Examining the spatial occurrence of carnivores across a gradient of anthropogenic pressure in southern Tanzania, with a focus on the Ruaha landscape and adjacent areas

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Abstract

Tanzania's Ruaha landscape harbours some of the most important carnivore population strongholds in East Africa. However, ongoing human-induced changes of natural habitat expose these carnivore populations to increased anthropogenic pressure, even within protected areas. Such habitat changes can disrupt carnivore distribution and species interactions, which can be detrimental for species conservation. Yet, there is limited understanding about how anthropogenic-related variables influence carnivore occurrence and interspecific interactions in this landscape, which hinders the development of strategies to conserve carnivores. In this thesis, I examined the spatial occurrence of carnivores across the gradient of anthropogenic pressure in the Ruaha landscape and adjacent areas. In the first data chapters I investigated how landscape and human-related variables influenced carnivore site occupancy and interspecific interactions in the Ruaha National Park (RNP), surrounding wildlife management area, and village lands through extensive camera-trapping data. I found a consistent and steady decline in carnivore detections with increasing distance from RNP, especially closer to human households. Large carnivores, specifically, were not detected anywhere in the village lands. There was a notable variation on the influence of anthropogenic and landscape variables to carnivore site use: large carnivores were influenced by prey biomass and anthropogenic variables, whereas mesocarnivores were largely influenced by distance to the Great Ruaha River. In addition, mesocarnivore detections were correlated with those of top-order carnivores. Furthermore, increased probability for interspecific interactions between mesocarnivores was influenced by proximity to households. Overall, I identified that the village lands were likely acting as a hard edge that limited carnivore distribution outside RNP. On my last data chapter, I investigated the determinants of carnivore habitat suitability beyond Ruaha, and generated a predictive map of highly suitable carnivore habitats for the human gradient between the Ruaha and Selous landscapes, using the lion (*Panthera leo*) as a key-species. Highly suitable habitats were associated with low human population density (<10 people/km^2) and rainfall, and over 75% of these habitats were limited to protected areas, with the remainder patchily distributed across village lands. The results suggested limited potential for landscape connectivity between Ruaha and Selous. Overall, this thesis provides a rigorous assessment of the first comprehensive baseline data of carnivore spatial occurrence within a gradient of anthropogenic pressure in this landscape. The framework presented here can be used to help informing carnivore conservation planning in Ruaha, with applications elsewhere where carnivores and humans overlap.

This thesis is dedicated to Nali, Mário and Luciano

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Alegria, o sol nascerá.

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Chapter 1: Introduction

1.1. An overview of the cultural, ecological and economic value of carnivores

1.1.1 Carnivores and their association with human cultures

The *Carnivora* order encompasses some of the most charismatic and iconic animal species (Dickman et al. 2015; Gross 2012; Macdonald et al. 2015), and throughout their distribution range, have had significant aesthetic, cultural, symbolic, spiritual and economic value in human societies through history (Kellert et al. 1996; Loveridge et al. 2010b). Large carnivores, in particular, have often being depicted as deities, and were often given sacred status. Tigers (*Panthera tigris*), for instance, have been historically worshipped as sacred animals by both Hindi and Muslims in Northern Bengal, and are portrayed as demigods used as vehicles by divine entities in Hinduism (Krishna 2010). The species is still worshipped in folkloric festivals such as the *puli kali* of Thekkikandu Maidan, in Kerala, India, in which men will dance simulating tiger movements before the start of the harvesting season for a good yield (Krishna 2010). Lions (*Panthera leo*) have historically been portrayed as a powerful, fierce and often-vengeful religious entity in ancient Graeco-Roman cultures and in early Christian religion, surpassing humans in both virtue and courage (Gilhus 2006). They are found portrayed as ravenous man-eating beasts (i.e. the Myth of the Sphinx; the Nemean Lion), and to give power, courage, and strength to those bearing lion fur - Heracles was often depicted using the Nemea lion skin to subdue and capture Cerberus (Connor 2003). In traditional African cultures, both lions and leopards (*Panthera pardus*) are still closely associated with religious beliefs, and the possession of their body parts is thought to imbue people with bravery, social status and spiritual protection (Dickman 2008; Goldman et al. 2013). In Tanzania, for example, tribes such as the Sukuma and Barabaig still conduct traditional lion hunting - either to retaliate against/or prevent livestock loss, and as a way of demonstrating bravery. In these hunts, young men are expected to spear and kill a lion, and then use their body parts as ornaments to earn the respect from other tribe members, and to claim rewards such as livestock from other villagers as acknowledgment for their bravery after a successful lion hunt (Fitzherbert et al. 2014). In other examples, leopard paws have been found to be used as talismans against bad luck in southern Africa (Warchol et al. 2003), whereas leopard coats are still used in Shembe religious ceremonies in Zulu communities in South Africa (Hunter et al. 2013).

Some carnivore species have been associated with witchcraft, and perceived as responsible for evil deeds such as predation upon people and livestock (Dickman 2015). Spotted hyaenas (*Crocuta crocuta*), for example, are often associated with magic (Dickman and Hazzah 2016), and believed to be used by witchdoctors to cause damage to enemies through livestock raiding and human predation in southern Tanzania (Dickman 2015). Similarly, grey wolves (*Canis lupus*) were historically associated with the devil, witchcraft and death, which contributed to their eradication from northern Germany in the 18th and 19th century (Rheinheimer 1995). The ability of these large carnivores to subdue and predate on humans and livestock (Inskip and Zimmermann 2009; Madden 2004; Packer et al. 2005b; Sillero-Zubiri and Laurenson 2001), and their potential to inflict severe economic losses through livestock and game killing (Dickman et al. 2011; Nyhus et al. 2005; Ogada et al. 2003), have contributed to their stigma of pest animals or "vermin" species (Ginsberg and Macdonald 1990; Linnell et al. 1999), and even to the title of "harbingers of death" (Clark et al. 1996; Rheinheimer 1995). This negative perception – either due to a perceived or actual threat (Bruskotter et al. 2017)- unsurprisingly, has contributed to people's intolerance towards carnivores (Dickman and Hazzah 2016; Inskip et al. 2016). Such intolerance often translates into direct persecution and carnivore killing (Bruskotter et al. 2017; Hazzah et al. 2017; Inskip et al. 2016; Kansky et al. 2014), and has contributed to widespread carnivore population declines and range contractions that currently threaten their conservation (Inskip and Zimmermann 2009; Ripple et al. 2014; Woodroffe et al. 2005b).

Independently of the values attributed to a particular species, carnivores have long been deeply entwined with humans through history, influencing long-lasting traditions (Kellert et al. 1996). Their relationship with people still exerts a powerful influence on the human psyche and behaviour through their range (Bruskotter and Wilson 2014; Carter et al. 2012; Dickman and Hazzah 2016).

1.1.2. Carnivores as key players for maintaining ecosystem health

From an ecological standpoint, carnivores are vital components of a healthy, functioning ecosystem (Estes et al. 2011; Ripple et al. 2014; Ritchie and Johnson 2009). Large carnivores (those above 15 kg) often act as keystone species, and are instrumental in regulating ecological interactions on lower trophic levels (Haswell et al. 2016; Ripple et al. 2014; Ripple et al. 2016b;

Ritchie et al. 2012). For example, they influence the densities, behaviour and sex ratios of prey species, and suppress the deleterious effects of large ungulates on vegetation (Bowyer et al. 2005; Everatt et al. 2014; Ford et al. 2014; Hobbs 1996; Licht et al. 2010; Terborgh et al. 2001). Their removal from the ecosystem can result in significant alterations in predator-prey equilibrium and dynamics, irruptions on mesopredator populations (Elmhagen and Rushton 2007; Estes et al. 2011; Ripple et al. 2014; Ritchie and Johnson 2009), and in the loss of species richness and diversity (Estes et al. 2011; Krebs et al. 2001; Licht et al. 2010).

The consequences of apex predator removal to a trophic system are well illustrated by the long-term extirpation of grey wolves from Yellowstone National Park, USA, in the early 1920s. During the 70 years post-wolf extirpation, the increase of ungulate populations – largely attributed to the lack of top-down regulation by wolf predation – intensified herbivory and overgrazing, and compromised overall vegetation structure due to low plant recruitment (Licht et al. 2010; Ripple and Beschta 2012; Smith et al. 2003). These changes in vegetation compromised the hydrology of the region through displacement of beaver (*Castor canadensis*) damming (Wolf et al. 2007), and limited connectivity of streams with adjacent floodplains around Yellowstone (Beschta and Ripple 2006; but see Marshall et al. 2014). Moreover, in the absence of wolves, the increased populations of subordinate carnivores released from intraguild competition caused substantial suppression of smaller prey species (Ripple et al. 2013; Smith et al. 2003), and contributed to simplification of the ecosystem (Licht et al. 2010).

In the context of the African savannah, mesocarnivore trophic cascades (i.e. from large carnivores to mesocarnivores and their associated prey – Ripple et al. 2014) have been observed following the removal of a guild of apex carnivores encompassing lions, leopards and spotted hyaenas from six protected areas in Ghana. Following carnivore removal, mostly due to poaching, the population of olive baboons (*Papio anubis*), a subordinate mesopredator, increased in >300%, and contributed to the decline, and eventually local extinction of antelope and primate species due to increased baboon predation (Brashares et al. 2010).

It is important to remark that mesocarnivores also play an important role in ecosystem services. For example, in systems where large dominant carnivores are absent, mesocarnivores can become the apex predators themselves, and will drive community structure. They can provide important ecosystem services such as regulation of smaller prey such as rodents (Byrom et al. 2014), which can cause severe economic losses due to crop raiding (Naughton-Treves and Treves 2005), and are carriers of zoonosis of sanitary risk to humans such as hantaviruses, plague, leptospirosis and toxoplasmosis (Schmaljohn and Hjelle 1997; Taylor et al. 2008). Furthermore, mesocarnivores often contribute to primary and secondary seed dispersal (Hämäläinen et al. 2017), plant recruitment and dispersal, and nutrient cycling, which can influence landscape and vegetation structures (Roemer et al. 2009). In one example, the introduction of the Artic fox (*Alopex lagopus*) to the Aleutian Islands, Alaska, has resulted in substantial changes in vegetation type (from grassland to maritime tundra) as the increased predation of costal bird populations by the foxes has led to decrease in guano deposition, which interfered in nutrient cycling and henceforth decreased soil fertility (Roemer et al. 2009).

Thus, carnivore removal from ecosystems can result in severe negative impacts on ecosystem services and trophic equilibrium, and their conservation is important for maintenance of species and overall biodiversity (Brashares et al. 2010; Estes et al. 2011; Ripple et al. 2014; Ritchie et al. 2012; Terborgh et al. 2001).

1.1.3. Large carnivores as economic assets

Large carnivores are key species for the multi-million dollar tourism and trophy hunting industries, especially in sub-Saharan African countries (Campbell 2013; Di Minin et al. 2016a; IUCN 2016; Macdonald et al. 2016; Nelson et al. 2013). For example, wildlife tourism, which is largely based on wildlife watching of large carnivores and other megafauna, has generated approximately US $108 billion to sub-Saharan African countries GDP in 2016 (Price 2017). In Tanzania, wildlife tourism has been estimated to underpin a market worthy of over US $700 million/year, and that accounted for 5-10% of the country's GDP in 2002 (Nelson et al. 2007). Similarly, it contributes to the yearly US $620 million Zimbabwe's tourism revenue, and to 5% of the country's GDP since 2008 (Meer et al. 2016). Large carnivores such as lions and leopards are among the most sought-after species by tourists, and are significantly important to the profitability of the tourism industry across Africa (Grünewald et al. 2016; Maciejewski and Kerley 2014; Meer et al. 2016; Mossaz et al. 2015). Previous estimates of carnivore 'worth' ranged from US $50,000/year for leopards in

Londoloze Game Reserve in South Africa, and US $128,750/year for lions in Amboseli National Park, Kenya (Sillero-Zubiri and Laurenson 2001). In another example, Thresher (1981) has estimated the economic tourist value of a lion for a 15 year period (1977-1992) to reach US $1,195,000, and to be tied to the maintenance of 2,000 jobs at Amboseli National Park, Kenya.

Despite divergences on the true contribution of the overall hunting industry to the gross domestic product of African countries (Booth 2010; Campbell 2013; Lindsey et al. 2007) - hunting *per se* has been suggested to contribute to less than 2% of the overall tourism revenues (Campbell 2013)-, figures for overall species hunting range from US$ 190 - 217 million for the estimated yearly minimum gross revenue of international agencies and governments in the sub-Saharan Africa (Booth 2010; Di Minin et al. 2016a; Jorge et al. 2013; Lindsey et al. 2006; Lindsey et al. 2012; Lindsey et al. 2007).

In the context of large carnivore trophy hunting, lions, for example, are one of the most iconic and expensive trophy species in Africa, with hunting prices in 2012 estimated to range from US $24,000 – 71,000 depending on the country (for instance, lion hunting prices were only exceeded by those associated with elephant *Loxodonta africana* and rhinoceros *Ceratotherium simum* and *Diceros bicornis* hunting respectively in South Africa and Namibia; Lindsey et al. 2012). Lion hunting in isolation has contributed to 5 - 17% to national economies of five sub-Saharan countries between 2005 and 2011 (Lindsey et al. 2012). In South Africa, lion hunting alone generated ~54% (>US $15 million) of the overall gross hunting revenue in 2012 (Di Minin et al. 2016a). Leopard sport hunting was estimated to generate 8 to 20% of the annual gross income of the trophy hunting industries in Eastern and Southern Africa for the period between 2005 and 2011 (Lindsey et al. 2012). In Tanzania, lion and leopard hunting was estimated to contribute to roughly 20% of the US $27.6 – 36.1 million annual revenue of hunting activities during a review of over 20 years of trophy hunting data (Baldus and Cauldwell 2004; Lindsey et al. 2006; Lindsey et al. 2007).

1.1.3.1. Implications of tourism and trophy hunting for carnivore conservation

The accrued revenue from tourism and hunting often represents substantial income for governments, environmental agencies and individuals, and can contribute positively to carnivore and overall wildlife conservation in a scenario of effective governance and management (IUCN 2016; Naidoo et al. 2016). For example, Buckley et al. (2012) estimated that the conservation of at least 5% of over half of the red-listed mammal species is dependent on tourism revenues, with approximately 29% of the extant lion population conserved through tourism revenues to protected areas. Governments, private and communal landholders will use hunting and tourism revenues to cover, for instance, the costs associated with wildlife management, salaries for rangers and guards, anti-poaching patrolling, and investments in equipment and infrastructure (IUCN 2016; Macdonald et al. 2016). For example, in Tanzania, 22% (>US $12 million) of the 2008's hunting revenue was allocated to the Wildlife Division (Di Minin et al. 2016a), which is responsible to manage wildlife services such as anti-poaching patrolling and combat to wildlife crime. In another example, all the 2015 lion hunting revenue (>US $1.2 million) was invested in the maintenance costs of the Bubye Valley Conservancy, Zimbabwe, and contributed to lion conservation by supporting activities such as anti-poaching, fencing maintenance and research (Macdonald et al. 2016).

The flow of revenues into rural communities engaged in hunting and tourism contributes to their economic welfare by paying wages, creating employment opportunities and improving communal infrastructure (Naidoo et al. 2016). In Uganda, for example, a tourism revenue-sharing scheme implemented around three parks resulted in >US $80,000 that were used to build 21 schools and four health-care clinics, and helped to improve people's attitudes towards the parks (Archabald and Naughton-Treves 2001; Dickman et al. 2011). Similarly, tourism and hunting related revenues have contributed to increase livelihood security by creating job opportunities and increasing household incomes, besides financing provision of water supply to households, and construction of 35 houses in three villages in the Okavango delta, Botswana (Mbaiwa and Stronza 2010). In addition, communities that benefit from such revenue-sharing schemes often show increased awareness and tolerance towards carnivore presence in communal lands, and reduced human-wildlife conflict and retaliatory killing of perceived-problem animals (Booth 2010; Di Minin et al. 2016a; Lindsey et al. 2013c; Naidoo et al. 2016). For example, in the Kenyan Ewaso ecosystem, tolerance towards large carnivores such as cheetahs (*Acinonyx jubatus)* and lions by community members was correlated with direct or expected gains from wildlife use (Romanach et al. 2011). However, it is noteworthy that the correlation between benefit gains and increased tolerance to a given carnivore species is not always that clear. People might appreciate receiving the revenues and benefits associated with tourism and hunting activities, and still show low tolerance to carnivores when the costs of bearing such species in their lands, and the economic losses due to livestock predation are not offset (Lindsey et al. 2013c; Walpole and Thouless 2005). For instance, even when people received substantial direct monetary benefits from jaguar presence, they did not show increased tolerance towards the species, as shown by Harvey et al. (2016).

Besides generating economic revenues and benefits to governments and communities, the maintenance of photographic areas and hunting reserves for carnivores have also been linked to the conservation of large swathes of intact wildlife habitats (Di Minin et al. 2016a; Fitzgerald and Stronza 2016; Lindsey et al. 2006; Lindsey et al. 2007; Macdonald et al. 2016). This is an important conservation contribution, especially in the context of rapid loss of wildlife due to the conversion of habitats to farming and grazing (Brink et al. 2016; Caro et al. 2009b; Lindsey et al. 2013b). In fact, areas set aside for large carnivore hunting has been estimated to span 1.3 million km^2, exceeding in 22% the total area protected by national parks in sub-Saharan Africa (Lindsey et al. 2007). In addition, the intensive management and surveillance required to maintain the trophy species within hunting areas helps minimising the threat of bushmeat poaching, and carnivore killing (Brink et al. 2016; Di Minin et al. 2016a), contributing to overall wildlife conservation.

As shown above, carnivores represent substantial economic assets for countries, governments and communities, and their well-managed use have the potential to generate significant economic benefits, and can contribute to human welfare and development, and wildlife conservation. However, tourism and trophy hunting are not a panacea, and can have detrimental effects on carnivore conservation. The literature is fraught with empirical examples in which carnivore overharvesting due to unsustainable hunting practices and poor governance has contributed to their population decline (Brink et al. 2016; Creel et al. 2016; Crosmary et al. 2015; IUCN 2016; Lindsey et al. 2016; Loveridge et al. 2016a; Packer et al. 2011; Ripple et al. 2016c). Trophy hunting has been shown to be the main cause of lion mortality and population decline in Zambia's South Luangwa National Park and adjacent game areas (Rosenblatt et al. 2014), whereas it has affected population size, sex ratio, number of male coalitions, and ultimately survival of offspring and adult lions in Hwange National Park (Loveridge et al. 2016a). Lions are particularly sensitive to overharvesting as the removal of young males in their prime, often the most targeted by hunters, can disrupt pride demography patterns, increase male turnover rates, and thereby infanticide and cub mortality, creating a draining population dynamics that can lead local populations to extinction (Barthold et al. 2016; Loveridge et al. 2010a; Loveridge et al. 2016a; Loveridge et al. 2016b; Packer et al. 2004). However, it is worth noting that very little comparable research has been conducted on the magnitude and impacts of other forms of anthropogenic killing, such as from conflict, and the level of that killing often substantially exceeds trophy hunting (Panthera et al. 2017).

In regards to tourism, the overall benefits to carnivore conservation have also been questioned. Unregulated or mismanaged tourism activities have been shown to contribute to landscape changes from rural to a more urban setting (Rastogi et al. 2015), disturbance of ecological corridors by tourism infrastructure building (DeFries et al. 2010; Karanth and Karanth 2012), disruption of physiological and behavioural patterns (Penteriani et al. 2017; Rastogi et al. 2015), changes in predator-prey interactions (Geffroy et al. 2015), and harm to animal welfare (Moorhouse et al. 2015). In some instances, the detrimental high footprint of tourism activities to carnivore conservation have led governments to propose tourism ban to tiger sanctuaries in an attempt to minimise the adverse effects of mass wildlife tourism in India (Karanth and Karanth 2012). Furthermore, the lack of engagement with communities living adjacent to tourism areas (which can be excluded from their traditional practices and land for the benefit of tourism, as observed with Maasai communities in the Ngorongoro area), and the poor equity in revenue-sharing can undermine the living conditions and economic welfare of local communities (Cater 1995; Walpole and Goodwin 2002; Walpole and Thouless 2005). In fact, the exclusion of local communities from tourism activities is likely to further exacerbate antagonism and hostility towards wildlife and protected areas, with detrimental consequences to the long-term conservation of species (Newsome et al. 2004; Walpole and Thouless 2005). Even though tourism on its own is unlikely to achieve wildlife conservation (Walpole and Thouless 2005), it can be a powerful tool to help improving tolerance towards carnivores given the adequate involvement of local communities, planning, and use of financial instruments to alleviate the opportunity costs associated with carnivore presence (Walpole and Thouless 2005).

1.2. Population declines of large carnivores

Large carnivores are naturally rare, have low reproductive rates and generally occur in low densities (Noss et al. 1996; Ray et al. 2005; Ripple et al. 2014). Such rarity, related to high energetic requirements and large home range requirements (Carbone and Gittleman 2002; Carbone et al. 1999; Woodroffe and Ginsberg 1998), make them particularly sensitive to human encroachment and associated changes in habitat quality (Cardillo et al. 2004; Riggio et al. 2012; Woodroffe 2000), and more extinction-prone than many other terrestrial mammals (Caro and Durant 1995; Woodroffe and Ginsberg 2005).

Among the 31 extant large terrestrial carnivores, 23 are undergoing population declines, and 19 are listed as “Threatened” by the International Union for the Conservation of Nature (IUCN) and are at risk of local or complete extinction (Ripple et al. 2014). Among those, large canids and felids experienced some of the most pronounced range and population contractions (Karanth and Chellam 2009; Ripple et al. 2014). These declines have been associated with human-mediated activities such as habitat alteration and fragmentation (Crooks et al. 2011), persecution and direct killing as a result of conflict (Bruskotter et al. 2017; Dickman and Hazzah 2016; Dickman et al. 2014), prey depletion resulting from bushmeat poaching and livestock encroachment of wilderness

(Ripple et al. 2016a; Ripple et al. 2015; Wolf and Ripple 2016), and exploitation for body parts and medicine (Ripple et al. 2014). A brief overview on the conservation status and population declines of lions and leopards, the main large carnivores studied in this research, is provided in the next sections.

1.2.1. Conservation status of large African carnivores with a focus on lions and leopards

1.2.1.1. Lions

Lions have disappeared from 92% of their historical range over the past few centuries (Bauer et al. 2016), and have suffered a reduction in population size of at least 42% between 1993 to 2014 (Bauer et al. 2016). Lions were totally extirpated from North Africa before the 1950s (Nowell and Jackson 1996a), and only relict and scattered populations remain in West and Central Africa (Frank et al. 2006; Henschel et al. 2010). In East Africa, lions are found distributed within a metapopulation context, in which core lion populations are fragmented amidst a matrix of human dominated landscape that is suggested to limit their connectivity and compromise lions' long-term conservation (Dolrenry et al. 2014). Riggio et al. (2012) recently estimated significant and sizeable lion populations limited to only 10 remaining population 'strongholds' (protected areas or hunting zones sustaining continuous populations with more than 500 individuals) distributed across 25% of the remaining African savannah. Of these, four strongholds are located in Eastern Africa, with the remaining in Southern Africa (Riggio et al. 2012). Despite controversies on the current number of lions in Africa, studies concur on the declining trend in the overall lion population (Bauer et al. 2016; Riggio et al. 2012). Lions are considered Vulnerable to extinction (Bauer et al. 2016), and according to Riggio et al. (2012), viable populations are mainly found in Kenya, Botswana, Zimbabwe, Mozambique, South Africa, Namibia, Zambia and Tanzania, the last representing the main stronghold for around 9,900 out of 24,000 lions estimated to remain in the wild (Dickman et al., in prep.).

The most pressing threats to lions are, as for other large carnivores, habitat destruction and fragmentation, prey depletion, illegal or unsustainable hunting, and persecutory killing resulting from conflict with humans (Bauer et al. 2015; Bauer et al. 2016; Brink et al. 2016; Riggio et al. 2012). Lions figure as one of the main large carnivores associated with creating conflict with people within their African range either due to predation on humans or livestock (de Boer et al. 2010; Frank et al. 2006; Hazzah et al. 2009; Packer et al. 2005b; Packer et al. 2013; Woodroffe et al. 2007). The reliance of many lions on non-protected areas (Oriol-Cotterill et al. 2015a; Schuette et al. 2013a; Tuqa et al. 2014), means that close interactions with humans and consequent human-induced mortality pose a major challenge for their conservation (Bauer et al. 2016; Packer et al. 2013).

1.2.1.2. Leopards

The leopard is currently listed as Vulnerable by the IUCN (Stein et al. 2016). The species have lost 63-75% of their original range (Jacobson et al. 2016), especially in North and West Africa, South Africa and the Horn of Africa (Hunter et al. 2013; Jacobson et al. 2016; Nowell and Jackson 1996a). As for lions, range contraction and population decline has been associated with human encroachment, habitat destruction, retaliatory killing, overexploitation for pelt and body parts trade, prey base depletion and unsustainable trophy hunting (Jacobson et al. 2016; Stein et al. 2016). Even though the species is still widely distributed across the sub-Saharan Africa, occurring from mountainous areas such as Mount Kenya to rainforests and deserts (Hunter et al. 2013), remaining populations are scattered in patches that are often located outside protected areas (Jacobson et al. 2016). The leopard's ecological plasticity to adjust to various habitat types and levels of anthropogenic pressure (Jacobson et al. 2016) means that leopards will often inhabit human-dominated landscapes (Athreya et al. 2016; Athreya et al. 2013). In such landscapes, leopards are more likely to create conflict through human and livestock depredation, and of being killed in retaliation (Ghosal et al. 2013; Stein et al. 2016). The species is, as for lions, one of the main reported culprits of livestock depredation across its range in Africa (Dickman et al. 2014; Henschel et al. 2008; Ogada et al. 2003; Swanepoel et al. 2015; Swanepoel et al. 2014). Currently, there is no reliable estimation of the number of leopards living in the wild (Hunter et al. 2013). Previous attempts estimated a sub-Saharan population of 740,000 individuals (Martin and De Meulenaer 1988), which was later considered an unrealistic and flawed over-estimate (Henschel et al. 2008).

1.3. Human-carnivore conflict and implications for large carnivore conservation

The accelerated rate of human encroachment into wild areas, with a noticeable growth rate around protected areas in sub-Saharan African (Wittemyer et al. 2008), has led to the replacement of natural systems with largely human-dominated landscapes. Consequently, people and carnivores increasingly impinge upon each other (Chapron and Lopez-Bao 2016; Lindell et al. 2005; López-Bao et al. 2017), provoking widespread and often intense human-carnivore conflict (Bruskotter et al. 2017; Chapron and Lopez-Bao 2016). One of the key drivers of this conflict is depredation of livestock by large predators such as lions and leopards (Dickman et al. 2014; Hemson et al. 2009; Jacobson et al. 2016; Kuiper et al. 2015; Loveridge et al. 2010b). Such depredation can impose debilitating economic costs to livestock owners, and compromise the livelihood of entire communities (Dickman et al. 2011). For example, lion depredation of livestock across 199 households was estimated to cost over US $380,000, and US $1,952 per household during a 18-month study in the surroundings of Amboseli National Park, Kenya (Muriuki et al. 2017), whereas Holmern et al. (2007) estimated an economic loss of approximately US $12,846 (19.2% of the overall local annual income) across 481 households due to livestock depredation by large carnivores in the borders of Serengeti National Park, Tanzania. Taking the example of Tanzania, where 13% of the income of rural households depend on livestock (Covarrubias et al. 2012), such depredation events can be financially devastating, generate extreme hardship to entire households, contributing to long-term poverty and creating poverty traps (Dickman et al. 2011).

Besides the economic costs, conflict exacerbates intolerance towards carnivore presence and contributes to pre-emptive or retaliatory carnivore killing (Bauer et al. 2017; Carter et al. 2017; Dickman et al. 2014; Hazzah et al. 2017). In some areas, retaliatory killing can be the most important source of direct carnivore mortality, significantly contributing to their local extirpation (Butler et al. 2004; Kissui and Packer 2004). For example, intense human-lion conflict around Kenya's Amboseli National Park, driven by livestock depredation and animosity towards the government, led villagers to exterminate all the lions within the park between 1991 and 1994 (Hazzah et al. 2009; Maclennan et al. 2009). Although lions later recolonised the area from adjacent communal lands, the population again declined due to retaliatory killing (Frank et al. 2006b). Similarly, the lion population of Maasai Mara National Reserve, Kenya, decreased to 12% of its original size due to lethal control to prevent livestock predation (Frank et al. 2006a; Ogutu et al. 2005). In Tanzania, 71 hyaenas were poisoned in only three villages during a 19-month study (Kissui 2008), while, in seven months of research, at least nine hyaenas were killed in Laikipia, Kenya, where Frank (2011) already suggested a steep decline in the local hyaena population.

The expected dramatic population growth in human communities in Africa (e.g., a predicted population doubling by 2050, reaching 2.5 billion people - (PRB 2016)) and their estimated encroachment around protected areas - with an associated 70% conversion of sub-Saharan habitats into agro-pastoral land (Prestele et al. 2016)-, will likely increase the area of overlap between humans and carnivores. This could increase competition over finite resources and space, with an expected increase in conflict and detrimental effects on carnivore survival. In this likely scenario, understanding how, which and to what extent environmental and anthropogenic variables contribute to carnivore occurrence and persistence within human-dominated landscapes becomes a pressing issue in carnivore conservation. This information could help guide the development of strategies for minimising conflict, carnivore mortality and ultimately promote coexistence between carnivores and humans (Carter and Linnell 2016; Chapron and Lopez-Bao 2016).

1.4. The importance of human-dominated landscapes for carnivore conservation

Protected areas, such as national parks, act as vital refugia for wildlife and plant biodiversity, safeguarding large-scale ecological processes and ecosystem functions (Di Minin et al. 2016b; Le Saout et al. 2013; Treves 2008; Woodroffe and Ginsberg 1998). However, increased human encroachment adjacent to protected areas contributes to their fragmentation and isolation (Wittemyer et al. 2008). In this way, protected areas are increasingly becoming isolated within a sea of human-dominated landscapes (Athreya et al. 2013; Montgomery et al. 2014). These protected areas are often too small, isolated, and ineffectual to conserve large wide-ranging mammal species such as large carnivores (Crooks et al. 2011; Ginsberg 2017; Lindsey et al. 2017a). For example, land use changes around protected areas have been found to limit lion movement patterns, and to compromise their immigration and emigration (Cushman et al. 2015; Cushman et al. 2006), negatively affecting the functional connectivity and gene flow between populations (Cushman et al. 2015; Morandin et al. 2014). Furthermore, and as shown above (Section 1.3), humans will often persecute and kill carnivores over concerns relating to real or perceived attacks upon livestock and people in these areas, which is a major driver of their population declines through their range (Bruskotter et al. 2017; Dolrenry et al. 2016; Hazzah et al. 2017; López-Bao et al. 2017). Besides conflict, carnivore survival in human-dominated areas is further threatened by bushmeat poaching and prey depletion, which is a common threat around protected areas (Loveridge et al. 2016b; Ripple et al. 2016a; Ripple et al. 2015).

These additive human-mediated threats can result in high levels of carnivore mortality and create a source-sink dynamic (Furrer and Pasinelli 2016), with sink effects that can extend from the human-dominated land into source protected areas (Woodroffe and Frank 2005), potentially leading to the extirpation of carnivore populations (Barthold et al. 2016; Loveridge et al. 2016b). For example, high rates of human-induced mortality around Hwange National Park led to the extinction of 10 out of 22 lion prides inhabiting areas near the park boundary between 1997 and 2007, while, during the same period, only one pride out of the 15 inhabiting the core areas of the reserve died out (Loveridge et al. 2010a). Similarly, Rosenblatt et al. (2016) reported 67% higher density of leopards inside Zambia's South Luangwa National Park in relation to the peripheral areas of the park, where leopards were exposed to higher mortality due to illegal hunting, exploitative competition over prey with poachers and intraguild competition.

1.4.1. A brief overview of carnivore occurrence in human-dominated habitats

Paradoxically, given their relatively large home range requirements and wide ranging tendencies, much of the habitat necessary to sustain robust large carnivores populations occurs outside of protected areas (Nowell and Jackson 1996b). For example, approximately 44% of African lion range is found outside formally protected areas (Lindsey et al. 2017a), whereas less than 20% of the overall leopard range falls inside protected areas (Jacobson et al. 2016); in South Africa, 68% of the leopard range is estimated to fall outside legally protected areas (Swanepoel et al. 2013). Similarly, 77% of the current cheetah (*Acinonyx jubatus*) distribution range is located outside protected areas (Durant et al. 2017). Thus, the fate of large carnivore populations may lie in the often unprotected and largely human-dominated habitat surrounding protected areas, exactly where they are more vulnerable to extinction (Carter and Linnell 2016; Crooks et al. 2011; López-Bao et al. 2017; Woodroffe 2000; Woodroffe and Ginsberg 1998).

The occurrence of carnivores in human-dominated landscapes is a result of complex interactions involving landscape characteristics (Llaneza et al. 2012; Swanepoel et al. 2013), prey availability (Alexander et al. 2016a; Henschel et al. 2011; Loveridge et al. 2009; Valeix et al. 2012), interspecific interactions

(Dorresteijn et al. 2015; Rota et al. 2016a), and behavioral adaptations to cope with anthropogenic pressure (Boydston et al. 2003; Oriol-Cotterill et al. 2015a; Oriol-Cotterill et al. 2015b; Valeix et al. 2012). For example, leopards have been found to survive by feeding on domestic dogs and livestock in human-dominated areas in India, and to rely on field crops as refuge (Athreya et al. 2016; Athreya et al. 2013). Lions have been found to change their activity patterns to avoid temporal overlap with periods of intense human activity, and to move straighter and faster whilst moving across human-dominated habitats to reduce exposure to pastoralists and risk of anthropogenic mortality (Oriol-Cotterill et al. 2015a; Oriol-Cotterill et al. 2015b; Valeix et al. 2012). Similarly, hyaenas changed their use of time and space to minimise exposure to intense pastoralism, and traded-off using areas of higher prey availability for those of lower prey density and human disturbance in the Maasai Mara National Reserve, Kenya (Boydston et al. 2003). These behavioral and spatial adjustments to avoid exposure to humans can compromise interactions among carnivores, and result in increased opportunities for intraguild aggression and predation, with potential suppression of a subordinate predator (Crooks et al. 2010; Lewis et al. 2015; Lewis et al. 2017; May et al. 2008). For example, Lewis et al. (2015) suggested that the spatiotemporal adjustments of carnivores to avoid humans could increase the rates of aggressive interactions and mortality from interspecific competition between pumas (*Puma concolor*) and bobcats (*Lynx rufus*) across urbanized areas of Colorado, USA. Furthermore, carnivores have been shown to increase predation on prey to compensate for decline in feeding time as a response to fear of humans, which could result in human-mediated trophic cascades. For instance, Smith et al. (2017) have found pumas *Puma concolor* to flee more frequently from kill sites, and reduce overall feeding time by over 50% in response to hearing the sound of humans. Due to reduction in feeding time, pumas increased predation rates on deer to compensate for low food intake, which could result in suppression, and even extinction of prey population (Ryall and Fahrig 2006).

The influence of human disturbance on carnivore occurrence patterns and interspecific interactions is, however, species-specific and context dependent (Haswell et al. 2016). Whilst some large carnivore species which are less tolerant of anthropogenic impacts might be negatively influenced by human pressure (Woodroffe 2000), subordinate predators such as the cheetah, or more generalist, ecologically flexible mesocarnivores (Roemer et al. 2009), may fare better in human-dominated areas (Durant et al. 2017; Ginsberg 2017; Haswell et al. 2016). Lions, for instance, have been suggested to disappear from human-dominated landscapes with a minimum of 25 people/km^2, a threshold that could relate to those areas undergone intense land-use conversion and habitat degradation (Riggio et al. 2012; Woodroffe 2000). However, generalist carnivores such as the African civets (*Civettictis civetta*) and black-backed jackals have been found to have higher probability of occupancy in human-dominated habitats than within Moremi Gamer Reserve, Botswana (Rich et al. 2016).

As shown above, humans can have a substantial influence on carnivore behaviour, trophic interactions, occurrence patterns, and can ultimately determine their survival. In an ever-increasing scenario of human encroachment into wilderness, determining the extent to which carnivore species can occupy areas of increasing human pressure is of major importance for their conservation. This information is much needed to support the development of targeted and species-specific strategies aiming at reducing the immediate and long-term anthropogenic threats to carnivore conservation in an increasingly human-dominated landscape.

1.5. An overview of the spatial ecology of carnivores in Tanzania's Ruaha landscape

Tanzania's Ruaha landscape harbours an intact guild of carnivores, and is estimated to support some of largest populations of lions (Riggio et al. 2012), cheetahs and African wild dogs (*Lycaon pictus*) left in Africa, as well as significant populations of leopards, spotted hyaenas and mesocarnivores (Mills et al. 2001; TAWIRI 2007, 2009a, b, 2012).

Previous studies conducted in this area attempted to determine the contributory role of bioclimatic and landscape variables on defining habitat suitability for lions, leopards and spotted hyaenas across the Ruaha National Park, Wildlife Management Area and village lands, and to map important areas for large carnivore conservation based on the outputs of species distribution modelling algorithms (Abade et al. 2014b). In this study, habitat suitability was calculated based on environmental features extracted from georeferenced presence-only carnivore location data, which was primarily collected within Ruaha National

Park during 2011 to 2013. This study found that habitats with increased suitability for large carnivore were those closer to rivers, and that experienced above average annual precipitation. Furthermore, the predictive models suggested that 95% of the highly suitable habitats for large carnivores were located within 30 km of the Park-village borders, raising concerns about human-carnivore conflict. This was of particular concern for spotted hyaenas, as they were located significantly closer to the Park boundary than lions and leopards. Another studies investigated community richness, composition and structure, and the potential determinants of kleptoparasitic and predatory tendencies of large carnivores in the Ruaha National Park (Cusack et al. 2016; Cusack et al. 2015). These studies provided important insights on carnivore ecology in this area; however, their limited focus and reliance on data primarily collected within Ruaha National Park has prevented better understanding of carnivore occurrence patterns of the human-dominated landscape where they create intense conflict with people and are killed in retaliation (Abade et al. 2014a; Abade et al. 2014b; Dickman et al. 2014). For example, over 37 lions and other carnivores were killed due to conflict with pastoralists in less than 500 km^2 in a single year, which represents the highest known rate of human-induced carnivore mortality in East Africa (Dickman; in prep.). However, and despite the importance of the surrounding village lands for carnivore conservation, limited data has been collected on any aspects of carnivore spatial ecology in the non-protected areas surrounding Ruaha National Park. In fact, very little data exists on the potential influence of human activities and landscape structure (e.g. land-use classes, human and livestock density) on carnivore occurrence patterns across the gradient of anthropogenic pressure in Ruaha, with information about carnivores largely limited to the core areas of Ruaha National Park. This paucity of data limits in-depth understanding of carnivore occurrence patterns, and hinders the development of contextualised species-specific, and effective strategies for mitigating anthropogenic threats to carnivores in these human-dominated landscapes. Given this lack of data, the Greater Ruaha landscape has been listed as a top-priority area for research by the Tanzanian Wildlife Research Institute (TAWIRI 2009a, 2012).

This study aims to generate much-needed data on the occurrence patterns of carnivores across the gradient of anthropogenic pressure extending from Ruaha National Park into surrounding village lands. Carnivore occurrence patterns will be investigated using a combination of presence-absence and presence-only analytical methods (further explanation in the next sections), and as a function of land use, human and livestock densities, prey availability, and environmental variables, in order to try to identify key determinants for their spatial distribution across the study area. A brief description of the modelling methods used through the thesis is provided in the next sections. Further details on the specific methods used for data collection and processing, environmental variable development, and model implementation are further provided in each data chapter.

1.6. Occupancy modelling techniques in the study of carnivore occurrence patterns

The elusive nature of most large carnivores, combined with their rarity, low densities and large home ranges, make them particularly challenging to detect in ecological surveys (Long et al. 2011). Researchers often lack the resources to use intensive sampling methods and to survey vast landscapes due to logistical constraints (Karanth et al. 2011). Such surveys are particularly subject to detection errors – these errors occur when a particular species may not be detected even when it was present, resulting in a false negative (detection) error (type II error) – that may lead to severe underestimates of the spatial distribution and demographics of the species (Clement 2016; Gu and Swihart 2004; MacKenzie et al. 2002). This imperfect detection undermines efforts of investigations of species occurrence (MacKenzie et al. 2002), as they result in inaccurate estimates of true habitat occupancy and species distribution (Karanth et al. 2011).

Recently, new analytical methods have been developed to enable the unbiased estimation of species site occupancy and occurrence patterns, by explicitly accounting for imperfect detections (Karanth et al. 2011; MacKenzie et al. 2003; MacKenzie et al. 2002; Royle and Dorazio 2008; Royle et al. 2007; Tyre et al. 2003). These models attempt to disentangle false absences (i.e. where the survey failed to register the species) from true absences, by using information from species detectability gathered from areas where the species was identified at least once, to estimate the probability of patch occupancy for those sites where the species was never observed (MacKenzie et al. 2003). These 'hierarchical' models recognise species observations as the combined result of a particular state process (i.e. abundance; occupancy; species richness) that determines species occurrence at each surveyed site, and the detection process that yields observing the species conditionally to the state process. The final model for the state process will convey information on the species occurrence at each surveyed site taking into account the imperfect detection (Fiske and Chandler 2011).

The occupancy analyses are performed based on values of encounter histories, which summarise the number of surveys performed in a particular site and the observations for the species studied at each sampling occasion, and on the frequencies of encounter histories (Donovan and Hines 2007). Assuming that the state variable site occupancy for a particular species is binary where Zi=0 when site *i* is not occupied and Zi=1 when occupied; *p* is the probability of detecting the species in each survey *j*, and that the occupancy remains constant within the surveying period, the joint distribution of the observations conditional on the latent occupancy state is given by:

Z_i~Bernoulli (ψ) ; describes the state variable

$y_{i,j}|Z_i$ ~Bernoulli ($Z_i p$) ; describes the observation process (i.e. detection)

in which occupancy (Z_i) is modelled as a Bernoulli random variable probability dependent on parameter (ψ; occupancy probability).

These models also enable assessing the influence of environmental variables on both occupancy and detection estimates, which is given by the following equations:

$\text{logit}(\psi_i) = x_i\beta$,

where x_i represents the site-level covariates at each sampling unit *i*, and β the corresponding effect parameters, and:

$\text{logit}(p_{ij}) = v_{ij}\alpha$,

where where v_{ij} represents the observation covariates at each sampling unit *i* and during each survey replicate *j*, and α the corresponding effect parameters.

This class of model is particularly useful to assess, predict and determine species occurrence patterns based on noninvasive presence-absence survey data such as those collected in camera-trapping studies (Long et al. 2011). Given their statistical flexibility and robustness in dealing well with limited sample, complex interactions among variables, and good predictive power (MacKenzie et al. 2002; Vaughn 2008), they have become a useful methodology for the study of carnivore spatial distribution, species interactions, and population demography (Burton et al. 2012; Elliot and Gopalaswamy 2017; Rich et al. 2016; Rota et al. 2016a; Rota et al. 2016b).

1.7. Species distribution models in the study of carnivore occurrence patterns

Environmental variables such as prey availability, vegetation cover, and human density affect habitat quality and suitability, influencing carnivore behaviour, distribution and habitat use (Kolowski and Holekamp 2009; Oriol-Cotterill et al. 2015a; Rota et al. 2016a; Valeix et al. 2010). For example, increased habitat suitability for lions has been linked to proximity to water sources (Abade et al. 2014b), as these habitats have been found to contribute to better hunting and reproductive success (Mosser et al. 2009).

Recently, environmental variables have been incorporated into species distribution models (SDMs) aiming to predict carnivore distribution across a landscape (Abade et al. 2014b; Rodríguez-Soto et al. 2011). These models compare environmental covariates from a species presence point with those found across the landscape, and use algorithms to predict areas with increased likelihood of species presence based on estimated habitat suitability (Elith et al. 2006; Guisan et al. 2006; Guisan et al. 2013; Guisan and Zimmermann 2000). These model outputs have implication for carnivore conservation as they depict potential hotspots of carnivore occurrence, and enable the predictions of areas where conservation efforts should be prioritised (Rodríguez-Soto et al. 2011). For example, SDMs were used to predict the distribution of jaguars (*Panthera onca*) in Mexico, relating the presence of the species to lowland rainforest areas with flooded vegetation and increased prey abundance, thereby identifying previously-unknown areas of potential importance for the species' conservation

(Rodríguez-Soto et al., 2011). Additionally, these predictive models revealed that landscape-level variables such as vegetation cover classes and altitude were associated with increased risk of livestock depredation by jaguar and puma (*Puma concolor*) in Mexico, enabling the prediction of high-risk areas for conflict, where mitigation strategies aiming conflict reduction should be prioritised (Zarco-González et al., 2013). Such detailed ground-level information provides valuable support to the development of contextualized, and applied conservation planning strategies (Elith et al. 2006; Guillera-Arroita et al. 2015; Guisan et al. 2013; Miller 2015).

Predictive modelling algorithms such as boosted regression trees (Elith et al. 2008) represents one of the specific SDMs that can be used to study the spatial ecology and distribution of species (Elith et al. 2008), with applications for research on carnivore spatial ecology (McCue et al. 2014). This algorithm has the capability to generate valid outputs while dealing with recurrent problems in large carnivore research such as small sample size, presence-only data and biased sampling due to survey gaps in inaccessible or remote areas (Elith et al. 2008; Papes and Gaubert 2007) - further information on the specific statistical details of boosted regression trees is provided in Chapter 5. The ability of this algorithm to perform well using presence-only data provides an alternative to the well-established and data-intensive presence-absence models, as often, species surveys, especially for large carnivores, cannot reliably identify areas of total absence of occurrence for a particular species within its distribution range, and have low sample sizes (Gu & Swihart, 2004). This is important as the use of unreliable absence records in predictive modelling leads to unrealistic and misleading scenarios of potential species distribution (Gu & Swihart, 2004; Jiménez-Valverde et al., 2008). The use of these predictive modelling algorithms are of particular relevance for conservation planning, as a lack of financial resources usually prevents the extensive surveys that would be required to accurately determine presence-absence of species across vast landscapes.

1.8. Thesis overview

Chapter 1. General Introduction

The first chapter of the thesis provides a brief overview of the value of carnivore species for human societies and the regulation of ecosystem services, and the importance of anthropogenic landscapes for carnivore conservation. It also provides an overview of the current status of knowledge for carnivore spatial distribution in Tanzania's Ruaha landscape, the aim of the present study, and briefly describes the methods that will be used to further investigate carnivore spatial distribution across gradients of anthropogenic pressure in the study area.

Chapter 2: Examining patterns of lion (*Panthera leo*) occurrence across a gradient of anthropogenic pressure in southern Tanzania

The study is the first to assess and quantify the influence of landscape and anthropogenic variables on lion occurrence patterns in a multiple land-use area including Ruaha National Park and surrounding village land. We use camera-trapping data and Bayesian hierarchical occupancy modelling to provide the first assessment of the potential role of habitats bordering protected areas for lion distribution and conservation in this landscape. We show that high rates of anthropogenic disturbance and mortalities create a "hard edge" for lions, compromising lion persistence outside the National Park. We demonstrate that even in systems with robust lion populations, anthropogenic pressure can significantly limit lion occurrence patterns.

Chapter 3: The importance of the wildland-human interface for carnivore ecology: a case study of leopard (*Panthera pardus*) site use in Tanzania

In this study, we investigated the factors affecting the probability of leopard site use at the interface of protected and unprotected habitat in the Ruaha landscape, in an area encompassing the eastern portions of Ruaha National Park, the adjacent semi-protected Pawaga-Idodi Wildlife Management Area (WMA), and unprotected village lands. Specifically, we assessed spatial variation in leopard site use in response to (*i*) anthropogenic disturbance, as indicated by distance to households and livestock presence, (*ii*) the availability of primary prey species, and (*iii*) proximity to water sources. We show that high rates of anthropogenic disturbance, represented by proximity to human households and livestock presence, coupled with the intense underlying carnivore persecution and killing, are the main limiting factors of leopard distribution outside Ruaha National Park, rather than being influenced by primary prey availability.

Chapter 4: **Evaluating the spatial ecology of a carnivore guild across a gradient of anthropogenic pressure using camera-trapping and multispecies occupancy models**

We evaluate the influence of environmental variables on the occurrence patterns of a carnivore guild composed of aardwolf (*Proteles cristata*), bat-eared fox (*Otocyon megalotis*), black-backed jackal, civet and leopard, across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape, while accounting for the potential for interspecific interactions (i.e. described as the degree of dependence in occurrence probability between two species, as explained in Mackenzie et al. 2004). We examine the conditional detection probability of subordinate carnivore species at each camera-trap station as a function of detecting leopards - a dominant carnivore species; estimate the independent site occupancy for each species solely as a function of the environmental variables; and investigate site co-occurrence as a response to both changes in environmental variables and presence or absence of any other carnivore species. We provide the first in-depth analyses of the occurrence patterns of a carnivore guild across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape.

Chapter 5: Mapping the suitability of habitat for lions (*Panthera leo*) across two stronghold populations in southern Tanzania

We investigate the spatial distribution of highly suitable lion habitats across the gradient of human occupation between Ruaha National Park and Selous Game Reserve. We quantify the variables determining lion habitat suitability and map prime habitats for lion conservation. We show that low human population density and moderate rainfall are the key predictors of habitat suitability for lions. We show that most (60.2%) of all highly suitable habitats are in game reserves where lions are often hunted as trophies. In village lands, highly suitable lion habitats are fragmented and usually within 10 km of protected area borders. If these areas become converted to other land-use types, lions might lose substantial portions of their habitats in southern Tanzania. We highlight that the maintenance of these key protected areas under a wildlife-based land-use play a central role in lion conservation in East Africa.

Chapter 6: General Discussion

This chapter consists of the general synthesis of the findings of study. It contextualises the findings of each chapter and discusses how this knowledge advances our understanding of carnivore spatial ecology in human-dominated landscapes, and its implications for helping to formulate effective strategies for carnivore conservation outside protected areas.

Annexes: R Scripts used in this study

Annex 1. Annotated JAGS model used in Chapter 2: "Examining patterns of lion (*Panthera leo*) occurrence across a gradient of anthropogenic pressure in southern Tanzania"

Annex 2. Annotated JAGS model used in Chapter 3: "The importance of the wildland-human interface for carnivore ecology: a case study of leopard (*Panthera pardus*) site use in Tanzania"

Annex 3. Annotated STAN model used in Chapter 4: "Evaluating the influence of environmental variables and interspecific interactions on multicarnivore occurrence across a gradient of anthropogenic pressure in southern Tanzania"

Annex 4. Annotated R script used in Chapter 5: "Mapping the suitability of habitat for lions (*Panthera leo*) across two stronghold populations in southern Tanzania"

Annex 5. List of contributed papers published during the study period

Chapter 2: Examining patterns of lion (*Panthera leo*) occurrence across a gradient of anthropogenic pressure in southern Tanzania

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*An adapted version of this chapter is currently in preparation for re-submission to Ecology and Evolution

Abstract

Lion (*Panthera leo*) populations in Africa have been reduced by almost half in the past two decades, with stronghold populations centered in national parks and game reserves, particularly in East Africa. Much of the habitat necessary to support lion populations occurs in the borderlands around these national park and game reserves, and typically has no protected status. This study, conducted on one of these last remaining stronghold lion populations, the Ruaha landscape, evaluated the spatial variation in lion occurrence patterns along a gradient of anthropogenic pressure extending from inside of Ruaha National Park (RNP) into a multi-use landscape encompassing a wildlife management area (WMA) and surrounding unprotected village lands. We collected lion occurrence data via extensive camera-trapping across multiple sampling areas. We calculated lion occupancy and detection probability using a Bayesian framework, which enabled identifying the key covariates associated with patterns of lion occurrence. We recorded 157 lion detections across 127 camera-trap stations. From this total, 143 lion detections were within the national park, 14 in the WMA, and none in the village lands. This suggests that lions do not regularly occupy the gradient of anthropogenic pressure surrounding Ruaha National Park during the dry season (May – December). Within the national park, lion occupancy was principally associated with the availability of primary prey. Our results suggest that high rates of anthropogenic disturbance and mortalities could be creating a "hard edge" for lions, compromising lion occurrence outside of the national park. This demonstrates that even in systems

with robust lion populations, anthropogenic pressure can significantly limit lion occurrence patterns. Our results highlight the need for local, regional, national and international stakeholders to address anthropogenic threats in reserve-adjacent areas, in order to improve the chances of landscape-level lion persistence and conservation.

Keywords: Bayesian, conservation, hierarchical occupancy modelling, human-carnivore conflict, *Panthera leo*, Ruaha

Author contributions to the manuscript:

Experimental design: LA, RM; Data collection: LA, JC; Data analysis: LA, RJM (guidance on model implementation); Writing of 1st draft of manuscript: LA; Improvements to manuscript: PS, DM, AD & RM

2.1. Introduction

Protected areas, such as national parks, act as vital refugia for both wildlife and plant biodiversity, serving as protection for large-scale ecological processes and ecosystem functions (Di Minin et al. 2016b; Le Saout et al. 2013; Treves 2008; Woodroffe and Ginsberg 1998). However, sustained human-related activities adjacent to the borders of protected areas contribute to their fragmentation and isolation (Wittemyer et al. 2008). In this way, protected areas are increasingly becoming islands situated within a sea of human-dominated, multi-use landscapes (Athreya et al. 2013; Montgomery et al. 2014). These protected areas are often too small, isolated, and ineffectual to conserve large wide-ranging mammal species (Crooks et al. 2011; Ginsberg 2017; Lindsey et al. 2017a). For instance, land use change around protected areas can alter species immigration/emigration behaviour (Cushman et al. 2015; Cushman et al. 2006), limit the genetic diversity of wildlife populations (Frankham et al. 2014), and create source-sink dynamics (Furrer and Pasinelli 2016; Hansen 2011). These issues are particularly apparent in Africa, where dramatic human population growth has rapidly intensified conversion of wilderness and greatly fragmented protected areas (Wittemyer et al. 2008). Correspondingly, large mammal populations have declined by almost 60% in the past 40 years, apart from in intensively managed and often fenced ecosystems in southern Africa (Craigie et al. 2010). Consequently, human encroachment and habitat conversion around protected areas present some of the greatest conservation challenges in the 21st century (Lande 1998; Woodroffe and Ginsberg 1998).

Large carnivore persistence is particularly affected by human encroachment and habitat conversion around protected areas (Woodroffe 2000, 2001). Within the human-wildlife interface, large carnivores are exposed to, and imperiled by, various sources of anthropogenic mortality (Durant et al. 2017; Lindell et al. 2005; Woodroffe 2001; Woodroffe and Ginsberg 1998). These include conflict related killings (Dickman et al. 2014; Kissui 2008), illegal trophy-hunting (Balme et al. 2010), and poaching (Becker et al. 2013). These borderland habitats often act as population sinks, where carnivores experience perilously high mortality. For example, the high offtake observed in these areas affects the demographic structure of the carnivore populations bordering protected areas, and can drive entire populations to local extinction (Loveridge et al. 2010a; Pitman et al. 2015; van der Meer et al. 2014; Woodroffe and Ginsberg 1998). Paradoxically, given relatively large home range requirements and wide ranging tendencies, much of the habitat necessary to sustain robust large carnivores populations can occur outside of protected areas (Nowell and Jackson 1996b). Thus, the fate of large carnivore populations may lie in the often unprotected and largely human-dominated habitat surrounding protected areas (Carter and Linnell 2016; Crooks et al. 2011).

African lions (*Panthera leo*) present a particularly interesting case study for examination of this topic. Approximately 44% of African lion range currently has no official protected status (Lindsey et al. 2017a). African lion populations have reduced by almost half in the last 20 years because of habitat loss, prey depletion, unregulated trophy hunting, and conflict-related mortality (Bauer et al. 2015; Lindsey et al. 2017a). All these sources of mortality are more likely to occur in unprotected habitat where intense human activities interfere with lion movement patterns and dispersal ability, genetic diversity and fitness, reducing population recruitment and population viability (Cushman et al. 2015; Elliot et al. 2014; Loveridge et al. 2016b; Morandin et al. 2014). Given prevailing anthropogenic disturbance, these are the areas where lions are most vulnerable to mortality and extinction risk (Woodroffe 2000; Woodroffe and Ginsberg 1998). Dramatic population growth in the human communities in Africa (e.g., a predicted population doubling by 2050; (PRB 2016)), will likely increase human-lion interactions in the periphery of protected areas. This could increase competition over finite resources and space, with an expected increase in conflict and its ensuing detrimental effects on lion survival.

Hence, determining the extent to which lions can occupy areas of increasing human pressure, including pressures such as trophy hunting and agro-pastoralism, is of major importance for the conservation of this species. This information is vital to support conservation strategies aiming at reducing anthropogenic threats found in these landscapes. Here we investigated the environmental and anthropogenic factors associated with spatial variation in lion occupancy along a gradient of anthropogenic pressure, from within RNP to ~40 km into surrounding village lands in the Ruaha landscape of southern Tanzania. This system is one of the six largest strongholds for lion populations, as well as a region where lions experience some of the highest known rates of conflict-related mortality in East Africa (Dickman, in. prep.). Despite its significance for lion conservation globally (Riggio et al. 2012), the paucity of information about the spatial ecology and distribution of lions in this landscape has hindered conservation planning for the species, with the Tanzanian government listing this area as a national priority for lion research (TAWIRI 2007, 2009a). In this study, we provide the first assessment of the potential role of habitats bordering protected areas for lion distribution and conservation in the Ruaha landscape by using camera-trapping data and Bayesian hierarchical occupancy modelling. Assessments such as this provide valuable data to help quantify the relative importance of anthropogenic habitats for lions in southern Tanzania, and can be used to support management strategies aiming at promoting conservation of large carnivores in human-dominated landscapes, both locally and elsewhere where there is overlap between lions and people.

2.2. Methods

2.2.1. Study Area

The study area is a multi-use landscape located in southern Tanzania (Fig. 2.1). The greater Ruaha system, which encompasses the Ruaha National Park (RNP), adjacent game reserves, the Pawaga-Idodi Wildlife Management Area (WMA), and village lands, covers ~50,000 km^2. Ruaha National Park is one of the largest national parks in Africa, spanning over 20,226 km^2. Trophy hunting of wildlife, including lions, is permitted in limited sections of the WMA, but prohibited in RNP and village lands. In the village lands, large carnivores are often killed due to conflict, cultural hunting, and bushmeat snaring (Abade et al. 2014a; Dickman 2015; Knapp et al. 2017).

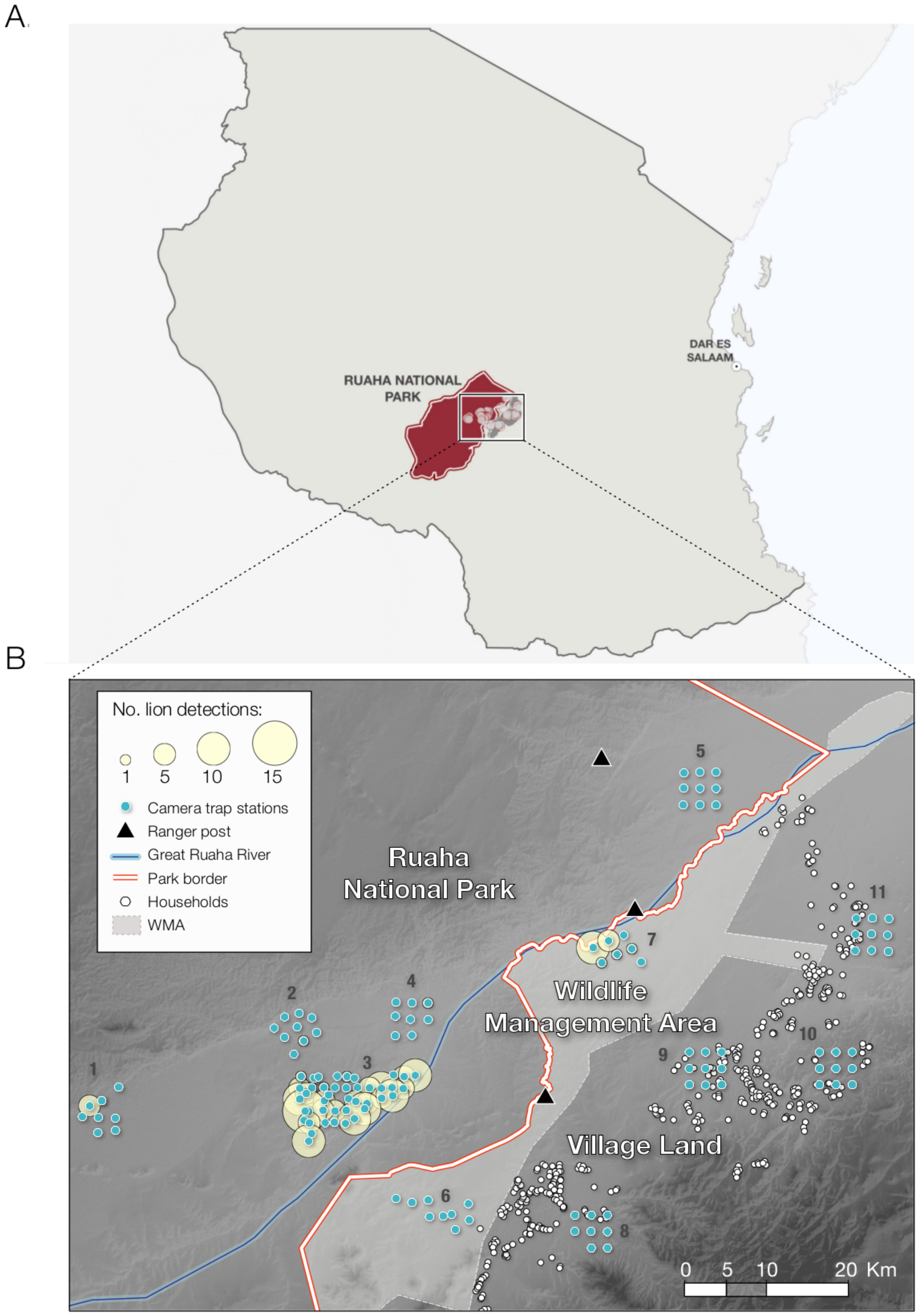

Figure 2.1. Location of the study site, and distribution of camera-trap stations (blue shaded circles) across the Ruaha landscape, southern Tanzania, during our surveys in the dry seasons of 2014-2015. 1-11 represents sampling areas: 1. Mdonya; 2. Kwihala; 3. Msembe; 4. Mwagusi; 5. Lunda-Ilolo; 6. Pawaga; 7. Lunda; 8. Idodi; 9. Malinzanga; 10. Nyamahana; 11. Magosi. The yellow shaded circles represent the number of independent detections of lions (*Panthera leo*) at each camera-trap station (> 5 min between detections).

This system features a varied large carnivore assemblage, including globally-important populations of lions, cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), leopards (*Panthera pardus*) and spotted hyaenas (*Crocuta crocuta*; (Abade et al. 2014b; Cusack et al. 2015)).

The climate of the region is semi-arid to arid, with an average rainfall of 500 mm/year, and a bimodal rainy season from December to January and March to April (Walsh 2000b). The temperature ranges from 15 to 35°C (Darch 1996), and the elevation from 696 to 2,171 m (ESA 2009). The vegetation is a mosaic of semi-arid savannahs, Zambesian *miombo* woodlands (Sosovele and Ngwale 2002), *Acacia* sp., *Combretum* sp. and *Commiphora* sp. Land cover varies substantially across the gradient of anthropogenic pressure from RNP into the village lands. Grasslands and woodlands are most common, although there are at least 17 different vegetation classes (ESA 2009) occurring in RNP and WMA. In contrast, the village lands are primarily agricultural fields and livestock grazing areas. The Great Ruaha River is the main water source for wildlife and livestock, especially during the dry season.

2.2.2. Village lands

The village lands around RNP and WMA (Fig. 2.1) are inhabited by over 60,000 people distributed across 22 villages (Green and Adams 2015). Human livelihood is primarily based on agriculture and rearing of domestic livestock such as donkeys, goats, sheep and cattle (NBS 2013). Although no official estimates of livestock abundance are available for this area, the overall Iringa region, within which Ruaha National Park sits, contains a fifth of Tanzania's total domestic animals, with > 620,000 livestock and > 1.5 million poultry (NBS 2013).

Local attitudes towards large carnivores among village members tend to be very negative, mainly due to the actual or perceived risk of depredation upon livestock (Dickman et al. 2014). Despite the fact that carnivore depredation accounts for comparatively little stock loss when compared to diseases (Dickman et al. 2014), carnivore attacks generate intense hostility and lead to high levels of retaliatory and preventative lion killings (Abade et al. 2014b; Dickman 2015; Dickman et al. 2014).

2.2.3. Lion occurrence data

We collected data on the occurrence of lions and their prey during the dry seasons (May-December) of 2014 and 2015, via 127 non-baited remotely triggered single camera-trap stations (CTs) installed in 11 sampling areas in the study area (Fig. 2.1). We initiated the survey in 2014 by placing 42 CTs inside RNP. These CTs were randomly placed along animal trails found in areas exposed to low anthropogenic pressure near the park headquarters (Cusack et al. 2015). In 2015 we added 34 CTs to the national park across four sampling areas, 16 in the WMA across two sampling areas, and 35 in the village lands across four sampling areas (Fig. 2.1). We distributed the CTs across a range of distances from the border of the national park (0-10 km; 10-20 km; >30 km) to facilitate an examination of evident spatial variation in lion occurrence (Fig. 2.1). We set the CTs facing animal trails when the pre-defined GPS coordinates were found within 5 meters from the nearest open path showing signs of animal use. We adopted this design so as to increase detection of more elusive species (Wearn et al. 2013). All the CTs were placed in trees or poles at a height of 0.3-0.5 meters off the ground. We visited the CTs every 30-50 days to retrieve data and service the traps.

We collapsed the temporal extent of the survey into seven-day interval bins, across our 32-week survey (~210 days), to minimize potential issues of non-population closure (Kendall and White 2009; MacKenzie et al. 2002). Given the wide-ranging patterns of lions (Cushman et al. 2015; Dolrenry et al. 2014), occupancy in our study represents the probability that a given site was used during the survey period, rather than the probability of continuous site occupation (MacKenzie et al. 2006). We thus modelled lion occupancy as the probability of site use during the study period at the CTs level, and hereafter, the term occupancy refers to site use. We identified the mammals recorded at each CTs to the species level based on published reference guides of African mammals (Kingdon 2013).

2.2.4. Covariates development

We developed a geographic information system to depict nine covariates (Table 2.1) hypothesised to influence lion detection and occupancy (Abade et al. 2014b; Cusack et al. 2016; Henschel et al. 2016; Midlane et al. 2014). We represented each covariate as a raster across our study area at a resolution of 500 x 500 meters, with exception for prey biomass and trail type (Fig. 2.2; more details below), which were calculated at the CTs level. We generated these rasters in QGIS 2.6.0 (QGIS) from freely available geoprocessed satellite imagery and data collected by University of Oxford's Wildlife Conservation Research Unit Ruaha Carnivore Project (RCP).

Table 2.1. Covariates predicted to influence lion occupancy* in the Ruaha landscape, southern Tanzania.

Covariates	**Model type**
Density of humans	Ψ
Density of livestock	Ψ
Distance to Greater Ruaha	Ψ
Distance to household	Ψ
Distance to ranger post	Ψ
Large prey (CPUE)	Ψ; P
Medium prey (CPUE)	Ψ
VCF(Townshend et al. 2011)	Ψ
Trail type	P

*Ψ. probability of occupancy; P. probability of detection. VCF: Vegetation Continuous Fields. CPUE: catch-per unit effort index of prey biomass

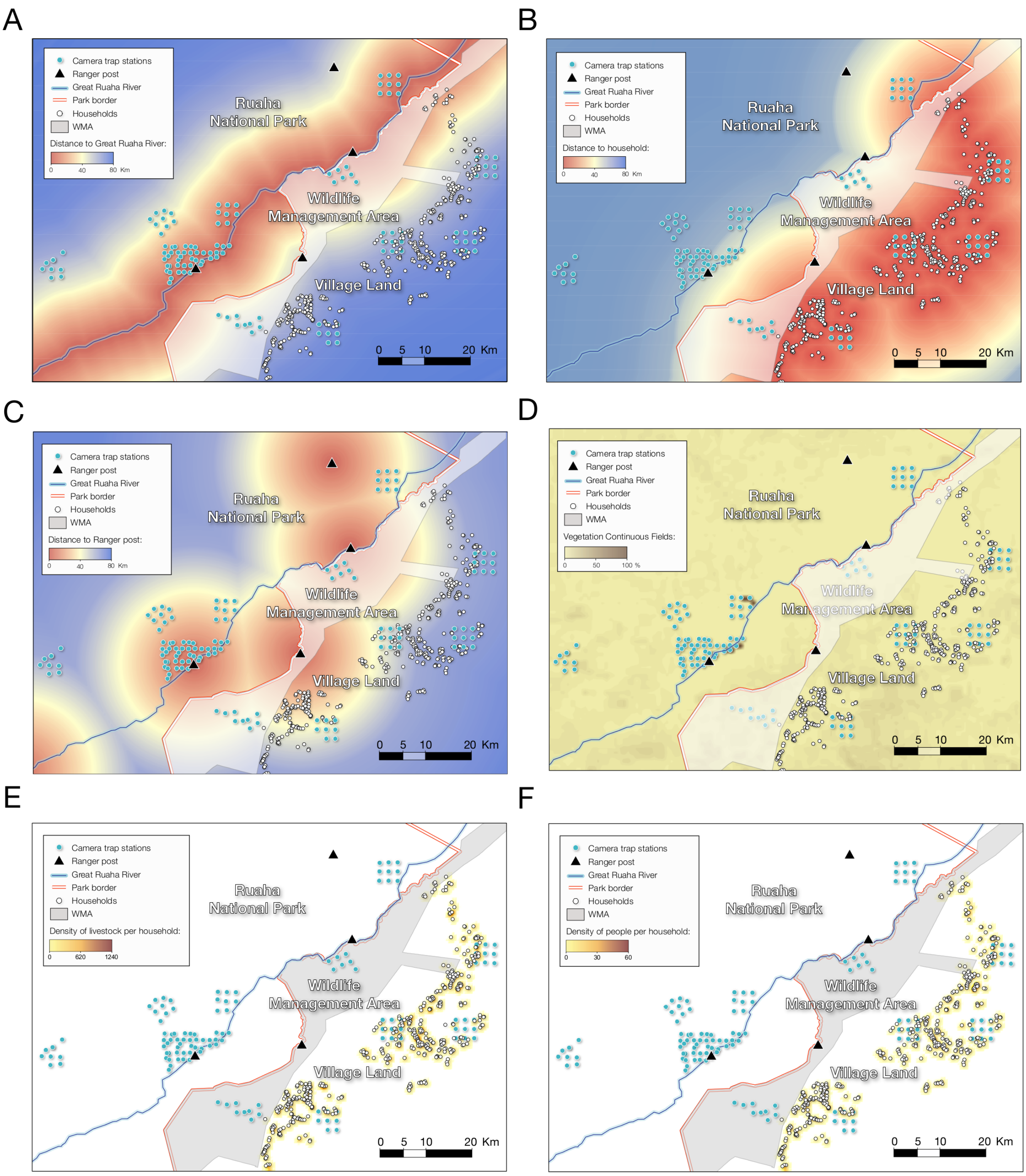

Figure 2.2. Set of covariates hypothesised to influence probability of occupancy by lions (*Panthera leo*) across the Ruaha landscape, southern Tanzania, during our surveys in the dry seasons of 2014-2015. **A.** Distance to the Great Ruaha River; **B.** Distance to households; **C.** Distance to ranger posts; **D.** Vegetation continuous fields (VCF); **E.** Density of livestock per household; **F.** Density of people per household. Biomass index of large and medium prey (CPUE), and trail type not represented here.

First, we considered trail type (animal trails, no-trails and man-made roads) as previous studies have found an influence of trail type on probability of carnivore detection in this study area (Cusack et al. 2015). We hypothesised that increased lion detection would be associated with higher large prey biomass given that prey abundance is a key covariate influencing lion distribution and habitat use within a home range (Everatt et al. 2015). We also hypothesised that lion occupancy was associated with proximity to the Great Ruaha River (Abade et al. 2014b; Cusack et al. 2016), farther from households and areas of higher human and livestock density (Everatt et al. 2014; Oriol-Cotterill et al. 2015a; Schuette et al. 2013a), and in areas of increased surveillance, where anti-poaching patrolling efforts could be more frequent, as recent studies have found a positive influence of patrol intensity on lion occupancy (Henschel et al. 2016). Thus, we calculated rasters representing distance to the Great Ruaha river, human households (mapped by RCP), and ranger posts (Tanzania National Parks; TANAPA), respectively, using the Euclidean Distance function in QGIS 2.6.0 (QGIS). We calculated the rasters of human and livestock density based on the number of people co-habiting each property mapped in the study site, and the total number of domestic stock (goats, donkey and cattle) owned per household through the kernel density estimator tool in QGIS 2.6.0 (QGIS). We hypothesised a positive association of lion occupancy and increased vegetation cover, as vegetation structure has been suggested to be an important component of lion-prey interaction by substantially influencing prey catchability (Hopcraft et al. 2005) and lion hunting success (Davies et al. 2016) in savannah ecosystems. We characterised percentage of vegetation cover using data on

Vegetation Continuous Fields (VCF) derived from the MOD44B product (Townshend et al. 2011) and depicted the mean VCF values over the past decade (2006-2015). VCF ranges from 0 to 100, and describes the percent of a pixel that is covered by tree cover layer, with higher values indicating forested areas with dense tree canopy cover (Townshend et al. 2011).

We calculated a temporal catch-per unit effort (CPUE) index of prey biomass for each CTs based on the number of independent records (> 5 min; Burton et al., 2012) for large and medium prey photographed during the survey, hypothesising lion occupancy to be positively associated with high values of large and medium prey biomass. We classified large prey as those herbivores with mean body weight > 100 kg (Ripple et al. 2015), and medium prey those weighing between 18 to 100 kg (Hayward and Kerley 2005; Owen-Smith and Mills 2008). Prey weight was based on reference guides (Tacutu et al. 2013). We calculated the CPUE by multiplying the number of independent events at each station by the species average weight, divided by the CTs sampling effort, and standardised per 100 camera trap days (Burton et al. 2012).

Prior to model fitting, we standardized (z-score) all the covariates (Long et al. 2011), and assessed for potential multi-collinearity and correlation based on the results of Pearson correlation and variance inflation factor tests. We only considered those minimally correlated covariates in the models (Pearson <0.7, VIF <3 (Zuur et al. 2010); see Table S2.1; S2.2 in Supporting Information). Thus, we removed distance to the Great Ruaha River and livestock density from the analyses due to high correlation with the other covariates.

2.2.5. Model analyses and averaging

We modelled lion occupancy in a hierarchical Bayesian framework. We used temporally replicated surveys (i.e. weeks) to estimate the latent, unobserved occupancy at each CTs Z_i, where Z_i = 1 if site i is occupied and 0 otherwise, and detection probability $p_{i,j}$, where $p_{i,j}$ is the probability that lions are detected at site i during replicate j, given the proportion of site occupancy (i.e., Z_i = 1) (MacKenzie et al. 2002; Tyre et al. 2003). We generated a global model for the whole study site (i.e. including data from the national park, WMA and village land), and two individual models for the Ruaha National Park (Ruaha model) and for the areas outside of the park (WMA and village land; WMA+VL model). This approach enabled us to investigate the relative influence of the national park and village lands on lion site occupancy independently. To minimise issues of potential spatial autocorrelation among model residuals, we included a random intercept indexed by sampling area (n = 11), where each area consists of a grid of CTs (Moll et al. 2016; Rhodes et al. 2009) (Fig. 2.1; see Fig. S2.1.1). Our final models to estimate occupancy were implemented as follows:

$$\text{logit}(\Psi_i) = \alpha_{area} + \alpha_1{*}\text{CPUE\_Medium\_Prey}_i + \alpha_2{*}\text{CPUE\_Large\_Prey}_i + \alpha_3{*}\text{Distance\_Household}_i + \alpha_4{*}\text{Distance\_Ranger\_Post}_i + \alpha_5{*}\text{VCF}_i \qquad \textit{(Eq. 2.1)}$$

where Ψ_i represents the probability of lion site occupancy at the i^{th} CT, α_{area} represents a random intercept indexed by area with estimated hyperparameters μ (mean) and τ^2 (variance), and $\alpha_{1,2,\ldots 5}$ represent the influence of associated covariates at the i^{th} CT (Table 2.1).

The final detection models were implemented as follows:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1\text{*CPUE\_Large\_Prey}_i + \beta_k\text{*Trail}_i \qquad \textit{(Eq. 2.2)}$$

where $p_{i,j}$ represents the probability of detection at the i^{th} CT during survey j given that a site is used (i.e., Z_i = 1), β_0 is the intercept, β_1 represents the influence of large prey biomass, and β_k represents the effect of the k^{th} trail type on lion detection at each CT (k = 3), with animal trail as the reference category.

For the Ruaha model, we reclassified the covariate trail type to binary because the CTs deployed in the park were either on or off animal trails, but never on man-made roads.

We analysed the models using a Bayesian framework and Markov chain Monte Carlo (MCMC) simulations in R v.2.13.0 (R Core Team 2012) and JAGS (Plummer 2003) through the package 'R2jags' (Su and Yajima 2012). We estimated the degree of support for the effect of each covariate on occupancy through the Bayesian inclusion parameter (w_c) (Kuo and Mallick 1998), which had a Bernoulli distribution and an uninformative prior probability of 0.5. The posterior probability of w_c corresponds to the estimated probability of any given covariate ('C') to be included in the best model of a set of 2^C candidate models (Burton et al. 2012; Moll et al. 2016; Royle and Dorazio 2008). We calculated model-averaged estimates for the covariate coefficients over the global models from MCMC posterior histories, as described by Royle & Dorazio (2008). We used uninformative uniform priors and implemented the models using three chains of 20,000 iterations each, discarding the first 5,000 as burn-in, and thinned the posterior chains by 10. We assessed the convergence of the models by ensuring R-hat values for all parameters were <1.1 (Gelman and Hill 2007).

2.3. Results

Over 12,987 camera-trap days we recorded 157 independent lion detections (> 5 minutes; n = 2,505 lion pictures) at 35 (28%) of the 127 CTs. We registered 14,422 independent events of lion prey in the WMA and national park and 334 in the village lands (see Table S2.3). We also had over 2,800 independent events of livestock in 32 out of 35 village land CTS, where we did not register some of the main lion prey species such as buffalo, giraffe and zebra. We documented spatial variation in the number of lion detections across sampling areas, with the highest detection coming from within the national park (136 out of 143 detections solely in the Msembe sampling area of RNP; Fig. 2.1). The WMA had far fewer detections (14 detections in Lunda; Fig. 2.1; Table 2.2) and we did not detect lions in any of the sampling areas in the village lands. The naïve occupancy estimates ranged from 27.6% for the global model, to 39% for the model implemented on the data derived from the 77 CTs in the national park, and 10% for the model based on the data from the 50 CTs in WMA and village land. We observed an increase in the estimated occupancy from the naïve estimate when accounting for imperfect detection for all models, with 33.2% for the global model, 47.4% for the Ruaha model, and 14% for the WMA+VL models (Table 2.3).

We found a high degree of overlap in the outputs of the global and Ruaha model, with lion occupancy significantly influenced by increased biomass of large and medium prey (Table 2.3, Fig. 2.3a-2.3b). We found a negative association between proximity to households and ranger posts as well as increased vegetation cover to lion occupancy, although all three of these relationships demonstrated considerable variability (i.e., large credible intervals) over the range of covariate values (Table 2.3, Fig. 2.3a-2.3b). Large and medium prey biomass indices and distance to household were the most common covariates included in these models (Table 2.3). Lion detection probability was positively influenced by large prey biomass at the CTs level, and we found a negative association between detection and CTs installed outside animal trails or man-made roads (Table 2.3).

Table 2.2. Total number of independent lion detections per sampling areas used to model lion occupancy in the Ruaha landscape, southern Tanzania, during the camera-trapping survey (dry seasons 2014-2015). * Σ of all independent events (> 5 minutes interval between detections).

Land-management	Area	CT effort (days)	Σ Events*
National Park	Kwihala	196	1
	Lunda-Ilolo	196	0
	Mdonya	226	5
	Msembe	7,447	136
	Mwagusi	173	1
Wildlife Management Area	Lunda	867	14
	Pawaga	738	0
Village land	Idodi	674	0
	Magosi	656	0
	Malinzanga	718	0
	Nyamahana	1,059	0

CT effort (days): Number of active days of survey; each day = 24h.

Table 2.3. Posterior means, standard deviations, 95% credible intervals (C.I.), and Bayesian inclusion parameters (w_c) of lion occupancy models fit to camera-trap data from the Ruaha landscape, southern Tanzania during the dry seasons of 2014-2015.

Model	Covariate	Parameter	Mean	SD	95% C.I.	w_c
	Medium prey (CPUE)	α_1	1.8	1.05	0.03, 4.12	0.59
	Large prey (CPUE)	α_2	3.19	1.11	1.01, 4.90	0.98
	Distance to household	α_3	2.61	1.84	-2.04, 4.89	0.61
	Distance to ranger post	α_4	0.97	2.08	-3.38, 4.53	0.41
	VCF	α_6	1.16	0.78	-0.08, 3.06	0.39
Global	Mean random intercept	α_{site}	-4.77	3.47	-12.35, 1.19	-
	Large prey (CPUE)	β_1	0.26	0.09	0.08, 0.44	0.68
	Intercept	B_0	-0.57	1.13	-3.25, 0.75	-
	Trail type.N	B_{k2}	-1.97	0.84	-3.89, -0.61	0.27
	Trail type.RD	B_{k3}	0.28	0.33	-0.37, 0.88	0.27
	CTs occupied	Ψ	42.24	4.09	37.00, 53.00	-
	Medium prey (CPUE)	α_1	1.75	1.13	-0.12 , 4.30	0.52
	Large prey (CPUE)	α_2	3.12	1.15	0.90, 4.91	0.97
	Distance to household	α_3	1.15	2.56	-4.29, 4.83	0.48
	Distance to ranger post	α_4	2.63	1.71	-1.22, 4.91	0.6
	VCF	α_6	1.2	0.94	-0.21, 3.55	0.35
Ruaha	Mean random intercept	α_{site}	-3.86	4.02	-12.67, 3.42	-
	Large prey (CPUE)	β_1	0.28	0.09	0.10, 0.45	0.76
	Intercept	B_0	0.02	2.89	-4.78, 4.70	-
	Trail type.N	B_{k2}	-2.33	1.89	-4.86, 2.08	0.56
	Trail type.RD	B_{k3}	-	-	-	-
	CTs occupied	Ψ	36.47	4.83	31.00, 50.00	-
	Medium prey (CPUE)	α_1	1.91	1.91	-2.11, 4.83	0.43
	Large prey (CPUE)	α_2	1.66	2.22	-3.31, 4.85	0.46
	Distance to household	α_3	1.39	2.67	-4.32, 4.86	0.52
	Distance to ranger post	α_4	-2.69	1.96	-4.92, 2.43	0.62
	VCF	α_6	0.24	2.45	-4.43, 4.47	0.41
	Mean random intercept	α_{site}	-6.6	5.88	-19.34, 3.37	-
	Large prey (CPUE)	β_1	0.27	0.59	-0.68, 1.54	0.11
	Intercept	B_0	-1.75	2.91	-8.01, 2.57	-
WMA + VL	Trail type.N	βk_2	-3.15	3.25	-8.93, 1.96	0.24
	Trail type.RD	B_{k3}	-1.44	3.18	-6.78, 2.96	0.24
	CTs occupied	Ψ	7.03	1.91	5.00, 11.00	-

CPUE: catch-per unit effort index of prey biomass; VCF: Vegetation Continuous Fields; Trail type.N: off roads; Trail type.RD: on man-made roads; CTs: camera-trap station

The outputs for the WMA and village land model suggest that proximity to ranger post, increased medium and large prey biomass index, and distance to households had a weak positive influence on occupancy. Detection probability was positively influenced by large prey biomass and negatively by no-trails and man-made roads (Table 2.3, Fig. 2.3c).

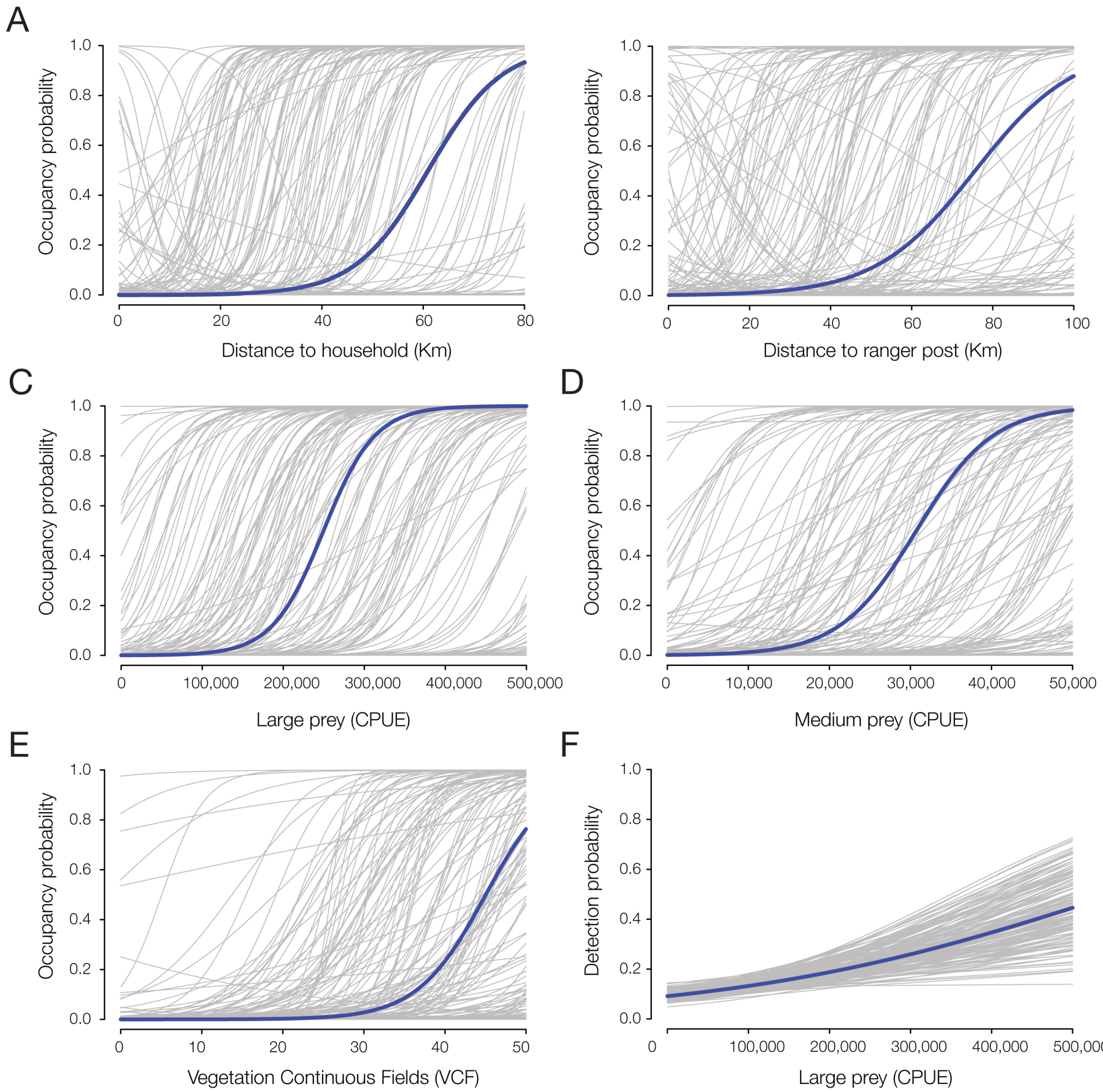

Figure 2.3a. Predicted association of the hypothesised covariates to the probability of occupancy (A-E) and detection (F) of lions (*Panthera leo*) for the **global** model. The solid blue line represents the posterior mean, and the light grey lines represent the estimated uncertainty based on a random posterior sample of 200 iterations.

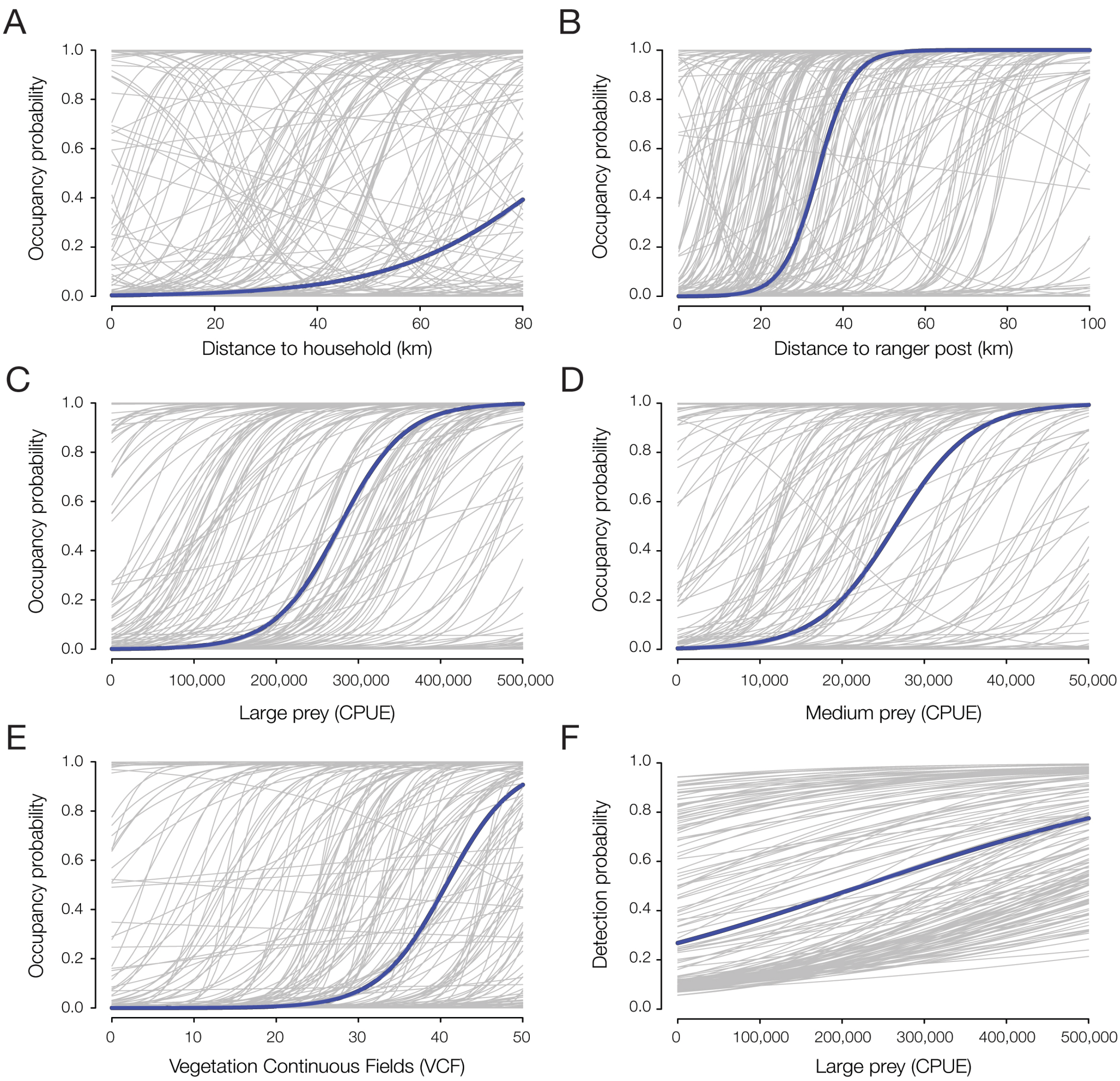

Figure 2.3b. Predicted association of the hypothesised covariates to the probability of occupancy (A-E) and detection (F) of lions (*Panthera leo*) for the **Ruaha** model. The solid blue line represents the posterior mean, and the light grey lines represent the estimated uncertainty based on a random posterior sample of 200 iterations.

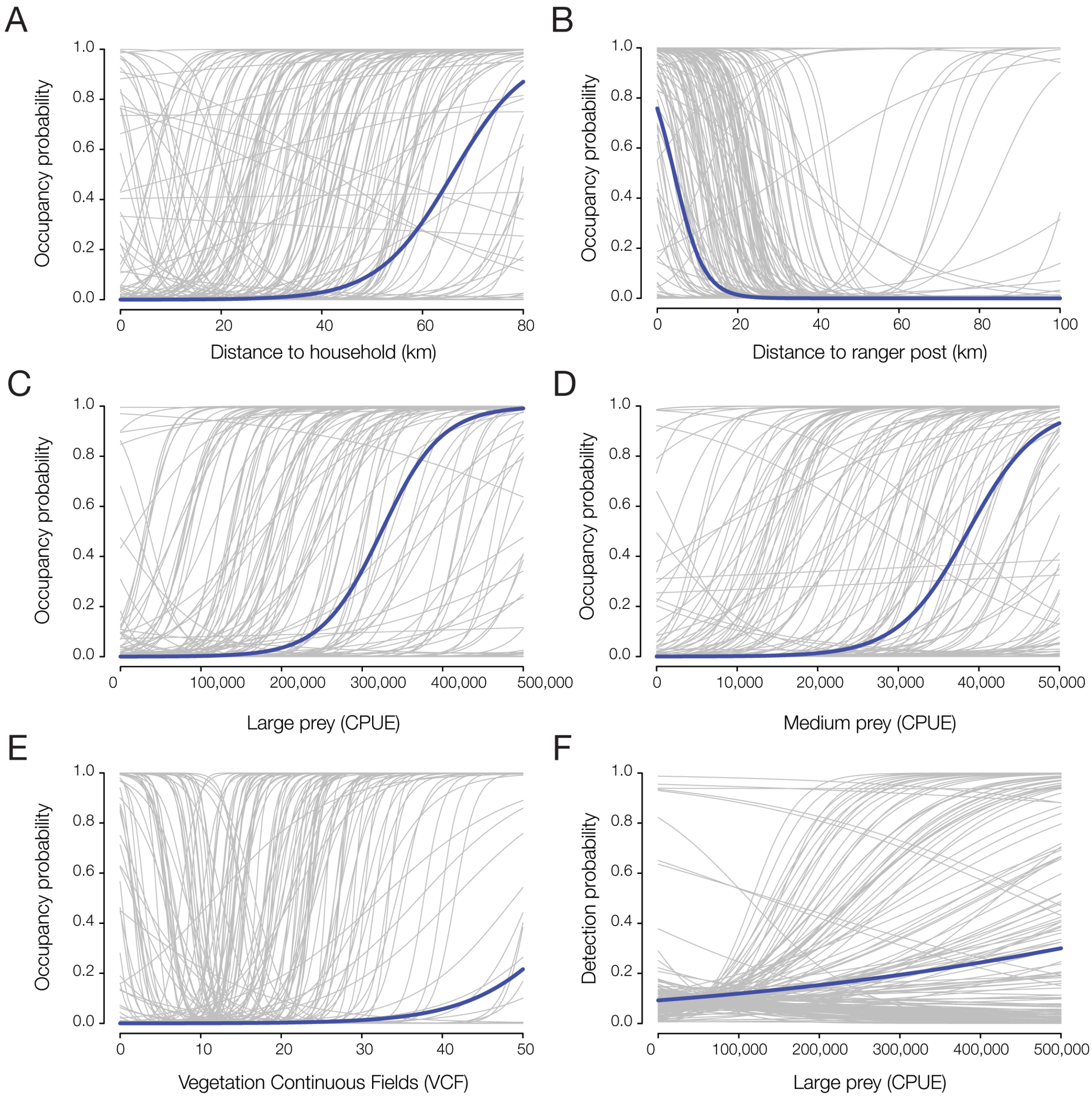

Figure 2.3c. Predicted association of the hypothesised covariates to the probability of occupancy (A-E) and detection (F) of lions (*Panthera leo*) for the **WMA+VL** model. The solid blue line represents the posterior mean, and the light grey lines represent the estimated uncertainty based on a random posterior sample of 200 iterations.

2.4. Discussion

In this study, we only detected lions in habitats that had a protected status, increased prey availability, or were likely under some level of surveillance as represented by closer proximity to ranger posts outside RNP. We did not detect lions in the unprotected village lands. We know that lions periodically use the village lands, as evidenced by spoor, depredations of livestock, and direct conflict with people. However, our extended camera trap surveys did not detect them. As such, models describing lion occupancy across the national park, WMA, and village lands varied little from those models fitted at the national park level. We suspect that anthropogenic pressure in the village lands presents a key limiting factor on lion spatial distribution, given land conversion and human encroachment (Lankford et al. 2009; Wenban-Smith 2015), prey depletion (Knapp et al. 2017), and high levels of human-carnivore conflict in this area (Abade et al. 2014a; Dickman et al. 2014). In this way, our results add to a growing body of research demonstrating the importance of protected areas as key refugia for lions (Bauer et al. 2015; Lindsey et al. 2017a; Packer et al. 2013). However, our analysis also highlights the importance of addressing threats immediately adjacent to national parks, as even in areas where lions occur at high numbers, such as in Ruaha (Riggio et al. 2012), the effects of human disturbance can significantly affect their occurrence.

2.4.1. Determinants of lion occupancy

Lion occupancy patterns varied substantially between the national park and village lands. In the national park, lion occurrence was strongly and positively associated with higher levels of prey occurrence (Table 2.3). This is unsurprising, as the availability of large-bodied prey species shapes lion spatial distribution and habitat use (Davidson et al. 2013; Hayward and Kerley 2005; Loveridge and Canney 2009; Valeix et al. 2009). Our findings are similar to those presented by Cusack et al. (2016) that observed significant effects of large prey species on lion occupancy and detection in the national park.

However, and despite the relative importance of human-dominated landscapes for lion distribution (Blackburn et al. 2016; Dolrenry et al. 2016), and their known presence in the village lands around RNP (e.g. frequent lion killings in village lands; Dickman, in. prep.), we found little evidence of lion occupancy of unprotected habitats around RNP. The lack of lion detections in the most disturbed areas of the gradient of anthropogenic pressure is alarming, as it could indicate the species low densities outside the protected area (Royle and Nichols 2003). It is noteworthy that we did record 14 lion detections in the northern portion of the WMA in a region with minimal human activity, and no livestock grazing. This area is also relatively close to national park ranger posts, where both park and private anti-poaching patrolling activities exist. In the village lands, we found signs of indiscrimate bushmeat poaching (head and foot snares), registered a high number of livestock in all but three CTs, and we did not detect some lion main large prey species, including zebra, buffalo and giraffe in the village lands. It is also important to notice that our results suggest that lions could be avoiding the use of animal trails outside Ruaha, especially in those areas of increased anthropogenic pressure, which could be a strategy to minimise encounters with humans. Lions show risk-avoidance strategies, and adjust their spatiotemporal behaviour selecting for those habitats of lower anthropic pressure to minimise exposure to people and livestock (Oriol-Cotterill et al. 2015a; Oriol-Cotterill et al. 2015b; Valeix et al. 2012). Large carnivores are known to avoid using trails and roads in areas of increased anthropogenic pressure and hunting (Foster et al. 2010; Kays et al. 2017), and this could help explaining the low detection rates of lions in village lands.

Poaching and displacement by livestock are known factors contributing to prey depletion (Ripple et al. 2015), which can be even more detrimental to carnivores than direct anthropogenic mortality (Rosenblatt et al. 2016). These effects can importantly alter lion populations (Henschel et al. 2016; Wolf and Ripple 2016), and are likely a contributing factor to the low levels of occupancy that we identified outside of the national park. Besides potential prey depletion, lions are one of the most persecuted large carnivores around RNP due to intense rates of human-carnivore conflict (Dickman et al. 2014), and are exposed to high rates of human-induced mortality. For instance, over 100 lions were killed by humans in the villages around RNP between 2010 and 2016 (Dickman, in. prep.). Although the effect of such killings on local or regional lion populations in Ruaha is yet to be quantified, they might be contributing to reduced lion numbers in the village lands, and hence to the observed low detection and site occupancy. Of substantial concern here is the potential for these killings to lead to source-sinks for lions locally, with possibility to affect the population within the national park as well, as observed elsewhere in Africa (Loveridge et al. 2010a; Loveridge et al. 2016b). Furthermore, it is also possible that given the vast pristine lion habitats within RNP, lions are less likely to rely on the sub-optimal human-dominated habitats found in the periphery of the protected area, although further studies based on high-resolution analyses of movement patterns would help to clarify such hypothesis.

We acknowledge that the precise mechanistic connections between low-levels of lion detection in the village lands and the variety of sources of anthropogenic pressure remains elusive. Our results are limited in their ecological inference because of the inherent sampling limitation of camera trapping surveys - CTs only sample a fraction of the landscape, which is a challenge when surveying wide-ranging species (Cusack et al. 2016). However, given the outputs of our models and the results herein presented, we surmise that human-related top-down processes (i.e. poaching; human-related lion mortality; prey depletion) are likely the key limiting factors of lion occupation as soon as they enter village lands. These results are in line with other studies across Africa that found higher occupancy estimates for lions exactly in areas of limited human activities, such as pastoralism, and with lower levels of illegal wildlife exploitation (Everatt et al. 2015), and in areas of increased surveillance (Henschel et al. 2016) such as those closer to the ranger posts in our study area.

2.4.2. Implications for lion conservation

Here, we showed that lion occurrence outside the national park was majorly limited to areas of increased prey availability, exposed to relatively lower levels of anthropogenic disturbance, and increased surveillance closer to ranger posts, where they are less likely to experience conflict-related killing (although illegal cultural and retaliatory lion hunting and bushmeat poaching are pervasive across all land-use classes in this landscape). Furthermore, we show that village lands represent a "hard edge" that limits lion occurrence and distribution outside RNP.

Thus, if lions are to be conserved in the village lands around RNP, it is crucial that actions should foster coexistence and tolerance to the presence of this iconic species as this could help lessening the current burden of the human-related threats on lion survival in this area. Additionally, our results reinforce the necessity to protect and maintain prey base given their strong influence on determining lion occupancy and detection. Conservation strategies should ensure that lions and other large carnivores represent a positive presence instead of a potential perceived hazard (Dickman et al. 2014), and work closely with all stakeholders to reduce the costs of lion presence and increase the tangible benefits of having these species in the village lands (Blackburn et al. 2016; Dickman 2015; Hemson et al. 2009). For instance, when lions generate direct benefits for pastoralists, they are more likely to tolerate and not retaliate against depredations (Blackburn et al. 2016), which lessens conflict-related killings. The provisions of benefits such as veterinary medicines, health care and education associated with lion presence as part of a community-based conservation approach in some of the villages around RNP has resulted in 80% decline of large carnivore killing, although those initiatives currently operate across less than half of the village land due to limited resources (Dickman 2015). Finding avenues to adapt and increase benefit provisions to all the 22 villages surrounding RNP could help to promote widespread large carnivore conservation across the study site, although the complexity and associated financial costs of such community-based approach might be challenging (Dickman 2015). Monetary incentives for local tribes not to kill lions, and financial inducements for village land scouts to perform anti-poaching patrolling in human-dominated lands could also be a viable alternative to help promote conservation outside RNP (Caro and Davenport 2016). In addition, increasing people's awareness and accessibility to effective actions to reduce the perceived hazard originated from carnivore presence could help to increase tolerance and attitudes towards lions and other large carnivores locally (Bruskotter and Wilson 2014). For example, the widespread concerted efforts to systematically improve husbandry practices using predator-proof bomas (Abade et al. 2014a; Lichtenfeld et al. 2015), and prevention of human-carnivore conflict, could lead to a substantial reduction in lion and other large carnivore mortality, and contribute to conservation of these species in village lands. Lastly, efforts to improve food security, diversifying access to protein sources other than wild prey, and minimizing the potential economic reliance on bushmeat trade by local villagers could help alleviating unsustainable bushmeat harvesting (van Vliet et al. 2016), and the ensuing negative effects of prey depletion on lion conservation locally.

It is vital that strategies aimed at conserving large carnivores within human-dominated lands should be implemented in collaboration with local communities, as they will bear the costs of co-existing with lions, and ultimately be responsible for deciding upon the conservation of the species (Dolrenry et al. 2016). Multi-lateral strategies for promoting community-based conservation (Newmark and Hough 2000) and participatory monitoring whereby locals actively engage in the conservation of the species, such as those implemented in some villages around Ruaha National Park by the RCP, could be extended to further villages, as this could have direct implications for the conservation of wildlife.

Acknowledgments

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Chapter 2. Supporting Information

Table S2.1. Pearson's correlation of the putative ecological variables used to model lion occupancy in the Ruaha landscape, southern Tanzania.

Ecological Covariates	Dist. household	Dist. Greater Ruaha	Dist. ranger post	ρ people	ρ livestock	Large prey (CPUE)	Medium prey (CPUE)	VCF
Dist. household	1	-	-	-	-	-	-	-
Dist. Great Ruaha	-0.43	1	-	-	-	-	-	-
Dist. ranger post	-0.33	0.86	1	-	-	-	-	-
ρ people	-0.27	0.28	0.24	1	-	-	-	-
ρ livestock	-0.29	0.28	0.24	0.94	1	-	-	-
Large prey (CPUE)	0.35	-0.4	-0.38	-0.14	-0.15	1	-	-
Medium prey (CPUE)	0.34	-0.25	-0.15	-0.11	-0.12	0.63	1	-
VCF	0.09	0.34	0.23	-0.13	-0.14	-0.21	-0.02	1

Dist. Distance; ρ. density; CPUE. catch-per unit effort index of prey availability for each camera-trap station based on the number of independent records for lion prey species photographed during the survey. VCF. Vegetation continuous fields.

Table S2.2. Variance inflation factor (VIF < 3) of the ecological covariates used to model lion occupancy in the Ruaha landscape, southern Tanzania.

Ecological covariates	VIF
Distance household	1.34
Distance ranger post	1.36
Density people	1.15
Large prey (CPUE)	2.03
Medium prey (CPUE)	1.77
VCF	1.18

Table S2.3. Estimated index of biomass (CPUE) for lion prey species registered during the survey in Ruaha landscape, southern Tanzania, in the dry seasons of 2014-2015. $\bar{X}$ weigh values according to (Tacutu et al. 2013). *Σ of independent events (> 5 minutes interval between detections).

Species	Prey Class	$\bar{X}$ Weigh	Σ Events*	$\bar{X}$ CPUE (Min-Max)
Buffalo *Syncerus caffer*	Large	700	75	272.58 (0-13,031.91)
Eland *Taurotragus oryx*	Large	500	46	180.87 (0-6,250)
Elephant *Loxodanta africana*	Large	4800	2893	87,616.95 (0-829,090.91)
Giraffe *Giraffa camelopardalis*	Large	800	1395	9,477.11 (0-91,851.85)
Greater kudu *Tragelaphus strepsiceros*	Large	217.5	909	1,192.45 (0-5,553.19)
Hippo *Hippopotamus amphibious*	Large	3750	392	7,043.43 (0-425,159.24)
Waterbuck *Kobus ellipsiprymnus*	Large	175.3	39	46.10 (0-2,337.33)
Zebra *Equus quagga*	Large	280	404	960.57 (0-16,210.53)
Bush pig *Potamochoerus larvatus*	Medium	88.5	33	20.59 (0-465.79)
Bushbuck *Tragelaphus scriptus*	Medium	60	79	44.63 (0-3200)
Duiker *Sylvicapra grimmia*	Medium	18.5	199	36.71 (0-678.33)
Grant's gazelle *Nanger granti*	Medium	67	59	44.01 (0-2,153.57)
Impala *Aepyceros melampus*	Medium	52.5	6775	2,459.56 (0-34,687.5)
Lesser kudu *Tragelaphus imberbis*	Medium	82.5	213	125.41 (0-1,787.50)
Warthog *Phacochoerus africanus*	Medium	100	181	173.89 (0-5,000)

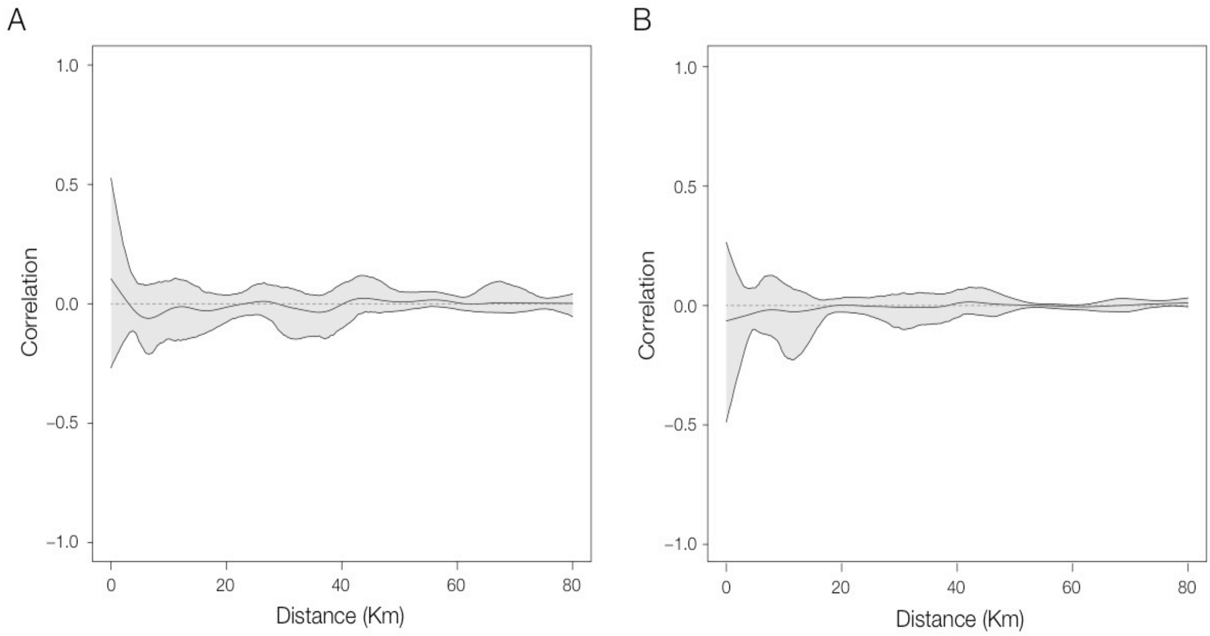

Figure S2.1.1. Spline correlograms for the lion (*Panthera leo*) occupancy models. Spline correlograms from a generalized linear model (a) and a generalized linear mixed model that included a random intercept at the CT level (b) showing a reduction in spatial autocorrelation. Distance between paired sample locations in kilometres (Km).

Chapter 3: The importance of the wildland-human interface for carnivore ecology: a case study of leopard (*Panthera pardus*) site use in Tanzania

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Abstract

Understanding large carnivore occurrence patterns in multiple use landscapes beyond protected areas is central to developing actions for species conservation in an increasingly human-dominated world. Among large carnivores, leopards (*Panthera pardus*), the most widely distributed felid, often occupy anthropogenic landscapes where they are frequently reported to create - and are killed as a result of - human-carnivore conflict. Leopards' ecological plasticity to anthropogenic landscapes, and their frequent involvement with conflict make them an insightful study-model for understanding the determinants of carnivore occurrence across human-dominated habitats. We evaluated the spatial variation in leopard site use throughout a multiple use landscape extending from the Ruaha National Park (RNP) into a Wildlife Management Area (WMA) and surrounding human-dominated village lands in southern Tanzania. We collected leopard data via extensive camera trapping, and estimated site use as a function of landscape and anthropogenic variables using hierarchical occupancy models under a Bayesian framework. We recorded 197 leopard detections within RNP, 35 in the WMA, and none in the village lands. Proximity to human households and livestock presence exerted stronger influence on leopard site use than prey availability. Conservation strategies should prioritise mitigating the negative effects of intense pastoralism, conflict and large carnivore killing around RNP, as even in areas where leopards are believed to occur at high numbers, such as in Ruaha, the effects of human disturbance can significantly limit their distribution. Such approaches to mitigation are timely

for conservation of large carnivores in increasingly human-dominated habitats in areas of wildland-human interface.

Key-words: large carnivores; conservation; occupancy; Bayesian; human-carnivore conflict

Author contributions to the manuscript:

Experimental design: LA, RM; Data collection: LA, JC; Data analysis: LA; Writing of 1st draft of manuscript: LA, Improvements to manuscript: RJM, PS, DM, AD & RM

3.1. Introduction

As apex predators, large-bodied mammalian predators of the order *Carnivora* may influence faunal and floral communities, trophic interactions and in regulating ecosystem functions (Beschta and Ripple 2009; Ford et al. 2014; Pitman et al. 2012; Ripple et al. 2014). In addition to this regulatory role, large carnivores have had aesthetic and cultural importance to human societies throughout history (López-Bao et al. 2017; Ray 2005). Large carnivores are also important revenue-generators for a multimillion-dollar ecotourism and sport hunting industry that contributes to national economies, and to the conservation and management of wildlife and wilderness, particularly in Africa (Creel et al. 2016; Di Minin et al. 2016a; Lindsey et al. 2006; Lindsey et al. 2013b; Packer et al. 2011). Despite these critical roles, large carnivore populations are in jeopardy, with 24 of the remaining 31 species documented to be declining (Ripple et al. 2014). Such population losses are attributable to habitat conversion, human persecution, prey depletion, unsustainable hunting and exploitation for body parts (Macdonald 2016; Ripple et al. 2016a; Ripple et al. 2014). Human population growth and urbanization around protected areas, especially in the sub-Saharan African countries (Newmark 2008; Wittemyer et al. 2008) where large carnivores can still be found in almost ecologically intact guilds (Dröge et al. 2017), present imminent challenges for carnivore conservation. For example, mortality is higher along the boundaries of protected areas where large carnivores are subject to interaction and conflict with people, and risk being killed preventatively or in retaliation to predation events (Balme et al. 2010; Loveridge et al. 2010a; Loveridge et al. 2016b; Woodroffe and Ginsberg 1998). The habitats associated with this human-carnivore interface can function as population sinks, whereby the high human-induced large carnivore offtake can "drain" populations from the bordering protected areas and compromise population persistence (Loveridge et al. 2010a; Loveridge et al. 2016b). However, as large carnivores are often wide-ranging and maintain large home ranges (Ripple et al. 2014; Treves and Karanth 2003), they will resort not only on the core of protected areas but also on its periphery (Burton et al. 2012; Loveridge et al. 2010a; O'Brien et al. 2003; Pitman et al. 2015; Rosenblatt et al. 2016). Thus, the habitat bordering protected areas is essential to the conservation of large carnivore populations (Loveridge et al. 2010a; Pitman et al. 2015; van der Meer et al. 2014; Woodroffe and Ginsberg 1998). Thereby, determining the extent to which large carnivores can occupy areas of increasing human pressure, such as those represented by human encroachment of wildlands and agro-pastoralism, is of major importance for their conservation. This information is much needed to support conservation strategies aiming at reducing anthropogenic threats found in these increasingly human-dominated landscapes.

Among large carnivores, leopards (*Panthera pardus*) are the most widespread felid species (Jacobson et al. 2016), occupying the most diverse habitat types including deserts, forests, and savannahs (Jacobson et al. 2016; Nowell and Jackson 1996b; Pitman et al. 2012). The behavioural flexibility and dietary plasticity of leopards facilitates this widespread distribution (Jacobson et al. 2016; Stein et al. 2016). Such adaptations enable leopards to use sub-optimal habitats such as those found outside protected areas, in heavily disturbed human-dominated landscapes (Athreya et al. 2016; Athreya et al. 2013; Jacobson et al. 2016). For instance, given tolerance to their presence, leopards can live alongside people even in densely populated areas (400 people/km^2) by mostly feeding on livestock and domestic dogs, and finding refuge in crops and agricultural lands (Athreya et al. 2016; Athreya et al. 2013). Despite such ecological plasticity, the conservation of leopards is threatened by rampant destruction and fragmentation of habitat, primary prey depletion due to bushmeat poaching and overgrazing, conflict-related mortality, and unsustainable harvest resulting from mismanaged sport hunting and to attend demands for pelts and body parts (Jacobson et al. 2016; Packer et al. 2011; Stein et al. 2016; Wolf and Ripple 2016). As a result, leopard populations have experienced >30% global range contraction in the past 20 years (Jacobson et al. 2016). In Africa, leopards have lost 48-67% of their historical distribution with even more pronounced and critical range reductions in northern and western Africa (Jacobson et al. 2016). In East and West Africa, leopard populations have suffered an estimated 50% decline fuelled by habitat conversion and reduction in many of their prey populations (Stein et al. 2016). The species is expected to undergo further population decline across its overall Sub-Saharan African range given the observed high rate of prey depletion (Wolf and Ripple 2016) and increasing human population in the next 50 years (Stein et al. 2016). Leopard's wide-ranging behaviour and ability to cover multi-use landscapes (Pitman et al. 2015), frequent overlap with humans on anthropogenic areas (Athreya et al. 2016; Athreya et al. 2013; Stein et al. 2016), common association with livestock depredation, and the levels of persecution by humans (Athreya et al. 2016; Athreya et al. 2013; Ramesh et al. 2017; Rosenblatt et al. 2016), make them a good model for understanding large carnivore occupancy of human-dominated habitats, as well as typifies the challenges in the conservation of large carnivores elsewhere (Pitman et al. 2015).

Tanzania is one of the most important countries for leopard conservation in Africa, where its vast array of national parks and game reserves protects substantial portions of the leopard's extant range, and significant and sizeable populations (Jacobson et al. 2016). Leopards represent an important economic asset for Tanzania, as the species is among the top three most exported trophy species, besides hippos (*Hippopotamus amphibious*) and elephants (*Loxodonta africana*), and contributes to a US $56,3 million revenue for hunting operators and governments (Di Minin et al. 2016a). Despite the ecological and economic importance of leopards, the current lack of empirical field data on leopard ecology hinders the development of effective conservation strategies designed to protect the species in Tanzania (TAWIRI 2007, 2009a).

In this study, we investigated the factors affecting the probability of leopard site use at the interface of protected and unprotected habitat in southern Tanzania's Ruaha landscape, in an area encompassing the eastern portions of Ruaha National Park, the adjacent semi-protected Pawaga-Idodi Wildlife Management Area (WMA), and unprotected village lands. Specifically, we assessed spatial variation in leopard site use in response to (*i*) anthropogenic disturbance, as indicated by distance to households and livestock presence, (*ii*) the availability of primary prey species, and (*iii*) proximity to water sources. We hypothesised that leopard site use would be negatively related to habitats associated with increased human occupation represented by those closer to households, and of intense livestock rearing and grazing, similar to those found in the most populated portions of the village land. Furthermore, we expected a positive association between leopard site use, increased prey availability and proximity to water sources, as these features are known determinants of habitat quality, and to influence leopard spatial distribution (Abade et al. 2014b; Bailey 2005; Balme et al. 2007; Gavashelishvili and Lukarevskiy 2008; Pitman et al. 2012). Documenting the factors associated with carnivore site use is central to efforts prioritising the conservation of these species. Tools like this are going to become ever more important in increasingly human-modified protected to unprotected habitat interfaces.

3.2. Material and methods

3.2.1. Study Area

We examined leopard site use in a multi-use landscape encompassing the eastern portions of Ruaha National Park (RNP), the Pawaga-Idodi Wildlife Management Area (WMA), and surrounding village lands (Fig. 3.1). Further information on the study area, including a detailed description of ecogeographic characteristics is provided in Chapter 2 - Section 2.2.

3.2.2. Village lands

The socio-economic characteristics of the village lands surrounding Ruaha National Park, as well a description of human-carnivore conflict in these areas is provided in Chapter 2 – Section 2.2.

3.2.3. Leopard occurrence data

We collected data on leopard occurrence during the dry seasons (May-December) of 2014 and 2015, via the deployment of 127 non-baited remotely triggered single camera-trap stations (CTs) across 11 sampling areas in the study site (Fig. 3.1). The data on leopard occurrence was collected using the same methodological approach described in Chapter 2. A detailed description on the survey design and implementation, camera-trapping setup and data collection is provided in Chapter 2. It is noteworthy that in this study, as in Chapter 2, site use equates to the probability that a given site was used during the survey period, rather than the probability of continuous site occupation (MacKenzie et al. 2006). Thus, we modelled leopard occupancy as the probability of site use during the study period at the CT level. We considered independent detection events for leopard, prey and livestock as those with > 5 minutes between records (Burton et al. 2012).

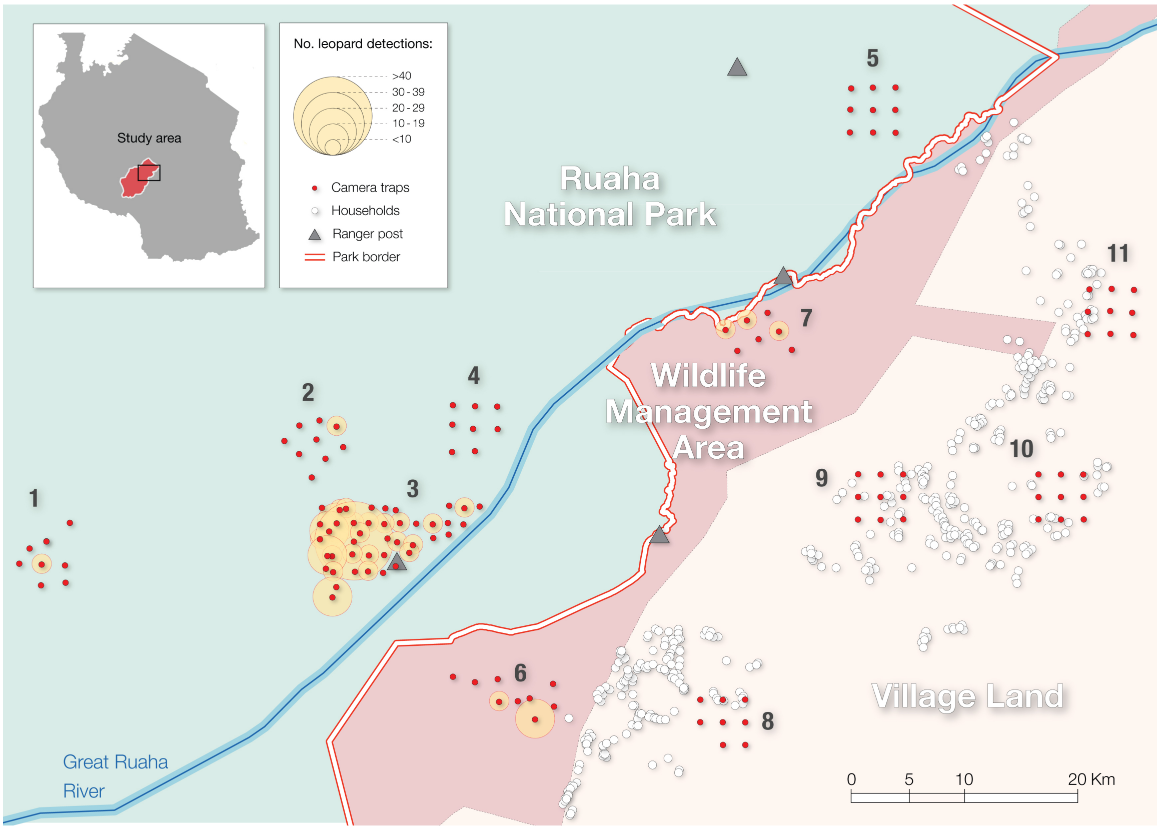

Figure 3.1. Location of the study site and distribution of camera-trap stations (red shaded circles) across the Ruaha landscape, southern Tanzania. 1-11 represents sampling areas: 1. Mdonya; 2. Kwihala; 3. Msembe; 4. Mwagusi; 5. Lunda-Ilolo; 6. Pawaga; 7. Lunda; 8. Idodi; 9. Malinzanga; 10. Nyamahana; 11. Magosi. The yellow shaded circles represent the number of independent detections of leopards (*Panthera pardus*) at each camera-trap station (> 5 minutes between detection).

3.2.4. Environmental covariates

We predicted leopard site use as a function of five environmental covariates known to influence leopard habitat selection (Table 3.1). We represented the distance to Great Ruaha River and distance to household covariates as rasters at a resolution of 500 x 500 meters (See Supporting Information – Fig. S3.1). We generated the rasters in QGIS 2.6.0 (QGIS) from freely available geoprocessed layers of satellite imagery and data collected by University of Oxford's Wildlife Conservation Research Unit, Ruaha Carnivore Project (RCP). We calculated the livestock number covariate by summing the total independent livestock detections at each CTs (we considered detections for cattle, goats and donkeys altogether). We also developed a primary prey availability covariate for leopards. To do so, we calculated a temporal catch-per unit effort (CPUE) index of prey availability for each CTs based on the number of independent records for the main five leopard prey species (Hayward et al. 2006), namely bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), and warthog (*Phacochoerus africanus*) photographed during the survey. We calculated the CPUE by multiplying the number of independent events at each CTs by the species average weight, divided by the CTs sampling effort, and standardised per 100 camera trap days (Burton et al. 2012). Prey weight was based on standard reference guides (Tacutu et al. 2013).

We considered trail types [animal trails (AT); no-trails (NT); human-made roads (RD)], as a covariate influencing detection of leopards as trail types have been found to influence on probability of carnivore detection in this study area (Cusack et al. 2015).

Table 3.1. Covariates and corresponding expected influence on the estimates of leopard site use and detection in the Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015.

Covariates	**Class**	**Model type**	**Expected influence**
No. livestock	Anthropogenic	Ψ	-
Dist. Great Ruaha River	Habitat	Ψ	+
Dist. household	Anthropogenic	Ψ	+
Medium prey (CPUE)	Habitat	Ψ	+
Trail type	Habitat	P	+

[a]Ψ. probability of site use; P. probability of detection; Dist. Distance; CPUE. catch-per unit effort index of prey availability for each camera-trap station based on the number of independent records for the main five leopard prey species (Hayward et al. 2006) photographed during the survey.

Prior to model fitting, we standardized (z-score) all covariates (Long et al. 2011), and assessed predictor collinearity using Pearson correlation and variance inflation factor tests. All the covariates used in the models were those minimally correlated (Pearson <0.7, VIF <3 (Zuur et al. 2010); Table S3.1; S3.2.).

3.2.5. Model analyses and averaging

We modelled leopard site use in a hierarchical Bayesian framework. We used temporally replicated surveys (i.e. weeks) to estimate the latent, unobserved probability of site use of each CTs Z_i, where $Z_i = 1$ if site i is occupied and 0 otherwise, and detection probability $p_{i,j}$, where $p_{i,j}$ is the probability that leopards are detected at site i during replicate j, given use of that site (i.e., $Z_i = 1$) (MacKenzie et al. 2002; Tyre et al. 2003). We fit the model with a random intercept at the level of each of the sampling areas (Fig. 3.1) in the study site

(Moll et al. 2016; Rhodes et al. 2009) to minimise issues of potential spatial autocorrelation among model residuals (Fig. S3.2). Our final model to estimate leopard site use was implemented as follows:

$\mathrm{logit}(\Psi_i) = \alpha_{area} + \alpha_1$*livestock number_i + α_2*distance river_i + α_3*distance $\mathrm{household}_i$ + α_4*medium prey$(\mathrm{CPUE})_i$

(*Eq. 3.1*)

where Ψ_i represents the probability of leopard site use at the i^{th} CT, α_{area} represents a random intercept indexed by area with estimated hyperparameters μ (mean) and τ^2 (variance), and $\alpha_{1,2,\ldots5}$ represent the influence of associated covariates at the i^{th} CT (Table 3.1).

The final detection model was implemented as follows:

$\mathrm{logit}(p_{i,j}) = \beta_0 + \beta_k$*$\mathrm{trail}_i$

(*Eq. 3.2*)

where $p_{i,j}$ represents the probability of detection at the i^{th} CT during survey j given that a site is used (i.e., $Z_i = 1$), β_0 is the intercept, and β_k represents the effect of the k^{th} trail type on leopard detection at each CT ($k = 3$), with animal trail (AT) as the reference category.

We implemented and analysed the models using a Bayesian framework and Markov chain Monte Carlo (MCMC) simulations in R v.2.13.0 (R Core Team 2012) and JAGS (Plummer 2003) through the package 'R2jags' (Su and Yajima 2012). We estimated the degree of support for the effect of each covariate on site use through the Bayesian inclusion parameter w_c (Kuo and Mallick 1998), which had a Bernoulli distribution and an uninformative prior probability of 0.5. The posterior probability of w_c corresponds to the estimated probability of any given covariate ('C') to be included in the best model of a set of 2^C candidate models (Burton et al. 2012; Moll et al. 2016; Royle and Dorazio 2008). We calculated model-averaged estimates for the covariate coefficients over the global models from MCMC posterior histories, as described by Royle & Dorazio (2008). We used uninformative uniform priors and implemented the models using three chains of 100,000 iterations each, discarding the first 10,000 as burn-in, and thinned the posterior chains by 10. We assessed the model convergence by ensuring R-hat values for all parameters <1.1 (Gelman and Hill 2007).

3.3. Results

We recorded a total of 232 independent leopard events over 12,987 camera-trap days at 42 of the 127 CTs (33%). We recorded 197 leopard detections in 36 out of 77 CTs in the national park, 35 detections in 6 out of 16 CTs in WMA, and we recorded no detections in the 35 CTs installed in the village lands (Fig. 3.1). The naïve site use estimate of 33% increased to 40.8% when we accounted for imperfect detection.

We had a total of 8,120 independent detections of the primary prey of leopards (Fig. 3.2; Fig. 3.3). We observed spatial variation in the number of primary prey detections, with a total of 5,766 independent prey records in the national park, 2,116 in the WMA, and 238 in the village lands (Fig. 3.3). We registered 2,811 independent events of livestock in 32 out of 35 village land CTs.

We found a strong negative relationship between the probability of leopard site use and habitat that: had increased livestock presence, was closer to households, and was farther from the Great Ruaha River (Table 3.2; Fig. 3.4). We found a weak relationship between prey availability and probability of leopard site use (Table 3.2; Fig. 3.4). The relatively high Bayesian inclusion parameter values (w_c – Table 3.2) for both proximity to households and livestock presence, in comparison to prey availability, suggest that leopard site use was primarily influenced by lower levels of anthropogenic pressure than prey availability during the survey. We found a lack of effect of trail type on detection probability, as the credible intervals (C.I.) of the trail parameters strongly overlapped zero and had Bayesian inclusion parameters near zero (Table 3.2).

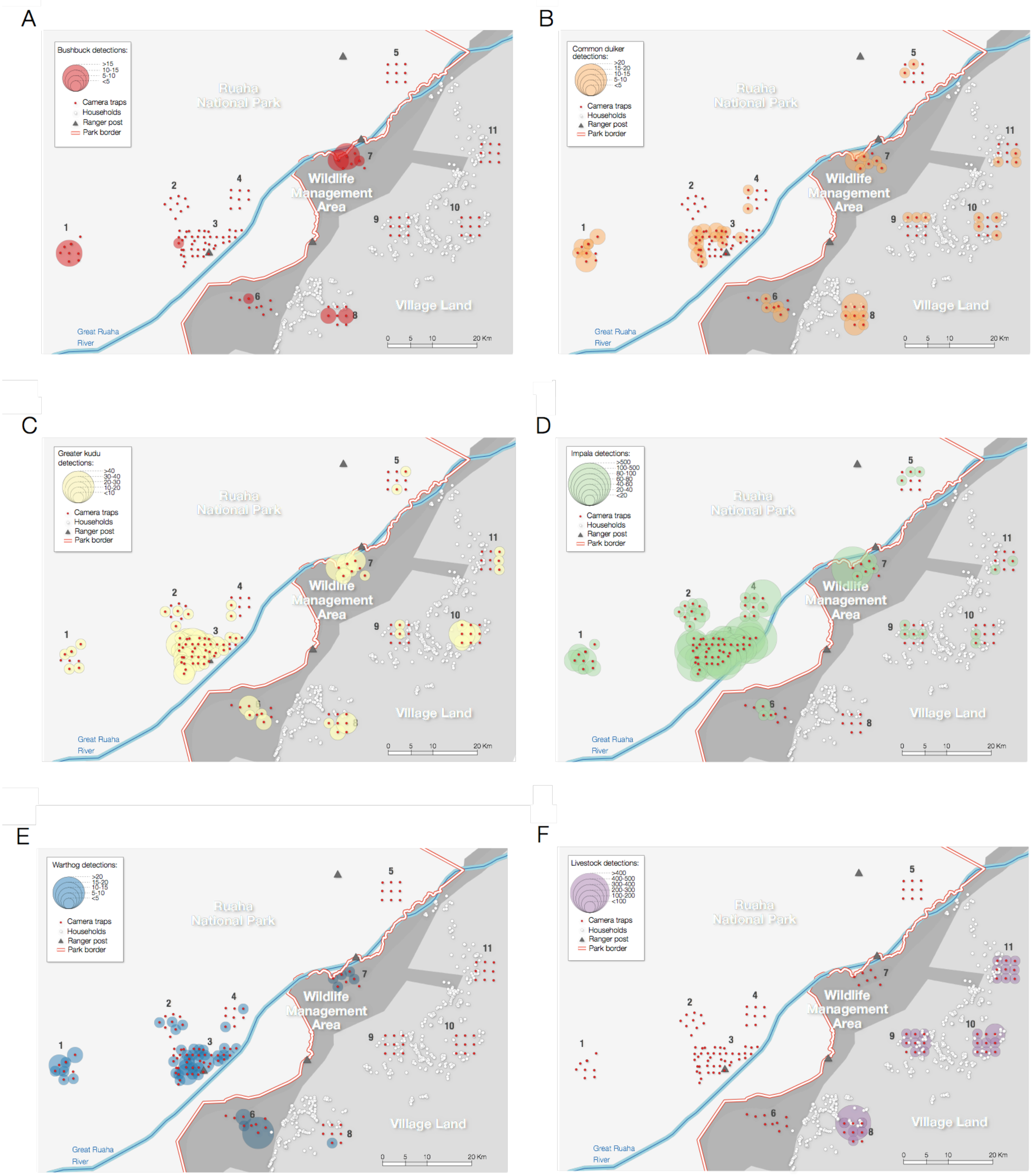

Figure 3.2. Map of independent detections (> 5 minutes between detection) of the main leopard prey species at each camera-trap station across the Ruaha landscape, southern Tanzania, in the dry seasons of 2014-2015. A. Bushbuck (*Tragelaphus scriptus*); B. Common duiker (*Sylvicapra grimmia*); C. Greater kudu (*Tragelaphus strepsiceros*); D. Impala (*Aepyceros melampus*); E. Warthog (*Phacochoerus africanus*); F. Livestock. 1-11 represents sampling areas: 1. Mdonya; 2. Kwihala; 3. Msembe; 4. Mwagusi; 5. Lunda-Ilolo; 6. Pawaga; 7. Lunda; 8. Idodi; 9. Malinzanga; 10. Nyamahana; 11. Magosi.

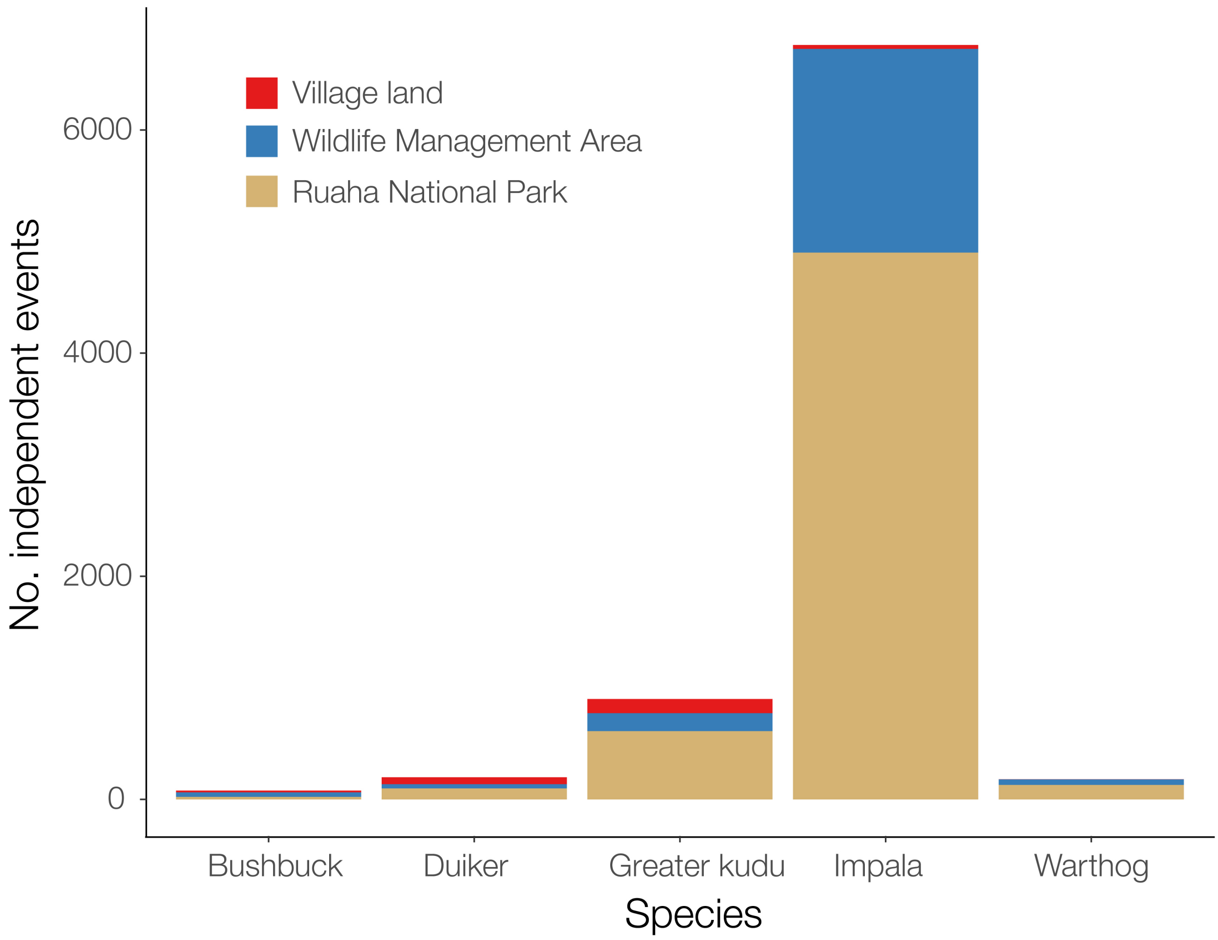

Figure 3.3. Variation in prey detection across the gradient of anthropogenic pressure in the Ruaha landscape. Independent events (> 5 min interval between detection). Bushbuck (*Tragelaphus scriptus*); Common duiker (*Sylvicapra grimmia*); Greater kudu (*Tragelaphus strepsiceros*); Impala (*Aepyceros melampus*); Warthog (*Phacochoerus africanus*).

Table 3.2. Posterior means, standard deviations (S.D.), 95% credible intervals (C.I.), and Bayesian inclusion parameters (w_c) of leopard site use models fit to camera-trap data from the Ruaha landscape, southern Tanzania, collected during the dry seasons of 2014-2015.

Covariates	Parameter	Mean	S.D.	95% (C.I.)	w_c
No. livestock	α_1	-5.5	2.97	-9.82, 0.09	0.47
Dist. Great Ruaha River	α_2	-1.94	1.66	-5.66, 1.27	0.33
Dist. households	α_3	2.96	1.48	0.46, 6.31	0.73
Prey availability (CPUE)	α_4	0.62	0.58	-0.23, 2.04	0.1
Intercept	β_0	-1.59	0.09	-1.77, -1.41	NA
Trail type N	β_{k2}	-0.21	0.45	-1.05, 0.61	0.01
Trail type RD	β_{k3}	-0.55	0.39	-1.4, 0.15	0.01
Estimated no. sites used	Ψ	51.83	4.02	45, 60	NA

Dist. distance; CPUE. catch-per unit effort index of prey availability for each camera-trap station based on the number of independent records for the main five leopard prey species (Hayward et al. 2006) photographed during the survey; Trail type.N: off roads; Trail type.RD: on man-made roads; CTs: camera-trap station

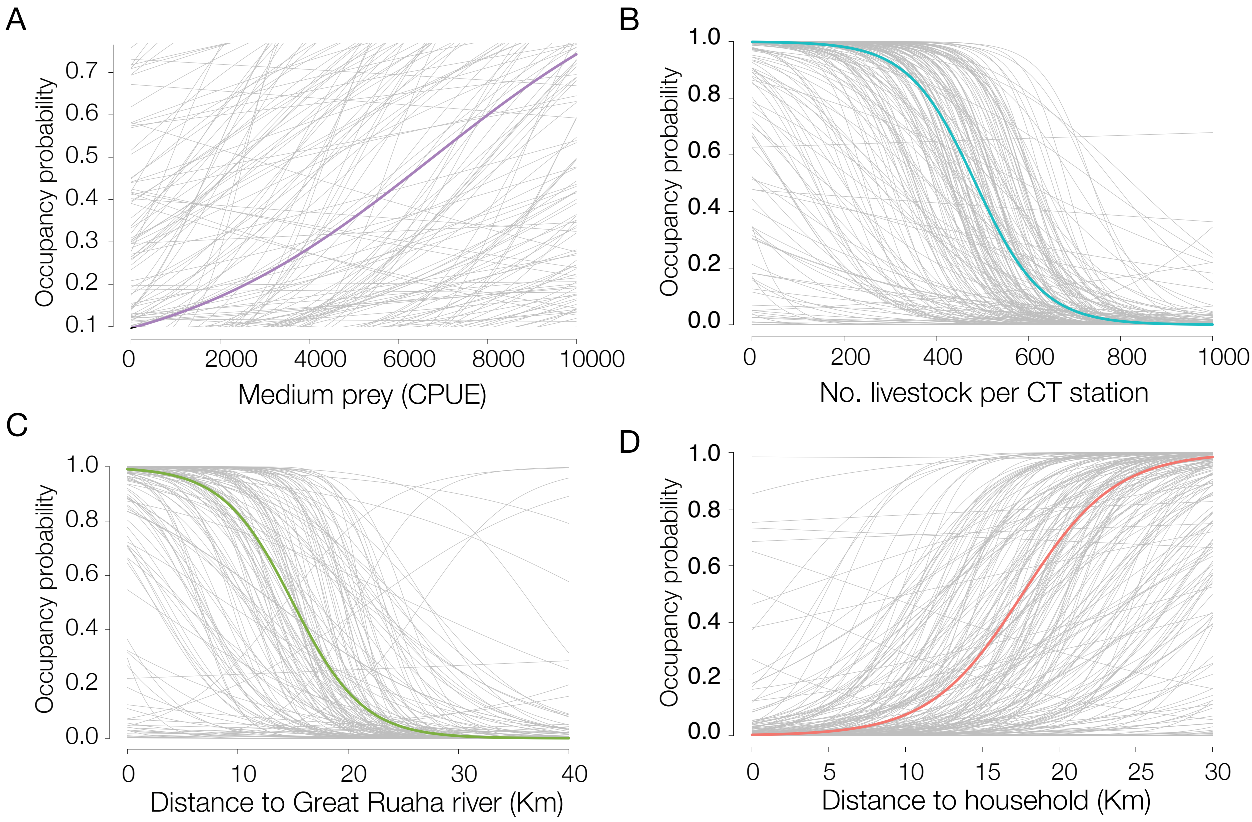

Figure 3.4. Predicted association of the hypothesised covariates to the probability of site use of leopards (*Panthera pardus*) across the Ruaha landscape, southern Tanzania, during the surveys in the dry seasons of 2014-2015. The solid line represents the posterior mean, and the light grey lines represent the estimated uncertainty based on a random posterior sample of 150-200 iterations. Occupancy probability = site use.

3.4. Discussion

Our findings suggest that human-related activities such as increased livestock presence and proximity to human households exerted stronger influence than prey availability on leopard site use, and were the major limiting factors of leopard distribution across the gradient of human pressure, especially in the village lands outside Ruaha National Park. Leopards are a species that can adapt to heavily disturbed anthropogenic environments, occurring in areas with high human densities (e.g. 400 people/km^2) and of low wild prey density (Athreya et al. 2013; Athreya et al. 2015; Jacobson et al. 2016). Our results however, suggest that such adaptations to human-pressure and threats may be context-specific, as observed in other studies (Alexander et al. 2016b; Haswell et al. 2016). It is important to highlight that the limited leopard site use observed outside the national park should not be interpreted as a result of the anthropogenic factors considered in this study in isolation, but also as a consequence of the underlying high persecution and human induced mortality of large carnivores in the study site (Dickman 2015; Dickman et al. 2014). The combination of these factors are likely thwarting leopard occurrence outside the protected area in the Ruaha landscape.

3.4.1. Determinants of leopard site use

The lack of leopard detections in the village lands suggests low population densities for the species in the unprotected areas surrounding Ruaha National Park. This area, as many other rural areas of Tanzania, has undergone rapid conversion of habitats due to intense human and livestock encroachment

(Lankford et al. 2009; Wenban-Smith 2015), intense conflict and high human-induced carnivore killing (Dickman 2015; Dickman et al. 2014), with all these factors likely contributing towards creating a "hard edge" for leopard populations in these non-protected areas. These results are similar to those presented by Henschel et al. (2011) and Ramesh et al. (2017), that found leopard use of habitat and abundance to be negatively influenced by areas with high human activity or increased bushmeat poaching. The negative influence of livestock presence on leopard site use could suggest a potential risk-avoidance strategy targeted at areas of intense human exposure. Large carnivores have been found to change and adjust spatiotemporal behaviour and home range in areas of intense herding activities to minimise exposure to human herders and livestock (Kolowski and Holekamp 2009; Oriol-Cotterill et al. 2015a). Alternatively, intense livestock herding could be associated with overgrazing and potential displacement of wild prey across the village lands, although our analyses showed little support for this hypothesis. It is noteworthy that despite the lack of leopard detections in village lands, leopards undoubtedly use these areas as indicated by the common livestock depredation events reported by villagers (Dickman et al. 2014), and the corresponding number of leopard killings in the village lands (A., Dickman; pers. comm.). Thus, we acknowledge that the precise mechanisms influencing leopard detections in the village lands remain elusive. However, our results are the first to investigate the environmental determinants of leopard site use across the gradient of anthropogenic pressure in the Ruaha landscape, and provide much needed data to help furthering our understanding of the effects of human activities on limiting leopard spatial distribution across one of the most important large carnivore strongholds in East Africa.

The observed weak association between leopard site use and primary prey availability (Table 3.2; Fig. 3.4) was contrary to our original hypotheses. Prey availability is a known determinant of site use, spatial distribution, and population density of leopards (Balme et al. 2007; Balme et al. 2013; Rosenblatt et al. 2016) and other carnivores (Carbone and Gittleman 2002; Hayward et al. 2007; Wolf and Ripple 2016). In fact, recent studies have shown that areas of increased leopard population density were linked to high abundance of medium-sized wild prey (Ramesh et al. 2017; Rosenblatt et al. 2016). One explanation of the observed weak relationship is that leopards could be relying on smaller prey species than those considered in this study, especially outside RNP, as a potential response to larger prey scarcity. Leopards are known to shift and rely on small-sized prey species (<20 kg) in areas of increased bushmeat hunting and intense competition with humans for limited food resources (Hayward et al. 2006; Henschel et al. 2011; Pitman et al. 2014), similar to those of the village lands around RNP. The relatively fewer prey detected across village lands where they are exposed to intense bushmeat poaching (Knapp et al. 2017) could help to corroborate such hypothesis (Fig. 3.2; 3.3). Large scale surveys using complementary sampling surveys such as sign surveys could help to further assess this association, as observed by Alexander et al. (2016a). Even though we found weak association between leopard site use and prey availability, it is nonetheless important to highlight that prey depletion could still pose a serious threat to leopards locally. Prey depletion is one of the main limiting factors to leopard occurrence and population density across their extant range (Alexander et al. 2016a; Jacobson et al. 2016; Ramesh et al. 2017; Rosenblatt et al. 2016), and potentially more detrimental to their survival than direct human-induced killings (Rosenblatt et al. 2016).

It is difficult to determine the role of trail types in this study given the lack of contribution of this covariate to the overall model estimates. Yet, the lack of effect of trail type on leopard detection could suggest that leopards could be avoiding using trails in areas of increased human activities, especially in the village lands, as observed for other large carnivores elsewhere (Foster et al. 2010; Kays et al. 2017). For RNP and WMA, where human activities are limited, the lack of influence of trail on detection could be associated with risk-avoidance strategy to minimise overlap and exposure to more dominant carnivores such as lions and spotted hyaenas. Such patterns have been observed elsewhere where leopards had 47-52% lower detection rates in areas of overlap with the more dominating tiger (*Panthera tigris*) (Steinmetz et al. 2013). In the context of the present study, lion detections have been positively influenced by trail types in the National Park and WMA (Abade et al., submitted – Chapter 2), which could help explain these results.

3.4.2. Implications for leopard conservation

Our results highlight the importance of protected areas on the conservation of wide-ranging large carnivores such as the leopard. Large protected areas such as Ruaha National Park are fundamental in protecting important habitats for leopards and other large carnivores (Di Minin et al. 2016b; Lindsey et al.

2017a) against the increasing human pressure observed in village lands surrounding protected areas across Africa (Lankford et al. 2009; Newmark 2008; Wittemyer et al. 2008). We observed a steadily decline in leopard site use with downgrading protected area status from the national park to the WMA and village lands. Our findings suggest that intense human activities (represented by proximity to human households and increased livestock numbers), likely coupled with underlying high levels of human-induced carnivore mortality due to conflict (Abade et al. 2014a; Abade et al. 2014b; Dickman et al. 2014), represent key-limiting factors to leopard spatial distribution in the human-dominated non-protected areas around RNP. Similar results have been found elsewhere in Africa, where the spatial distribution and population density of leopards (Rosenblatt et al. 2016), as well as of other large carnivores such as lions (Everatt et al. 2015) and other smaller carnivores (Burton et al. 2012; Rich et al. 2016) have been thwarted by increased human and livestock encroachment, pastoralism, conflict and human-mediated mortality in anthropogenic landscapes surrounding protected areas. If leopards are to be successfully conserved in such areas of human occupation, it is thus vital to address the threats imposed by people and livestock immediately adjacent to protected areas. In the context of this study, one much-needed strategy is the mitigation of carnivore-related conflict with people (Abade et al. 2014a; Dickman 2015; Dickman et al. 2014). Increasing people's awareness and accessibility to effective actions to reduce the perceived hazard originating from carnivore presence could help to increase tolerance and improve attitudes towards leopards and other large carnivores locally (Bruskotter and Wilson

2014). For example, systematically widespread improvement of husbandry practices using predator-proof bomas (Abade et al. 2014a; Lichtenfeld et al. 2015), and prevention of human-carnivore conflict could lead to a substantial reduction in leopard and other large carnivore mortality, and contribute to conservation of these species in the village lands (Dickman 2015). Additionally, developing strategies to reduce the associated costs of leopards and other large carnivores presence, and increase the tangible benefits of having these species in the village lands could help to promote their conservation (Blackburn et al. 2016; Dickman 2015; Hemson et al. 2009). When large carnivores generate direct benefits for pastoralists, people are more likely to tolerate and not retaliate against depredations (Blackburn et al. 2016; Romanach et al. 2011), which lessens conflict-related killings. Providing incentives and financial inducements for local tribes not to kill leopards and other large carnivore species in human-dominated lands could be a viable alternative to help promote their conservation (Caro and Davenport 2016) outside Ruaha National Park. For instance, the provisions of veterinary medicines, health care and education associated with large carnivore presence as part of a community-based conservation approach in some of the villages around Ruaha National Park resulted in 80% decline of large carnivore killing, although those initiatives currently operate across less than half of the village land (Dickman 2015).

On a landscape-level, concerted efforts to develop integrated management strategies and adaptive livestock and wildlife foraging systems could help limit the impact of livestock on rangeland habitats and wildlife (du Toit et al. 2017; Fynn et al. 2016). Guaranteed access to optimum foraging sites by livestock, and the implementation of planned grazing strategies – which consists of establishing several grazing paddocks that enable livestock rotation based on forage growth rate - across rangelands could help minimising competition with wildlife, prey depletion, habitat degradation due to overgrazing, and ultimately promote wildlife conservation (Fynn et al. 2016; Odadi et al. 2017). These foraging systems have been shown to increase livestock productivity by guaranteeing access to forage resources even in the driest periods of the year (Tyrrell et al. 2017), which could be an incentive for the adoption of this system by livestock owners in this landscape. Although, these strategies can be difficult to implement in areas where livestock owners can be highly nomadic and transient, as is the case in the vicinity of Ruaha National Park.

Strategies aimed at conserving leopards and other large carnivores within human-dominated lands should be implemented in collaboration with local communities given that these local communities will bear the costs of co-existing with these species, and ultimately be responsible for deciding upon their conservation (Dolrenry et al. 2016). Action plans for promoting community-based conservation (Newmark and Hough 2000) and participatory monitoring whereby locals actively engage in the conservation of the species, such as those implemented in some villages around Ruaha National Park by the RCP, are vital, and could be extended to further villages, as this could have direct implications for the conservation of wildlife.

In conclusion, concerted efforts by local, regional, national and international stakeholders are needed to address the anthropogenic threats in the wildland-human interface areas, in order to improve the chances of landscape-level leopard persistence and conservation. Conservation strategies should prioritise mitigating the negative effects of intense pastoralism, conflict and large carnivore killing around RNP, as our results highlight that even in areas where leopards are believed to occur at high numbers, such as in Ruaha, the effects of human disturbance can significantly limit their distribution. Approaches such as this are timely for helping large carnivore conservation elsewhere, and specially in increasingly human-dominated habitats in areas of wildland-human interface.

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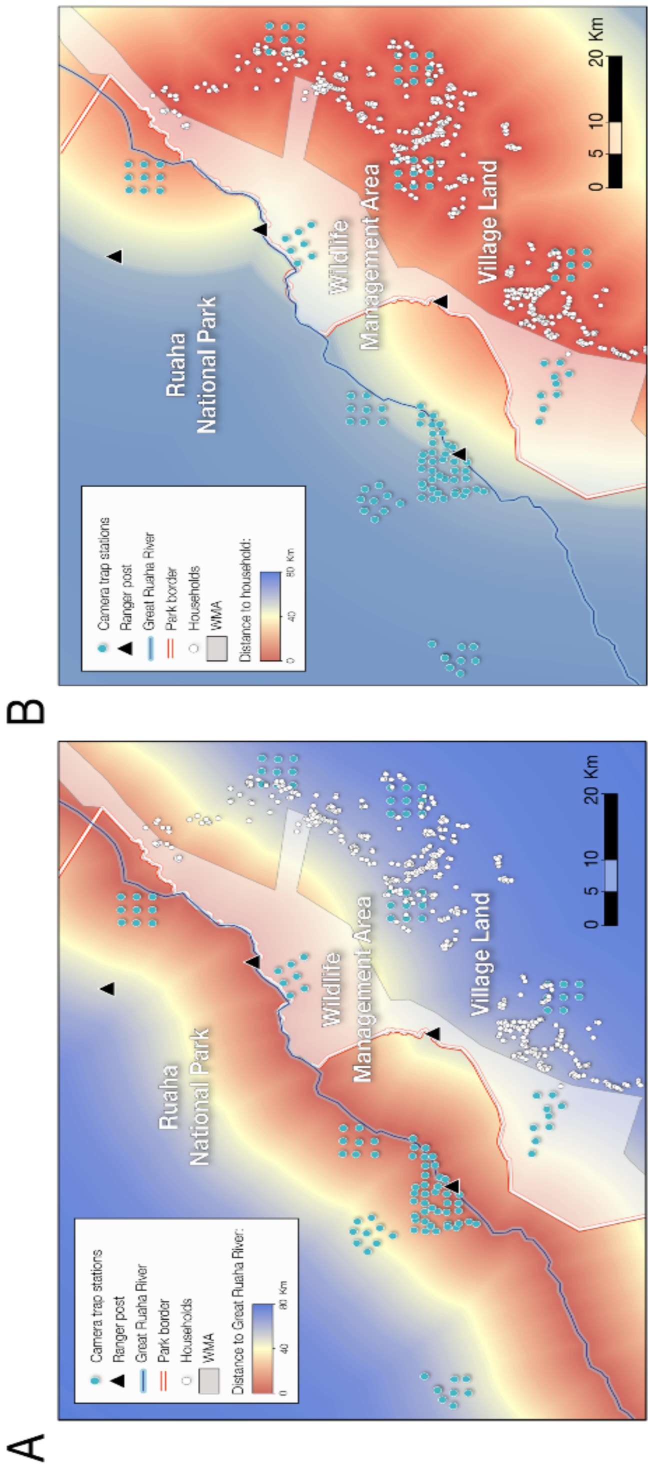

Figure S3.4. Set of covariates hypothesised to influence site use by leopards (*Panthera pardus*) across the Ruaha landscape, southern Tanzania, during our surveys in the dry seasons of 2014-2015. A. Distance to the Great Ruaha River; B. Distance to households.

Table S3.1. Pearson's correlation of the putative ecological variables used to model leopard (*Panthera pardus*) site in the Ruaha landscape, southern Tanzania. Dist.: distance

Ecological Covariates	Dist. household	Dist. Greater Ruaha river	Livestock No.	Medium prey (CPUE)
Dist. household	1	-	-	-
Dist. Great Ruaha river	-0.43	1	-	-
Livestock No.	-0.18	0.86	1	-
Medium prey (CPUE)	0.38	-0.26	-0.09	1

Table S3.2. Variance inflation factor (VIF < 3) of the ecological covariates used to model site use by leopards (*Panthera pardus*) in the Ruaha landscape, southern Tanzania.

Ecological covariates	**VIF**
Dist. household	1.36
Dist. Great Ruaha river	1.27
Livestock no.	1.05
Medium prey (CPUE)	1.18

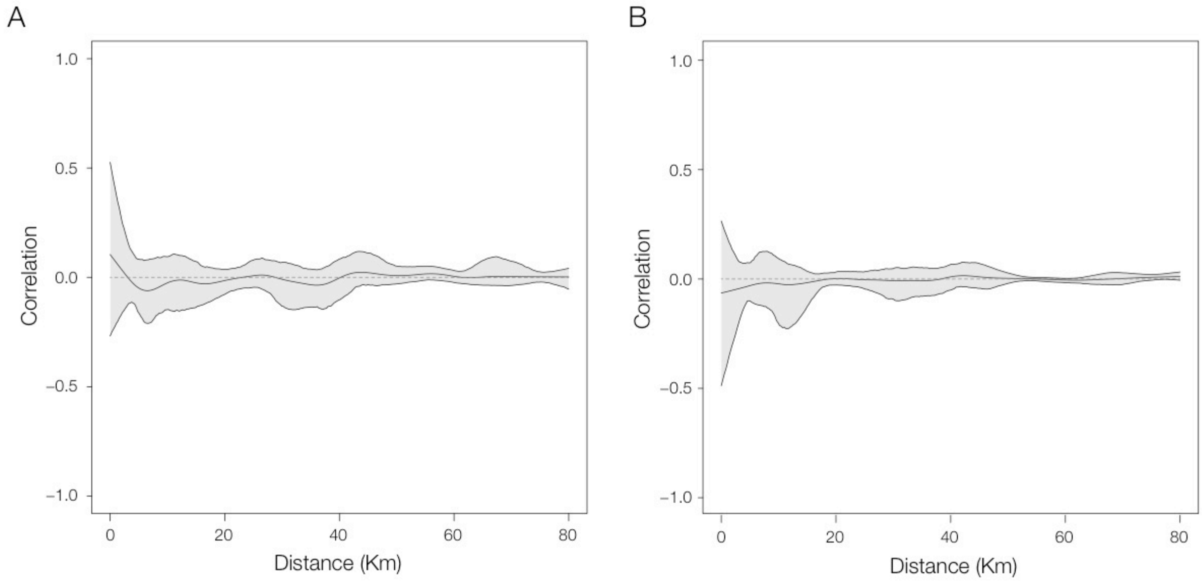

Figure S3.2. Spline correlograms for the leopard (*Panthera pardus*) occupancy models. Spline correlograms from a generalized linear model (A) and a generalized linear mixed model that included a random intercept at the CT level (B) showing a reduction in spatial autocorrelation. Distance between paired sample locations in kilometres (Km).

Chapter 4: Evaluating the spatial ecology of a carnivore guild across a gradient of anthropogenic pressure using camera-trapping and multispecies occupancy models

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*An adapted version of this chapter is currently under review status in

Journal of Animal Ecology

Abstract

Terrestrial carnivores have undergone pronounced human-induced range contractions, and experienced perilously high population declines that currently threaten their survival. Widespread land use changes, associated with human population growth, have constrained the habitat availability for carnivores, increasing range overlap of sympatric species. Despite the prevalence of these dynamics in the 21st century, there is relatively limited understanding of how carnivores inhabit shared areas along gradients of anthropogenic pressure. We investigated occupancy and interspecific interactions among a sympatric carnivore guild in Ruaha National Park, Tanzania and the village lands adjacent to the park. More specifically, we studied a dominant top-order carnivore (leopard *Panthera pardus*) and several subordinate mesocarnivores (aardwolf *Proteles cristata*, bat-eared fox *Otocyon megalotis*, black-backed jackal *Canis mesomelas*, and African civet *Civettictis civetta*). We (*i*) investigated the spatiotemporal variation in mesocarnivore detections as a function of the presence of the leopard; and (*ii*) estimated site occupancy and co-occupancy as a function of environmental, anthropogenic and potential interspecific interactions among carnivore species in Ruaha National Park, surrounding wildlife management area and village lands. We found a steady decline and lower carnivore detection in areas of increased anthropogenic pressure. Our results showed a positive spatiotemporal association in detections for black-backed jackals, African civets, and leopards. Additionally, we identified important heterogeneity on the influence of anthropogenic disturbance and landscape variables to carnivore spatial occurrence: site occupancy for most mesocarnivores was strongly determined by distance to river, whereas anthropogenic variables were the main limiting factors to civets and leopards site use. The co-occupancy models estimated increased co-occupancy probability for bat-eared foxes and black-backed jackals in areas closer to human households, although they were more likely to be found independently from each other otherwise. In this study we present an in-depth analysis of carnivore occurrence across a gradient of human occupation, as a function of anthropogenic, landscape and non-asymmetric interspecific interactions on carnivore spatial distribution. Our methods and results have applications elsewhere where humans and carnivore impinge upon each other, and further understanding of carnivore spatial distribution is needed to guide the development of targeted and contextualised conservation strategies.

Key-words: leopard; mesocarnivores; conservation; occupancy; Bayesian; human-carnivore conflict

Author contributions to the manuscript:

Experimental design: LA, RM; Data collection: LA, JC; Data analysis: LA & BL (guided the STAN model implementation); Writing of 1st draft of manuscript: LA, Improvements to manuscript: RJM, AD, DM & RM.

4.1. Introduction

The spatial distribution of wildlife species is predicated on a complex array of environmental factors that comprise habitat (Wisz et al. 2013). For instance, carnivore spatial distribution has been correlated to rainfall patterns, which influence both the allocation and availability of prey, and other variables such as soil type, land cover and elevation (Abade et al. 2014b; Loveridge et al. 2009; Moll et al. 2016; Packer et al. 2005a; Valeix et al. 2010). Additionally, interspecific interactions such as competition can have substantial effects on patterns of carnivore occurrence. This is particularly true for competitively subordinate carnivore species that might be excluded from resource-rich areas by sympatric top-order carnivores (Donadio and Buskirk 2006; Gompper et al. 2016; Swanson et al. 2016). For example, the spatial distribution of the competitively subordinate African wild dog (*Lycaon pictus*) has been shown to be limited to less optimum areas when occurring in sympatry with the more dominant lion (*Panthera leo*) to minimise the deadly risks of interspecific aggression (Creel et al. 2001; Dröge et al. 2017; Mills and Gorman 1997; Swanson et al. 2014; Vanak et al. 2013). Similarly, the arctic fox (*Alopex lagopus*) distribution has been limited to higher and less-productive altitudes due to increased competition with red foxes (*Vulpes vulpes*) in the Norwegian tundra ecosystems (Tannerfeldt et al. 2002). In another example, black-backed jackals (*Canis mesomelas*) have been found to influence habitat use and denning site of the subordinate bat-eared (*Otocyon megalotis*) and cape foxes (*Vulpes chama*) through interference competition (Kamler et al. 2012).

The multiple mechanisms that regulate interspecific interactions among carnivores (i.e. dietary, temporal and spatial niche overlap; (Broekhuis et al. 2013; Cozzi et al. 2012; Dröge et al. 2017; Hayward and Slotow 2009; Vanak et al. 2013)) are subject to external anthropogenic disturbances when carnivores occupy human-dominated landscapes (Dorresteijn et al. 2015; Haswell et al. 2016). Human-induced changes in habitat structure and subsequent disturbance of carnivore populations can increase competition and aggression over limited resources and suppress subordinate species. Such a changes can have implications for potential cascading effects on trophic systems (Dorresteijn et al. 2015; Linnell and Strand 2000), and broader influence on carnivore distribution (Haswell et al. 2016). For example, the highly competitive pumas (*Puma concolor*) and bobcats (*Lynx rufus*) have been found on increased spatiotemporal overlap in anthropogenic areas to minimise exposure to humans, which could prompt the species into intense competition and aggression over limited resources (Lewis et al. 2015). In another example, carnivores have been shown to overuse and deplete prey stock in anthropogenic landscapes to compensate decreasing feeding time due to human disturbance of their kill sites (Smith et al. 2017). As humans encroach into the most remote wilderness, there is widespread and increased competition with carnivores over limited space and resources (Chapron and Lopez-Bao 2016; López-Bao et al. 2017) that could lead to direct carnivore displacement and contribute to increased human-mediated changes in carnivore interactions (i.e. interference competition) that could result in species suppression (Kuijper et al. 2016). Thus, recent studies have highlighted the importance of investigating and understanding the combined effects of anthropogenic and landscape factors and their potential to disrupt and interfere on interspecific interactions, as these are fundamental determinants of carnivore spatial distribution and habitat use within human landscapes (Kuijper et al. 2016; Magle et al. 2012; Rota et al. 2016a; Rota et al. 2016b).

In this study, we evaluate the influence of environmental variables on occurrence patterns of a carnivore guild, composed of aardwolf (*Proteles cristata*), bat-eared fox, black-backed jackal, African civet (*Civettictis civetta*) and leopard (*Panthera pardus*), across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape while accounting for potential interspecific interactions, hereafter understood as the degree of dependence in occurrence probability between two species (MacKenzie et al. 2004). We selected these species based on their known potential to interact interspecifically and the dietary overlap that they might exhibit (Caro and Stoner 2003; Palomares and Caro 1999). The Ruaha landscape is one of the most important strongholds for carnivore conservation in Tanzania, and yet has been understudied, with little information available about the potential influence of anthropogenic pressure on carnivore distribution and conservation in the village lands around Ruaha National Park (TAWIRI 2009a). We specifically: (i) examine the conditional detection probability of subordinate carnivore species at each camera-trap station as a function of detecting leopards - a dominant carnivore species; (ii) estimate the independent site occupancy for each species solely as a function of the environmental variables; and (iii) investigate species site co-occurrence as a response to both changes in environmental and presence or absence of any other carnivore species.

We provide the first in-depth analyses of the occurrence patterns of a carnivore guild across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape. This biotic-landscape modelling approach provides more robust outputs for understanding the relation between carnivore occurrence patterns and environmental features (Gompper et al. 2016; Rota et al. 2016a), and furthers our understanding of the role of anthropogenic threats on carnivore spatial distribution across human-dominated lands, with potential implications for carnivore conservation.

4.2. Material and methods

4.2.1. Study Area

The study area is located within the 50,000 km^2 Greater Ruaha landscape of southern Tanzania, and is composed of a multiple use landscape that extends from the eastern portions of Ruaha National Park - RNP, to the Pawaga-Idodi Wildlife Management Area - WMA, and surrounding village lands. Further information on the study area, including a detailed description of ecogeographic characteristics is provided in Chapter 2 - Section 2.2.

4.2.2. Village lands

The socio-economic characteristics of the village lands surrounding Ruaha National Park, as well a description of human-carnivore conflict in these areas is provided in Chapter 2 – Section 2.2.

4.2.3. Environmental variables

We investigated carnivore occurrence as a function of anthropogenic and environmental variables with known potential to influence carnivore distribution (Table 4.1). We represented the distance to Great Ruaha River and distance to household covariates as rasters at a resolution of 500 x 500 meters (See Supporting Information – Fig. S4.1). We generated the rasters in QGIS 2.6.0 (QGIS) from freely available geoprocessed layers of satellite imagery and data collected by University of Oxford's Wildlife Conservation Research Unit, Ruaha Carnivore Project (RCP). We calculated the percentage of vegetation cover around each CT using raster data derived from the GlobCover project (ESA 2009) and land-use conversion extracted from Jacobson et al. (2015). We reclassified the vegetation types in the study site into three main categories: open natural fields, human converted lands, and vegetated areas. The reclassified raster was used to estimate the proportion of vegetation coverage surrounding each CT within a 1 km buffer based on FRAGSTATS (McGarigal et al. 2012) metrics estimated in R v.2.13.0 (R Core Team 2012) through the 'raster' (Hijmans and van Etten 2014), 'sp' (Pebesma and Bivand 2005), 'rgdal' (Bivand et al. 2017) and SDMTools (VanDerWal et al. 2014) packages. We calculated the livestock number covariate by summing the total independent livestock detections at each CTs (we considered detections for cattle, goats and donkeys altogether).

Prior to model fitting, we standardized (z-score) all covariates (Long et al. 2011), and assessed predictor collinearity using Pearson correlation and variance inflation factor tests. All the covariates used in the models were those minimally correlated (Pearson <0.7, VIF <3 (Zuur et al. 2010); Table S4.1-4.2).

Table 4.1. Environmental variables used to assess carnivore occupancy and detection in the Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015.

Variables	Class	Model type	Published evidence of influence on carnivore occurrence
No. livestock	Anthropogenic	Ψ	Schuette et al. 2013
Dist. Great Ruaha River	Habitat	Ψ	Abade et al. 2014; Cusack et al. 2015
Dist. household	Anthropogenic	Ψ	Schuette et al. 2013; Henschel et al. 2008
Vegetation cover (%)	Habitat	Ψ	Abade et al. 2014; Rich et al. 2017
Trail type	Habitat	P	Cusack et al. 2015

[a]Ψ. probability of site use; P. probability of detection; Dist. Distance.

4.2.4. Multispecies carnivore data

We collected occurrence data on the assemblage of carnivores during the dry seasons (May-December) of 2014 and 2015, via the deployment of 127 non-baited remotely triggered single camera-trap stations – CTs, across 11 sampling areas in the study site (Fig. 4.1).

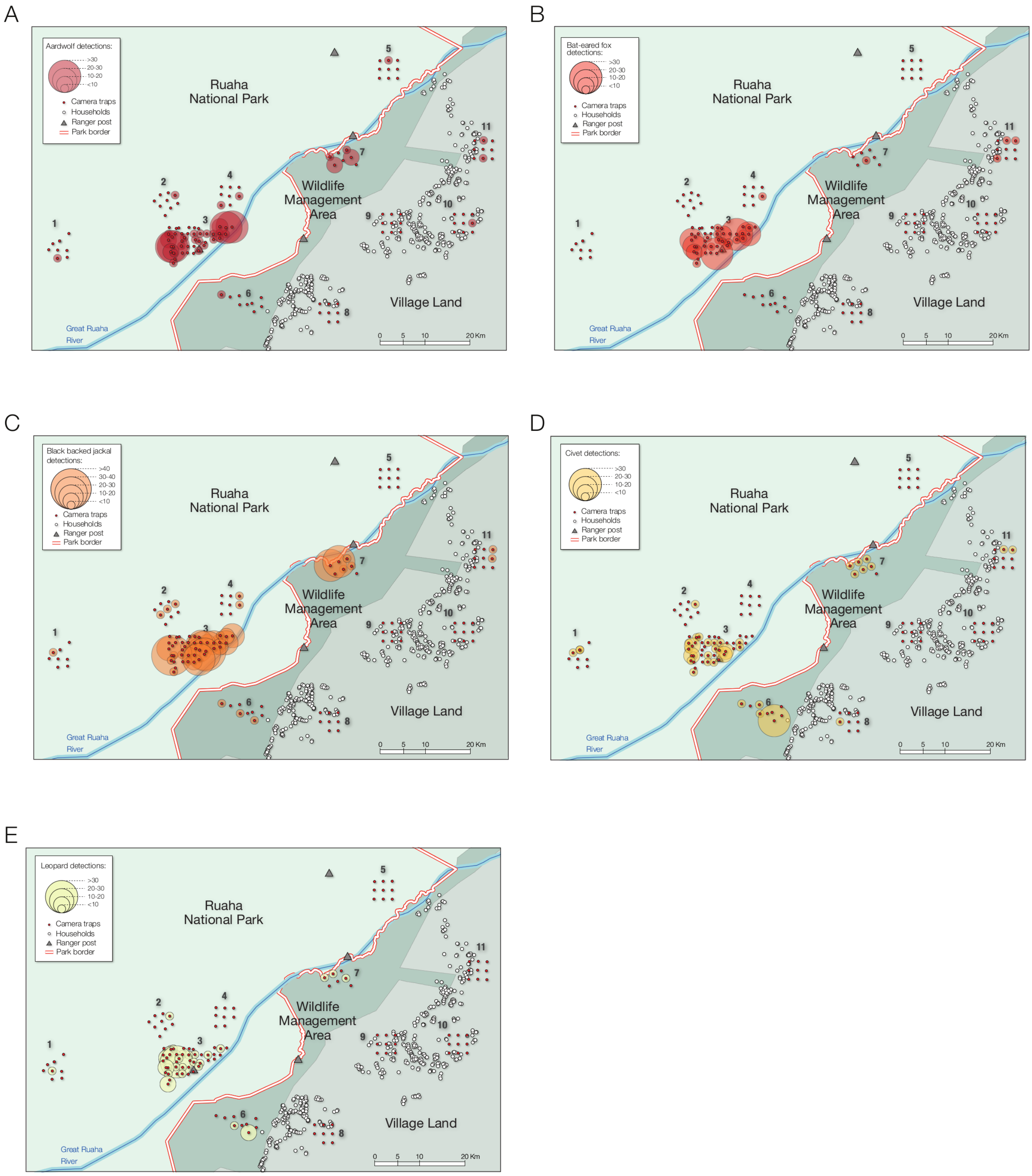

Figure 4.1. Location of the study site and distribution of camera-trap stations (red shaded circles) across the Ruaha landscape, southern Tanzania. 1-11 represents sampling areas: 1. Mdonya; 2. Kwihala; 3. Msembe; 4. Mwagusi; 5. Lunda-Ilolo; 6. Pawaga; 7. Lunda; 8. Idodi; 9. Malinzanga; 10. Nyamahana; 11. Magosi. The shaded circles represent independent carnivore detections (> 5 minutes between detection) at each camera-trap station across the study site. A. Aardwolf (*Proteles cristata*); B. Bat-eared fox (*Otocyon megalotis*); C. Black-backed jackal (*Canis mesomelas*); D. African civet (*Civettictis civetta*); E. Leopard (*Panthera pardus*).

The data on carnivore occurrence was collected using the same methodological approach described in Chapter 2. A detailed description on the survey design and implementation, camera-trapping setup and data collection is provided in Chapter 2. It is noteworthy that in this study site use equates to the probability that a given site was used during the survey period, rather than the probability of continuous site occupation (MacKenzie et al. 2006). Thus, we modelled carnivore occupancy as the probability of site use during the study period at the CT level. We considered independent detection events for carnivores and livestock as those with > 5 minutes between records (Burton et al. 2012).

4.2.5. Modelling carnivore occurrence patterns

4.2.5.1. Conditional detection probability of carnivores

The conditional detection probability model was developed assuming that the presence of the more dominant leopard could limit the probability of detection of the smaller carnivores, and was based on the outputs of a survival analysis, also known as time-to-event analysis. For each camera station at which both leopard and a given small carnivore were captured, we first evaluated the time delay (in hours) between each leopard detection and the next detection of the smaller carnivore (i.e. an event). If either another leopard detection or camera failure occurred before the small carnivore was detected, we assigned a censored status to the time observation. We then fitted four different types of parametric survival functions to the combined observed and censored events: exponential, Weibull, log-normal and log-logistic distributions. Model selection was based on Akaike's Information Criteria (AIC) (Akaike 1981). After identifying the best function (Table S4.3), we predicted the hazard rate for 120 hours, which translates as the instantaneous probability of detecting any subordinate carnivore species over time following the detection of a leopard at the same CT. We then generated a null expectation for the hazard rate curve by randomizing the timing of the observed subordinate species detections 1,000 times, taking into account the CT location and the species' activity pattern (derived from the pooled survey data), and fitting the same models as for the observed dataset. It is important to note that a simple exponential distribution cannot be considered as the null model in this case owing to the higher likelihood of a small carnivore detection occurring soon after a leopard detection. Indeed, longer delays are more likely to be censored by another detection of a leopard or camera failure. Finally, for each hour, we obtained a two-tailed p-value (with sequential Bonferroni correction) describing the probability of observing a hazard rate that was lower or higher than the null distribution. These analyses were performed in R v.2.13.0 (R Core Team 2012).

4.2.5.2 Site occupancy models

The site occupancy models were developed using a hierarchical Bayesian framework based on single-season occupancy models (MacKenzie et al. 2002). We used temporally replicated surveys (i.e. weeks) to estimate the latent, unobserved probability of site use of each CTs Z_i, where $Z_i = 1$ if site i is occupied and 0 otherwise, and detection probability $p_{i,j}$, where $p_{i,j}$ is the probability that each carnivore species are detected at site i during replicate j, given use of that site (i.e., Z_i = 1) (MacKenzie et al. 2002; Tyre et al. 2003). Our model to estimate carnivore occurrence was implemented as follows:

$$\text{logit}(\Psi_i) = \alpha_0 + \alpha_1{*}\text{livestock number}_i + \alpha_2{*}\text{distance river}_i + \alpha_3{*}\text{distance household}_i + \alpha_4{*}\text{vegetation cover}_i$$

(*Eq. 4.1*)

where Ψ_i represents the probability of carnivore site use at the i^{th} CT, and $\alpha_{1,2,\ldots5}$ represent the influence of associated covariates at the i^{th} CT (Table 4.1).

The detection model was implemented as follows:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_k{*}\text{trail}_i$$

(*Eq. 4.2*)

where $p_{i,j}$ represents the probability of detection at the i^{th} CT during survey j given that a site is used (i.e., Z_i = 1), β_0 is the intercept, and β_k represents the effect of the k^{th} trail type on carnivore detection at each CT (k = 3), with animal trail (AT) as the reference category.

We implemented and analysed the models using a Bayesian framework and Markov chain Monte Carlo (MCMC) simulations in R v.2.13.0 (R Core Team 2012) and JAGS (Plummer 2003) through the package 'R2jags' (Su and Yajima 2012). We estimated the degree of support for the effect of each covariate on carnivore site use through the Bayesian inclusion parameter w_c (Kuo and Mallick 1998), which had a Bernoulli distribution and an uninformative prior probability of 0.5. The posterior probability of w_c corresponds to the estimated probability of any given covariate ('C') to be included in the best model of a set of 2^C candidate models (Burton et al. 2012; Moll et al. 2016; Royle and Dorazio 2008). We calculated model-averaged estimates for the covariate coefficients over the global models from MCMC posterior histories, as described by Royle & Dorazio (2008). We used uninformative uniform priors and implemented the models using three chains of 100,000 iterations each, discarding the first 10,000 as burn-in, and thinned the posterior chains by 10. We assessed the model convergence by ensuring R-hat values for all parameters <1.1 (Gelman and Hill 2007).

4.2.5.3. Species co-occupancy

We investigated species co-occupancy based on a generalization of MacKenzie et al.'s single-season single species occupancy model (MacKenzie et al. 2002), following a recently developed co-occurrence model developed by Rota et al. (2016a). This model framework assumes that the latent site occupancy state equates to a multivariate Bernoulli random variable, which enables constructing a covariates model for species co-occurrence that does not require assumptions of asymmetric interactions (Rota et al. 2016a). The model enables obtaining results from pairwise correlation between species using basic probability theory, and has the advantage of allowing the influence of any environmental variable on a given species to vary in the presence or absence of another; this enables assessing whether the probability of co-occurrence for two species vary along an environmental gradient (Rota et al. 2016a). The latent co-occurrence, hereafter, co-occupancy model of species s at site i as a multivariate Bernoulli random variable (MVB) was implemented as such:

$$\mathbf{Z}_i \sim \mathrm{MVB}(\Psi_i)$$

(*Eq. 4.3*)

where $\mathbf{Z}_i = (z_{1i}, z_{2i}, \ldots, z_{Si})$ is a S-dimensional vector of 1's and 0's for the latent occupancy state for all S species, Ψ_i is a 2^{S-} dimensional vector denoting the probability of all possible sequences of 1's and 0's for $\mathbf{Z}_i$, such as the probability sum equals to 1 (Rota et al. 2016a). We investigated the probability of co-occupancy for species as a function of species-specific and pairwise interaction parameters (Table 4.2), assuming a logistic prior distribution for all parameters (Rota et al. 2016a).

We modelled carnivore detection probability solely as a function of environmental variables, similarly to Eq. 4.2. It is important to notice that our detection model here was species-specific and implemented solely as a function of trail types.

We implemented models in STAN v.2.8.0 using RSTAN v.2.8.0 in R v.2.13.0 (R Core Team 2012). We ran models using four chains, and determined convergence according by ensuring R-hat values for all parameters <1.1 (Gelman and Hill 2007). All models achieved convergence after 1,000 iterations, and a burn-in phase of 500.

Table 4.2. Models used to estimate conditional site co-occupancy for the assemblage of carnivores in Tanzania's Ruaha landscape, during the dry seasons of 2014-2015.

Species	Model
AAD (*f*1)	
BEF (*f*2)	
BBJ (*f*3)	$\alpha_0 + \alpha1$*livestock number$i$ + $\alpha2$*distance river$i$ + $\alpha3$*distance household$i$ + $\alpha4$*vegetation cover$i$ + $\beta0$ + βk*trail$i$
CIV (*f*4)	
LEOP (*f*5)	
AAD+BEF	$\text{logit}^{-1}(f1 + f2 + f1,2)$
AAD+BBJ	$\text{logit}^{-1}(f1 + f3 + f1,3)$
AAD+CIV	$\text{logit}^{-1}(f1 + f4 + f1,4)$
AAD+LEOP	$\text{logit}^{-1}(f1 + f5 + f1,5)$
BEF+BBJ	$\text{logit}^{-1}(f2 + f3 + f2,3)$
BEF+CIV	$\text{logit}^{-1}(f2 + f4 + f2,4)$
BEF+LEOP	$\text{logit}^{-1}(f2 + f5 + f2,5)$
BBJ+CIV	$\text{logit}^{-1}(f3 + f4 + f3,4)$
BBJ+LEOP	$\text{logit}^{-1}(f3 + f5 + f3,5)$
CIV+LEOP	$\text{logit}^{-1}(f4 + f5 + f4,5)$

*f*1 to *f*5 are the species-specific site occupancy models. The additive interactions represent the conditional co-occupancy models. AAD. Aardwolf; BEF. bat-eared fox; BBJ. black-backed jackal; CIV. African civet; LEOP. leopard.

4.3. Results

4.3.1. Conditional detection models

Our conditional detection models suggested that none of the species showed significant spatiotemporal avoidance from a site that had just been used by a leopard (Fig. 4.2). Conversely, the results suggested that black-backed jackals had a slight non-significant increase in detection probability following a leopard detection event, and African civets' detection probability was significantly higher within the first 40 hours of detecting a leopard (Fig. 4.2).

4.3.2. Site occupancy

We recorded a total of 357 aardwolves, 286 bat-eared foxes, 642 black-backed jackals, 244 African civets and 232 leopard independent detections over 12,987 camera-trap days (Fig. 4.1, Table 4.3). The total number of detections varied according to the gradient of anthropogenic pressure, with all species (except bat-eared fox) being consistently more likely to be detected within RNP and in the WMA (Table 4.3). Leopard was the only carnivore species not detected in the village lands. We registered a total of 2,811 independent events of livestock in 32 out of 35 village land CTs.

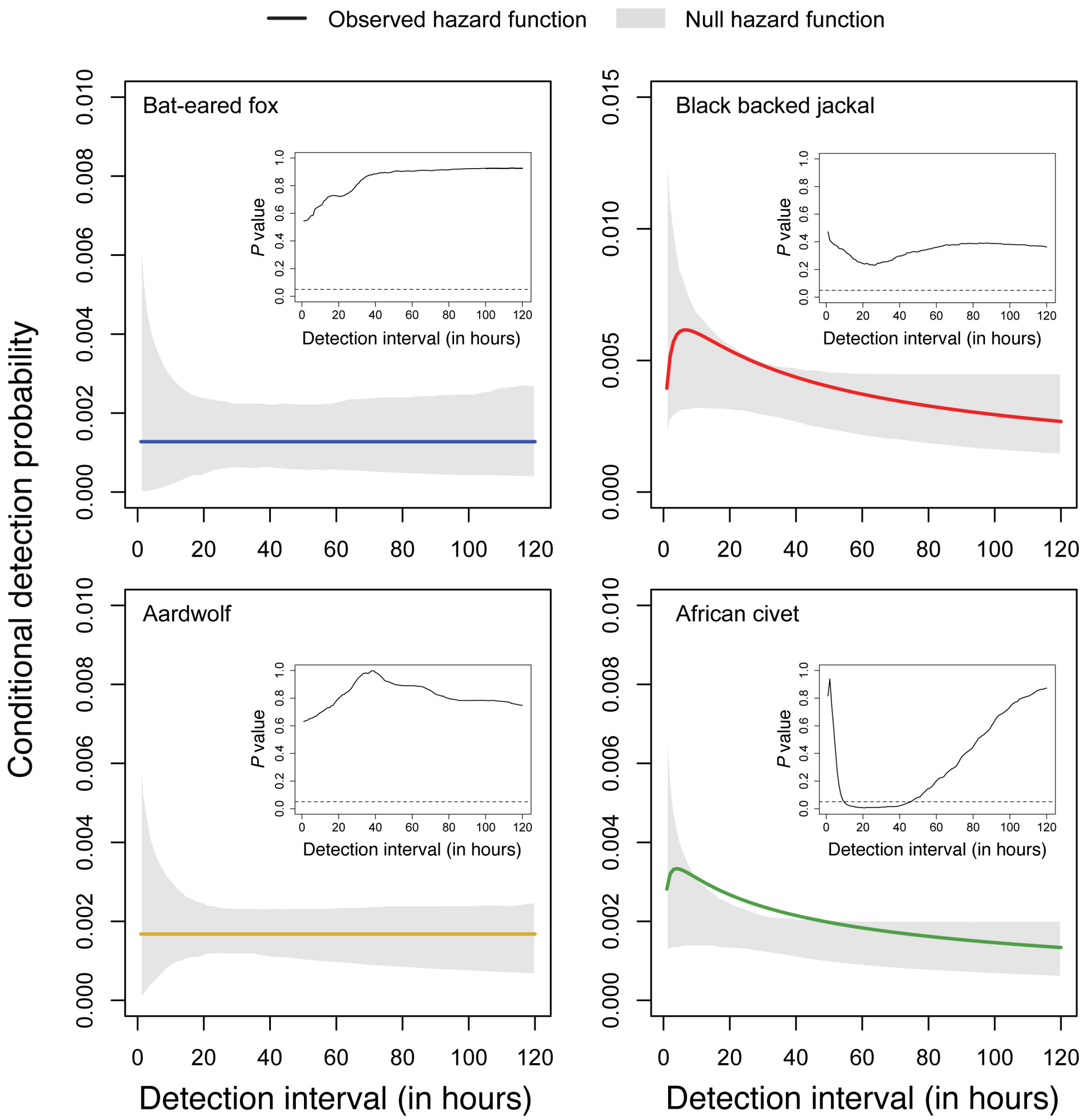

Figure 4.2. Conditional detection probability estimates for carnivores as a function of leopard detection at each camera-trap station. The colored line represents the hazard function estimated from the observed data, the shaded grey polygon represents the "null space" based on 1,000 null hazard functions, and the inset shows detection probability significance as a function of leopard detection for each hour.

Table 4.3. Total number of detections and (%) site occupancy estimates for carnivores across the gradient of anthropogenic pressure in Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015.

	No. Detections				
Species	**RNP**	**WMA**	**VL**	**(%)Naïve Occu**	**(%) Occu**
AAD	308	38	11	38.5	44.9
BEF	263	4	19	30	37.1
BBJ	532	102	8	48	54.4
CIV	152	82	10	42.5	56.8
LEOP	197	35	0	33	43.8

AAD. Aardwolf; BEF. bat-eared fox; BBJ. black-backed jackal; CIV. African civet; LEOP. leopard. RNP. Ruaha National Park; WMA. Wildlife Management Area; VL. Village Land. Occu. Occupancy estimates accounting for imperfect detection.

The set of variables determining carnivore site occupancy varied according to each species. Aardwolf, bat-eared fox and black-backed jackal occupancy was primarily influenced by proximity to the Great Ruaha River (Table 4.4). Additionally, bat-eared fox occupancy was also associated with those habitats closer to households; conversely, African civet and leopard site occupancy was strongly limited by increased number of livestock and proximity to households. Leopards were also influenced by proximity to the Great Ruaha River (Table 4.4). Trail type showed no major influence on the detection of the carnivore species, although we found bat-eared foxes less likely to be detected on roads (Table 4.4).

Table 4.4. Posterior means, standard deviations (S.D.), 95% credible intervals (C.I.), and Bayesian inclusion parameters (w_c) for carnivore occupancy models fit to camera-trap data from the Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015. Significant effects highlighted in bold.

Species	Variables	Mean	SD	2.50%	97.50%	w
	No Livestock CT	-1.7	1.63	-6	0.21	0.13
	Dist River	**-2.24**	**0.53**	**-3.33**	**-1.28**	**1**
	Dist Household	-0.63	0.58	-1.87	0.43	0.11
Aardwolf	% Vegetation Cover	0.14	0.24	-0.32	0.64	0.03
	Trail N	-0.78	0.36	-1.57	-0.1	0.02
	Trail Road	0	0.28	-0.58	0.53	0.02
	Sites occupied	57.1	2.75	52	63	NA
	No Livestock CT	-1.66	1.7	-6.02	0.32	0.13
	Dist River	**-3.17**	**1.13**	**-5.77**	**-1.43**	**1**
	Dist Household	**-2.32**	**1.15**	**-4.87**	**-0.38**	**0.64**
Bat-eared fox	% Vegetation Cover	-0.69	0.35	-1.4	0	0.24
	Trail N	-1.06	0.97	-2.78	1.01	0.16
	Trail Road	-1.69	0.78	-3.27	-0.22	0.16
	Sites occupied	47.13	3.63	41	56	NA
	No Livestock CT	-2.46	1.92	-7.23	0.06	0.22
	Dist River	**-2.11**	**0.48**	**-3.08**	**-1.2**	**1**
	Dist Household	0.28	0.46	-0.61	1.21	0.06
Black-backed jackal	% Vegetation Cover	0.19	0.25	-0.29	0.69	0.04
	Trail N	-0.33	0.25	-0.82	0.13	0
	Trail Road	-0.28	0.23	-0.72	0.15	0
	Sites occupied	69.11	2.54	64	74	NA
	No Livestock CT	**-7.05**	**2.27**	**-9.9**	**-1.74**	**0.91**
	Dist River	-0.41	0.69	-1.61	1.11	0.11
	Dist Household	**1.55**	**0.7**	**0.35**	**3.09**	**0.67**
African Civet	% Vegetation Cover	0.44	0.37	-0.29	1.16	0.09
	Trail N	0.28	0.32	-0.3	0.94	0
	Trail Road	0.24	0.29	-0.35	0.81	0
	Sites occupied	72.11	3.94	65	80	NA
	No Livestock CT	**-5.67**	**2.88**	**-9.83**	**-0.1**	**0.5**
	Dist River	**-2.27**	**1.06**	**-4.65**	**-0.36**	**0.65**
	Dist Household	**2.77**	**1.06**	**0.97**	**5.07**	**0.98**
Leopard	% Vegetation Cover	0.84	0.46	0	1.8	0.26
	Trail N	-0.33	0.46	-1.35	0.48	0.01
	Trail Road	-0.48	0.42	-1.4	0.36	0.01
	Sites occupied	55.65	3.87	48	63	NA

4.3.3. Co-occupancy models

Our co-occupancy models found a positive conditional occupancy for bat-eared foxes and black-backed jackals (i.e. the 95% credible intervals for the intercept parameter for the co-occupancy model did not overlap 0) (Table 4.5). These species showed independent site occupancy patterns across most of the gradient of anthropogenic pressure, but were more likely to co-occupy the same sites when in close proximity to human households, with no significant influence from the other variables (Table 4.6; Fig. 4.3).

Table 4.5. Posterior means, standard deviations (S.D.), and 95% credible intervals (C.I.), for pairwise carnivore interaction and co-occupancy estimates. Models fit to camera-trap data collected in the Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015. Significant interactions highlighted in bold.

Interacting species	Mean	SD	2.50%	97.50%
AAD + BEF	1.17	0.78	-0.20	2.69
AAD + BBJ	0.56	0.76	-0.94	2.22
AAD + CIV	-0.45	0.73	-1.83	0.90
AAD + LEOP	-0.66	1.06	-2.66	1.35
BEF + BBJ	**2.67**	**0.85**	**1.13**	**4.31**
BEF + CIV	0.81	0.80	-0.77	2.23
BEF + LEOP	-1.52	1.17	-3.98	0.51
BBJ + CIV	1.27	0.74	-0.11	2.84
BBJ + LEOP	1.49	0.96	-0.41	3.49
CIV + LEOP	1.27	0.85	-0.26	2.83

AAD. Aardwolf; BEF. bat-eared fox; BBJ. Black-backed jackal; CIV. African civet; LEOP. leopard

Table 4.6. Posterior means, standard deviations (S.D.), and 95% credible intervals (C.I.), for pairwise carnivore interaction and co-occupancy estimates for bat-eared fox (*Otocyon megalotis*) and black-backed jackal (*Canis mesomelas*). Models fit to camera-trap data collected in the Ruaha landscape, southern Tanzania, during the dry seasons of 2014-2015. Significant effects highlighted in bold.

Variables	Mean	SD	2.50%	97.50%
No Livestock CT	0.12	1.22	-2.19	2.26
Dist River	-0.49	1	-2.55	1.41
Dist Household	**-1.94**	**0.99**	**-3.92**	**-0.01**
% Vegetation Cover	0.03	0.83	-1.52	1.56

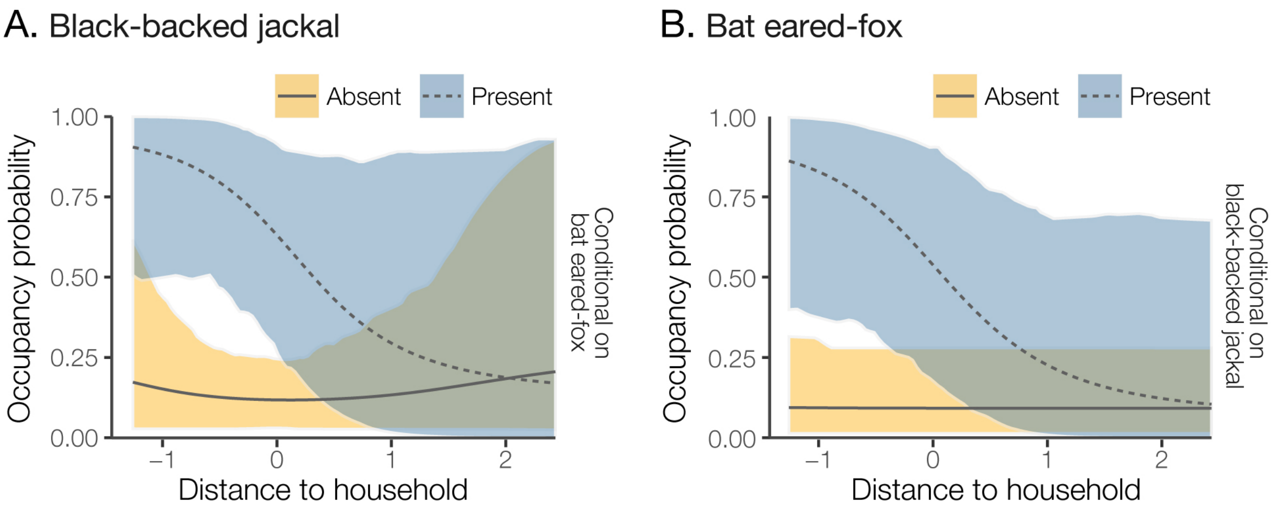

Figure 4.3. Site occupancy probability of black-backed jackal (*Canis mesomelas*) and bat-eared fox (*Otocyon megalotis*) conditional on the presence and absence of each of the other species. The plot in column 1 represents black-backed jackal occupancy probability, conditional on the presence and absence of bat-eared fox. The solid and dashed lines represent posterior means, and the shaded polygons the 95% credible intervals. Distance to household in standardised values (z-score), rescaled to have a mean of zero and a standard deviation of one. The variables not represented in the plot are assumed fixed at their observed mean (Rota et al. 2016).

4.4. Discussion

An understanding of the functional mechanisms by which environmental and anthropogenic variables affect carnivore occupancy patterns, mediate interspecific interactions, and determine their spatial distribution in increasingly anthropogenic landscapes provides much needed information that can be used to help guiding strategies to conserve carnivores outside protected areas (Kuijper et al. 2016; Magle et al. 2012). In this study, we investigated the determinants of the spatial distribution of a carnivore guild across a multi-use landscape in southern Tanzania, using a novel approach that facilitated examination of the combined effects of environmental, anthropogenic, and interspecific interactions on carnivore species occurrence.

4.4.1. Carnivore spatial distribution patterns

We found a consistent decline in carnivore detections outside Ruaha National Park (Fig. 4.1; Table 4.3), with carnivores detected in only 6 out of 35 camera-stations in the village lands (Fig. 4.1), mostly in the northern sections of the study site. Fewer detections are often associated with small population sizes in surveyed areas (Royle and Nichols 2003), which could be an indication of comparatively low carnivore densities in the village lands. The association of unsuitable environmental conditions (e.g. distance to the Great Ruaha River), with intense pastoralism, rapid conversion of habitats due to human and livestock encroachment (Lankford et al. 2009; Wenban-Smith 2015), bushmeat poaching (Knapp et al. 2017), and the widespread conflict-related carnivore killing (Dickman 2015; Dickman et al. 2014) could be contributing to the low carnivore numbers and consequently, lower detections in these habitats. Indeed, mesocarnivores like civets and black-backed jackals can also create conflict with people either due to real or perceived risk (Kissui 2008; Mateos et al. 2015; Nattrass et al. 2017). Consequently, these species are subject to human persecution, which represents a major cause of mortality for these species through their range (Carpaneto and Fusari 2000; Croes et al. 2008; Nattrass et al. 2017; Ray et al. 2005; Stein et al. 2016; Thorn et al. 2012). That being said, most of the reported human-induced carnivore killings in this area are associated with retaliatory and cultural hunts of larger species such as lions and leopards (Abade et al. 2014a; Dickman 2015; Dickman et al. 2014). Thus, other underlying factors unaccounted here such as habitat loss, change in vegetation structure, and prey depletion could be influencing mesocarnivore distribution in the village lands. For example, the associated changes in habitat structure and increased shrub cover from intense livestock grazing has been found to limit the abundance of smaller prey items such as rodents, termites and beetles, and the diversity of mesocarnivores in savannahs (Blaum et al. 2007; Blaum et al. 2009). Additionally, the increased number of potential predators such as domestic and free-ranging dogs around households, which are known to limit mesocarnivore distribution in human landscapes (Craft et al. 2017; Lepczyk 2015; Young et al. 2011), could be contributing to the low detections of the smaller carnivores in the village lands. Nonetheless, the results presented here are concurrent with previous studies (Abade et al., under review) that suggest the human-dominated landscapes as a “hard edge” that limits carnivore distribution outside Ruaha National Park. We acknowledge that the precise causes and the mechanistic connections between low carnivore detections and the variety of sources of anthropogenic pressure in the village lands are elusive and difficult to quantify. However, our results are among the first to characterise site occupancy by a carnivore guild across a gradient of anthropogenic pressure in East Africa, and help furthering our understanding of the effects of human activities on limiting carnivore spatial distribution outside protected areas.

When carnivores co-occur, subordinate species will often spatiotemporally adjusts their habitat use in areas of overlap with larger, higher trophic order dominant carnivores to reduce the associated risks of predation (Broekhuis et al. 2013; Dröge et al. 2017; Palomares and Caro 1999; Vanak et al. 2013). Such changes can have profound effects on carnivore detection rates (Farris et al. 2016; Steinmetz et al. 2013), with some studies reporting over 50% decline in detecting subordinate species where they overlap with dominant carnivores (Steinmetz et al. 2013). Our results however, suggest that leopards had limited influence on the detection of the subordinate carnivores when they overlapped in this study area. Conversely, we found a positive association between detections for civets and black-backed jackals, and those for leopards (Fig. 4.2). These patterns are likely associated to the opportunistic scavenging behaviour exhibited by these smaller carnivores (Bothma 1971; Loveridge and Macdonald 2002; Newmark et al. 1996; White and Diedrich 2012), despite their overall limited reliance on carrion and carcass feeding (Benbow et al. 2015; Hunter et al. 2007).

The site occupancy patterns observed in our study suggest heterogeneity in carnivore responses to human disturbances, and that species tolerance to anthropogenic pressure is both context and species-specific. Site occupancy for aardwolves, bat-eared foxes and black-backed jackals was primarily determined by landscape traits such as proximity to the Great Ruaha River, whereas leopards and civets were mostly limited by anthropogenic disturbance (Table 4.4). Our results corroborate previous findings (Abade et al. 2014b; Cusack et al. 2016; Cusack et al. 2015), and highlight the importance of the Great Ruaha River on determining carnivore spatial distribution during the dry seasons in the Ruaha landscape. In addition, the strong negative influence of anthropogenic variables on civet occupancy detected here is surprising as the species is often described as ecologically tolerant to highly anthropogenic habitats such as farmlands and crop fields across Africa (Do Linh San et al. 2015; Mateos et al. 2015; Ray et al. 2005). Yet, similar findings have been reported in other multiple use landscapes in Africa, where civet occurrence was correlated with distance to households (Craft et al. 2017; Schuette et al. 2013b), which suggests that this species is relatively sensitive to anthropogenic disturbance, as observed here. Additionally, the negative influence of anthropogenic-related variables to leopard site occupancy is concurrent with other studies in Africa that found leopard use of habitat and abundance to be negatively influenced by high human activity, pastoralism and increased bushmeat (Henschel et al. 2011; Ramesh et al. 2017; Schuette et al. 2013b). These results are of conservation concern, as they show that even in landscapes where carnivores are believed to occur at high numbers, such as in Ruaha, the effects of human disturbance can significantly limit their distribution.

The pair-wise site co-occupancy models provided an interesting insight into the factors determining species occurrence across the gradient of anthropogenic pressure. These observations could not have been made if not for the application of this multi-species framework. For example, black-backed jackals and bat-eared foxes were more likely to be found independently from each other in those habitats closer to the Great Ruaha River; however, the models suggested an increased co-occupancy conditional probability determined by proximity to human households when these species were found in the village lands. One possible explanation for these results is the potentially increased availability of anthropogenic food resources around households in the village lands, as this type of "unnatural" food subsidy has been correlated with enhanced mesocarnivore numbers in anthropogenic landscapes (Mohammadi et al. 2017; Newsome et al. 2015). Black-backed jackals, which show dietary niche overlap with bat-eared foxes (Fleming et al. 2017), have been found to rely substantially on anthropogenic food waste (Kaunda and Skinner 2003; Lepczyk 2015; Nattrass et al. 2017) in areas of human occupation. Interestingly, black-backed jackals often act as predators of bat-eared foxes (Kamler et al. 2013), so the positive association found between these species requires further investigation. Similarly, domestic dogs, which are often numerous in the households across the study site (Dickman 2008), could limit the occurrence of these species through predation (Fleming et al. 2017; Lepczyk 2015), so again, the positive association with human households requires further investigation. We acknowledge that the limited number of records for these species in the village lands could be interfering in the co-occupancy model estimates, and further data collection efforts could help to investigate the patterns depicted here.

Our study presented an in-depth analysis of the ecological and anthropogenic factors influencing carnivore distribution. The framework used here represents an important improvement in our ability to investigate community-level carnivore spatial ecology while accounting for potentially complex interactions between species, imperfect detection and the influence of environmental variables, with applications elsewhere where carnivores occupy gradients of anthropogenic pressure.

4.4.2. Conservation implications

Whilst our findings suggest that site occupancy for each taxa was determined by a distinct combination of anthropogenic and landscape variables, they combined to highlight the limiting effect of the anthropogenic landscape on the overall carnivore distribution outside Ruaha National Park. Similar results have been found elsewhere in Africa, where carnivores' site occupancy, population density, and overall spatial ecology have been thwarted by increased human and livestock encroachment, intense pastoralism, conflict and human-mediated mortality in anthropogenic landscapes surrounding protected areas (Burton et al. 2012; Rich et al. 2016). Thereby, our results highlight the importance of the protected area to the conservation of the carnivore guild examined in this study. Large protected areas such as Ruaha National Park are fundamental to the preservation of important habitats for carnivores (Di Minin et al. 2016b;

Lindsey et al. 2017b) against the increasing human pressure observed in village lands surrounding protected areas across Africa (Lankford et al. 2009; Newmark 2008; Wittemyer et al. 2008). Furthermore, our findings suggest that carnivore conservation in the areas of human occupation is likely imperiled, and concerted efforts by local, regional, national and international stakeholders is needed to address the human-mediated threats to carnivores found immediately adjacent to protected areas. Conservation strategies should prioritise mitigating the negative effects associated to pastoralism, prey depletion, conflict, and carnivore killing around RNP, as our results highlight they can be of significant contribution to limiting carnivore distribution in Ruaha.

Chapter 4. Supporting Information

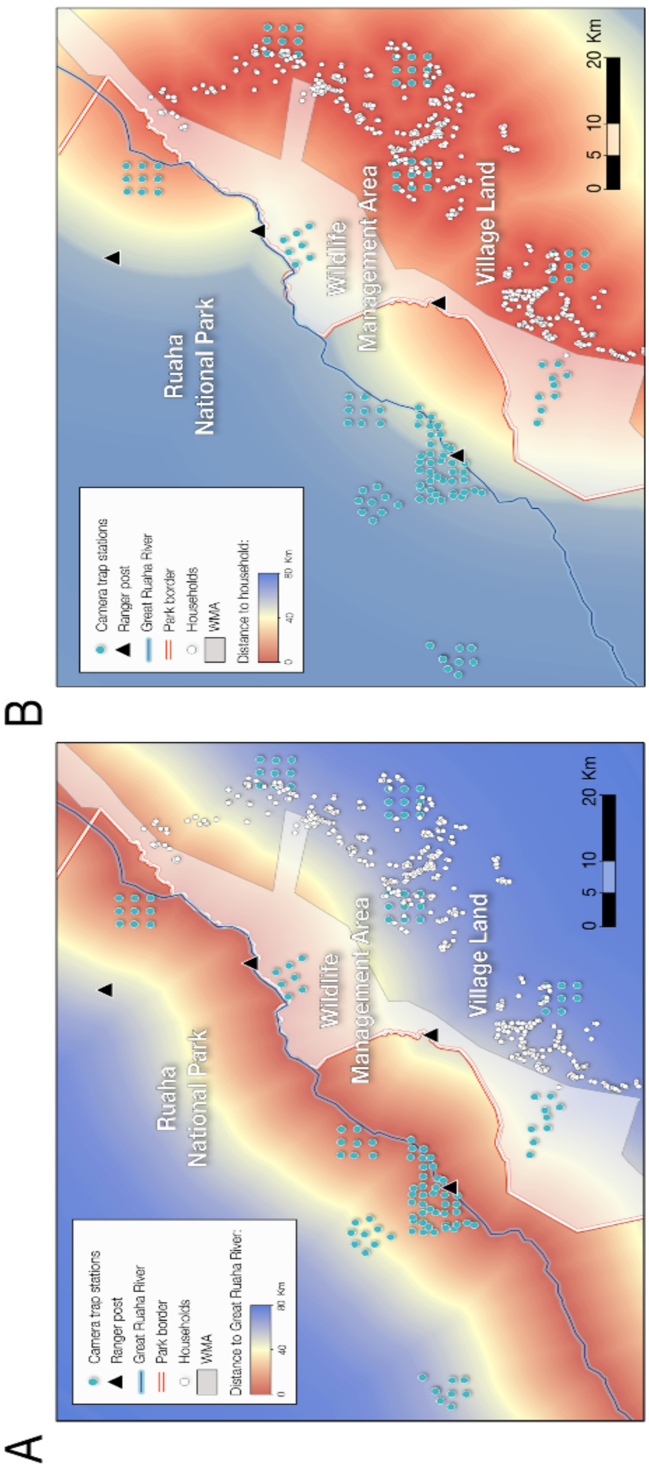

Figure S4.1. Set of covariates hypothesised to influence carnivore site use across the Ruaha landscape, southern Tanzania, during our surveys in the dry seasons of 2014-2015. A. Distance to the Great Ruaha River; B. Distance to households.

Table S4.1. Pearson's correlation of the putative ecological variables used to model carnivore site in the Ruaha landscape, southern Tanzania. Dist.: distance

Ecological Covariates	Dist. household	Dist. Greater Ruaha river	Livestock No.	% Vegetation cover
Dist. household	1	-	-	-
Dist. Great Ruaha river	-0.43	1	-	-
Livestock No.	-0.17	0.21	1	-
% Vegetation cover	-0.60	0.29	0.01	1

Table S4.2. Variance inflation factor (VIF < 3) of the ecological covariates used to model carnivore site use in the Ruaha landscape, southern Tanzania.

Ecological covariates	**VIF**
Dist. household	1.81
Dist. Great Ruaha river	1.26
Livestock no.	1.07
% Vegetation cover	1.6

Table S4.3. Survival distributions per species (based on the lowest AIC). Values indicated in bold represent the best parametric survival functions applied to the combined observed and censored detection events at each camera-trap station.

Species	**Exponential**	**Weibull**	**Log-normal**	**Log-logistic**
Bat-eared fox	**93.96**	95.93	96.16	95.99
Black-backed jackal	427.23	427.91	**423.94**	426.23
Aardwolf	**223.68**	225.65	224.12	225.25
African civet	401.42	401.15	**397.37**	400.35

Chapter 5: Mapping the suitability of habitat for lions (*Panthera leo*) across two stronghold populations in southern Tanzania

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*An adapted version of this chapter will be submitted to the journal Proceeding of the National Academy of Sciences

Abstract

Tanzania may hold >40% of the world's lions (*Panthera leo*), a species that faces substantial population declines across Africa. Around 70% of Tanzania's lions are thought to be distributed in two population strongholds: the Ruaha-Rungwa and Selous-Mikumi landscapes. These populations are predominantly in national parks and game reserves, and separated by human-dominated land. Despite the importance of this area for lion conservation, there is a paucity of information on the potential suitability of habitat for lions across the anthropogenic mosaic separating these populations, and to which extent these human-dominated landscapes may interfere in lion population connectivity. Here, we investigated the spatial distribution of highly suitable lion habitats across these population strongholds. We quantified the variables determining lion habitat suitability and mapped prime habitats for lion conservation. We show that low human population density and moderate rainfall were the key predictors of habitat suitability for lions. We found that 60.2% (43,739 km^2) of all highly suitable habitats (55,741 km^2) were in game reserves where lions are often hunted as trophies. In village lands, highly suitable lion habitats were fragmented and majorly within 10 km of protected area borders. If game reserves become less profitable due to overhunting or hunting bans, these areas may be converted to other more profitable land-use types, and lions might lose substantial portions of their habitats in southern Tanzania. We highlight that the maintenance of these key protected areas under a wildlife-based land-use play a central role in lion conservation in East Africa.

Significance Statement

Lion populations have declined by half in the last 20 years, with habitat degradation and anthropogenic killing the primary threats. Only six lion stronghold populations remain in Africa, two of which (Ruaha-Rungwa and Selous-Mikumi) occur in southern Tanzania. These landscapes may still support around 30% of Africa's lions but remain under-studied. Our study reveals that suitable lion habitat is considerably fragmented, and particularly limited to game reserves. If game reserves become less profitable due to overhunting or hunting bans, they might be converted to non-wildlife based land use for livestock and agriculture, and the results could be catastrophic for lion conservation due to the loss of some of the most important swathes of highly suitable lion habitats in East Africa.

Key-words: predictive modelling; boosted regression trees; edge-effect; trophy hunting; Selous Game Reserve; Ruaha National Park

Author contributions to the manuscript:

Experimental design: LA, RM; Data contribution: HB, DI, PH; Data analysis: LA; MGUK & LH (helped with running the models); Writing of 1st draft of manuscript: LA, Improvements to manuscript: SB, PJ, DM, AD & RM

5.1. Introduction

Large carnivores have experienced dramatic population declines across the world over the last 100 years, imperiling the persistence of these species and the functioning of ecosystems (Bauer et al. 2015; Ripple et al. 2014). The effects of large carnivore extirpation can cascade down a trophic system, with ramifications for habitat structure, and correspondingly, biodiversity and heterogeneity of ecological systems (Ripple et al. 2014; Ripple et al. 2013). In Africa, the decline of large carnivore populations has been striking over recent decades (Ray et al. 2005; Ripple et al. 2014), resulting largely from human-induced habitat conversion, fragmentation, prey depletion (Dolrenry et al. 2014; Riggio et al. 2012; Ripple et al. 2015), unsustainable trophy hunting (Brink et al. 2016; Packer et al. 2011), and mortality resulting from human-carnivore conflict (HCC) (Winterbach et al. 2012; Woodroffe et al. 2005a).

The decline of the African lion (*Panthera leo*) is a particularly conspicuous example of the effects of anthropogenic disturbance on an apex predator (Morandin et al. 2014). Lions have lost 92% of their historic range with a 43% population reduction in just the last twenty years (Bauer et al. 2016). Robust populations with > 500 individuals (Riggio et al. 2012) are almost exclusively restricted to protected areas, including game reserves and national parks (Cushman et al. 2015; Riggio et al. 2012), that often lack the financial capacity and infrastructure to manage and protect the species (Bauer et al. 2015; Lindsey et al. 2017a).

Outside protected areas, lion populations are increasingly fragmented amidst a matrix of largely human-dominated habitats (Dolrenry et al. 2014; Riggio et al. 2012; Ripple et al. 2015). These anthropogenic landscapes can hinder lion movements and dispersion patterns (Cushman et al. 2015; Elliot et al. 2014), negatively affecting the functional connectivity and gene flow between populations (Cushman et al. 2015; Morandin et al. 2014). Small and isolated populations are more susceptible to the detrimental effects of environmental and demographic stochasticity (Winterbach et al. 2012), and genetic diversity loss via population bottlenecks (Morandin et al. 2014). For example, inbred lion populations have been found to be more susceptible to diseases (Trinkel et al. 2011), show lower fecundity and decreased reproductive success (Björklund 2003; Morandin et al. 2014; Packer et al. 1991; Trinkel et al. 2008). In addition, lions are subject to high mortality risk in anthropogenic areas with increased human-lion interactions. In these landscapes humans will often persecute lions over feelings of insecurity or concerns relating to real or perceived lion attacks upon livestock and people (Bruskotter et al. 2017; Packer et al. 2005b). Besides conflict, lion survival is further threatened by bushmeat poaching, which is a common threat around and even inside protected areas (Lindsey et al. 2013a; Ripple et al. 2016a; Ripple et al. 2015). The high levels of lion mortality in human borderlands can create a source-sink dynamic (Battin 2004), with sink effects that can extend from the human-dominated land into source protected areas (Woodroffe and Frank 2005) potentially leading to the extirpation of lion populations (Barthold et al. 2016; Loveridge et al. 2016b).

Over the next 50 years, lions are predicted to experience a further 50% population decline in West, Central, and East Africa, placing them on the brink of extinction particularly in the first two regions (Bauer et al. 2015). Within this timeframe, the human population in Africa is expected double (UN 2015) by the end of the century, with an associated 70% conversion of sub-Saharan habitats into agro-pastoral land (Prestele et al. 2016). Given that approximately 45% of estimated lion range falls outside protected areas (Lindsey et al. 2017a), anthropogenic pressure represents an imminent challenge for lion conservation. It is imperative that conservation strategies implement targeted and effective actions to protect the remaining lion habitats from the -often irreversible- threats posed by land-use conversion ensuing from human and livestock encroachment of wilderness.

Identifying and mapping suitable habitat for lions, both within and beyond protected areas, is a much-needed step toward effective lion conservation. Such efforts provide valuable information and opportunities for land management strategies to sustain ecologically functional areas (Dennis et al. 2003) for lions and other wildlife (Franklin and Lindenmayer 2009). Even though lions are among the most studied large carnivores in Africa (Brooke et al. 2014), there is a dearth of information on the spatial distribution of highly suitable habitats for lions, especially outside protected areas. Within their African distribution, Tanzania is immensely important for lion conservation given that over 40% of the continent-wide population may reside in this country (Riggio et al. 2012). Nevertheless, several fundamental aspects of lion spatial ecology remain understudied, and studies have been limited to few portions of the country

(TAWIRI 2009a). Most of Tanzania's lion populations occur within an array of protected areas (i.e. national parks, game reserves and wildlife management areas) (Bauer et al. 2015; Bauer et al. 2016) encompassing 32.2% of the country. The majority (26.4%) of this habitat is located in game reserves (Di Minin et al. 2016a) where lions tend to be managed as a trophy species. Tanzania has partially three of the four East African lion strongholds, and two of these lion populations are located in the Selous Game Reserve (within the Selous-Mikumi landscape), and the Ruaha-Rungwa area (part of the Katavi-Ruaha stronghold) (Dolrenry et al. 2014; Riggio et al. 2012). Although a precise estimate of the number of lions remaining in Africa is lacking - especially for Tanzania (Bauer et al. 2015), this area is estimated to support approximately 30% of the global population (Bauer et al. 2016). At their closest point, these landscapes are separated by just ~180 km. Thus, ecologists have long speculated about the degree to which these two stronghold populations may be, or could be, functionally connected (Epps et al. 2011; Jones et al. 2009).

Importantly, there has never been detailed assessment of suitable habitat outside of the stronghold populations. Additionally, in the face of the recent debate about the implications of the sanctions fostered by the U.S. Fish and Wildlife Service (USFWS 2015) on the lion trophy hunting industry (Creel et al. 2016; Di Minin et al. 2016a; Ripple et al. 2016c) for the viability of hunting industry in Tanzania (Lindsey et al. 2012), identifying the role of the game reserves in maintaining and securing highly suitable habitats for lions in this area is timely. Wildlife areas such as game reserves can protect intact habitats against the growing threats of human and livestock encroachment, and ensuing land-use conversion (Creel et al. 2016; Di Minin et al. 2016a). Here, we use species distribution modelling based on machine learning algorithms (boosted regression trees; BRT) to investigate (*i*) the ecologic and anthropogenic covariates that define areas of optimum-niche and of high suitability for lions; (*ii)* the size of highly suitable lion habitats under various levels of protection; and (*iii*) the configuration of habitat suitability between the Ruaha-Rungwa and Selous-Mikumi landscapes to examine the potential for functional connectivity. We present the ecological implications of our results and discuss the role of this research in future conservation planning for this iconic species.

5.2. Materials and Methods

5.2.1. The Ruaha and Selous landscapes

The joint area of Ruaha National Park, Mikumi National Park and Selous Game Reserve (Fig. 5.1) covers over 100,000 km^2 including village lands, and may protect up to ~30% of the world's remaining lion population (Riggio et al. 2012). This area encompasses a variety of land-use classes including: Ruaha, Mikumi, Kilombero Valley and Udzungwa Mountains national parks; the Kisigo, Rungwa, Muhezi and Selous game reserves; wildlife management areas, forest and nature reserves; and an extensive matrix of human occupation with > 125 villages and over 2 million people (further explanation on the study area provided on SI; Table S5.1).

Despite of the geographical proximity of the Ruaha-Selous areas (~180 km apart), and shared similarities in habitat conditions for harbouring significant populations of carnivores, the human-dominated matrix between these protected areas has been suggested to limit carnivore movements, and threat the connectivity between these populations (Dolrenry et al. 2014; Epps et al. 2011; Jones et al. 2009).

5.2.2. Lion occurrence and pseudo-absence data

We compiled 2,393 georeferenced lion presence-only occurrence data opportunistically collected through multiple methods (Table S5.2) across the study area between 2006-2015 (Table S5.2). We used the occurrence data for characterizing the ecological covariates associated with each lion location. In presence-only studies based on regression analyses, pseudo-absence points are required as true absence points are generally unavailable. We randomly generated 5,000 pseudo-absence (i.e. background) points biased towards the human population data in order to account for potential sampling bias in data collection. We weighted each pseudo-absence record so the total sum of all pseudo-absence records is equal to the total number of all presence records, whereas each presence record is weighted as one in the dataset (Barbet-Massin et al. 2012).

5.2.3. Spatial thinning

We used a spatial thinning method based on nearest neighbour distance using the *spThin* package (Aiello-Lammens et al. 2015) in R (RStudioTeam 2015) to minimize spatial autocorrelation associated with non-standardized data collection. We generated 20 thinned dataframes; each composed of 302-305 randomly selected presence-points that were at least 2 km apart from each other. This threshold of distance helped to minimize spatial correlation between occurrence points and model performance.

5.2.4. Ecological covariates

We estimated suitability based on elevation, slope, mean rainfall index (mm), distance to water sources (km), human population density (people/km^2), vegetation continuous field (VCF), and vegetation classes (ESA 2009) reclassified into the following: bushed grassland, cropland, shrubland, woodland, urban areas, bare areas, and water bodies (see SI for additional information on covariate data processing).

5.2.5. Boosted regression trees

We implemented the boosted regression trees algorithm (BRT) (see SI for additional information) on the lion data for mapping their spatial distribution, identifying areas of niche-optimum for the species, and the presence and extent of suitable patches within protected areas and human-dominated landscape. We estimate the relative contribution of each ecologic covariate to the potential habitat suitability (HS) and distribution of the species across the landscape from the BRT ensemble outputs. We used the BRT outputs to identify those highly suitable habitats of niche-optimum for lions. Additionally, the functional relationships between HS and each covariate could be approximated via partial dependence plots.

5.2.6. Model processing

We adopted an ensemble approach of 200 sub-models predicting the distribution of highly suitable habitats for lions, following Kraemer et al. (2015). The final output map was generated based on the mean of all the 200 sub-model outputs implemented in the 20 thinned dataframes (see SI for additional information on model processing). We assessed pixel-based uncertainty by calculating 95% confidence interval from the 200 sub-models (Kraemer et al. 2015). Modelling was performed using the gbm (Ridgeway 2013), dismo (Hijmans et al. 2012), raster (Hijmans and van Etten 2014) and seegSDM (Golding 2014) R packages (RStudioTeam 2015). We evaluated the predictive performance of each sub-model based on the values of the area under the receiver operating characteristic (ROC) curve (AUC), and Cohen's Kappa statistic (Cohen 1960). The final predictive accuracy of the ensembled model was derived from the mean and standard deviation of these AUCs across all 200 sub-models (Hijmans 2012).

5.2.7. Identifying highly suitable habitats for lions

The final predictive model was converted into a suitability map to facilitate model interpretation (0-100), with higher values indicating high suitability. Highly suitable habitats (i.e. niche-optimum areas) were identified and mapped based on the mean value of a threshold probability by which model sensitivity equalled model specificity. This choice of threshold selection is recommended for generating low rates of false negatives and positives in predictive modelling (Liu et al. 2005).

We assessed the variation in the distribution of suitable habitats for lions across the study area through a chi-square test applied to the BRT results. We examined the influence of edge effect on habitat suitability in the Ruaha-Rungwa and Selous-Mikumi areas through a chi-square test. We assigned high edge effect levels to those areas within the first 10 km to the borders of the protected areas; moderate edge effect was assigned to those areas between 10 and 20 km to the borders; and low edge effect areas were those over 20 km to the borders. Moreover, we investigated the potential variation in density distribution of the highly suitable habitats within and around the Rungwa-Ruaha and Selous-Mikumi using a kernel-density estimator analysis (KDE). We considered habitat continuity between highly suitable grid-cells when the maximum Euclidean distance between centroids was below 1 km, and assumed a “patch size” to be suitable for supporting a lion population when its area was >86 km^2 following Dolrenry et al. (Dolrenry et al. 2014). The combination of these spatial filters enabled mapping highly suitable continuous and sizeable patches with the potential to support lion populations across the study area.

5.3. Results

5.3.1. Model performance

Our model validation statistics indicated high predictive performance of our BRT ensemble mean model, with the area under the receiver operating characteristic (AUC/ROC) of 0.84 (±0.1 SD, n=200 trees), and the Kappa statistic showing good discriminatory power (0.66; ±0.17 SD, n=200 trees). The results of our pixel level uncertainty analyses also identified high model accuracy and good fit to data (Figure S5.1).

5.3.2. Contribution of covariates to habitat suitability for lions

Our results indicated that lion habitat suitability (HS) was most strongly associated with human population density and precipitation. Highly suitable habitats (HS≥48.7) were those with low human population density (<10 people/km^2) and average rainfall of between 600 to 1,200mm/year. Habitat suitability was also associated with low to intermediate elevations (up to 500 meters above sea level) and proximity to water sources. For example, habitat suitability decreased in areas >10 km from rivers (Table 5.1; Fig. S5.2). Slope, vegetation cover (VCF), and vegetation classes contributed to less than 20% of the overall habitat suitability for lions (Table 5.1; Fig. S5.2).

Table 5.1. Contribution of ecologic covariates to habitat suitability for lions in Tanzania's Ruaha-Selous landscape according to boosted regression trees (BRT) modelling

Ecologic Covariate	Mean Contribution	95% Confidence Interval
Human Density (Afripop)	29.3	25.3-34
Rainfall (Bio12)	23.6	18.4-27.8
Elevation (DEM)	17.2	13.1-21.9
Distance to Water Sources	12.3	9.3-16.5
Slope	9.3	6.8-12.2
Vegetation Continuous Field (VCF)	7.4	4.8-10
Vegetation Class (GlobCover)	0.8	0.2-1.8

5.3.3. Mapping habitat suitability for lions

The BRT model coefficients revealed significant variability in the suitability of habitat for lions across the study area (X^2= 19,730, 1, p <0.01; Fig. 5.1). Habitat with un-protected status (i.e. village land) had the lowest mean suitability value (HS= 26.9; SD ±29). In contrast, habitat within protected areas had considerably higher mean suitability level (HS= 51.5; SD±34.3) (Fig. 5.2). The mean lion habitat suitability calculated for the whole study area (HS=41; SD±34) was below the defined threshold of habitat that was considered to have high suitability (HS≥ 48.7). Highly suitable habitats comprised 42.7% (72,774 km^2) of the study area (170,629 km^2), and were patchily distributed (Fig. 5.1A-B). These patches tended to be located within protected areas –either in national parks, nature, forest and game reserves, and wildlife management areas (76.6%; 55,741 km^2; 32.6% of the study area; Table 5.2)-, whereas the remaining 23.4% (17,032 km^2; 10% of the study area) were scattered across human-dominated areas (Table 5.2). Game reserves represented the most important land-use class for lions, encompassing 60.2% (43,739 km^2; 25.7% of the study area) of the mapped highly suitable lion habitats. In relative proportions, 65% of the habitats within game reserves were highly suitable for lions, in comparison to 47% in national parks and 28% in village lands (Table 5.2).

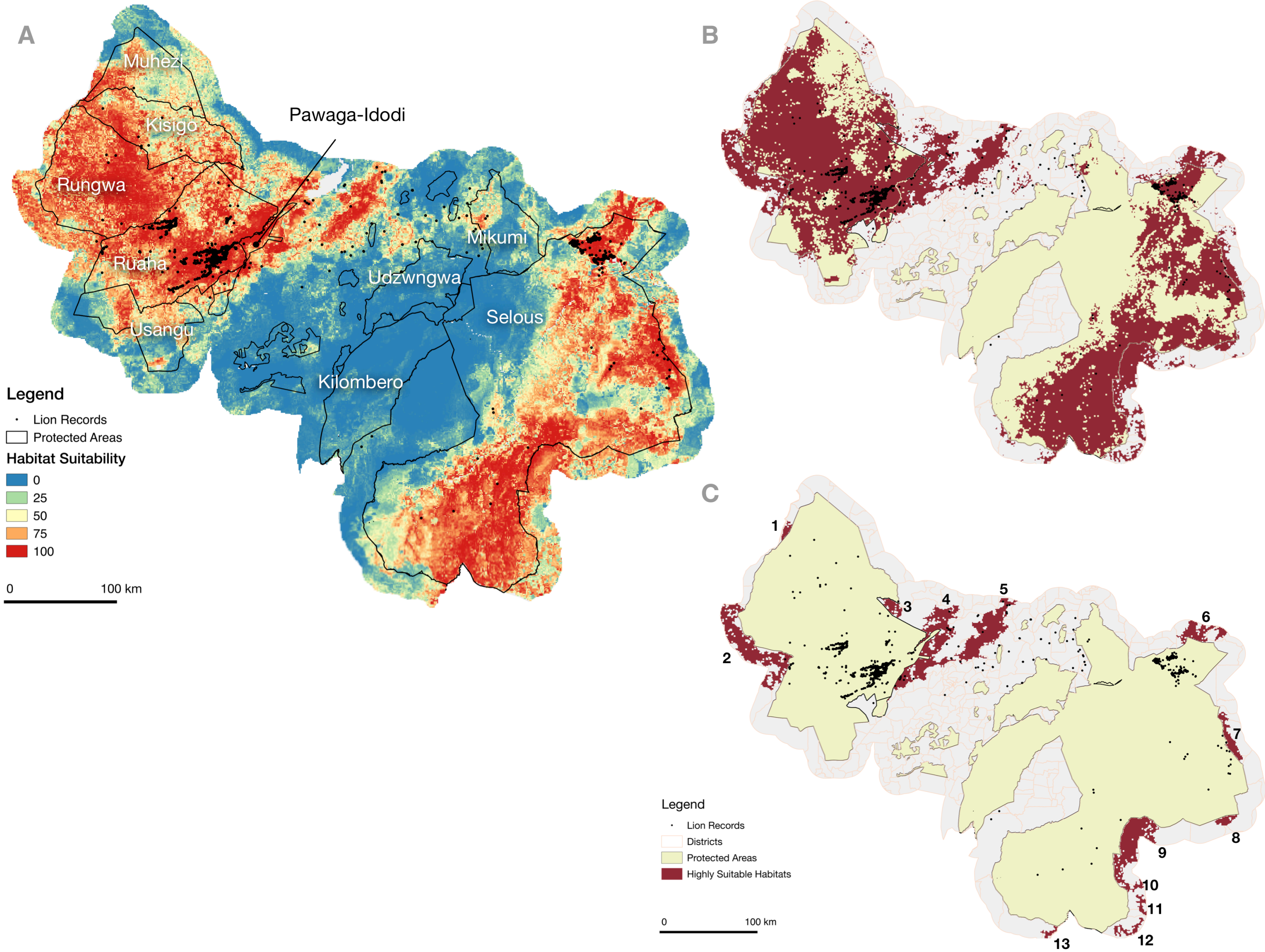

Figure 5.1. **A.** Predictive map of habitat suitability (HS) for lions in Tanzania's Ruaha-Selous landscape. The warmer areas represent higher values of habitat suitability for lions, and indicate increased probability of species occurrence. **B.** Distribution of highly suitable habitats (HS≥48.7) for lions in Tanzania's Ruaha-Selous landscape. **C.** Distribution of highly suitable and ecologically functional habitats to support lion populations outside protected areas (i.e. in the gradient of human occupation) in Tanzania's Ruaha-Selous landscape.

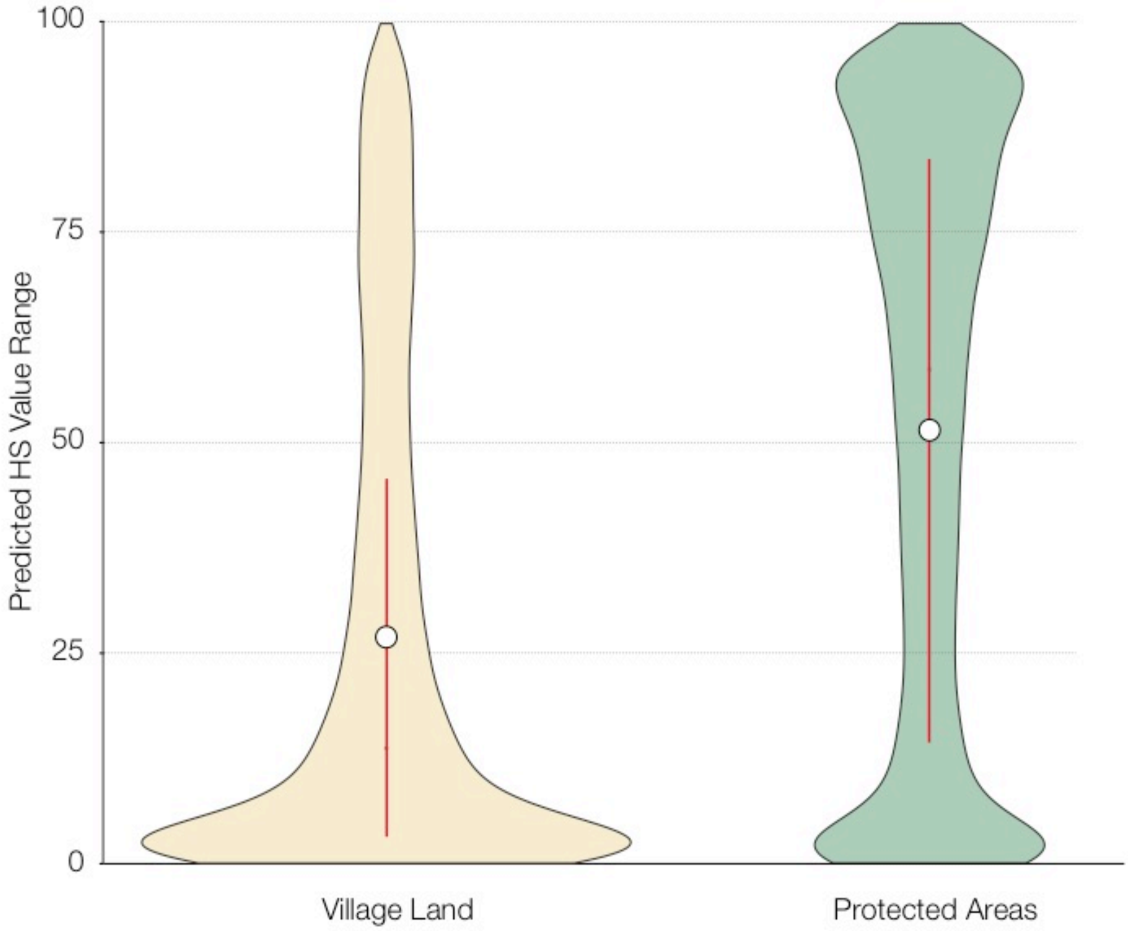

Figure 5.2. Distribution of predicted suitability (HS) for lion habitats across village land and protected areas in the study area. The white circle represents the suitability mean. The red bar represents the first-to-third interquartile range of suitability values.

Table 5.2. Highly suitable areas (HSA) for lions according to each main land-use class across the study area. $\overline{X}$ HS: mean habitat suitability value; SD: standard deviation

Land-use	Consumptive use	Total Area (Km²)	HSA (Km²)	% HSA*	% HAS in Study Area	$\overline{X}$ HS (SD)
FR	Y	6,650.5	14.9	0.22	<0.1	55.5 (6.2)
GR	Y	65,967.3	42,865.7	65	25.1	78.5 (13.8)
NP	N	25,642.2	12,001.9	47	7.0	79.5 (14)
NR	Y	9,269.08	1.8	0.02	<0.1	61 (6.6)
VL	Y	61,454.5	17,032.5	27.72	10.0	73.4 (13.8)
WMA	Y	1,645.2	857.2	52.09	0.5	81.8 (14.1)
Total	-	170,629	72,774.0	-	42.7	77.5 (14)

FR. Forest reserve (Table S1); GR. Game reserve (Muhezi, Kizigo, Rungwa, Selous); NP. National Park (Ruaha, Mikumi, Udzungwa); NR. Nature Reserve (Kilombero); VL. Village land; WMA. Wildlife management area (Pawaga-Idodi/MBOMIPA, Waga). *Proportion of highly suitable areas (HSA) by the total area of its respective land-use class.

Table 5.3. Highly suitable and sizeable habitat patches (>86 km²) for lions within the gradient of human occupation in the Ruaha-Selous landscape. Area (ID): identifier for each habitat patch. HS ($\overline{x}$): mean habitat suitability value

Area (ID)	**Area (Km²)**	**HS ($\overline{x}$)**
1	106.4	81.5
2	1,791.9	76.1
3	217.1	78.3
4	2,515	80.3
5	1,527.2	83.2
6	445.8	84.4
7	100.9	85
8	370.1	79.4
9	157.7	76.2
10	1,567	79.7
11	117.5	70.2
12	189.1	75.5
13	107.5	72.9

We identified 13 potential sizeable patches (see Dolrenry et al. 2014; Fig. 5.1C; Table 5.3) that ranged from 100.9 km^2 to 1,791.9 km^2 in area ($\bar{x}$ area= 708.7 km^2) outside protected areas. The habitat suitability index within these patches varied from 70.2 to 85 ($\bar{x}$ suitability= 78.7). These patches accounted for 53.5% (9,105 km^2; 5.3% of the study area) of the highly suitable habitats identified in non-protected areas. It's noticeable that all but one of these patches were located close (<10 km) to protected areas where human population density is low (Fig. 5.1C; Fig. S5.2; S5.3).

We found significant differences in the distribution of habitat suitability in relation to protected area edge within Ruaha-Rungwa (X^2= 1,843.5, df = 2, p <0.01) and Selous-Mikumi (X^2= 4,052.7, df = 2, p <0.01). Habitat suitability was clearly higher closer to cores of the protected areas (Fig. 5.3). This trend was particularly evident in the Ruaha-Rungwa landscape, where 44% of highly suitable habitats occurred in low edge effect areas, in comparison to the 36% mapped across areas exposed to high and moderate edge effect. A similar, but less pronounced trend was observed in the Selous-Mikumi area, where 25% of the highly suitable habitats occurred in low edge effect areas, against 21% observed in those high and moderate edge effect areas (Fig. 5.3). In the Ruaha-Rungwa area, 18% of highly suitable habitats were found at areas of high edge effect, a pattern not observed in the Selous-Mikumi area, likely due to the lower density of people in the first 10 km around Ruaha-Rungwa ($\bar{x}$: 0.12 people/km^2; 0.008 – 3.11 people/km^2) in comparison to Selous-Mikumi ($\bar{x}$: 0.28 people/km^2; 0.03 – 28.9 people/km^2). Despite the noticeable influence of edge effect on habitat suitability, our KDE analysis suggests that approximately 70% (50,941 km², 29.85% of the study area) of the highly suitable habitats in the study area occurred within 20 km of the boundaries of the protected areas, and along 15 km in the surrounding lands of the protected areas (Fig. 5.4).

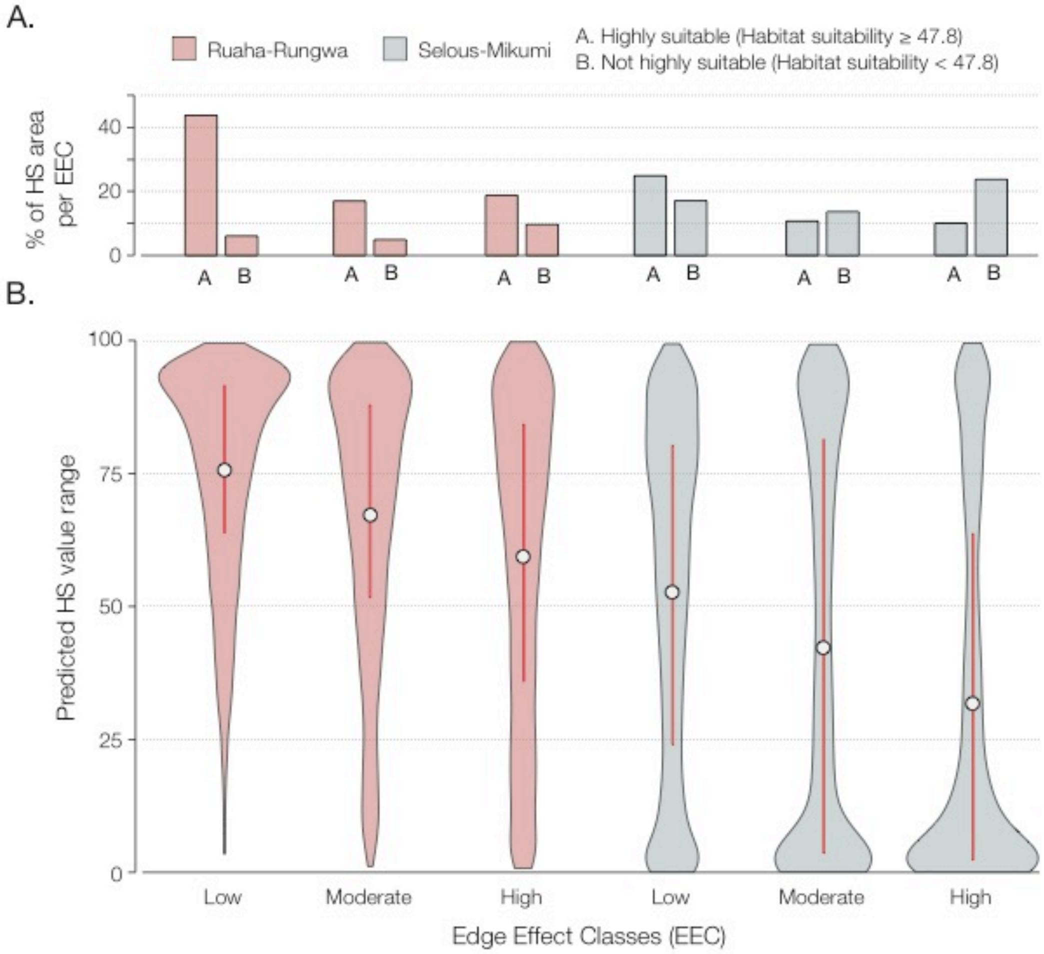

Figure 5.3. A. % Distribution of habitat suitability (HS) in Km² for lions in relation to exposure to edge effect classes (EEC) within protected areas in the Mikumi-Selous and Ruaha-Rungwa landscapes in Tanzania. EEC classes: High: <10 km into the protected area; Moderate: 10-20 km into the protected area; Low: >20 km into the protected area. B. Variation in the distribution of predicted suitability of lion habitats in relation to exposure to EEC within protected areas in the Mikumi-Selous and Ruaha-Rungwa landscapes in Tanzania. The white circle represents the suitability mean in each gradient of distance within the protected areas. The red bar represents the first-to-third interquartile range of suitability values.

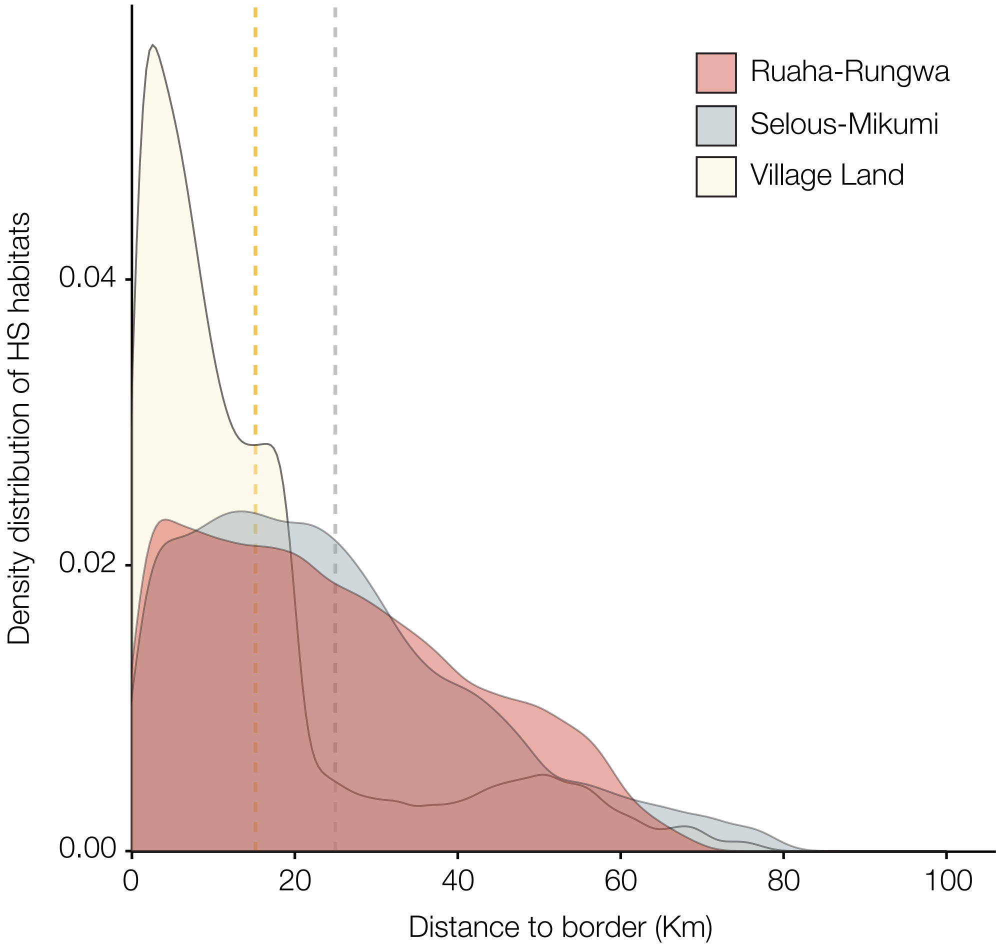

Figure 5.4. Density distribution of highly suitable habitats (HS) for lions within protected areas and village land across Tanzania's Ruaha and Selous landscapes. The dashed line represents the mean distance of highly suitable habitats to the borders of the protected areas. Mean distance for Ruaha-Rungwa and Selous-Mikumi: 25 km; Village land: 15 km.

5.4. Discussion

5.4.1. Characteristics of highly suitable habitats for lions

We identified a fragmented distribution of highly suitable lion habitats across the Ruaha-Rungwa and Selous-Mikumi landscapes. Habitat suitability was associated with a combination of environmental and anthropogenic features, but chiefly influenced by low human population density and moderate rainfall. The negative effect of human population on lion habitat suitability observed here is consistent with expectations (Abade et al. 2014b). In our study area even relatively low human population densities (<10 people/km^2) were correlated with low habitat suitability for lions, a much lower value than observed elsewhere in Africa (Woodroffe and Ginsberg 1998) (Fig. S5.2; S5.3). These patterns are likely associated to relatively high levels of human activities, occupation and habitat conversion for livestock grazing and agriculture in the study area (Brink et al. 2016; Packer et al. 2011; Salerno et al. 2014). In fact, highly suitable habitats outside protected areas occurred in the most remote areas of the human-dominated landscape, where human density and pressure is still relatively low (Fig. S5.3). The influence of rainfall on suitability is also expected as higher pluviosity relates to increased net primary productivity, and abundance of large sized ungulates (Ogutu et al. 2008) that compose the bulk of lion diet (Hayward et al. 2011; Hayward and Kerley 2005), which ultimately shapes lion distribution (Davidson et al. 2013; Spong 2002; Valeix et al. 2010; Valeix et al. 2009). Finally, the increased suitability in areas of low-to-intermediate elevation range and in those closer to rivers is also associated to the increased distribution of wild prey around perennial water sources in lower elevation ranges in Ruaha-Rungwa (Abade et al. 2014b) and Selous-Mikumi (Spong 2002). Riverine areas are known to attract prey species (Davidson et al. 2013), provide shelter (Mosser et al. 2009) and cover for hunting (Hopcraft et al. 2005), and are associated with lion's high-reproductive success (Mosser et al. 2009). However, it is important to notice that riverine habitats are also often associated with intense HCC due to the overlap between grazing livestock, wild prey, lions and other large carnivores (Abade et al. 2014a; Valeix et al. 2010). This is particularly true in Ruaha, where the Great Ruaha River - one of the main water sources for livestock and wildlife - forms the southern borders of the National Park and creates a landscape of increased livestock vulnerability to predation (Abade et al. 2014a; Abade et al. 2014b). These areas are, therefore, of concern for lion conservation as the species is likely to be exposed to high human-induced mortality, and should be prioritised in strategic conflict mitigation planning.

5.4.2. Distribution of highly suitable habitats, and implication for conservation

Our results indicate that game reserves contain the greatest share of highly suitable habitats for lions in southern Tanzania. The joint area of the highly suitable habitats encompassed by these reserves is equivalent to over threefold the suitable habitats found in Ruaha, Mikumi and Udzungwa National Parks, and twice that in the surrounding village lands (Table 5.2).

Game reserves are important for lion conservation by protecting intact habitats against the pressing land-use conversion rates due to farming and grazing

(Brink et al. 2016; Caro et al. 2009b), and the serious loss of habitat and wildlife ensuing from such a changes (Lindsey et al. 2013b). In addition, the intensive management and surveillance required to maintain the trophy species within game reserves helps minimising the threat of bushmeat poaching, and direct and indirect lion killing (Brink et al. 2016; Di Minin et al. 2016a). Sport hunting of lions has become a highly contentious issue in recent years (Lindsey et al. 2013b; Lindsey et al. 2007; Nelson et al. 2013). Proposals have been entertained to ban lion trophy hunting altogether, with some countries like Botswana already imposing a ban on any type of safari hunting (Di Minin et al. 2016a; Mbaiwa 2017). This presents a potentially important problem for lion conservation given that there is more land set aside for hunting in Africa than there is protected by national parks (Lindsey et al. 2017a; Nelson et al. 2013). If trophy hunting is banned, what will become of the land is an enduring question. Concerns relate to the often-definitive conversion and fragmentation of these prime wildlife habitats for grazing and farming as observed elsewhere in Africa, removal of financial incentives for communities reliant on hunting revenues, lower tolerance towards wildlife, increased bushmeat poaching, and the ensuing declines of wildlife populations (Caro et al. 2009b; Di Minin et al. 2016a; Lindsey et al. 2006; Mbaiwa 2017). Thus, in a scenario where trophy hunting becomes less profitable as a result of overhunting and wildlife depletion (Brink et al. 2016), and 'emptied' hunting areas are set aside for other non-wildlife based land use such as livestock farming and agriculture, lions could lose some of their most highly suitable habitats in one of the most important landscapes for their conservation in Africa. Therefore, ensuring the maintenance of these game reserves under a wildlife status seems central for sustaining lion conservation across these large landscapes.

The presence of suitable habitat is not of course enough to ensure lion populations are secure. Game reserves need to maintain high trophy hunting standards to benefit lion conservation. For example, lions in the Selous Game Reserve have experienced disproportionally high mortality due to increased unsustainable hunting offtake that occurs in its several hunting concessions (Brink et al. 2016). This demonstrates that poorly managed hunting activities, resulting from a complex and misbalanced equation involving short hunting block tenure, quota misregulation and lion overharvesting (Brink et al. 2016), can accelerate the decline of the Selous lion population since the late 1990s. Although, the inferred 21% lion population decline observed in Selous between 1993 and 2014 was less pronounced than those observed in some other areas across Africa where hunting is not permitted (Packer et al. 2011) such as in Tarangire (-44% population decline) and Katavi (-100% population decline) National Parks, with an overall continental population decline of around 66% (Bauer et al. 2015; UNEP-WCMC 2015).

Overall, the scenario depicted by our study represents a conundrum for lion conservation, in which the Selous Game Reserve, in particular, has some of the most substantial portions of highly suitable and sizeable habitat for lions in Africa, but where the current hunting activities have been clearly associated with lion decline. It is imperative that this area should be maintained under a wildlife-based land use. One option, apart from reforming trophy hunting in the area to establish sustainable quotas (Brink et al. 2016), would be to substitute photo tourism for trophy hunting across more of this area, as that is likely to be less damaging to lion populations . However, given that existing national parks in southern Tanzania tend not to be profitable (Lindsey et al. 2017a), and there is no guarantee that highly suitable areas for lions are also highly suitable for photographic tourism, this may not be an economically viable strategy. There is currently increasing pressure on the trophy hunting industry, as the U.S. Fish and Wildlife service is evaluating whether trophy hunting is beneficial for lion populations. However, if Tanzania fails to demonstrate that benefit, then it is likely that trophy hunting of lions will contract, lowering the economic return from game reserves. Unless there is a better economic alternative, there is a risk of land conversion to anthropogenic uses, which is likely to have very damaging consequences as land managed under neither hunting nor photographic tourism has been shown as the most negative outcome for lion populations (Lindsey et al. 2006; Lindsey et al. 2007). In the short term, it is imperative that managers implement strict regulation and control of the consumptive use of lions in Tanzanian Game Reserves and their surroundings, effective governance and management strategies, and increase law enforcement to minimize wildlife overexploitation (Brink et al. 2016; Packer et al. 2011).

5.4.3. Highly suitable habitats in landscapes of anthropogenic mortality

Our findings depict a worrying scenario for the conservation of lions outside protected areas in southern Tanzania. We found a highly fragmented matrix of suitable lion habitats, where sizeable and highly suitable habitats with the potential to support lion populations in southern Tanzania are almost exclusively limited to game reserves and national parks. Similar observations have been reported for other important lion populations in West (Henschel et al. 2014) and Central Africa (Bauer et al. 2015), where lion populations are largely restricted to protected areas.

We found that approximately 70% of the highly suitable habitats for lions occurred within 30 km of the edges of protected areas (Fig. 5.3-5.4), where lions are exposed to high rates of human-induced lion mortality as a result of intense poaching, illegal trophy hunting, and HCC (Abade et al. 2014a; Dickman et al. 2014). These 'landscapes of anthropogenic mortality' (Loveridge et al. 2016b), are known to function as critical ecological traps (Battin 2004), and population sinks that can destabilize lion populations accelerating extinction processes (Loveridge et al. 2010a; Woodroffe and Frank 2005; Woodroffe and Ginsberg 1998). In the surroundings of Ruaha National Park for instance, over 100 lions have been indiscriminately killed between 2010 and 2016 due to human-wildlife conflict and traditional lion hunting in the fringes of Ruaha National Park and Pawaga-Idodi/MBOMIPA Wildlife Management Area (Dickman.; in prep.). The consequences of these killings upon the long-term survival of the lion populations in Ruaha remains unknown (Dickman 2015), but data from similar studies (Barthold et al. 2016; Loveridge et al. 2010a; Loveridge et al. 2016b) suggest that high levels of anthropogenic mortality, like these, can affect the viability of populations across a wide area (Loveridge et al. 2010a; Loveridge et al. 2016b; Woodroffe and Frank 2005).

Likewise, conflict-related killings and unsustainable hunting has contributed to lion population declines around Selous Game Reserve (Brink et al. 2016), an area deemed to harbour 8 of the 13 highly suitable and sizeable habitat patches for lions according to our findings (Fig. 5.1).

Human occupation of the habitat bordering both the Ruaha-Rungwa and Selous-Mikumi has accelerated in recent years (Salerno et al. 2014). This, coupled with increases in livestock numbers and associated habitat conversion (Bamford et al. 2014; Mtahiko et al. 2006), is likely to exacerbate HCC, bushmeat poaching and defaunation (Bamford et al. 2014; Kideghesho et al. 2013; Knapp et al. 2017; Ripple et al. 2016a; Ripple et al. 2015). These mechanisms all contribute to increased lion mortality risk. Therefore, implementation or improvement of husbandry techniques such as the adoption of livestock guarding dogs and predator-proof enclosures, associated with community-based approaches aiming at limiting damages arisen from livestock losses by large carnivores, similar to those adopted in some villages around Ruaha National Park (Abade et al. 2014a; Dickman 2015) could help to minimise both HCC and human-induced mortality of lions.

5.4.4. Insights into potential connectivity between Ruaha and Selous

The existence of highly suitable and sizeable patches to support lion populations between Ruaha-Rungwa and Selous-Mikumi (Fig. 5.1) could suggest a potential connectivity route, especially in the northern sections of the study area. However, these potential lion habitats are fragmented and surrounded by human-dominated areas where HCC and human-induced carnivore mortality might impose an immediate threat to lions. Thus, even though crossing between these landscapes could be possible solely in terms of distance - lions travel up to 251 km whilst dispersing and searching for areas to establish territories (Cushman et al. 2015; Elliot et al. 2014), which is more than the distance between these protected areas -, the human matrix could be a limiting barrier. Indeed, previous studies suggested the existence of a potential corridor of connectivity for wildlife from Rungwa-Ruaha to Selous-Mikumi through the gradient of human occupation; however, such corridor was considered extremely degraded and likely to disappear within 5 years from its original 2009 assessment (Caro et al. 2009a; Jones et al. 2009). In addition, this potential corridor has been suggested to be more functional for less ecologically demanding species such as spotted hyaenas than lions (in terms of sensitivity to human pressure and ecological flexibility) (Epps et al. 2011). Thus, even though our results suggest the existence of a potential route of connectivity for carnivores, ground-truthed data is required to assess the existence of an ecologically functional corridor of connectivity. Lastly, our results corroborate recent findings by Riggio and Caro (2017) that identified a potential connectivity route for wildlife between Ruaha and Selous, although noting the threat imposed by intense human occupation and habitat conversion to the long-term viability of such corridor. We however, note that predictive habitat suitability should not be directly translated into potential connectivity maps as they may be limited to reflect the effect of the different spatial scales (Ziółkowska et al. 2016) and the complex array of ecologic factors that determine population connectivity (Cushman et al. 2015; Elliot et al. 2014).

Further studies should therefore prioritise data collection on wide-scale lion movements, and genetic data to truly assess the connectivity between lion populations from these areas, as well as to better assess how human-related habitat conversion and fragmentation influence on the landscape connectivity between Ruaha and Selous.

5.5. Conclusion

Our results suggest that highly suitable, and contiguous habitat patches with the potential to sustain lion populations are primarily limited to protected areas and their immediate surroundings in the last two lion strongholds remaining in southern Tanzania. We found that game reserves encompassed the largest swathes of highly suitable habitats. Thus, if trophy hunting becomes less profitable due to lion overhunting and depletion, or due to bans, these prime lion landscapes risk being lost by replacement to anthropogenic-based land uses such as agriculture and livestock grazing. In this scenario, lions could lose substantial highly suitable habitats in one of the most important landscapes for their conservation in Africa. Therefore, ensuring the maintenance of these game reserves under a wildlife status will be central to sustaining lion conservation in these areas. Additionally, fostering conservation actions and stricter regulation of wildlife use is urgent, as well as the development of land-use strategies to protect key lion habitats beyond current protected areas, as we found that anthropogenic pressure negatively influenced habitat suitability in the village lands and even within adjacent habitat in the protected areas. These steps are crucial for the long-term conservation of the lion, as we have shown that bordering village land does play an important role on the maintenance of highly suitable patches for the species. Most importantly, we illustrate that game reserves are particularly important to lions in Tanzania emphasizing the importance of effective and appropriate management of the species in those reserves.

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Chapter 5: Supporting Information

S.I. Material and Methods

S.I. The Ruaha and Selous landscapes

The Rungwa-Ruaha landscape spans over 45,000 km^2, and encompasses the Ruaha National Park -where consumptive use of wildlife is strictly forbidden; Kisigo, Rungwa, Muhezi Game Reserves, and Pawaga-Idodi/MBOMIPA Wildlife Management Area -where there is regulated consumptive use of wildlife; and adjacent village land -where agropastoral is the main type of human activity, and wildlife is exposed to poaching. The climate is semi-arid to arid, with bimodal rainfall peaks between December to January and March to April, with ~500 mm rain/year (Walsh 2000a). The temperature ranges from 15 to 35C (Darch 1996). The altitude ranges from 696 to 2,171 m (ESA 2009). The vegetation cover is a mosaic of East African semi-arid savannah and Zambesian miombo woodland, *Acacia* sp., *Combretum* sp. and *Commiphora* sp (Sosovele and Ngwale 2002). The Ruaha River is the main water supply in the study area, providing key resources for wildlife. During the driest season, the river and 20 natural water holes become the most important water source for wildlife and livestock (Epaphras et al. 2008), attracting species towards the park borders with the Pawaga-Idodi/MBOMIPA Wildlife Management Area and village land (Abade et al. 2014b).

The Mikumi-Selous region spans over 50,000 km^2, which makes it one of the largest protected areas in Africa (Brink et al. 2013), and a world renowned trophy hunting destination (Brink et al. 2016). The Selous Game Reserve encompasses a diversity of vegetation classes within its 43 different hunting blocks, though being dominated by deciduous Miombo woodland (UNESCO 2014). The Mikumi-Selous area encompasses the Selous Game Reserve, the Mikumi National Park on its northern border, and the Kilombero Valley and Udzungwa Mountains National Park on its west borders. The area is exposed to substantial differences in rainfall, with the east receiving ~750 mm rain/year, whereas the west is exposed to ~1,300 mm rain/year (Caro et al. 2009b).

The gradient of human occupation between Ruaha and Selous contains > 125 villages and over 2 m people residing within these regions. There are a few small forest and nature reserves (Table S5.1) scattered among these villages.

Despite of the geographical proximity of the Ruaha-Selous areas (~180 km apart), and their shared similarities in habitat and environmental conditions for harbouring significant populations of carnivores, the human-dominated matrix between these protected areas has been suggested to create a barrier for carnivore movements, and pose an imminent threat to the connectivity between these populations (Dolrenry et al. 2014; Epps et al. 2011; Jones et al. 2009).

Table S5.1. Protected areas according to official land-management category across the Ruaha-Selous landscape, southern Tanzania

Protected Area	Official Land Use Category	Area (Km^2)
Forest Reserve No. 1	Forest Reserve	0.56
Forest Reserve No. 4	Forest Reserve	7.33
Gulosilo	Forest Reserve	36.50
Image	Forest Reserve	90.31
Irunda	Forest Reserve	3.90
Iwande	Forest Reserve	124.34
Kisinga-Rugaro	Forest Reserve	59.76
Kisinga-Rugaro	Forest Reserve	118.02
Luhombero Luwegu	Forest Reserve	402.05
Lulanda	Forest Reserve	11.54
Lungonya	Forest Reserve	1,985.45
Mang'alisa	Forest Reserve	58.75
Mufindi Scarp	Forest Reserve	392.19
Mufindi Tea Estate Land	Forest Reserve	356.72
Nambiga	Forest Reserve	15.88
New Dabaga-Ulongambi	Forest Reserve	37.48
Ngindo/North East Undendeule	Forest Reserve	188.91
Ngongwa-Busangi	Forest Reserve	30.77
North East Undendeule	Forest Reserve	1,591.57
Nyanganje	Forest Reserve	190.28
Pala Mountain	Forest Reserve	108.02
Ruande	Forest Reserve	5.70
Ruande	Forest Reserve	6.26
Sao Hill	Forest Reserve	288.83
Ukwiva	Forest Reserve	357.24
Uzungwa Scarp	Forest Reserve	182.16
Kizigo	Game Reserve	5,333.60
Muhezi	Game Reserve	3,769.62
Rungwa	Game Reserve	9,729.38
Selous Game Reserve	Game Reserve	47,134.77
Ruaha	National Park	20,226
Mikumi	National Park	3,327.56
Udzungwa Mountains	National Park	2,088.69
Kilombero	Nature Reserve	95.44
Kilombero	Nature Reserve	1,219.70
Kilombero Valley Floodplain	Wetlands of International Importance (Ramsar)	7,953.93
MBOMIPA	Wildlife Management Area	740.35
Ngarambe-Tapika	Wildlife Management Area	787.20
Waga	Wildlife Management Area	117.68

S.I. Ecological covariates

We selected a candidate set of covariates known or hypothesized to influence lion spatial distribution (Abade et al. 2014b; Packer et al. 2005a; Valeix et al. 2010). We rejected collinearity among the candidate set of covariates based on Pearson correlation and variance inflation factor tests (Pearson<0.7, VIF <10 (Naimi et al. 2014)). The covariates data were converted in habitat-grid cells of approximately 1 km^2 according to their original resolution size (Table S5.3; Fig. S5.4). We performed the spatial data analyses in ArcGIS v.10.2. We defined the relative contribution of each covariate to habitat suitability following Friedman (2001), by estimating the number of times in which a covariate is selected for splitting the trees, and weighted by the square improvement to the model resulting from each split, and then averaged over all trees generated during model implementation.

S.I. Boosted regression trees

The BRT models combine the flexibility of decision trees with the powerful ensemble approach of gradient boosting (Elith et al. 2008; Friedman 2001; Salonen et al. 2014). The principle behind the BRT algorithm is the construction of a forward stage wise additive ensemble of decision trees, where each added decision tree is maximally correlated with the negative gradient of a general loss function (e.g. squared loss). This modelling approach has been shown to have a superior predictive performance when compared to other predictive algorithms (Heikkinen et al. 2012; Marmion et al. 2009) due to its capabilities of handling complex, and interacting relationships between species probability of occurrence and covariates (Elith et al. 2006; Elith et al. 2008; Kraemer et al. 2015). In the forward stage wise fitting it is easy for the BRT to completely overfit the observed data; to prevent this overfitting and maximise generalizability, regularisation is performed via K-fold cross validation and shrinkage (reducing the contribution of an individual tree). Gradient minimisation was performed using a squared loss function (i.e. the deviance).

S.I. Model processing

We adopted an ensemble approach of 200 sub-models predicting the distribution of highly suitable habitats for lions, following Kraemer et al. (Kraemer et al. 2015). Prior to run the final 200 BRT models, we fit 100 BRT models on each of the 20 thinned dataframes. Using the optimally learnt hyperparameters from these models we refit on the whole lion dataset, and then add this output to the ensemble BRT model. We fitted each model iteration to a distinct bootstrap resampling of the resulting dataset, and then used for deriving the final ensemble map of habitat suitability for lions in the study area. The final output map was generated based on the mean of all the 200 sub-model outputs implemented in the 20 thinned dataframes. We assessed pixel-based uncertainty by calculating 95% confidence interval from the 200 sub-models (Kraemer et al. 2015). We performed regularisation using a penalized forward stepwise search with generalisation error evaluation via cross-validation to minimize model overfitting and identify the BRT optimal hyperparameters (Elith et al. 2008; Kraemer et al. 2015). Modelling was performed using the gbm (Ridgeway 2013), dismo (Hijmans et al. 2012), raster (Hijmans and van

Etten 2014) and seegSDM (Golding 2014) R packages (RStudioTeam 2015). We evaluated predictive performance of each sub-model based on the values of the area under the receiver operating characteristic (ROC) curve (AUC), and Cohen's Kappa statistic (Cohen 1960). The ROC/AUC was calculated based on the mean AUC value for each of the ten cross-validation folds evaluated against the other 90% of the data under the pairwise distance sampling procedure (Hijmans 2012). The final predictive accuracy of the ensembled model was derived from the mean and standard deviation of these AUCs across all 200 sub-models (Hijmans 2012).

S.I. Modelling notes

Most of the lion presence data were opportunistically collected within protected areas (Table S5.2), thus observational bias is a possibility, though we used spatial data thinning coupled with pseudo-absences weighing to minimise this issue. We acknowledge that limited data from Mikumi and western portions of Selous likely interfered with model predictive capability for these areas. We surmise that we incorporated any potential variation in the covariates between 2006-2015 by using their averaged values for the timespan of the study, excluding the human population density data. We highlight that our presence-only models covey information about predicted habitat suitability for lions instead of the actual probability of lion occurrence (Guillera-Arroita et al. 2015). We therefore recommend that further studies should prioritize standardized collection of presence-absence data across this ecosystem whenever possible, as this could yield better estimates of true probability of lion occurrence (Guillera-Arroita et al. 2015). Finally, even though the use of thresholds for transforming continuous model outputs into binary products for defining habitat suitability has been criticized (Guillera-Arroita et al. 2015), this approach is justifiable when the information derived from this transformation is required for supporting conservation planning as the case in this study (Liu et al. 2016). Despite these aforementioned challenges, this study collated the most representative dataset about lion presence available for these areas, and presented the first and much needed map of key habitats for lion conservation in this study area.

Table S5.2. Number of lion records (N=2,393) used for predicting the distribution of highly suitable habitats and the key conservation areas for the species across the Ruaha-Selous landscape, Tanzania

Area	Land-use	Lion records	Method		
			Camera trapping	Sighting	Questionnaire
Kizigo	GR	8	-	8	-
MBOMIPA	WMA	9	3	6	-
Mikumi	NP	2	-	2	-
Ruaha	NP	1953	15	1938	-
Rungwa	GR	9	-	9	-
Selous	GR	336	-	336	-
Village land	VL	76	2	19	55

GR. Game reserve; WMA. Wildlife management area; NP. National Park

Table S5.3. List of covariates used in the boosted regression tree models

Covariate	Source	Original Resolution
Elevation	www.worldclim.org	30 arc-seconds (~1 km)
Slope	Derived from elevation	-
Rainfall	www.worldclim.org	30 arc-seconds (~1 km)
Distance to water	Derived from www.fao.org/geonetwork/srv/en/main.home	-
Human population	www.afripop.org	0.000833333 (~100 metres)
Vegetation continuous fields (VCF)	lpdaac.usgs.gov/data_access/	250 metres
Vegetation class (Globcover)	due.esrin.esa.int/page_globcover.php	300 metres

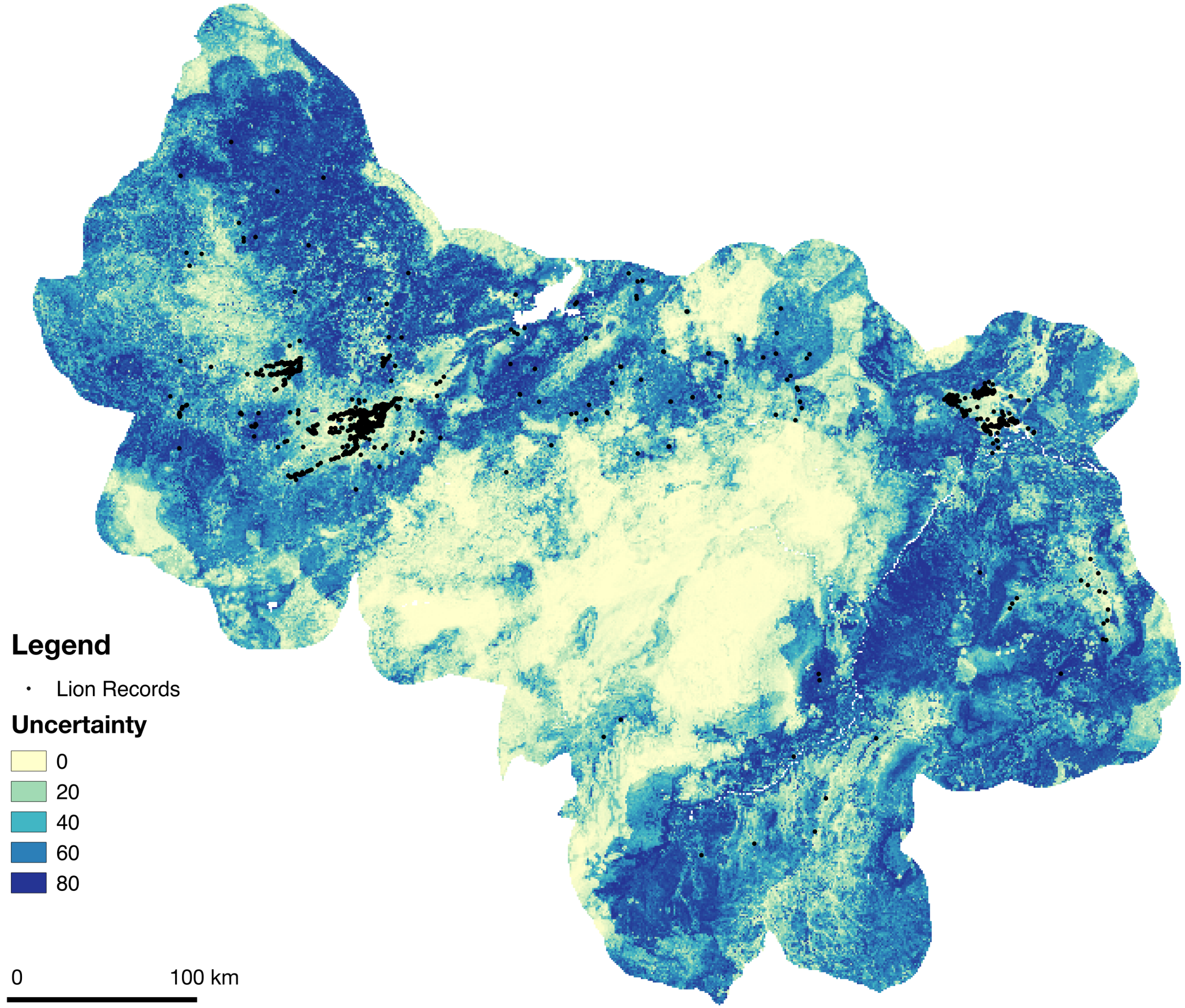

Figure S5.1. Estimated uncertainty for lion habitat suitability across the Ruaha-Selous landscape in southern Tanzania. Uncertainty ranges from very little (0) to greatest uncertainty (80) in suitability prediction. Lion records (N=2,393).

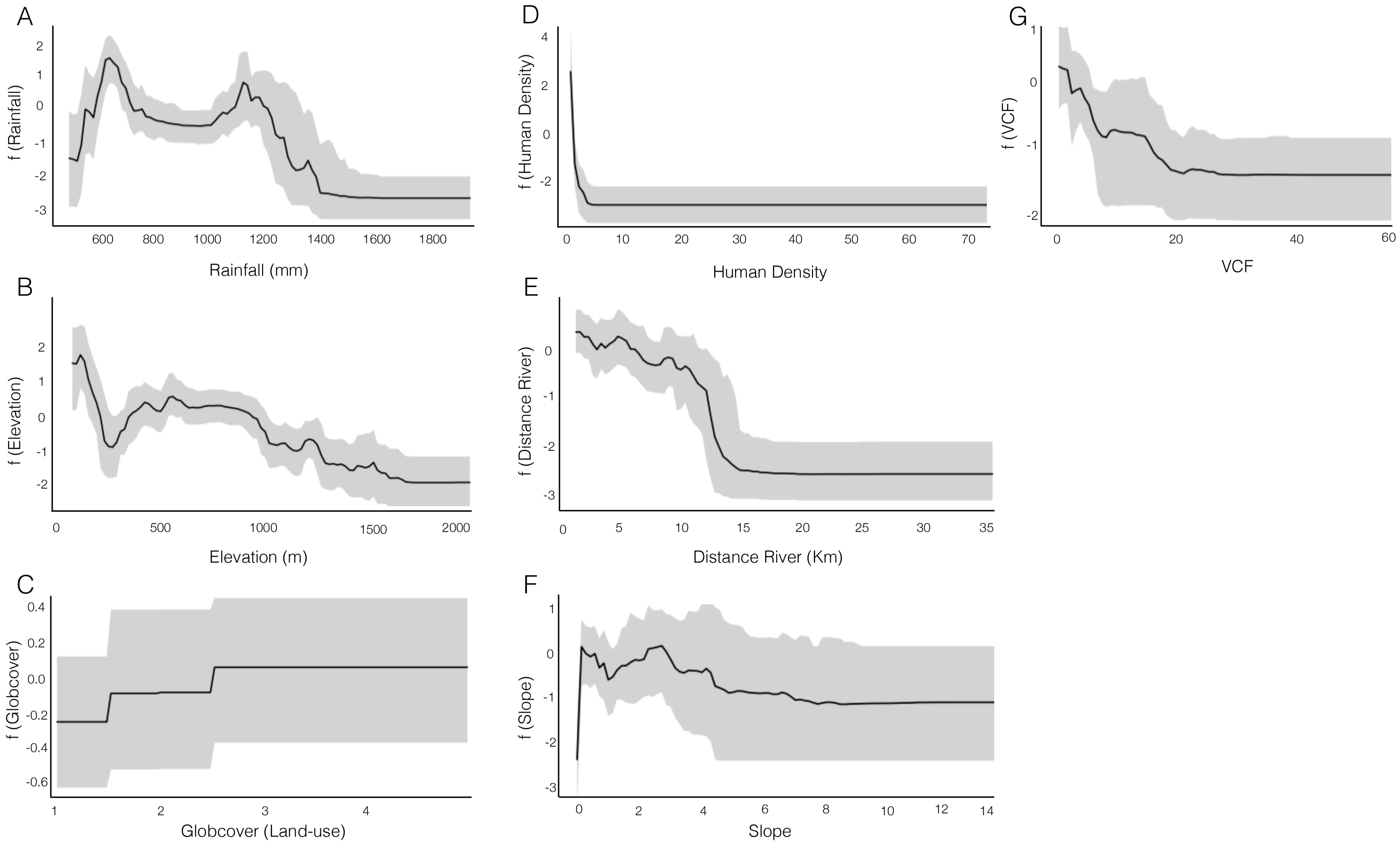

Figure S5.2. Effect plots for each ecogeographic variable used in the BRT modelling predictions for lion habitat suitability across the Ruaha-Selous landscape in southern Tanzania. A. Rainfall (mm); B. Elevation (m); C Globcover (Land-use: 1. Woodland, 2. Shrubland, 3. Bushed grassland, 4. Water, 5. Urban, 6. Bare, 7. Cropland); D. Human population density (Afripop); E. Distance to rivers (Km); F. Slope; G. Vegetation Continuous Fields (Land-cover).

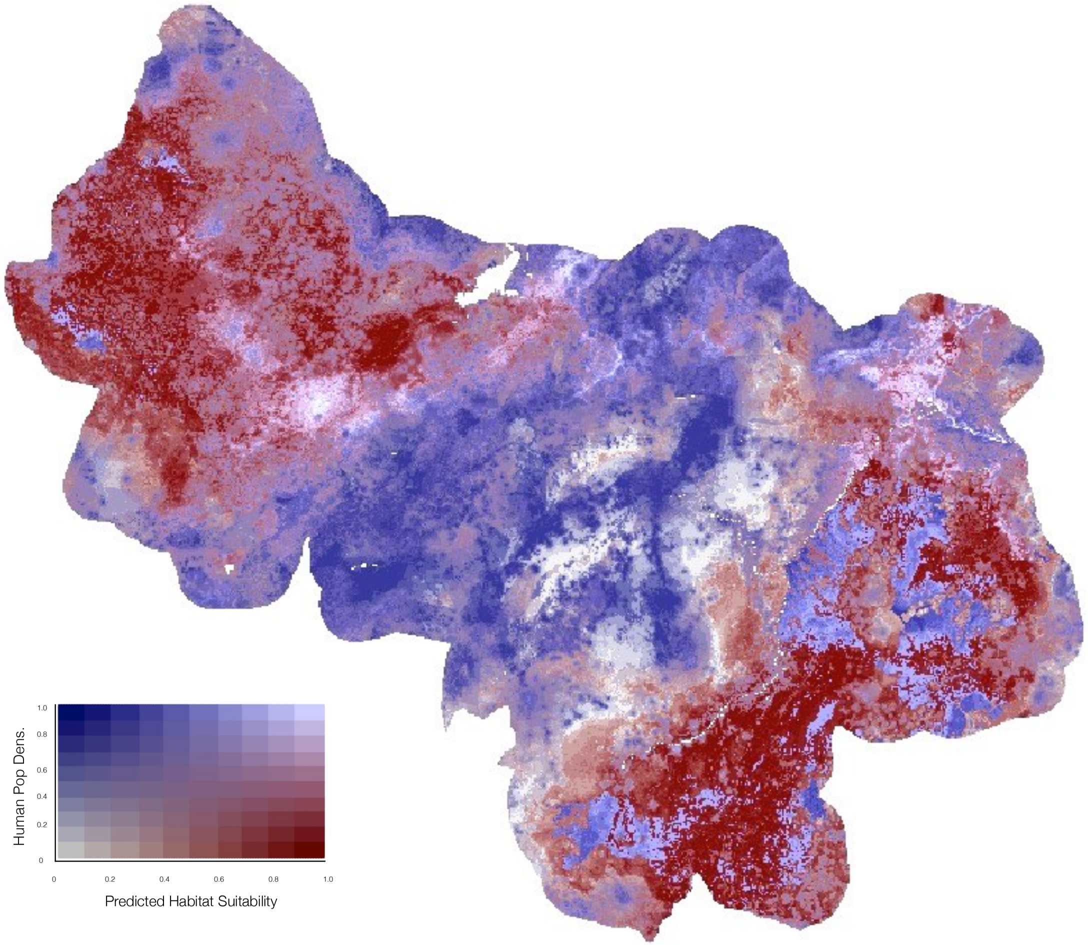

Figure S5.3. Choropleth map showing the overlap between the estimated habitat suitability for lions and human population density across the Ruaha-Selous landscape. Warmer areas indicate areas of high suitability for lions and low human population density.

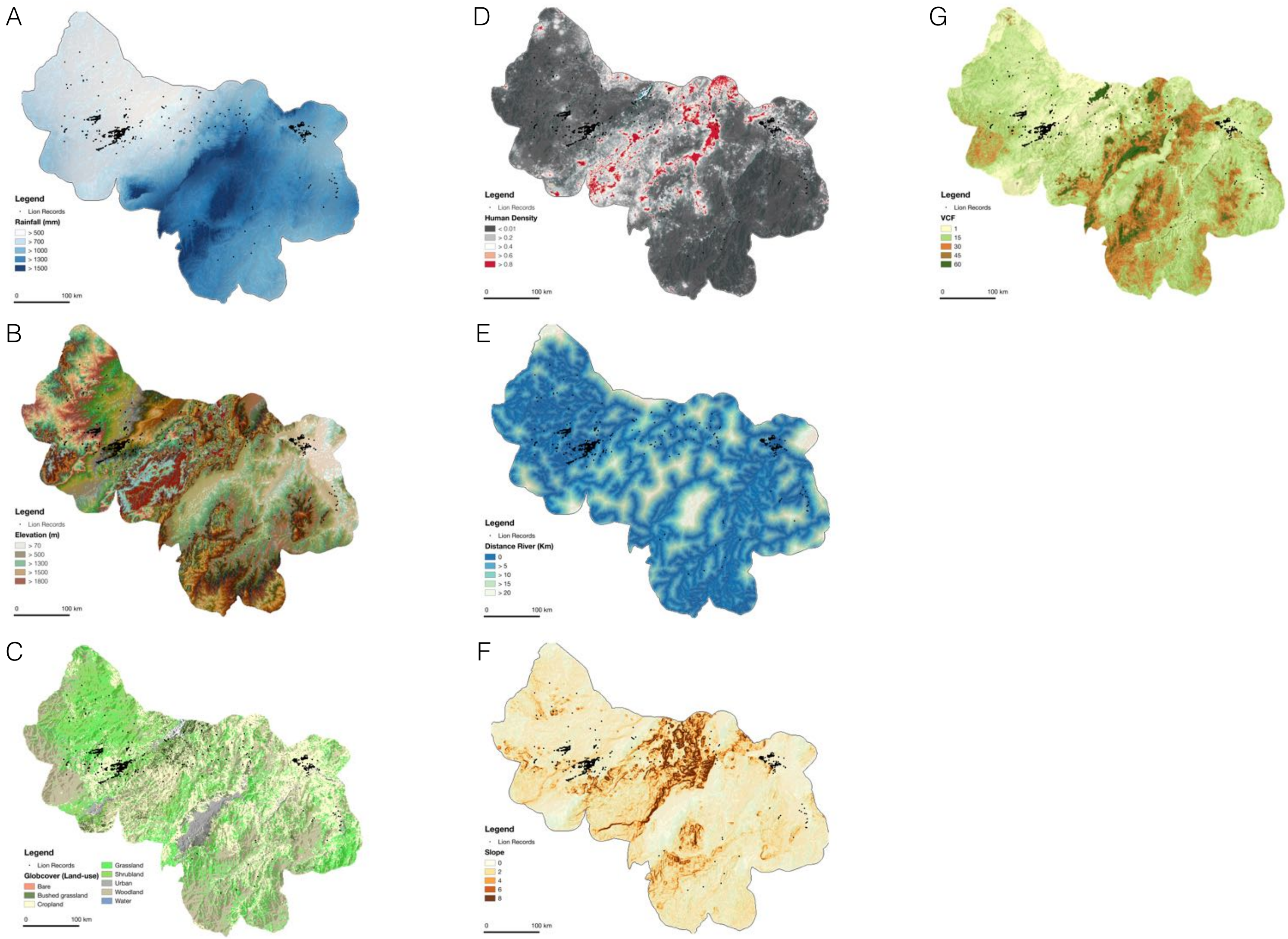

Figure S5.4. Ecogeographic variables used in the BRT modelling predictions for lion habitat suitability across the Ruaha-Selous landscape in southern Tanzania. A. Rainfall (mm); B. Elevation (m); C Globcover (Vegetation class); D. Human population density (Afripop); E. Distance to rivers (Km); F. Slope; G. Vegetation Continuous Fields (Land-cover).

Chapter 6: General Discussion

6.1. Overview

In this study I used a combination of carnivore presence data and bespoke advanced modelling techniques to provide the first in-depth analysis of carnivore occurrence patterns across a gradient of anthropogenic pressure in southern Tanzania, with a focus on the Ruaha landscape and adjacent areas. More specifically, I identified and quantified the influence of landscape and human-related variables on the spatial ecology of a carnivore guild across the multiple use landscapes within the study area. The study area investigated here encompasses some of the most important carnivore population strongholds in East Africa (Riggio et al. 2012; TAWIRI 2009a, 2012), and yet information is limited for most aspects related to the spatial ecology of carnivores, especially beyond protected areas. This knowledge gap represents an important obstacle to the development and implementation of targeted carnivore conservation practices (TAWIRI 2009). Therefore, improving the knowledge about the factors that determine carnivore distribution is key to better understanding their spatial ecology in this landscape, and, most importantly, to help inform action plans and the development of contextualized strategies for carnivore conservation. Thus, in this thesis I aimed to fill some of the current information gaps by providing novel data and insights to further identify the factors that most contribute to carnivore occurrence across human-dominated landscapes where anthropogenic pressure represents an increasing threat to their survival. Overall, the results presented in this study contribute to a better understanding of carnivore spatial ecology in human-dominated landscapes. Moreover, the methods described in each chapter can be applied in other areas where humans and carnivores overlap in order to better inform management and conservation strategies.

Chapter 2 investigated lion site use across multiple use landscapes extending from Ruaha National Park to the Wildlife Management Area and surrounding village lands. The occupancy models applied to extensive camera-trapping data identified prey availability and proximity to ranger posts (which could represent a proxy for areas of increased surveillance), as the determining factors of lion site use in this area. Lions were not detected in the village lands, which could be an indication of low population numbers resulting from anthropogenic pressures such as bushmeat poaching, habitat and prey loss, and conflict-related killings.

Chapter 3 investigated site use for the leopard, which is often deemed as a generalist predator, and ecologically less sensitive to human disturbance than lions (Athreya et al. 2016; Jacobson et al. 2016; Riggio et al. 2012; Woodroffe 2000). A similar analytical method was used as in *Chapter 2*, although models were based on species-specific variables with the potential to influence leopard site use. The model outputs indicated that, unlike for lions, leopard site use was largely limited by proximity to households and increased livestock numbers at each camera-trap station than by wild prey availability. Similarly to the observations from *Chapter 2*, leopards were not detected in village lands, suggesting that they are also sensitive to anthropogenic pressures in this area.

Chapter 4 evaluated the influence of environmental variables on the occurrence patterns of a carnivore guild, composed of aardwolf, bat-eared fox, black-backed jackal, civet and leopard, across the same sampling areas as the previous chapters, while accounting for potential interspecific interactions on detection and site occupancy. A conditional detection model was used to assess the dependency of mesocarnivore detections in relation to those of the more dominant leopard. Furthermore, the probability of site co-occupancy was estimated using a novel modelling approach that enabled assessing interspecific interactions without assuming hierarchical asymmetry between species in different trophic levels. As in the previous Chapters, there was limited detection for all carnivore taxa in the human-dominated landscapes. The models suggested a positive association – just to the level of statistical significance - for the conditional detection of black-backed jackals and civets in relation to leopards. As explained in *Chapter 4*, this could be associated with the opportunistic scavenging behaviour exhibited by these mesocarnivore species. Additionally, there was a notable difference in carnivore responses to anthropogenic disturbance and landscape variables: site occupancy for aardwolves, bat-eared foxes, and black-backed jackals was strongly determined by distance to the Great Ruaha River, whereas anthropogenic variables were the main limiting factors to site use by civets and leopards. Finally, bat-eared foxes and black-backed jackals were more likely to be found co-occupying the same sites in areas of increased anthropogenic pressure closer to human households, although they were more likely to be found independently outside village lands.

In *Chapter 5*, I investigated how the human gradient separating the largest carnivore strongholds in East Africa, the Ruaha and Selous landscapes, could be influencing or limiting the overall distribution of highly suitable habitats for large carnivores, using the lion as a key-species. I identified the most important predictors for habitat suitability, and mapped the predicted distribution of niche-optimum habitats for lions based on advanced boosted regression trees algorithms. The model outputs suggested a fragmented mosaic of sizeable and suitable habitat patches for lions amidst village lands between Ruaha and Selous Game Reserve. The results highlighted that game reserves encompassed the largest swathes of prime habitats for lions, and that the loss or conversion of these habitats to non-wildlife-based land-use types (such as livestock rearing or agriculture) could be highly detrimental to lion conservation.

6.2. Overall patterns of carnivore occurrence across the gradient of anthropogenic pressure around Ruaha National Park

The occupancy analyses performed in this study identified important heterogeneity in carnivore responses to both anthropogenic and landscape variables across the gradient of human occupation. For each species, the model outputs identified a particular set of ecological and human-related factors that determined carnivore occurrence, which provided interesting insights into carnivore spatial ecology. For instance, site use for lions was largely influenced by large prey biomass (i.e. CPUE index), whereas for leopards and civets, it was mostly limited by proximity to human households and high number of livestock detections at the camera-trap station level. Black-backed jackals, bat-eared foxes and aardwolves, on the other hand, were mostly influenced by proximity to the Great Ruaha River.

6.2.1. Lions

The association between lion site use and high prey biomass described here reinforced previous studies in the core areas of Ruaha National Park, which showed significant effects of large prey on lion occupancy and detection (Cusack et al. 2016). These results also concur with other studies that found large prey as a key-determining factor of lion spatial distribution and habitat use in other parts of the African savannah (Davidson et al. 2013; Hayward and Kerley 2005; Loveridge and Canney 2009; Valeix et al. 2009). However, it is important to notice that in systems of pronounced seasonality such as Ruaha, where water becomes a scarce resource during the dry season, prey are known to agglomerate around the few available water sources, which has a strong influence on carnivore spatial distribution (Davidson et al. 2013; Loveridge et al. 2009; Valeix et al. 2010). Thus, it is possible that the lion site use patterns observed here could be associated with the potential effects of seasonal prey distribution concentrated in the surroundings of the Great Ruaha River. Indeed, previous studies have found significant seasonal variations in species occurrence patterns in portions of Ruaha National Park, with increased prey and carnivore detection during the rainy season (Cusack et al. 2015). Hence, additional data from the wettest periods of the year could help to better understand the effects of seasonality on lion spatial distribution, especially for the village lands where water becomes more ubiquitous, and could influence distribution and availability of wild prey in this area.

6.2.2 Leopards

The results presented here suggest that leopard site use was largely limited by high livestock numbers and proximity to human households, rather than being primarily determined by prey biomass. Areas close to households with many livestock probably experience relatively high levels of livestock depredation and human-carnivore conflict, where leopards and other large carnivores are exposed to high conflict-related mortality (Abade et al. 2014a; Dickman 2015). Similar results have been found in Namibian farmlands, where leopard spatial ecology was limited as much by anthropogenic variables such as tolerance levels by farmers, as by prey availability (Marker and Dickman 2005). In another example, leopard density and distribution have been found to decrease in areas of high livestock density and conflict with farmers in communal lands in southern Africa (Constant 2014). Furthermore, the low number of leopard detections in village lands could reflect a potential risk-avoidance strategy to minimise exposure to those riskier areas of the anthropogenic landscape where there is high human-induced mortality (Loveridge et al. 2016b; Oriol-Cotterill et al. 2015a; Valeix et al. 2012). Thus, these occurrence patterns likely corresponded to leopards' ecological responses to the habitat changes associated with intense human occupation and agro-pastoral activities outside Ruaha National Park (as discussed in *Chapters 2* and *3*), and the combined effects of high conflict and mortality found in the village lands.

The weak influence of prey biomass on leopard site use could indicate reliance on smaller prey than those considered in the analyses (e.g. bushbuck, common duiker, impalas, greater kudu, warthog – which are commonly favoured by the species (Hayward et al. 2006)), especially in the village land, where there were low prey detections and likely abundance (Fig 3.3). This could be a response to prey depletion in the village land, as leopards are known to shift and rely on small-sized prey species in areas of increased bushmeat hunting, and of intense competition with humans for limited food resources where their favoured prey are scarce (Ghoddousi et al. 2016; Hayward et al. 2006; Henschel et al. 2011).

6.2.3. Mesocarnivores

The strong association between mesocarnivore occurrence and proximity to water sources depicted here were concurrent with findings from across 11 study sites in northern Tanzania, where proximity to water was a major key-variable determining the spatial distribution of a whole carnivore guild (Pettorelli et al. 2010). However, they differed from studies in Botswana's Okavango Delta and in some areas of the Serengeti, where the spatial distribution of black-backed jackals, bat-eared foxes and aardwolves was either unaffected by the presence of water sources (Rich et al. 2016), or associated with those areas further from rivers (Durant et al. 2010). One possible explanation for such differences is that the carnivore surveys of the present study were limited to the dry seasons, when the Great Ruaha River becomes the only water source available for wildlife, and exerts substantial influence on carnivore and prey distribution in this landscape (Cusack et al. 2016). Additional data collected during the rainy season, when water sources become ubiquitous and more evenly distributed across village lands, could help to further investigate the role of the Great Ruaha River on determining mesocarnivore spatial occurrence in this area. It is also noticeable the limited contribution of increased vegetation cover to mesocarnivore occurrence patterns here, as this variable has been found to influence site occupancy of a whole carnivore guild - with a particular strong effect on black-backed jackal and civets - in savannah areas of northern Botswana (Rich et al. 2017). Such differences could be attributed to the lack of forested vegetation types in the surveyed areas of the Ruaha landscape.

The low mesocarnivore detection on village land was noteworthy, suggesting that anthropogenic pressures are not only affecting highly visible and conflict-causing species such as lions, but also smaller members of the carnivore guild. Anthropogenic factors, including proximity to human settlements, have been found to limit site occupancy for carnivores such as aardwolves, civets and black-backed jackals in similar areas of human-carnivore interface elsewhere in Africa (Schuette et al. 2013b). However, the relatively low influence of human-related variables (e.g. proximity to human households, and livestock presence at camera-trapping station) to mesocarnivore site use could suggest that other unaccounted factors such as habitat loss, change in vegetation structure, and prey depletion, could be influencing mesocarnivore distribution in the village lands. For example, changes in habitat structure and increased shrub cover, which is often associated to intense livestock grazing, can limit the abundance of smaller prey items such as rodents, termites and beetles, and the diversity of mesocarnivores in savannahs (Blaum et al. 2007; Blaum et al. 2009). Further investigation is therefore required to better understand mesocarnivore occurrence in village lands.

6.3. The importance of anthropogenic pressures around Ruaha National Park in determining carnivore occurrence

Despite the observed variation in carnivore responses to environmental traits, there was a consistent and steady decline in carnivore detections with increasing distance from Ruaha National Park, especially in those areas of increased anthropogenic pressure closer to human households. These findings could be indicating low carnivore abundance in the village lands, as low detections have been shown to often correlate with low population densities (MacKenzie et al. 2003; MacKenzie et al. 2002). The Ruaha landscape has undergone substantial changes over the past decades following rapid increases in human and livestock populations around the National Park (Green and Adams 2015; Williams 2005). The increased populations of herders and farmers has led to intensification of agropastoral practices in the village lands, and caused major habitat conversion and degradation (Morris et al. 2002). Increased human populations have been associated with increased threats to carnivores, such as bushmeat hunting and poaching, logging, livestock encroachment, and human-wildlife conflict (Lindsey et al. 2017a). Therefore, these anthropogenic pressures associated with rapidly growing human populations are likely to be a limiting factor for both carnivore and wild prey occurrence around Ruaha

National Park, as observed in other areas across Africa. For example, leopard density decreased around Zambia's South Luangwa National Park due to intense bushmeat poaching and low prey availability (Rosenblatt et al. 2016), while human-induced killings represented the main cause of leopard and lion mortality outside protected areas in parts of South Africa and Kenya respectively (Ogutu et al. 2005; Oriol-Cotterill et al. 2015a; Williams et al. 2017). Similarly, Henschel et al. (2011) found lower leopard densities in closer proximity to human households and areas of intense poaching in the Congo basin.

In Ruaha, despite the limited information about the major causes of carnivore mortality and associated consequences to local population survival, over 100 lions and other large carnivores have been killed just as a result of conflict and cultural hunting in the village lands around Ruaha National Park between 2010 and 2016 (Dickman, in prep.), which could be contributing to reduced large carnivore numbers in the village lands. As discussed in *Chapter 2*, the potential for village land to become a sink for carnivores is a concern, as these source-sink dynamics can affect adjacent protected-area carnivore populations as well, as observed elsewhere in Africa (Balme et al. 2010; Loveridge et al. 2010a; Loveridge et al. 2016b). It is noteworthy that even mesocarnivores had low detection on village land, despite their often common association with areas closer human households due to increased food subsidies (Newsome et al. 2015), and are more likely to be found in areas where competition from larger carnivores is reduced (Prugh et al. 2009). The lack of a potential release of mesopredators in village lands is somehow surprising given the known high levels of top-predator removal (Dickman 2015; Dickman et al. 2014), and the likely low numbers of top-order carnivores in these areas (as suggested by the lack of large carnivore detections outside the protected area). Blaum et al. (2009), for instance, have shown an increased abundance of mesocarnivores such as bat-eared foxes in farmlands, where more dominant carnivores have been commonly removed due to conflict in the southern Kalahari. However, the results presented here are similar to those by Schuette et al. (2013), which did not find evidences of high mesocarnivore occupancy estimates to be inversely correlated with apex predators. Thus, it is possible that wider anthropogenic pressures not examined here, such as habitat conversion and likely prey depletion, could be having a marked impact on the mesocarnivore spatial distribution outside Ruaha National Park. Thus, it is not just the obvious direct carnivore killings that need to be considered for conservation planning, but also the less visible - and likely as important - pressures such as habitat and prey loss, as these combined factors could be a major threat to the overall carnivore guild in this area.

6.4. Distribution of highly suitable habitats for carnivores across the Ruaha and Selous landscapes

The model outputs from *Chapter 5* suggested that habitat suitability for lions (which was used as a study-model due to its high ecological requirements for habitats and resources) was chiefly influenced by human-related variables, with low human population density as the major determining factor of habitat suitability. Thus, approximately 77% of the predicted highly suitable habitats with the potential to support lion populations were exclusively limited to game reserves and national parks, with the remainder patchily distributed across human-dominated landscapes. These findings are concurrent with other studies which suggest that lion populations are often largely restricted to protected areas, as observed in West (Henschel et al. 2014), Central and Southern Africa (Bauer et al. 2015) – although it is important to note that ~44% of the remaining lion range is estimated to fall outside formally protected areas (Lindsey et al. 2017a).

In this study, it was noteworthy that 70% of highly suitable habitats for lions occurred within 30 km of the edges of protected areas, and this relative proximity to human-dominated areas means that lions are likely to be exposed to anthropogenic mortality, for example as a result of conflict (Abade et al. 2014a; Bamford et al. 2014; Brink et al. 2013; Brink et al. 2016; Dickman et al. 2014). These areas, which have been described as landscapes of anthropogenic mortality (Loveridge et al. 2016b), can function as ecological traps and population sinks that can destabilize lion populations and accelerate extinction processes (Loveridge et al. 2010a; Woodroffe and Frank 2005; Woodroffe and Ginsberg 1998). Therefore, though most of the highly suitable habitats in this study were within game reserves and national parks (in relative proportions, 65% of the habitats within game reserves were highly suitable for lions, in comparison to 47% in national parks and 28% in village lands), they were located in areas where carnivores could still be subject to increased anthropogenic-induced mortality, so still need very careful monitoring and conservation management.

Outside protected areas, the results depicted a worrying scenario, where there was a highly fragmented and degraded matrix of suitable lion habitat. In here, and as observed in the other Chapters, the gradient of anthropogenic pressure was the major limiting factor to habitat suitability, and thus lion spatial distribution outside Ruaha National Park and Selous Game Reserve. Interestingly, even relatively low human population densities (<10 people/km^2) were correlated with low habitat suitability for lions, which is much lower than the 25 people/km^2 suggested as a limiting threshold to lion distribution by other studies (Riggio et al. 2012; Woodroffe 2000). As discussed above, these patterns could be associated with human occupation and habitat conversion for livestock grazing and agriculture, following the trends seen over recent decades (Brink et al. 2016; NBS 2013; Packer et al. 2011; Salerno et al. 2014; Wittemyer et al. 2008). It could also be that even relatively low densities of highly antagonistic people, such as traditional pastoralists who feel lions impose high costs and offer no benefits, can have severe impacts in terms of anthropogenic mortality (Bamford et al. 2014; Dickman 2015). In addition, the patchy distribution of highly suitable habitats, and the relatively high human density among them could mean substantially compromised landscape connectivity between Ruaha and Selous, corroborating previous studies that suggested critically limited potential for connectivity among these areas due to intense human-related habitat changes (Caro et al. 2009a).

The high proportion of highly suitable lion habitats within game reserves highlighted the importance for lion conservation of maintaining those areas under a wildlife-based land use status. As discussed in *Chapter 5*, in a scenario where trophy hunting becomes less profitable as a result of poorly managed quotas, overhunting and wildlife depletion (Brink et al. 2016), and 'emptied' hunting areas are set aside for other non-wildlife based land use such as livestock farming and agriculture, lions could lose some of their most highly suitable habitats their conservation in East Africa. Therefore, ensuring the maintenance of these game reserves under a wildlife status seems central for sustaining lion conservation across these large landscapes, as these areas are important for overall wildlife conservation by protecting habitats against the pressing threats of land-use conversion, habitat loss and prey loss due to farming, settlement and grazing (Brink et al. 2016; Caro et al. 2009b; Lindsey et al. 2013b). Moreover, anti-poaching efforts in well-managed game reserves can help to minimise the threat of wildlife exploitation (Brink et al. 2016; Di Minin et al. 2016a). However, it is important to note that poorly regulated trophy hunting can have a devastating effect on carnivore populations (Bauer et al. 2015; Brink et al. 2016; Packer et al. 2011), so it is vital that any trophy hunting activities, particularly for infanticidal species such as lions and leopards, are strictly regulated and controlled (Lindsey et al. 2013b; Lindsey et al. 2016; Macdonald et al. 2016; Packer et al. 2011).

6.5. Implications for conservation

This study provided the first comprehensive data on the potential determinants of carnivore occurrence patterns in the Ruaha landscape and adjacent areas. Approaches like this are much needed as they enable understanding the variations of carnivore responses to ecological and anthropogenic factors, and provide important data for informing effective species conservation planning (Sanderson et al. 2002). For example, the results presented here suggest that even relatively low human population densities appear to have strongly negative associations with carnivore occurrence, and to limit site occupancy of both large and mesocarnivores across gradients of anthropogenic pressure. The likely association of areas of human occupation with habitat conversion for livestock grazing and agriculture, prey depletion, and high conflict-related carnivore mortality requires broad-ranging conservation strategies. For example, strategies should foster protection and maintenance of wild prey populations, given their strong association with lion site use across the gradient of anthropogenic pressure. Similarly, it should find avenues to minimise the potential detrimental effects of livestock grazing on displacement of wildlife, prey depletion, and overgrazing, as this cold be contributing to limit carnivore distribution outside Ruaha National Park, as observed elsewhere in East African rangelands (Schuette et al. 2016). Recent studies have highlighted the efficacy of using adaptive livestock and wildlife foraging systems, and planned grazing strategies (which is explained in detail in *Chapter 3*) to limit the impact of livestock on wild habitats and overall wildlife, as well as increasing livestock productivity, even during the driest periods of the year where grazing becomes scarce (Fynn et al. 2016; Odadi et al. 2017; Tyrrell et al. 2017). These strategies could help to minimise some of the negative effects of livestock grazing to the landscape, and ultimately help to conserve wildlife. However, this could be of limited application given the nomadic pastoralism observed in parts of the village land around Ruaha.

Moreover, the successful conservation of carnivores in the study area ultimately hinges on the implementation of measures aiming at improving human tolerance towards carnivores (such as those discussed in detail in *Chapters 2-4*), to reduce carnivore mortality and incentivise wider wildlife conservation in the village lands. One option would be the adoption of schemes that would enable local people to directly engage and profit from wildlife presence, and to receive tangible and commensurable benefits from carnivore conservation in their land. The use of community-based participatory monitoring schemes such as the Lion Guardians programme, in which young men are given access to education and formal employment as wildlife monitors, has contributed to a 99% decrease in lion killings in areas of Kenya (Dolrenry et al. 2016; Hazzah et al. 2014), and this initiative has now been started in Ruaha. In addition, strategies to improve husbandry through implementation of predator-proof bomas and provision of livestock guarding dogs can reduce conflict and retaliatory or preventative carnivore killings. Some of these strategies have now begun in some villages around Ruaha National Park, where communities receive benefits such veterinary, educational and healthcare benefits as a result of demonstrated wildlife presence on village lands. These initiatives have resulted in 80% decline of large carnivore killing in some core local villages, and could minimise anthropogenic pressures facing carnivore populations at a wider scale around Ruaha National Park. However, these initiatives are currently limited to less than half of the villages around Ruaha National Park, and many have only recently begun, and it will take time to change attitudes and actions at a landscape scale.

6.6. Future research

The ability to reliably study wild carnivores and derive inferences about ecological processes such as those determining their spatial distribution is a common and long-lasting challenge in wildlife studies (Burton et al. 2015; O'Connell et al. 2010). Large carnivores, specifically, are a challenging research subject due to their expansive habitat and resource requirements, naturally low densities and elusive nature (O'Connell et al. 2010). The upsurge of the camera-trapping methodology has facilitated such studies (Meek et al. 2014; Rowcliffe and Carbone 2008), and contributed to enhance the understanding of diverse aspects of carnivore ecology, ranging from population demographics and site occupancy (Alexander et al. 2015), activity patterns (Rowcliffe et al. 2014), interspecific interactions (Lewis et al. 2015; Rota et al. 2016a), and foraging behaviour in human-dominated landscapes (Smith et al. 2017).

By using extensive camera-trapping survey across a gradient of anthropogenic pressure, in combination with a multi-species approach, this study provides the first comprehensive and robust baseline data of carnivore spatial ecology in this globally important landscape, and that can be used for future carnivore research in human dominated landscapes elsewhere. There are many aspects that could build on this research to improve further understanding of the determinants of carnivore occurrence in anthropogenic landscapes. For example, complementary survey protocols such as track counts could be used, especially in the village lands around Ruaha National Park, to further investigate the determinants of carnivore occupancy in these areas, especially to clarify what determines mesocarnivore occurrence in village lands; although it is noteworthy that such methods are subject to species misidentification, observation bias and are highly dependent on substrate types, which could limit its applications as a survey tool across the study site (Hayward et al. 2015). Furthermore, unstructured spatial capture-recapture sampling of carnivore sightings could be used for evaluating carnivore spatial ecology and demography (Elliot and Gopalaswamy 2017); however, this method would have applications only for studies within Ruaha National Park as carnivore sightings are very unlikely in the village lands. Additionally, information on movement analyses from GPS-collaring of carnivores could provide finer-scale spatiotemporal data about site use and the interspecific interactions identified by this study, and on how sympatric species co-occur and avoid each other (Broekhuis et al. 2013; Cozzi et al. 2012; Dröge et al. 2017). For instance, simultaneous radio-tracking of carnivores could help to clarify how lions, leopards and mesocarnivores adjust their movement patterns to each other, whether the interspecific interactions suggested by this study could influence mesocarnivore use of the village lands (which would enable further understanding of the results depicted in *Chapter 4*), and how these carnivores could be using the village lands spatiotemporally. In addition, such data could help to identify which variables could be associated with increased livestock risk to predation in village lands (Loveridge et al. 2016b; Oriol-Cotterill et al. 2015a; Valeix et al. 2012); and where mitigation strategies to reduce conflict and carnivore mortality should be prioritised (Oriol-Cotterill et al. 2015b; Valeix et al. 2012). Such data are fundamental for in-depth understanding of carnivore spatial ecology in human landscapes (Oriol-Cotterill et al. 2015a), and have wider applications to guide conservations strategies in human dominated landscapes, however is it currently lacking for this area. Moreover, movement data could add to the results of *Chapter 5*, and enable mapping critical pathways connecting those habitats of high suitability across the gradient of human occupation between Ruaha and Selous, and that could facilitate carnivore movement between these protected areas (Cushman et al. 2015; Elliot et al. 2014). The information so far available for the potential landscape connectivity for these two carnivore strongholds has been derived from limited camera-trapping studies (Epps et al. 2011; Jones et al. 2009), and further movement data is needed to fully understand how carnivores use this landscape, whether connectivity is possible, and which would be the priority areas for conserving population connectivity. Lastly, the development and implementation of effective management and conservation strategies requires detailed data on species demographics, population trends and understanding of the major causes of mortality (Macdonald et al. 2017), which is currently lacking for any carnivore species in this area. Thus, further studies should consider addressing these fundamental knowledge gaps in order to best conserve carnivores in the study area, with special focus on the gradient of human occupation where carnivores are most threatened and vulnerable to local extinction.

Annexes: R Scripts used in this study

Annex 1. Annotated JAGS model used in Chapter 2: "Examining patterns of lion (Panthera leo) occurrence across a gradient of anthropogenic pressure in southern Tanzania"

```
############ Site occupancy for lions ##################
#################Final GLOBAL model for lion occupancy############
#-----model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w-----

# JAGS model
sink("model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w")
cat("
   model {

   # Occupancy priors
   alpha.ranger ~ dunif(-5,5)
   alpha.house ~ dunif(-5,5)
   alpha.lgprey ~ dunif(-5,5)
   alpha.medprey ~ dunif(-5,5)
   alpha.vcf ~ dunif(-5,5)

   # Detectin priors
   beta.trail[1]  <- 0 # Reference category for anthro pressure
   for (k in 2:3) {
   beta.trail[k] ~ dunif(-10,10)
   }
   beta.lgprey ~ dunif(-5,5)
   beta.0 ~ dunif(-5,5)

   # Occupancy random intercept indexed by site (k = 11)
   for (k in 1:11){
   alpha.0[k] ~ dnorm(mu.int.alpha, tau.alpha)
   }
   mu.int.alpha ~ dnorm(0,0.001)
   tau.alpha <- pow(sigma.alpha,-2)
   sigma.alpha ~ dunif(0,10)

   # Inclusion parameters
   for (m in 1:7){
   w[m] ~ dbern(0.5)
   }

   # Likelihood
   # Ecological model for true occurrence
   for (i in 1:R) {
```

```
    z[i] ~ dbern(psi[i])

    logit(psi[i]) <- alpha.0[Area[i]] +
    w[1] * alpha.house * Dist_Household[i] +
    w[2] * alpha.ranger * Dist_Ranger_Post[i] +
    w[3] * alpha.lgprey * CPUE_Large_Prey[i] +
    w[4] * alpha.medprey * CPUE_Medium_Prey[i] +
    w[5] * alpha.vcf * VCF[i]

    # Observation model for replicated detection/nondetection observations
    for (j in 1:T) {

    y[i,j] ~ dbern(z[i] * p[i,j])

    logit(p[i,j]) <- beta.0 +
    w[6] * beta.trail[trail_type[i]] +
    w[7] * beta.lgprey * CPUE_Large_Prey[i]

    } #j
    } #i

    # Derived quantities
    occ <- sum(z[])       # Number of occupied sites
    }
    ",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = data.lion.32,
              R = nrow(data.lion.32),
              T = ncol(data.lion.32),
              trail_type = trail_type,
              Dist_Household = Dist_Household,
              Dist_Ranger_Post = Dist_Ranger_Post,
              CPUE_Large_Prey = CPUE_Large_Prey,
              CPUE_Medium_Prey = CPUE_Medium_Prey,
              Area = Area,
              VCF = VCF)

# Initial values
zst <- apply(data.lion.32, 1, max, na.rm=TRUE)        # Observed occurrence as
starting values for z
wst <- rep(1,7)
inits <- function() list(z = zst,
                    w = wst,
                    sigma.alpha = runif(1,0,10),
                    mu.int.alpha = runif(1,-3,3),
                    alpha.house = runif(1,-3,3),
```

```
                    alpha.ranger = runif(1,-3,3),
                    alpha.lgprey = runif(1,-3,3),
                    alpha.medprey = runif(1,-3,3),
                    alpha.vcf = runif(1,-3,3),
                    beta.0 = runif(1,-3,3),
                    beta.trail = c(NA,1,1),
                    beta.lgprey = runif(1,-3,3))

# Parameters monitored
params <- c("occ",
          "mu.int.alpha",
          "alpha.house",
          "alpha.ranger",
          "alpha.lgprey",
          "alpha.medprey",
          "alpha.vcf",
          "beta.lgprey",
          "beta.trail",
          "alpha.0",
          "beta.0",
          "w",
          "z")

# MCMC settings
ni <- 20000
nt <- 4
nb <- 5000
nc <- 10

# Call JAGS from R (BRT < 1 min)
model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w <-
jags(win.data, inits, params,
"model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w", n.chains
= nc, n.thin = nt, n.iter = ni, n.burnin = nb, working.directory = getwd())
print(model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w,dig=2)

# save a text file of output
sink("model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w.txt")
print(model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w,dig=2)
sink()

# model averaged parameter estimates
out <- model.lion.det.trail.lgprey.occ.ri.house.ranger.lgprey.medprey.vcf.w
sims <- out$BUGSoutput$sims.list

house.incl <- sims$alpha.house[sims$w[,1] == 1]
house.incl.vec <- c(mean(house.incl),sd(house.incl),quantile(house.incl,probs =
c(0.025,0.975)))
```

```
ranger.incl <- sims$alpha.ranger[sims$w[,2] == 1]
ranger.incl.vec <- c(mean(ranger.incl),sd(ranger.incl),quantile(ranger.incl,probs
= c(0.025,0.975)))

lgprey.incl <- sims$alpha.lgprey[sims$w[,3] == 1]
lgprey.incl.vec <- c(mean(lgprey.incl),sd(lgprey.incl),quantile(lgprey.incl,probs =
c(0.025,0.975)))

medprey.incl <- sims$alpha.medprey[sims$w[,4] == 1]
medprey.incl.vec <-
c(mean(medprey.incl),sd(medprey.incl),quantile(medprey.incl,probs =
c(0.025,0.975)))

vcf.incl <- sims$alpha.vcf[sims$w[,5] == 1]
vcf.incl.vec <- c(mean(vcf.incl),sd(vcf.incl),quantile(vcf.incl,probs =
c(0.025,0.975)))

trail.n.incl <- sims$beta.trail[sims$w[,6] == 1,2]
trail.n.incl.vec <-  c(mean(trail.n.incl),sd(trail.n.incl),quantile(trail.n.incl,probs =
c(0.025,0.975)))

trail.rd.incl <- sims$beta.trail[sims$w[,6] == 1,3]
trail.rd.incl.vec <-
c(mean(trail.rd.incl),sd(trail.rd.incl),quantile(trail.rd.incl,probs =
c(0.025,0.975)))

lgprey.beta.incl <- sims$beta.lgprey[sims$w[,7] == 1]
lgprey.beta.incl.vec <-
c(mean(lgprey.beta.incl),sd(lgprey.beta.incl),quantile(lgprey.beta.incl,probs =
c(0.025,0.975)))

avg.params <- rbind(house.incl.vec,
    ranger.incl.vec,
    lgprey.incl.vec,
    medprey.incl.vec,
    vcf.incl.vec,
    trail.n.incl.vec,
    trail.rd.incl.vec,
    lgprey.beta.incl.vec,
    c(out$BUGSoutput$mean$mu.int.alpha,
      out$BUGSoutput$sd$mu.int.alpha,
      quantile(out$BUGSoutput$sims.list$mu.int.alpha, probs =
c(0.025,0.975))),
    c(out$BUGSoutput$mean$occ,
      out$BUGSoutput$sd$occ,
      quantile(out$BUGSoutput$sims.list$occ, probs = c(0.025,0.975))))
```

```
data.frame(avg.params)
rownames(avg.params) <-
c("alpha.house","alpha.ranger","alpha.lgprey","alpha.medprey","alpha.vcf","trail.
n","trail.rd","beta.lgprey",
                      "mu.alpha.int","sites.occ")
w.vals <- out$BUGSoutput$mean$w
w.vals <- append(w.vals,w.vals[6],6)
w.vals <- append(w.vals,c(NA,NA))
avg.params <- cbind(avg.params,w.vals)
colnames(avg.params) <- c("mean","sd","2.5%","97.5%","w")
avg.params <- round(avg.params,2)
avg.params

# save text file of avg.params in wd
sink("avg.params.lion.txt")
print(avg.params)
sink()

# model posterior probabilities
library(gtools)

# create all combinations of 7 inclusion parameters
models <- permutations(n=2,r=7,v=c(0,1),repeats.allowed=T)

# create and fill in probabilities for all combinations
model.probs <- NA
for (i in 1:nrow(models)){
  model.probs[i] <-  length(which(apply(out$BUGSoutput$sims.list$w, 1,
identical, models[i,])))/6000
}
model.probs <- round(model.probs,2)
model.probs <- data.frame(cbind(models,model.probs))
colnames(model.probs) <-
c("house","ranger","lgprey","medprey","vcf","trail","lgprey","prob")
model.probs <- model.probs[order(model.probs$prob, decreasing = T),]
model.probs

###### visualizing model predictions

# dist house
house.pred.vec <- seq(from = -1.5, to = 1, length.out = 100)
#house.pred.vec <- seq(from = 0.04, to = 10, length.out = 100) <- the orignial
raster goes till 80Km, but using 10 for better visualisation of the curve
house.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[1,1]*house.pred.vec)
plot(house.pred.vec,house.pred,
    type = "l",
    lwd = 3,
```

```
    ylab = "Occupancy probability",
    xlab = "Distance to household (standardized)",
    las = 1,
    frame.plot = T)

length(which(out$BUGSoutput$sims.list$w[,1]==1))

house.pred.array <- array(NA, dim =
c(length(house.pred.vec),(length(house.incl))))
for (i in 1:length(house.incl)){
  house.pred.array[,i] <- plogis(out$BUGSoutput$mean$mu.int.alpha
                              + house.incl[i]*house.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(house.incl), size = 200)
for (i in sub.set){
  lines(house.pred.vec, house.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(house.pred.vec, house.pred, type = "l", lwd = 3, col = "black")

# large prey on occ
lgprey.pred.vec <- seq(from = -1, to = 4, length.out = 100)
#lgprey.pred.vec <- seq(from = 0, to = 1, length.out = 100)
lgprey.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[3,1]*lgprey.pred.vec)
plot(lgprey.pred.vec,lgprey.pred,
    type = "l",
    lwd = 3,
    ylab = "Occupancy probability",
    xlab = "Large prey (standardized)",
    las = 1,
    frame.plot = F)

# generate all predictions
lgprey.pred.array <- array(NA, dim =
c(length(lgprey.pred.vec),(length(lgprey.incl))))
for (i in 1:length(lgprey.incl)){
  lgprey.pred.array[,i] <- plogis(out$BUGSoutput$mean$mu.int.alpha
                              + lgprey.incl[i]*lgprey.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(lgprey.incl), size = 150)
for (i in sub.set){
  lines(lgprey.pred.vec, lgprey.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(lgprey.pred.vec, lgprey.pred, type = "l", lwd = 3, col = "black")
```

```
# med prey on occ
medprey.pred.vec <- seq(from = -1, to = 5, length.out = 100)
medprey.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[4,1]*medprey.pred.vec)
plot(medprey.pred.vec,medprey.pred,
    type = "l",
    lwd = 3,
    ylab = "Occupancy probability",
    xlab = "Medium prey (standardized)",
    las = 1,
    frame.plot = F)

# generate all predictions
medprey.pred.array <- array(NA, dim =
c(length(medprey.pred.vec),(length(medprey.incl))))
for (i in 1:length(medprey.incl)){
  medprey.pred.array[,i] <- plogis(out$BUGSoutput$mean$mu.int.alpha
                              + medprey.incl[i]*medprey.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(medprey.incl), size = 150)
for (i in sub.set){
  lines(medprey.pred.vec, medprey.pred.array[,i], type = "l", lwd = 1, col =
"gray")
}
lines(medprey.pred.vec, medprey.pred, type = "l", lwd = 3, col = "black")


# large prey on det
lgprey.beta.pred.vec <- seq(from = -1, to = 4, length.out = 100)
lgprey.beta.pred <- plogis(out$BUGSoutput$mean$beta.0 +
avg.params[8,1]*lgprey.beta.pred.vec)
plot(lgprey.beta.pred.vec,lgprey.beta.pred,
    type = "l",
    lwd = 3,
    ylab = "Detection probability",
    xlab = "Large prey (standardized)",
    las = 1,
    frame.plot = F,
    ylim = c(0,0.4))

# generate all predictions
lgprey.beta.pred.array <- array(NA, dim =
c(length(lgprey.beta.pred.vec),(length(lgprey.beta.incl))))
for (i in 1:length(lgprey.beta.incl)){
  lgprey.beta.pred.array[,i] <- plogis(out$BUGSoutput$mean$beta.0
```

```
                        + lgprey.beta.incl[i]*lgprey.beta.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(lgprey.beta.incl), size = 150)
for (i in sub.set){
  lines(lgprey.beta.pred.vec, lgprey.beta.pred.array[,i], type = "l", lwd = 1, col =
"gray")
}
lines(lgprey.beta.pred.vec, lgprey.beta.pred, type = "l", lwd = 3, col = "black")

#-----Correlogram----
library(glmmML)
library(ncf)

# run a non mixed glm
Glm  <- glm(ever.detected.lion ~ Dist_Household + Dist_Ranger_Post +
            CPUE_Large_Prey + CPUE_Medium_Prey + VCF, family =
binomial)

Correlog.Glm <- spline.correlog(
  x = data.lion[, 2],
  y = data.lion[, 3],
  z = residuals(Glm, type = "pearson"),xmax = 80000)
plot.spline.correlog(Correlog.Glm)

# prepare data for the spline for the glmm
write.csv(ever.detected.lion, file = paste(getwd(),"ever_detected.csv", sep = "/"))
write.csv(VCF, file = paste(getwd(),"VCF.csv", sep = "/"))

# fit the mixed model with random intercept
Glmm  <- glmmML(ever.detected.lion ~ Dist_Household + Dist_Ranger_Post
+
              CPUE_Large_Prey + CPUE_Medium_Prey + VCF, cluster = Area,
family = binomial)

# load data for the pres.glmmML function
data.corr <- read.csv(paste(getwd(),"for_occu_lion_final_Pearson.csv", sep =
"/"), header = TRUE)

pres.glmmML<-function(model,data)
  #This function outputs a vector of
  #the Pearson residuals for a glmmML object
  #- "model" is a glmmML object, and "data"
  #is the data frame of the data to which "model"
  #was fitted. This function is based on
  #the glmmML package version 0.65-5 and
  #may not work properly in earlier or later
```

```
  #versions. Please report any bugs or
  #errors to Jonathan Rhodes (j.rhodes@uq.edu.au)
{
  Model<-model
  Data<-data

  #get the model frame
  ModelFrame<-model.frame(formula(terms(Model)),data=Data)

  #get the design matrix
  DesignMatrix<-model.matrix(terms(Model),data=ModelFrame)

  #get the linear predictor
  LP<-DesignMatrix %*% as.matrix(Model$coefficients)

  #get the cluster
  Cluster<-Data[,toString(Model$call$cluster)]
  Cluster<-as.factor(Cluster)

  #add the random-effect posterior modes
  for (i in 1:length(levels(Cluster)))
  {
    LP[Cluster == levels(Cluster)[i]] = LP[Cluster == levels(Cluster)[i]] +
Model$posterior.modes[i]
  }

  #get the response
  Response<-as.matrix(model.response(ModelFrame))

  if (is.null(Model$call$family) ||
(Model$call$family==as.name(paste("binomial(link =
",dQuote("logit"),")",sep=""))) || (Model$call$family==as.name("binomial")))
    #binomial response with logit link function
  {
    #get the fitted p values
    P<-exp(LP) / (1 + exp(LP))

    #get the pearson residuals
    if (ncol(Response) == 1)
      #bernoulli data
    {
      PRes<-(Response - P) / sqrt(P * (1 - P))
    }
    else if (ncol(Response) == 2)
      #binomial data
    {
      PRes<-(Response[,1] - (Response[,1] + Response[,2]) * P) /
sqrt((Response[,1] + Response[,2]) * P * (1 - P))
```

```
    }
    else
      #response matrix the wrong size
    {
      stop("wrong number of response variables")
    }

  }
  else if (Model$call$family==as.name(paste("binomial(link =
",dQuote("cloglog"),")",sep="")))
    #binomial response with complementary log-log link
  {

    #get the fitted p values
    P<-1 - exp(-exp(LP))

    #get the pearson residuals
    if (ncol(Response) == 1)
      #bernoulli data
    {
      PRes<-(Response - P) / sqrt(P * (1 - P))
    }
    else if (ncol(Response) == 2)
      #binomial data
    {
      PRes<-(Response[,1] - (Response[,1] + Response[,2]) * P) /
sqrt((Response[,1] + Response[,2]) * P * (1 - P))
    }
    else
    {
      stop("wrong number of response variables")
    }
  }
  else if ((Model$call$family==as.name(paste("poisson(link =
",dQuote("log"),")",sep=""))) || (Model$call$family==as.name("poisson")))
    #poisson response with log link function
  {

    #get the fitted count values
    C<-exp(LP)

    #get the pearson residuals
    PRes<-(Response - C) / sqrt(C)
  }
  else
    #response not binomial or poisson
  {
    stop("incompatible family specified")
```

```
  }

  return(as.vector(PRes))
}


# get the glmm correlelogram

Correlog.Glmm <- spline.correlog(
  x = data.lion[, 2],
  y = data.lion[, 3],
  z = pres.glmmML(model = Glmm, data = data.corr), xmax = 80000)

plot.spline.correlog(Correlog.Glmm)
```

Annex 2. Annotated JAGS model used in Chapter 3: "The importance of the wildland-human interface for carnivore ecology: a case study of leopard (Panthera pardus) site use in Tanzania"

```
########### Site occupancy for leopards #################
# JAGS model

sink("model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.w")
cat("
   model {

   # Occupancy Priors
   #alpha.humpop ~ dunif(-10,10)
   alpha.liv_n ~ dunif(-10,10)
   alpha.dist_riv ~ dunif(-10,10)
   alpha.dist_hh ~ dunif(-10,10)
   alpha.medprey ~ dunif(-10,10)

   # Detectin priors
   beta.trail[1]  <- 0 # Reference category for anthropogenic pressure
   for (k in 2:3) {
   beta.trail[k] ~ dunif(-10,10)
   }
   beta.0 ~ dunif(-10,10)


   # Occupancy random intercept indexed by site (k = 11)
   for (k in 1:11){
   alpha.0[k] ~ dnorm(mu.int.alpha, tau.alpha)
   }
   mu.int.alpha ~ dnorm(0,0.001)
   tau.alpha <- pow(sigma.alpha,-2)
   sigma.alpha ~ dunif(0,10)

   # Inclusion parameters
   for (m in 1:5){
   w[m] ~ dbern(0.5)
   }

   # Likelihood
   # Ecological model for true occurrence
   for (i in 1:R) {

   z[i] ~ dbern(psi[i])
```

```
  logit(psi[i]) <- alpha.0[Area[i]] +
  w[1] * alpha.liv_n * liv_n[i] +
  w[2] * alpha.dist_riv * dist_riv[i] +
  w[3] * alpha.dist_hh * dist_hh[i]+
  w[4] * alpha.medprey* medprey[i]

  # Observation model for replicated detection/nondetection observations
  for (j in 1:T) {

  y[i,j] ~ dbern(z[i] * p[i,j])

  logit(p[i,j]) <- beta.0 +
  w[5] * beta.trail[trail_type[i]]

  } #j
  } #i

  # Derived quantities
  occ <- sum(z[])      # Number of occupied sites
  }
  ",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = data.leop.32,
          R = nrow(data.leop.32),
          T = ncol(data.leop.32),
          trail_type = trail_type,
          liv_n = liv_n,
          dist_riv = dist_riv,
          dist_hh = dist_hh,
          medprey = medprey,
          Area = Area)

# Initial values
zst <- apply(data.leop.32, 1, max, na.rm=TRUE)      # Observed occurrence as
starting values for z
wst <- rep(1,5)
inits <- function() list(z = zst,
               w = wst,
               sigma.alpha = runif(1,0,10),
               mu.int.alpha = runif(1,-3,3),
               alpha.liv_n = runif(1,-3,3),
               alpha.dist_riv = runif(1,-3,3),
               alpha.dist_hh = runif(1,-3,3),
               alpha.medprey = runif(1,-3,3),
               beta.0 = runif(1,-3,3),
```

```
                    beta.trail = c(NA,1,1))

# Parameters monitored
params <- c("occ",
         "mu.int.alpha",
         "alpha.liv_n",
         "alpha.dist_riv",
         "alpha.dist_hh",
         "alpha.medprey",
         "beta.trail",
         "alpha.0",
         "beta.0",
         "w",
         "z")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 10000
nc <- 3

# Call JAGS from R (BRT < 1 min)
model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.w <- jags(win.data, inits,
params, "model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.w", n.chains =
nc, n.thin = nt, n.iter = ni, n.burnin = nb, working.directory = getwd())
print(model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.w,dig=2)

# model averaged parameter estimates
out <- model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.w
sims <- out$BUGSoutput$sims.list

liv_n.incl <- sims$alpha.liv_n[sims$w[,1] == 1]
liv_n.incl.vec <- c(mean(liv_n.incl),sd(liv_n.incl),quantile(liv_n.incl,probs =
c(0.025,0.975)))

dist_riv.incl <- sims$alpha.dist_riv[sims$w[,2] == 1]
dist_riv.incl.vec <-
c(mean(dist_riv.incl),sd(dist_riv.incl),quantile(dist_riv.incl,probs =
c(0.025,0.975)))

dist_hh.incl <- sims$alpha.dist_hh[sims$w[,3] == 1]
dist_hh.incl.vec <-
c(mean(dist_hh.incl),sd(dist_hh.incl),quantile(dist_hh.incl,probs =
c(0.025,0.975)))

medprey.incl <- sims$alpha.medprey[sims$w[,4] == 1]
```

```
medprey.incl.vec <-
c(mean(medprey.incl),sd(medprey.incl),quantile(medprey.incl,probs =
c(0.025,0.975)))


trail.n.incl <- sims$beta.trail[sims$w[,5] == 1,2]
trail.n.incl.vec <-  c(mean(trail.n.incl),sd(trail.n.incl),quantile(trail.n.incl,probs =
c(0.025,0.975)))

trail.rd.incl <- sims$beta.trail[sims$w[,5] == 1,3]
trail.rd.incl.vec <-
c(mean(trail.rd.incl),sd(trail.rd.incl),quantile(trail.rd.incl,probs =
c(0.025,0.975)))

avg.params <- rbind(liv_n.incl.vec,
                dist_riv.incl.vec,
                dist_hh.incl.vec,
                medprey.incl.vec,
                trail.n.incl.vec,
                trail.rd.incl.vec,
                c(out$BUGSoutput$mean$mu.int.alpha,
                  out$BUGSoutput$sd$mu.int.alpha,
                  quantile(out$BUGSoutput$sims.list$mu.int.alpha, probs =
c(0.025,0.975))),
                c(out$BUGSoutput$mean$occ,
                  out$BUGSoutput$sd$occ,
                  quantile(out$BUGSoutput$sims.list$occ, probs =
c(0.025,0.975))))

data.frame(avg.params)
rownames(avg.params) <- c("alpha.liv_n",
                     "alpha.dist_riv",
                     "alpha.dist_hh",
                     "alpha.medprey",
                     "trail.n",
                     "trail.rd",
                     "mu.alpha.int",
                     "sites.occ")
w.vals <- out$BUGSoutput$mean$w
w.vals <- append(w.vals,w.vals[5],5)
w.vals <- append(w.vals,c(NA,NA))
avg.params <- cbind(avg.params,w.vals)
colnames(avg.params) <- c("mean","sd","2.5%","97.5%","w")
avg.params <- round(avg.params,2)
avg.params

# save text file of avg.params in wd
sink("model.leop.det.trail.occ.liv_n.dist_riv.dist_hh.medprey.txt")
```

```
print(avg.params)
sink()

# model posterior probabilities
library(gtools)

# create all combinations of 5 inclusion parameters
models <- permutations(n=2,r=5,v=c(0,1),repeats.allowed=T)

# create and fill in probabilities for all combinations
model.probs <- NA
for (i in 1:nrow(models)){
  model.probs[i] <-  length(which(apply(out$BUGSoutput$sims.list$w, 1,
identical, models[i,])))/6000
}
model.probs <- round(model.probs,2)
model.probs <- data.frame(cbind(models,model.probs))
colnames(model.probs) <- c("liv_n","dist_riv","dist_hh","medprey",
"trail","prob")
model.probs <- model.probs[order(model.probs$prob, decreasing = T),]
model.probs

###### Visualizing model predictions

#### Livestock Number ####
original.liv_n.pred<-seq(0,1000, length.out = 100) #original values
liv_n.pred.vec <- seq(from = -1.5, to = 1, length.out = 100)
liv_n.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[1,1]*liv_n.pred.vec)
plot(original.liv_n.pred,liv_n.pred,
     type = "l",
     lwd = 3,
     ylab = "Occupancy probability",
     xlab = "N. livestock/station",
     las = 1,
     ylim = c(0,1),
     frame.plot = F)

length(which(out$BUGSoutput$sims.list$w[,1]==1))

liv_n.pred.array <- array(NA, dim =
c(length(liv_n.pred.vec),(length(liv_n.incl))))
for (i in 1:length(liv_n.incl)){
  liv_n.pred.array[,i] <- plogis(out$BUGSoutput$sims.list$alpha.0[i]
                          + liv_n.incl[i]*liv_n.pred.vec)
}

# subset 200 iterations
```

```
sub.set <- sample(1:length(liv_n.incl), size = 200)
for (i in sub.set){
  lines(original.liv_n.pred, liv_n.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(original.liv_n.pred, liv_n.pred, type = "l", lwd = 3, col = "black")

#####Distance to river######

original.river<- seq (from= 0, to = 40, length.out = 100) #original values
river.pred.vec <- seq(from = -1, to = 3, length.out = 100)
river.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[2,1]*river.pred.vec)
plot(original.river,river.pred ,
     type = "l",
     lwd = 3,
     ylab = "Occupancy probability",
     xlab = "Dist. river (Km)",
     las = 1,
     ylim=c(0,1),
     frame.plot = F)

# generate all predictions
river.pred.array <- array(NA, dim =
c(length(river.pred.vec),(length(dist_riv.incl))))
for (i in 1:length(dist_riv.incl)){
  river.pred.array[,i] <- plogis(out$BUGSoutput$sims.list$alpha.0[i]
                              + dist_riv.incl[i]*river.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(dist_riv.incl), size = 150)
for (i in sub.set){
  lines(original.river, river.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(original.river, river.pred, type = "l", lwd = 3, col = "black")

#### Distance to households####
original.house.pred<-seq(0,30, length.out = 100) #original values
house.pred.vec <- seq(from = -1.5, to = 1, length.out = 100)
house.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[3,1]*house.pred.vec)
plot(original.house.pred,house.pred,
     type = "l",
     lwd = 3,
     ylab = "Occupancy probability",
     xlab = "Distance to household (Km)",
     las = 1,
     ylim = c(0,1),
```

```
    frame.plot = F)

length(which(out$BUGSoutput$sims.list$w[,1]==1))

house.pred.array <- array(NA, dim =
c(length(house.pred.vec),(length(dist_hh.incl))))
for (i in 1:length(dist_hh.incl)){
  house.pred.array[,i] <- plogis(out$BUGSoutput$sims.list$alpha.0[i]
                          + dist_hh.incl[i]*house.pred.vec)
}

# subset 200 iterations
sub.set <- sample(1:length(dist_hh.incl), size = 200)
for (i in sub.set){
  lines(original.house.pred, house.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(original.house.pred, house.pred, type = "l", lwd = 3, col = "black")

####Medium prey on occupancy #####
original.mdprey <-seq(from = 0, to= 10000, length.out = 100) #original values
mdprey.pred.vec <- seq(from = -1, to = 4, length.out = 100)
mdprey.pred <- plogis(out$BUGSoutput$mean$mu.int.alpha +
avg.params[4,1]*mdprey.pred.vec)
plot(original.mdprey,mdprey.pred,
    type = "l",
    lwd = 3,
    ylab = "Occupancy probability",
    xlab = "Medium prey (CPUE)",
    las = 1,
    frame.plot = F)

# generate all predictions
mdprey.pred.array <- array(NA, dim =
c(length(mdprey.pred.vec),(length(medprey.incl))))
for (i in 1:length(medprey.incl)){
  mdprey.pred.array[,i] <- plogis(out$BUGSoutput$sims.list$alpha.0[i]
                          + medprey.incl[i]*mdprey.pred.vec)
}


# subset 200 iterations
sub.set <- sample(1:length(medprey.incl), size = 150)
for (i in sub.set){
  lines(original.mdprey, mdprey.pred.array[,i], type = "l", lwd = 1, col = "gray")
}
lines(original.mdprey, mdprey.pred, type = "l", lwd = 3, col = "black")
```

Annex 3. Annotated STAN model used in Chapter 4: “Evaluating the influence of environmental variables and interspecific interactions on multicarnivore occurrence across a gradient of anthropogenic pressure in southern Tanzania”

```
library(rstan)
Stan model from Rota et al. (2016):
 functions{
 int vectorEquality(row_vector aVector, int[] bVector){
   int aEqual;
   int aLen;
   aEqual = 1;
   aLen = num_elements(aVector);
   for(i in 1:aLen){
     if(aVector[i]!=bVector[i]){
       aEqual = 0;
       return(aEqual);
     }
   }
   return(aEqual);
 }
}
```

```
data{
  int numSpecies; // number of species
  int K;   // the number of occupancy parameters
  int L;   // the number of detection parameters
  int N;   // the number of sites
  int S;   // the number of unique combinations of 1s and 0s

  int obs[N];        // the number of replicate surveys at each site
  matrix[S, K] x[N];  // design matrix

  // detection model covariates -- assumed to be time-invariant
  matrix[N,L] detection;

  // detection counts over all sites and replicate surveys
  int Y[N,numSpecies];

  // all possible combinations of 0 and 1
  matrix[S,numSpecies] binaryCombinations;

}

transformed data{
  // indicators of whether each species was detected at least once at a site
  int Indicator[N,numSpecies];
  for(i in 1:N){
    for(j in 1:numSpecies){
      Indicator[i,j] = Y[i,j] > 0;
    }
  }
}

parameters{
  // detection model covariates
  matrix[numSpecies,L] a;

  // occupancy model covariates
  vector[K] beta;
}

model{

  matrix[N,S] psi;   // probability of each combination of 1s and 0s
  matrix[N,S] prob;  // psi * probability of detection history
  vector[N] marginalLogProb;

  // probability of observing the detection history at each site
  matrix[N,numSpecies] cd;
```

```
// priors
beta ~ logistic(0, 1);
for(i in 1:numSpecies){
  a[i] ~ logistic(0,1);
}

for(i in 1:N){

  // detection probability at each replicate survey
  vector[numSpecies] detectProb;
  int vIndicatorTemp[numSpecies];
  int aSum;
  int aSumSq;

  // Pr(detection) for a given site
  // detection is (N x L), a is (numSpecies x L). detection[i] is 1 x L
  // detectProb is of dimension numSpecies
  detectProb = to_vector(detection[i] * a');
  for(j in 1:numSpecies){
    detectProb[j] = inv_logit(detectProb[j]);
  }

  // by assuming independence amongst detections sum the log probs then
exponent to obtain
  // Pr(detection history at site i|z=1)
  for(j in 1:numSpecies){
    cd[i,j] = binomial_lpmf(Y[i,j]|obs[i],detectProb[j]);
  }


// Observation model starts here. This is equivalent to all lines of eqn. 2 in the
MS. This gives log psi for all possible z states
  psi[i] = to_row_vector(log_softmax(x[i] * beta));

  // Multiply the occupancy state by the conditional density for detection of log
scale - the p_sit in the eqns
  // to get the unconditional prob. I.e. p(y,z) = p(z) * p(y|z). Note that
p(y=0|z=0) = 1.
  // prob gives the joint probability of the occupancy (z) and all the detection
history (y).
  // psi[i] is (1 x S) binaryCombinations is (S x numSpecies). cd[i] is (1 x
numSpecies).
  // prob[i] is (1 x S)
  prob[i] = psi[i] + to_row_vector(binaryCombinations * cd[i]');

  // marginalise over z state by summing the appropriate probabilities (only
some are relevant because some yield
```

```
    //incongrous results)
    vIndicatorTemp = Indicator[i];
    aSum = sum(vIndicatorTemp);
    aSumSq = 1;
    for(j in 1:(numSpecies-aSum)){
      aSumSq = 2 * aSumSq;
    }
    if(aSum<0.5){
      marginalLogProb[i] = log_sum_exp(prob[i]);
    }else if(aSum>(numSpecies-0.5)){
      for(j in 1:S){
        if(vectorEquality(binaryCombinations[j],vIndicatorTemp)==1){
         marginalLogProb[i] = prob[i,j];
        }
      }
    }else{
      int vNonVariable[aSum];
      int count;
      vector[aSumSq] marginalLogProbTemp;
      count = 1;
      for(j in 1:numSpecies){
        if(vIndicatorTemp[j]==1){
          vNonVariable[count] = j;
          count = count + 1;
        }
      }
      count = 1;
      for(j in 1:S){
        row_vector[numSpecies] vBinaryTemp;
        vBinaryTemp = binaryCombinations[j];
       if(vectorEquality(vBinaryTemp[vNonVariable],rep_array(1,aSum))==1){
         marginalLogProbTemp[count] = prob[i,j];
         count = count + 1;
       }
      }
      marginalLogProb[i] = log_sum_exp(marginalLogProbTemp);
    }

    target += marginalLogProb[i];
  }
}

generated quantities{
  vector[N] logLikelihood;

  {

  matrix[N,S] psi;   // probability of each combination of 1s and 0s
```

```
 matrix[N,S] prob;  // psi * probability of detection history


 // probability of observing the detection history at each site
 matrix[N,numSpecies] cd;

 for(i in 1:N){

   // detection probability at each replicate survey
   vector[numSpecies] detectProb;
   int vIndicatorTemp[numSpecies];
   int aSum;
   int aSumSq;

   // Pr(detection) for a given site
   // detection is (N x L), a is (numSpecies x L). detection[i] is 1 x L
   // detectProb is of dimension numSpecies
   detectProb = to_vector(detection[i] * a');
   for(j in 1:numSpecies){
     detectProb[j] = inv_logit(detectProb[j]);
   }

   // by assuming independence amongst detections sum the log probs then
exponent to obtain
   // Pr(detection history at site i|z=1)
   for(j in 1:numSpecies){
     cd[i,j] = binomial_lpmf(Y[i,j]|obs[i],detectProb[j]);
   }


 // Observation model starts here. This is equivalent to all lines of eqn. 2 in the
MS. This gives log psi for all possible z states
   psi[i] = to_row_vector(log_softmax(x[i] * beta));

   // Multiply the occupancy state by the conditional density for detection of log
scale - the p_sit in the eqns
   // to get the unconditional prob. I.e. p(y,z) = p(z) * p(y|z). Note that
p(y=0|z=0) = 1.
   // prob gives the joint probability of the occupancy (z) and all the detection
history (y).
   // psi[i] is (1 x S) binaryCombinations is (S x numSpecies). cd[i] is (1 x
numSpecies).
   // prob[i] is (1 x S)
   prob[i] = psi[i] + to_row_vector(binaryCombinations * cd[i]');

   // marginalise over z state by summing the appropriate probabilities (only
some are relevant because some yield
   //incongrous results)
```

```
    vIndicatorTemp = Indicator[i];
    aSum = sum(vIndicatorTemp);
    aSumSq = 1;
    for(j in 1:(numSpecies-aSum)){
      aSumSq = 2 * aSumSq;
    }
    if(aSum<0.5){
      logLikelihood[i] = log_sum_exp(prob[i]);
    }else if(aSum>(numSpecies-0.5)){
      for(j in 1:S){
        if(vectorEquality(binaryCombinations[j],vIndicatorTemp)==1){
         logLikelihood[i] = prob[i,j];
        }
      }
    }else{
      int vNonVariable[aSum];
      int count;
      vector[aSumSq] marginalLogProbTemp;
      count = 1;
      for(j in 1:numSpecies){
        if(vIndicatorTemp[j]==1){
          vNonVariable[count] = j;
          count = count + 1;
        }
      }
      count = 1;
      for(j in 1:S){
        row_vector[numSpecies] vBinaryTemp;
        vBinaryTemp = binaryCombinations[j];
       if(vectorEquality(vBinaryTemp[vNonVariable],rep_array(1,aSum))==1){
         marginalLogProbTemp[count] = prob[i,j];
         count = count + 1;
       }
      }
      logLikelihood[i] = log_sum_exp(marginalLogProbTemp);
    }
  }
  }
}

 fMakeDesignMatrix <-
 function(numSpecies,numIndividualParams,numInteractionParams){
   nRow <- 2^numSpecies
   nCol <- numSpecies * numIndividualParams
   aDM_simple <- matrix(0,nrow = nRow,ncol = nCol)
   mComb <- combn(1:numSpecies,2)

   ## row names
```

```
 l <- rep(list(0:1), numSpecies)
 mRows <- expand.grid(l)

 ## simple
 for(i in 1:nRow){
   for(j in 1:numSpecies){
     if(mRows[i,j]==1){
       aDM_simple[i,(numIndividualParams*(j-1)+1):(numIndividualParams*j)]
<- 1
     }
   }
 }

 if(numSpecies > 2){
   nCol1 <- ncol(mComb) * numInteractionParams
   aDM_interactions <- matrix(0,nrow = nRow,ncol = nCol1)
   ## interaction
   for(i in 1:nRow){
     for(j in 1:numSpecies){
       onSpecies <- sum(mRows[i,])
       if(onSpecies > 1){
         indexOn <- which(mRows[i,]==1)
         if(length(indexOn)<=2){
           for(k in 1:ncol(mComb)){
             if(identical(indexOn,mComb[,k])){
               aDM_interactions[i,(numInteractionParams*(k-
1)+1):(numInteractionParams*k)] <- 1
             }
           }
         }else{
           mComb_short <- combn(indexOn,2)
           for(kk in 1:ncol(mComb_short)){
             for(k in 1:ncol(mComb)){
               if(identical(mComb_short[,kk],mComb[,k])){

                 aDM_interactions[i,(numInteractionParams*(k-
1)+1):(numInteractionParams*k)] <- 1
               }
             }
           }
         }
       }
     }
   }
 }else{
   aDM_interactions <- matrix(0,nrow = nRow,ncol = numInteractionParams)
   aDM_interactions[4,] <- 1
 }
```

```
  aDM <- cbind.data.frame(aDM_simple,aDM_interactions)
  return(aDM)
}
numSpecies <- 5
aDM <- fMakeDesignMatrix(numSpecies,3,3)

lAnimals <- list(aard,bef,bbj,civ,leop)

################
LOO_15_MODEL_LIVESTOCK_DIST_HH_RIVER_TREE_PERC
############

# filling in the design matrix

aDM <- fMakeDesignMatrix(numSpecies,5,5)
X1.array <- array(0, dim = c(nrow(largeCarnivore), 2^numSpecies, ncol(aDM)))
aNumRepeats <- numSpecies + cumsum(seq(1,(numSpecies-
1),1))[numSpecies-1]
for(i in 1:nrow(largeCarnivore)){
  print(i)
  for(j in 2:(2^numSpecies)){
    X1.array[i, j, aDM[j, ] == 1] <- rep(c(1, dist_to_hh[i], n_lvtck_std[i],
dist_greater_ruaha_std[i], tree_perc_std[i]),aNumRepeats)[aDM[j, ] == 1]
  }
}
aLen <- ncol(lion)
fPrepareY <- function(lAnimalsData,aDataStart){
  aLen <- length(lAnimalsData)
  aAnimal <- lAnimalsData[[1]]
  vCounts <- vector(length = aLen)
  bLen <- ncol(aAnimal)
  cLen <- nrow(aAnimal)
  mObs <- matrix(0,nrow = cLen,ncol = aLen)
  mCounts <- matrix(0,nrow = cLen,ncol = aLen)
  for(i in 1:aLen){
    aAnimal <- lAnimalsData[[i]]
    mObs[,i] <- apply(aAnimal[,aDataStart:bLen], 1,function(x) sum(!is.na(x)))
    mCounts[,i] <- apply(aAnimal[,aDataStart:bLen], 1,function(x) sum(x,na.rm
= T))
    vCounts[i] <- sum(aAnimal[,aDataStart:bLen],na.rm = T)
  }
  stopifnot(sd(colSums(mObs))<0.0001)
  stopifnot(sum(vCounts)==sum(mCounts))
  return(mCounts)
}

Y <- fPrepareY(lAnimals,2)
```

```
N <- nrow(lion)
trail1 <- ifelse(as.character(trailType$trail_type)=="AT",1,0)
trail2 <- ifelse(as.character(trailType$trail_type)=="RD",1,0)
detection <- as.matrix(data.frame(ones=rep(1,N),trail1=trail1,trail2=trail2))
l <- rep(list(0:1),numSpecies)
binaryCombinations <- expand.grid(l)
obs <- apply(largeCarnivore[,7:aLen], 1,function(x) sum(!is.na(x)))

dataList <- list(numSpecies=numSpecies,
            K = ncol(X1.array[1, , ]),
            L = 3,
            N = nrow(lion),
            S = 2^numSpecies,
            x = X1.array,
            obs=obs,
            detection=detection,
            Y=Y,
            binaryCombinations=binaryCombinations)

#aModel <- stan_model('anyNumberOfSpecies.stan')

aModel15 <-
stan_model('/Users/user/Dropbox/Occupancy_Files/leandro_data/for_lar_car_S
TAN/from_Ben_R_scripts/anyNumberOfSpecies.stan')

library(rstan)
options(mc.cores=4)
fit15 <- sampling(aModel15,data=dataList,iter=100,chains=4)
print(fit15)

## Estimating the predictive capability of the model
#install.packages('loo')
library(loo)
lLogLikelihood_15 <- extract_log_lik(fit15,'logLikelihood')
loo_15<-loo(lLogLikelihood_15)
```

Annex 4. Annotated R script used in Chapter 5: "Mapping the suitability of habitat for lions (*Panthera leo*) across two stronghold populations in southern Tanzania"

```
#install.packages('spThin')
library('spThin')
#install.packages('knitr')
library('knitr')
#install.packages('formatR')
library('formatR')

#Load original presence points with all the locations

sites <- read.csv('points_csv/all_lions_prj_with_brink_phil.csv',
              stringsAsFactors = FALSE)
loc.data <-sites
df <- data.frame(loc.data)
#add new colum
df["SPEC"] <- NA
#adding species name to the column recently created
df$SPEC <-'leo'

head (df)

#putting df in the format as described in spthin package
df<-df[,c(6,4,5,3)]
head(df)

a1<- thin(loc.data= df,
        lat.col = "Latitude",
        long.col = "Longitude",
        spec.col = "SPEC",
        thin.par= 2,
        reps= 20,
        locs.thinned.list.return = TRUE,
        write.files = TRUE,
        max.files = 20,
        out.dir =
("/users/User/Documents/for_brt/buffered/model_output/results/for_thd/thinn
ed_pnts/20_df/"),
        out.base = "thinned_data_a1",
        write.log.file = TRUE,
        log.file = "spatial_thin_log.txt",
```

```
        verbose = TRUE)

summaryThin(a1, show = TRUE)
plotThin(a1)
head(a1)
str (a1)

#creating individual dataframes from the 20 thinned dataframes
df_1<-a1[[1]]
df_2<-a1[[2]]
df_3<-a1[[3]]
df_4<-a1[[4]]
df_5<-a1[[5]]
df_6<-a1[[6]]
df_7<-a1[[7]]
df_8<-a1[[8]]
df_9<-a1[[9]]
df_10<-a1[[10]]
df_11<-a1[[11]]
df_12<-a1[[12]]
df_13<-a1[[13]]
df_14<-a1[[14]]
df_15<-a1[[15]]
df_16<-a1[[16]]
df_17<-a1[[17]]
df_18<-a1[[18]]
df_19<-a1[[19]]
df_20<-a1[[20]]

#to run the BRT on the phinned location points

nbg_pop <- 5000 #define here the number of bkg points
# install/loading packages
#install.packages('sp')
library('sp')
library('snow')
#install.packages('snowfall')
library('snowfall')
#install.packages('raster')
library('raster')
#install.packages('devtools')
library('devtools')
#install_github('SEEG-Oxford/seegSDM')
library('seegSDM')
library(foreach)
library('doParallel')

# load covariates
```

```
pop <- raster('asc/wgs84/afripop.asc')
bio12 <- raster('asc/wgs84/bio12.asc')
dem <- raster('asc/wgs84/dem.asc')
dist_pa <- raster('asc/wgs84/dist_pa.asc')
dist_river <- raster('asc/wgs84/dist_river.asc')
dist_road <- raster('asc/wgs84/dist_road.asc')
globcov <- raster('asc/wgs84/globcov.asc')
slope <- raster('asc/wgs84/slope.asc')
vcf <- raster('asc/wgs84/vcf.asc')

BG <- bgSample(pop,n=nbg_pop, prob=TRUE, spatial=FALSE)
head (BG)
colnames(BG)  <- c('Longitude', 'Latitude')
head (BG)

# add a presence/absence column onto each dataset

df_1 <- cbind(PA = rep(1, nrow(df_1)), df_1)
df_2 <- cbind(PA = rep(1, nrow(df_2)), df_2)
df_3 <- cbind(PA = rep(1, nrow(df_3)), df_3)
df_4 <- cbind(PA = rep(1, nrow(df_4)), df_4)
df_5 <- cbind(PA = rep(1, nrow(df_5)), df_5)
df_6 <- cbind(PA = rep(1, nrow(df_6)), df_6)
df_7 <- cbind(PA = rep(1, nrow(df_7)), df_7)
df_8 <- cbind(PA = rep(1, nrow(df_8)), df_8)
df_9 <- cbind(PA = rep(1, nrow(df_9)), df_9)
df_10 <- cbind(PA = rep(1, nrow(df_10)), df_10)
df_11 <- cbind(PA = rep(1, nrow(df_11)), df_11)
df_12 <- cbind(PA = rep(1, nrow(df_12)), df_12)
df_13 <- cbind(PA = rep(1, nrow(df_13)), df_13)
df_14 <- cbind(PA = rep(1, nrow(df_14)), df_14)
df_15 <- cbind(PA = rep(1, nrow(df_15)), df_15)
df_16 <- cbind(PA = rep(1, nrow(df_16)), df_16)
df_17 <- cbind(PA = rep(1, nrow(df_17)), df_17)
df_18 <- cbind(PA = rep(1, nrow(df_18)), df_18)
df_19 <- cbind(PA = rep(1, nrow(df_19)), df_19)
df_20 <- cbind(PA = rep(1, nrow(df_20)), df_20)

# add weights column

df_1 <- cbind(occurrence_weights = rep(1, nrow(df_1)), df_1)
df_2 <- cbind(occurrence_weights = rep(1, nrow(df_2)), df_2)
df_3 <- cbind(occurrence_weights = rep(1, nrow(df_3)), df_3)
df_4 <- cbind(occurrence_weights = rep(1, nrow(df_4)), df_4)
df_5 <- cbind(occurrence_weights = rep(1, nrow(df_5)), df_5)
df_6 <- cbind(occurrence_weights = rep(1, nrow(df_6)), df_6)
df_7 <- cbind(occurrence_weights = rep(1, nrow(df_7)), df_7)
```

```
df_8 <- cbind(occurrence_weights = rep(1, nrow(df_8)), df_8)
df_9 <- cbind(occurrence_weights = rep(1, nrow(df_9)), df_9)
df_10 <- cbind(occurrence_weights = rep(1, nrow(df_10)), df_10)
df_11 <- cbind(occurrence_weights = rep(1, nrow(df_11)), df_11)
df_12 <- cbind(occurrence_weights = rep(1, nrow(df_12)), df_12)
df_13 <- cbind(occurrence_weights = rep(1, nrow(df_13)), df_13)
df_14 <- cbind(occurrence_weights = rep(1, nrow(df_14)), df_14)
df_15 <- cbind(occurrence_weights = rep(1, nrow(df_15)), df_15)
df_16 <- cbind(occurrence_weights = rep(1, nrow(df_16)), df_16)
df_17 <- cbind(occurrence_weights = rep(1, nrow(df_17)), df_17)
df_18 <- cbind(occurrence_weights = rep(1, nrow(df_18)), df_18)
df_19 <- cbind(occurrence_weights = rep(1, nrow(df_19)), df_19)
df_20 <- cbind(occurrence_weights = rep(1, nrow(df_20)), df_20)

BG <- cbind(PA = rep(0, nrow(BG)), BG)
head (BG)

# tell it that dat and BG have equal weights

lengthBG <- nrow(BG)
WeightsBG <- (sum(df_1$occurrence_weights, na.rm = TRUE)/nrow(BG))

# create vector with BG Weights

WeightsBG <- rep(WeightsBG, nrow(BG))
BG <- cbind(WeightsBG, BG)
BG <- as.data.frame(BG)
colnames(BG) <- c('occurrence_weights', 'PA', 'Longitude', 'Latitude')
head(BG)

# combine these both into one dataframe

dat_1 <- rbind(df_1, BG)
dat_2 <- rbind(df_2, BG)
dat_3 <- rbind(df_3, BG)
dat_4 <- rbind(df_4, BG)
dat_5 <- rbind(df_5, BG)
dat_6 <- rbind(df_6, BG)
dat_7 <- rbind(df_7, BG)
dat_8 <- rbind(df_8, BG)
dat_9 <- rbind(df_9, BG)
dat_10 <- rbind(df_10, BG)
dat_11 <- rbind(df_11, BG)
dat_12 <- rbind(df_12, BG)
dat_13 <- rbind(df_13, BG)
dat_14 <- rbind(df_14, BG)
dat_15 <- rbind(df_15, BG)
dat_16 <- rbind(df_16, BG)
```

```
dat_17 <- rbind(df_17, BG)
dat_18 <- rbind(df_18, BG)
dat_19 <- rbind(df_19, BG)
dat_20 <- rbind(df_20, BG)

# put all Covariates into one RasterBrick

Covariates <- stack(bio12,
                    pop,
                    dem,
                    dist_river,
                    globcov,
                    slope,
                    vcf)

# extract covariates values for all of these datapoints

dat_1 <- dat_1[,c(2,1,3,4)]
extract_1 <- extract(Covariates, dat_1[, -1:-2])
dat_1 <- cbind(dat_1, extract_1) # add extracted values to the dataframe
dat_1 <- na.omit(dat_1) # make sure no NA values in dataframe
head(dat_1)

dat_2 <- dat_2[,c(2,1,3,4)]
extract_2 <- extract(Covariates, dat_2[, -1:-2])
dat_2 <- cbind(dat_2, extract_2) # add extracted values to the dataframe
dat_2 <- na.omit(dat_2) # make sure no NA values in dataframe

dat_3 <- dat_3[,c(2,1,3,4)]
extract_3 <- extract(Covariates, dat_3[, -1:-2])
dat_3 <- cbind(dat_3, extract_3) # add extracted values to the dataframe
dat_3 <- na.omit(dat_3) # make sure no NA values in dataframe

dat_4 <- dat_4[,c(2,1,3,4)]
extract_4 <- extract(Covariates, dat_4[, -1:-2])
dat_4 <- cbind(dat_4, extract_4) # add extracted values to the dataframe
dat_4 <- na.omit(dat_4) # make sure no NA values in dataframe

dat_5 <- dat_5[,c(2,1,3,4)]
extract_5 <- extract(Covariates, dat_5[, -1:-2])
dat_5 <- cbind(dat_5, extract_5) # add extracted values to the dataframe
dat_5 <- na.omit(dat_5) # make sure no NA values in dataframe

dat_6 <- dat_6[,c(2,1,3,4)]
extract_6 <- extract(Covariates, dat_6[, -1:-2])
dat_6 <- cbind(dat_6, extract_6) # add extracted values to the dataframe
dat_6 <- na.omit(dat_6) # make sure no NA values in dataframe
```

```
dat_7 <- dat_7[,c(2,1,3,4)]
extract_7 <- extract(Covariates, dat_7[, -1:-2])
dat_7 <- cbind(dat_7, extract_7) # add extracted values to the dataframe
dat_7 <- na.omit(dat_7) # make sure no NA values in dataframe

dat_8 <- dat_8[,c(2,1,3,4)]
extract_8 <- extract(Covariates, dat_8[, -1:-2])
dat_8 <- cbind(dat_8, extract_8) # add extracted values to the dataframe
dat_8 <- na.omit(dat_8) # make sure no NA values in dataframe

dat_9 <- dat_9[,c(2,1,3,4)]
extract_9 <- extract(Covariates, dat_9[, -1:-2])
dat_9 <- cbind(dat_9, extract_9) # add extracted values to the dataframe
dat_9 <- na.omit(dat_9) # make sure no NA values in dataframe

dat_10 <- dat_10[,c(2,1,3,4)]
extract_10 <- extract(Covariates, dat_10[, -1:-2])
dat_10 <- cbind(dat_10, extract_10) # add extracted values to the dataframe
dat_10 <- na.omit(dat_10) # make sure no NA values in dataframe

dat_11 <- dat_11[,c(2,1,3,4)]
extract_11 <- extract(Covariates, dat_11[, -1:-2])
dat_11 <- cbind(dat_11, extract_11) # add extracted values to the dataframe
dat_11 <- na.omit(dat_11) # make sure no NA values in dataframe

dat_12 <- dat_12[,c(2,1,3,4)]
extract_12 <- extract(Covariates, dat_12[, -1:-2])
dat_12 <- cbind(dat_12, extract_12) # add extracted values to the dataframe
dat_12 <- na.omit(dat_12) # make sure no NA values in dataframe

dat_13 <- dat_13[,c(2,1,3,4)]
extract_13 <- extract(Covariates, dat_13[, -1:-2])
dat_13 <- cbind(dat_13, extract_13) # add extracted values to the dataframe
dat_13 <- na.omit(dat_13) # make sure no NA values in dataframe

dat_14 <- dat_14[,c(2,1,3,4)]
extract_14 <- extract(Covariates, dat_14[, -1:-2])
dat_14 <- cbind(dat_14, extract_14) # add extracted values to the dataframe
dat_14 <- na.omit(dat_14) # make sure no NA values in dataframe

dat_15 <- dat_15[,c(2,1,3,4)]
extract_15 <- extract(Covariates, dat_15[, -1:-2])
dat_15 <- cbind(dat_15, extract_15) # add extracted values to the dataframe
dat_15 <- na.omit(dat_15) # make sure no NA values in dataframe

dat_16 <- dat_16[,c(2,1,3,4)]
extract_16 <- extract(Covariates, dat_16[, -1:-2])
dat_16 <- cbind(dat_16, extract_16) # add extracted values to the dataframe
```

```
dat_16 <- na.omit(dat_16) # make sure no NA values in dataframe

dat_17 <- dat_17[,c(2,1,3,4)]
extract_17 <- extract(Covariates, dat_17[, -1:-2])
dat_17 <- cbind(dat_17, extract_17) # add extracted values to the dataframe
dat_17 <- na.omit(dat_17) # make sure no NA values in dataframe

dat_18 <- dat_18[,c(2,1,3,4)]
extract_18 <- extract(Covariates, dat_18[, -1:-2])
dat_18 <- cbind(dat_18, extract_18) # add extracted values to the dataframe
dat_18 <- na.omit(dat_18) # make sure no NA values in dataframe

dat_19 <- dat_19[,c(2,1,3,4)]
extract_19 <- extract(Covariates, dat_19[, -1:-2])
dat_19 <- cbind(dat_19, extract_19) # add extracted values to the dataframe
dat_19 <- na.omit(dat_19) # make sure no NA values in dataframe

dat_20 <- dat_20[,c(2,1,3,4)]
extract_20 <- extract(Covariates, dat_20[, -1:-2])
dat_20 <- cbind(dat_20, extract_20) # add extracted values to the dataframe
dat_20 <- na.omit(dat_20) # make sure no NA values in dataframe

dat<-rbind(dat_1,dat_2,dat_3,
          dat_4,dat_5,dat_6,
          dat_7,dat_8,dat_9,
          dat_10,dat_11,dat_12,
          dat_13,dat_14,dat_15,
          dat_16,dat_17,dat_18,
          dat_19,dat_20)

dim(dat)

head(dat)

# run models

# set up the cluster on up to 64 cpus

sfInit(cpus= 2, parallel= TRUE)

sfLibrary(seegSDM)

# little function to subsample the dataset, for use in lapply so that a list is
returned

sub_1 <- function(i, dat_1) {
  subsample(dat_1,
           nrow(dat_1),
```

```
          min = c(10, 10),
          replace = TRUE)
}

data_list_1 <- lapply(1:100, sub_1, dat_1) # run the subsampling
#
sub_2 <- function(i, dat_2) {
  subsample(dat_2,
          nrow(dat_2),
          min = c(10, 10),
          replace = TRUE)
}

data_list_2 <- lapply(1:100, sub_2, dat_2) # run the subsampling
#
sub_3 <- function(i, dat_3) {
  subsample(dat_3,
          nrow(dat_3),
          min = c(10, 10),
          replace = TRUE)
}

data_list_3 <- lapply(1:100, sub_3, dat_3) # run the subsampling
#
sub_4 <- function(i, dat_4) {
  subsample(dat_4,
          nrow(dat_4),
          min = c(10, 10),
          replace = TRUE)
}

data_list_4 <- lapply(1:100, sub_4, dat_4) # run the subsampling
#
sub_5 <- function(i, dat_5) {
  subsample(dat_5,
          nrow(dat_5),
          min = c(10, 10),
          replace = TRUE)
}

data_list_5 <- lapply(1:100, sub_5, dat_5) # run the subsampling
#
sub_6 <- function(i, dat_6) {
  subsample(dat_6,
          nrow(dat_6),
          min = c(10, 10),
          replace = TRUE)
}
```

```
data_list_6 <- lapply(1:100, sub_6, dat_6) # run the subsampling
#
sub_7 <- function(i, dat_7) {
  subsample(dat_7,
            nrow(dat_7),
            min = c(10, 10),
            replace = TRUE)
}

data_list_7 <- lapply(1:100, sub_7, dat_7) # run the subsampling
#
sub_8 <- function(i, dat_8) {
  subsample(dat_8,
            nrow(dat_8),
            min = c(10, 10),
            replace = TRUE)
}

data_list_8 <- lapply(1:100, sub_8, dat_8) # run the subsampling
#
sub_9 <- function(i, dat_9) {
  subsample(dat_9,
            nrow(dat_9),
            min = c(10, 10),
            replace = TRUE)
}

data_list_9 <- lapply(1:100, sub_9, dat_9) # run the subsampling
#
sub_10 <- function(i, dat_10) {
  subsample(dat_10,
            nrow(dat_10),
            min = c(10, 10),
            replace = TRUE)
}

data_list_10 <- lapply(1:100, sub_10, dat_10) # run the subsampling
#
sub_11 <- function(i, dat_11) {
  subsample(dat_11,
            nrow(dat_11),
            min = c(10, 10),
            replace = TRUE)
}

data_list_11 <- lapply(1:100, sub_11, dat_11) # run the subsampling
#
```

```
sub_12 <- function(i, dat_12) {
  subsample(dat_12,
          nrow(dat_12),
          min = c(10, 10),
          replace = TRUE)
}

data_list_12 <- lapply(1:100, sub_12, dat_12) # run the subsampling
#
sub_13 <- function(i, dat_13) {
  subsample(dat_13,
          nrow(dat_13),
          min = c(10, 10),
          replace = TRUE)
}

data_list_13 <- lapply(1:100, sub_13, dat_13) # run the subsampling
#
sub_14 <- function(i, dat_14) {
  subsample(dat_14,
          nrow(dat_14),
          min = c(10, 10),
          replace = TRUE)
}

data_list_14 <- lapply(1:100, sub_14, dat_14) # run the subsampling
#
sub_15 <- function(i, dat_15) {
  subsample(dat_15,
          nrow(dat_15),
          min = c(10, 10),
          replace = TRUE)
}

data_list_15 <- lapply(1:100, sub_15, dat_15) # run the subsampling
#
sub_16 <- function(i, dat_16) {
  subsample(dat_16,
          nrow(dat_16),
          min = c(10, 10),
          replace = TRUE)
}

data_list_16 <- lapply(1:100, sub_16, dat_16) # run the subsampling
#
sub_17 <- function(i, dat_17) {
  subsample(dat_17,
          nrow(dat_17),
```

```
          min = c(10, 10),
          replace = TRUE)
}

data_list_17 <- lapply(1:100, sub_17, dat_17) # run the subsampling
#
sub_18 <- function(i, dat_18) {
  subsample(dat_18,
          nrow(dat_18),
          min = c(10, 10),
          replace = TRUE)
}

data_list_18 <- lapply(1:100, sub_18, dat_18) # run the subsampling
#
sub_19 <- function(i, dat_19) {
  subsample(dat_19,
          nrow(dat_19),
          min = c(10, 10),
          replace = TRUE)
}

data_list_19 <- lapply(1:100, sub_19, dat_19) # run the subsampling
#
sub_20 <- function(i, dat_20) {
  subsample(dat_20,
          nrow(dat_20),
          min = c(10, 10),
          replace = TRUE)
}

data_list_20 <- lapply(1:100, sub_20, dat_20) # run the subsampling

#catenate all the data_lists into one
data_list <- c(data_list_1,data_list_2,data_list_3,data_list_4,
            data_list_5,data_list_6,data_list_7,data_list_8,
            data_list_9,data_list_10,data_list_11, data_list_12,
            data_list_13,data_list_14,data_list_15,data_list_16,
            data_list_17,data_list_18,data_list_19,data_list_20)

# run a model on each dataset

model_list <- sfLapply(data_list,
                  runBRT,
                  5:ncol(dat),
                  1,
                  Covariates,
                  gbm.coords = 3:4,
```

```
                    wt = 2,
                    n.trees = 10,
                    step.size = 10)

# before we stop the cluster, get validation stats

stat_lis <- sfLapply(model_list, getStats)

stats <- do.call('rbind', stat_lis)

# to get the stats from the model output and save them as spreadsheet in .csv
b= summary (stats)
write.csv(b, file =
paste0("/users/User/Documents/for_brt/buffered/model_output/pop_bkg/",
'summary_stats_20df_thinned.csv'))
# ~~~~~~~~~~~~~~
# sort the results
# combine rasters
preds <- lapply(model_list, function(x) x$pred)
preds <- brick(preds)
preds <- combinePreds(preds, parallel = TRUE)
# stop the cluster
sfStop()
```

Annex 5. List of contributed papers published during the study period

Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., Hayward, M. W., Millspaugh, J. J. and Montgomery, R. A. (2017), The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. J Anim Ecol, 86: 749–765. doi:10.1111/1365-2656.12680

Rostro-García, S., Tharchen, L., Abade, L., Astaras, C., Cushman, S.A., Macdonald, D.W. (2016), Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. Landscape Ecology, 31(6), pp.1277-1298. https://doi.org/10.1007/s10980-015-0335-9

Moll, R. J., Kilshaw, K., Montgomery, R. A., Abade, L., Campbell, R. D., Harrington, L. A., Millspaugh, J. J., Birks, J. D. S. and Macdonald, D. W. (2016), Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. J Zool, 300: 177–185. doi:10.1111/jzo.12369

Faria, N.R., Azevedo, R.d.S.d.S., Kraemer, M.U.G., Souza, R., Cunha, M.S., Hill, S.C., Thézé, J., Bonsall, M.B., Bowden, T.A., Rissanen, I., Rocco, I.M., Nogueira, J.S., Maeda, A.Y., Vasami, F.G.d.S., Macedo, F.L.d.L., Suzuki, A., Rodrigues, S.G., Cruz, A.C.R., Nunes, B.T., Medeiros, D.B.d.A., Rodrigues, D.S.G., Nunes Queiroz, A.L., Silva, E.V.P.d., Henriques, D.F., Travassos da Rosa, E.S., de Oliveira, C.S., Martins, L.C., Vasconcelos, H.B., Casseb, L.M.N., Simith, D.d.B., Messina, J.P., Abade, L., Lourenço, J., Alcantara, L.C.J., Lima, M.M.d., Giovanetti, M., Hay, S.I., de Oliveira, R.S., Lemos, P.d.S., Oliveira, L.F.d., de Lima, C.P.S., da Silva, S.P., Vasconcelos, J.M.d., Franco, L., Cardoso, J.F., Vianez-Júnior, J.L.d.S.G., Mir, D., Bello, G., Delatorre, E., Khan, K., Creatore, M., Coelho, G.E., de Oliveira, W.K., Tesh, R., Pybus, O.G., Nunes, M.R.T., Vasconcelos, P.F.C., (2016), Zika virus in the Americas: early epidemiological and genetic findings. Science, *352*(6283), pp.345-349. doi:10.1126/science.aaf5036

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