2018) that devolve management and benefits to communities should also be encouraged alongside such efforts, to further promote conservation without compromising sustainable development priorities (Kremen & Merenlender, 2018; Tilman et al., 2017; Western et al., 2020). Large carnivore conservation requires balancing the need for legal protection of wildlife with the use of natural resources by rural people (Hutton & Leader-Williams, 2003), and improved governance and effectiveness of WMAs will be particularly crucial in this context (Caro & Davenport, 2016). Given current trends, the effective implementation of such measures over the next decade, which would have to be carried out at a national scale and with support from the highest levels of Government (and will require mapping effort such as those presented in Chapter 3 and recommended in Chapter 8), will be critical for the preservation of many of Tanzania's, and Africa's, last remaining wilderness areas.

9.4. LIMITATIONS

Specific limitations of each data chapter are explored in their respective discussion sections. In addition, there are also some more general limitations that are relevant to multiple components of this thesis.

The main such limitation for research carried out in Ruaha-Rungwa (Chapters 3, 4, 5, and 6) is that the data employed were only collected during the dry season. As a result, all conclusions made should be treated as relevant only to this period, and would have potentially differed if data had been collected at another time of the year. Significant seasonal differences in resource availability for herbivores would lead these to exhibit seasonally distinct ranging patterns, and carnivores would also be expected to adapt their habitat use as a result, as shown to be the case elsewhere (Schaller, 1972). Obtaining additional information on habitat use in the wet season would therefore help inform management; see Chapter 8 for recommendations on how to best achieve this in the study landscape.

An additional limitation of my research is that the nuances of the responses to anthropogenic pressures by large carnivores identified in Ruaha-Rungwa will vary across the species' range, as shown by the different persistence thresholds for some species in Ruaha-Rungwa and elsewhere (Chapter 3). This context-specificity must be kept into account, and additional efforts are required to understand the extent to which research findings from human-impacted landscapes can be generalised to elsewhere, and which responses are instead site-specific and expected to vary between areas and with time.

9.5. CONCLUSION

Through this thesis, I aimed to deliver an insightful look into an understudied yet globally significant large carnivore assemblage. At the same time, I hope to have provided a range of ecological, methodological, and applied conservation insights that can have wider applications and relevance. The research in this thesis shows that habitat requirements of large carnivores in human-shaped landscapes are multifaceted and complex, and that studies of an integrated nature can provide valuable insights for the conservation management of African large carnivore guilds (Chapters 3, 4). Large carnivore conservation in these systems will also depend on appropriate monitoring protocols, which will have to be standardised yet context-specific (Chapters 3, 5, 6, 7), and on evaluating the effectiveness of conservation strategies at meeting their biodiversity conservation targets, while generating both local and national-level benefits for a rapidly developing society in the process (Chapters 3, 5, 8).

Overall, this study aimed to cast some light on the complexities associated with conserving large carnivores in rapidly evolving African landscapes, where space for wildlife must not come at the detriment of human livelihoods, or of national economic and societal development. Improved understanding of large carnivore ecology in such landscapes, more nuanced appreciation of human-wildlife relations, and the development of novel solutions that benefit both wildlife and the human communities they live alongside, will all be critical if we are to provide safe passage to large carnivores through the 21st century, and ensure their persistence in humanity's most ancient home. It must also be appreciated that these novel systems do not signify "finis Africae" – the "end of Africa" (or, better, of the romanticised notion of wilderness that the term has become associated with in western discourse). Instead, increasing anthropogenic influence is an inevitability that the research and conservation communities must strive to understand, adapt to, and help guide in a direction that preserves ecological intactness, while also addressing the needs of the people and nations which oversee this globally important and dwindling natural wealth, and on whom its effective preservation will ultimately depend.



Rungwa South OA. A less-strictly protected area, it is used for trophy hunting and logging for charcoal by nearby communities. Comprising thick miombo woodlands interspersed with open patches ('mbugas'), the area plays a key role in connecting Ruaha-Rungwa with the Katavi-Rukwa-Lukwati complex to the west.

Being an OA, however, people can settle and graze livestock freely, and deforestation and bushmeat poaching are widespread. The area, like many others like it, is therefore severely threatened. Sustainable forest management programmes, as well as novel conservation-friendly revenue generation strategies, are urgently required to incentivise the protection of such areas in the face of rising demand for land in the country.

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APPENDIX I

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

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Submitted to *Biological Conservation* (in review)



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 riverine *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 the neighbouring MBOMIPA Wildlife Management Area (WMA). Density in the miombo (*Brachystegia-Jubelnardia*) woodland-dominated Ikiri block of Rungwa Game Reserve (3.36 ± 1.09 per 100 km^2), a trophy hunting area, was similar to miombo woodland in western Ruaha NP (3.23 ± 1.25 per 100 km^2). Our results illustrate that variation in density across the landscape is likely to be largely driven by differences in prey abundance, itself linked to differences in productivity between habitat types and differences in anthropogenic impacts. Our findings suggest that habitat type and human impacts play a key role in determining density of leopard populations, and that a trophy hunting area with significant protection investment supports a leopard density comparable to that in similar habitat in a photographic tourism area. We also provide evidence that community-managed WMAs have the potential to effectively conserve large carnivore populations at relatively high densities.

Manuscript submitted for publication can be accessed at: https://github.com/pstrampelli/DPhil-Supplementary-Manuscripts

APPENDIX II

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

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Submitted to *PLOS ONE* (in review)



ABSTRACT

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 miombo woodlands supported a higher serval density than the core tourist area and Wildlife Management Area, with 5.56 [±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 intraguild predation. 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.

Manuscript submitted for publication can be accessed at: https://github.com/pstrampelli/DPhil-Supplementary-Manuscripts

APPENDIX III

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)



ABSTRACT

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 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, 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.

Manuscript submitted for publication can be accessed at: https://github.com/pstrampelli/DPhil-Supplementary-Manuscripts