

**Human-carnivore conflict in Tanzania: modelling the spatial
distribution of lions (*Panthera leo*), leopards (*Panthera pardus*) and
spotted hyaenas (*Crocuta crocuta*), and their attacks upon livestock, in
Tanzania's Ruaha landscape**



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*Human-Carnivore Conflict in Tanzania: modelling the spatial distribution of lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyaenas (*Crocuta crocuta*), and their attacks upon livestock, in Tanzania's Ruaha Landscape*

Abstract

Tanzania's Ruaha landscape is an international priority area for large carnivore conservation, harbouring roughly 10% of the world's lions, and important populations of leopards and spotted hyaenas. However, these large carnivore populations are threatened by intense retaliatory killing due to human-carnivore conflict on village land around Ruaha National Park (RNP), mostly as a result of livestock predation by lions, leopards and spotted hyaenas. Moreover, a current lack of ecological data on the distribution of these carnivores hinders the development of effective strategies for conservation and targeted conflict mitigation in this landscape. This study aimed to identify the most significant ecogeographical variables (EGVs) influencing the distribution of lions, leopards and spotted hyaenas across the Ruaha landscape, and to map areas of conservation importance for these species. In addition, the study assessed the influence of EGVs on livestock predation risk by these carnivores in the village land around RNP, and generated a predictive map of predation risk. The relative importance of livestock husbandry practices and EGVs in terms of influencing predation risk within enclosures was also investigated. Proximity to rivers was the most important variable influencing the distribution of large carnivores in Ruaha, and contributed to predation risk of grazing livestock. The traditional livestock husbandry adopted in bomas appeared insufficient to alleviate the inherent risk of predation by large carnivores. The study produced the first detailed maps of lion, leopard and spotted hyaena distribution in the critically important Ruaha landscape, and identified likely livestock depredation hotspots. These results will target conflict mitigation approaches around Ruaha, by identifying particularly high-risk areas for livestock enclosures and grazing stock. Improving husbandry in these areas could help reduce livestock depredation and retaliatory carnivore killing, therefore reducing one of the most significant conservation threats in this critically important landscape.

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“The hills resound with their roaring. The wild animals tremble. They pull down cattle, spill men’s blood as well. Corpses of men, sheep and cattle lie in heaps as if the plague has killed them. Shepherds and herdsmen lament at what the lions have done. The villages are in mourning day and night.”

Records of Ashurbanipal, King of Assyria (668-627 BC)

“We are very worried. This is what happened last time. The lion ate dogs and goats first, then he began eating people”.

A villager in the borders of Serengeti National Park,

Tanzania (Paul Kvinta, 2006)

Chapter 1



General Introduction

1.1. Importance of large carnivore conservation

Large carnivores are some of the most charismatic and iconic animal species (Gross, 2012) and have had aesthetic, cultural, symbolic, spiritual and economic value in human societies throughout history (Loveridge et al., 2010b). In traditional African cultures, lions (*Panthera leo*) and leopards (*Panthera pardus*) are still closely associated with religious beliefs, and the possession of their body parts is often associated with bravery, social status and spiritual protection (Dickman, 2008). Leopard skins, for instance, are still used in religious ceremonies in Zulu communities in South Africa, and the possession of their paws is believed to protect against bad luck (Warchol et al., 2003). These associations can however be negative – for instance, spotted hyaenas (*Crocuta crocuta*) have long been associated with witchcraft in rural African communities (Dickman, 2008), but they still exert a powerful influence on the human psyche. Independently of the values attributed to a particular species by distinct cultures, these traditions and beliefs depict the deep entrenchment and long-term relationship of large carnivores with human cultures.

Currently, large carnivores can generate significant economic revenue, as they play a key role in the multi-million dollar trophy hunting and tourism industries (Lindsey et al., 2006; Jorge et al., 2013). Lions, for example, are one of the most expensive trophy species in Africa (only exceeded by elephants *Loxodonta africana* in South Africa and rhinoceroses *Ceratotherium simum* and *Diceros bicornis* in Namibia) with hunting prices ranging from US\$ 24,000 – 71,000 depending on the country (Lindsey et al., 2012b). Leopard sport hunting generates 8 to 20% of the annual gross income of the trophy hunting industry in Eastern and Southern Africa (Balme et al., 2012). Additionally, the economic benefits of tourism (Hemson et al., 2009; Funston et al.,

2013) and sustainable trophy hunting can potentially increase local tolerance of large carnivores, contributing to their conservation (Lindsey et al., 2006; Loveridge et al., 2006).

From an ecological standpoint, apex carnivores such as lions, leopards and spotted hyaenas are vital components of a healthy, functioning ecosystem (Ritchie & Johnson, 2009; Pitman et al., 2012). As keystone species, they play an important role in regulating ecological interactions, due to their considerable influence on lower trophic levels. For example, they influence the densities (Messier, 1994), behaviour and sex ratios of prey species (Bowyer et al., 2005), and suppress the deleterious effects of large ungulates on vegetation (Hobbs, 1996; Terborgh et al., 2001). Their removal from the ecosystem triggers trophic cascades leading to significant alterations in predator-prey balance and interspecific interactions (Terborgh, 2005; Ripple & Beschta, 2006; Beschta & Ripple, 2009), which can culminate in the loss of species richness and diversity (Krebs et al., 2001).

1.2. Population declines of large carnivores, with a focus on lions, leopards and spotted hyaenas

Despite their importance in regulating ecosystem services, large carnivores are naturally rare (Ray et al., 2005), have low reproductive rates (Noss et al., 1996) and generally occur in low densities (Hayward et al., 2007). Such rarity, related to high food intake and large home range requirements (Carrera et al., 2008), make them particularly sensitive to human encroachment and changes in habitat quality (Woodroffe, 2000), and more prone to extinction compared to many other terrestrial mammals (Caro & Durant, 1995; Woodroffe & Ginsberg, 2005).

Among the extant terrestrial mammals, large canids and felids show the most pronounced decline in population ranges and numbers (Karanth & Chellam, 2009), mostly due to habitat destruction and intentional killing by humans due to human-carnivore conflict (Woodroffe, 2000; Woodroffe, 2001). Lions, for example, have disappeared from 75% of their historical range over the past two centuries (IUCN, 2012), and have suffered a substantial reduction in population size of at least 30% over the past 20 years (IUCN, 2012), mainly due to habitat destruction and persecution (Riggio et al., 2012; Packer et al., 2013). Lions were totally extirpated from North Africa before the 1950s (Nowell & Jackson, 1996), and only relict and scattered populations remain in West and Central Africa (Frank et al., 2006a; Henschel et al., 2010). Significant and sizeable lion populations are only found in 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 (Riggio et al., 2012). Of these, four strongholds are located in Eastern Africa, with the remaining being in Southern Africa (Riggio et al., 2012). Lions are currently considered Vulnerable to extinction with a declining population trend (IUCN, 2012), with viable populations mainly found in Kenya, Botswana, Zimbabwe, Mozambique, South Africa, Namibia, Zambia and Tanzania, the last supporting approximately 40% of the 32,000 lions estimated to remain in the wild (Riggio et al., 2012).

Leopards, similarly to lions, have already lost at least 30% of their original range (Balme et al., 2007), especially in North and West Africa, South Africa and the Horn of Africa (Nowell & Jackson, 1996; Hunter et al., 2013) due to human encroachment and habitat alterations. 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 & De Meulenaer, 1988), which is considered an unrealistic and flawed over-estimate (Henschel et al., 2008). The species is currently considered Near Threatened by the IUCN (Henschel et al., 2008), but this conservation status is likely to change to Vulnerable under criterion A (Henschel et al., 2008), indicating a reduction in the number of mature individuals in the overall population (IUCN, 2001).

Even spotted hyaenas, which are considered to be the most abundant large carnivore in Africa (Smith & Holekamp, 2010), with an estimated extant population of 27,000 to 47,000 individuals (Honer et al., 2008), and more than 10,000 mature individuals in the wild (Honer et al., 2008), are facing population declines despite being categorized as Least Concern by the IUCN (Honer et al., 2008). Indiscriminate killing of the species and habitat loss are contributing to a decreasing population trend, especially in smaller and more isolated populations (Honer et al., 2008). Hyaenas are particularly predisposed to human persecution as they are associated with witchcraft and evil spirits (Glickman, 1995; Maddox, 2003).

1.3. Conflict involving humans and large carnivores

The accelerated rate of human encroachment into wild areas has led to the replacement of natural systems with largely human-dominated landscapes. One consequence of this is the creation of conflict-prone scenarios in areas of close interaction between humans and wildlife (Ray et al., 2005; Woodroffe et al., 2005a). Large carnivores are among the most common species associated with conflict with humans worldwide (Madden, 2004; Treves et al., 2006; Thorn et al., 2012). Their obligate carnivory predisposes them to compete with people for limited prey resources such as livestock and game meat (Ray,

2001; Henschel et al., 2011), which often results in severe economic losses to farmers and killing of the problem animal (Patterson et al., 2004). Apart from livestock predation, the ability of large carnivores to kill humans has contributed to their perception as “harbingers of death” (Clark et al., 1996), which has historically contributed to their persecution by humans (Sillero-Zubiri & Laurenson, 2001). In addition, their large home range requirements (Das, 2012) mean that they often roam beyond protected areas and into human-dominated landscapes, increasing the probability of creating conflict and being killed (Loveridge et al., 2010b; Nyhus & Tilson, 2010; Sanderson et al., 2010). Settlement areas and pasture lands surrounding protected areas are particularly prone to human-carnivore conflict, with relatively high probabilities of carnivore predation of livestock (Treves et al., 2004) and humans (Dhanwatey et al., 2013). In Tanzania, properties located within 3km from the borders of Serengeti National Park experienced increased rates of livestock predation by large carnivores (Holmern et al., 2007), while in India, tiger (*Panthera tigris*) and leopard were more likely to attack humans within the buffer zone surrounding Tadoba-Andhari Tiger Reserve (Dhanwatey et al., 2013). In addition, reserve-adjacent areas show increased rates of human-induced carnivore mortality (Loveridge et al., 2010a; Loveridge et al., 2010b), making them priority areas for conflict mitigation (Woodroffe & Ginsberg, 1998). In Hwange National Park, 10 out of 22 lion prides inhabiting areas near the Park boundary went extinct in nine years due to human-induced factors such as trophy hunting, snaring, spearing and poisoning, 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).

1.3.1. Impacts of Human-Carnivore Conflict (HCC)

Every year, thousands of people and livestock are injured or killed by large carnivores (Athreya et al., 2004; Inskip & Zimmermann, 2009; Barlow et al., 2010). These attacks compromise local economies (Dickman et al., 2011) and food security (Treves & Naughton-Treves, 1999), and also have psychological and physical impacts on people who directly or indirectly suffer the consequences of carnivore attacks (Barua et al., 2013). The following section will provide an overview and discuss the costs and consequences of HCC to both humans and carnivores.

1.3.2. Direct costs of HCC on human lives and subsistence

Carnivore depredation upon livestock is the main driver of HCC worldwide (Sillero-Zubiri & Laurenson, 2001; Inskip & Zimmermann, 2009). Livestock losses resulting from such attacks often significantly affect the livelihood of entire households, especially in impoverished and rural areas where livestock usually represents the main asset and source of subsistence (Dickman et al., 2011). In the borders of Serengeti National Park, Tanzania, 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 Zimbabwe, losses due to depredation by large predators, including spotted hyaenas, lions and leopards, accounted for 12% (US \$13/household) of the annual income of 130 households (Butler, 2000). In a similar study, a single hyaena predation event resulted in the loss of 70 animals among sheep and goats (Kolowski & Holekamp, 2006). In such extreme surplus killing scenarios, pastoralists that traditionally rely on their livestock as their exclusive source of income (Butler, 2000; Maddox, 2003) suffer severe economic losses that critically compromise their livelihood (Dickman et al., 2011; Barua et al.,

2013). Taking the example of Tanzania, where the average annual income of a rural household is approximately US \$609 (The World Bank, 2013), the cost of such losses is devastating and imposes extreme financial hardship to entire households, and this can exacerbate long-term poverty (Nowell & Jackson, 1996; Dickman et al., 2011).

Carnivore attacks on people are less common, yet incite particular horror, imposing a significant challenge to human-large carnivore coexistence (Quigley & Herrero, 2005). In Tsavo, Southern Kenya, a coalition of two man-eating lions killed at least 28 rail workers during 1898 (Yeakel et al., 2009). More recently, in Tanzania, lion attacks accounted for at least 563 human deaths and 308 additional human casualties between 1990 and 2004 (Packer et al., 2005b). From 2002 to 2004, at least 35 people were killed by man-eating lions in the surroundings of Dar Es Salaam, the largest city in the country (Baldus, 2004). In some tragic events the lions forced their way through the walls of the hut and dragged the victim outside for consumption (Baldus, 2004). These attacks mostly affect middle-age men, who represent the core of the working force in rural societies (Barua et al., 2013) and play a pivotal role in the generation of incomes in their household. Their removal, as a consequence of death or mutilation, results in immediate economic loss, reduces opportunities for future income generation and worsens pre-existing poverty conditions (Dickman et al., 2011).

From a broader perspective, carnivore predation imposes high costs on governments and entities if they are responsible for compensating losses inflicted by large carnivores (Nyhus et al., 2005; Karanth et al., 2012). The Italian government spent approximately US \$2 million to compensate damages caused by bear (*Ursus arctos*), wolf (*Canis lupus*) and feral dogs (*Canis familiaris*) (Nyhus et al., 2005), while in Norway, in 2001,

the government paid US \$6.2 million to compensate farmers for carnivore predation on sheep flocks (Linnell & Brøset, 2003).

1.3.3. Indirect costs of HCC

Carnivore attacks also incur highly significant indirect costs on human lives (Barua et al., 2013). For instance, the practice of guarding the livestock at night, often adopted in areas exposed to intense HCC, increases herders' vulnerability to attack by carnivores (Treves & Naughton-Treves, 1999; Baldus, 2004), whilst sleeping outside to protect livestock also exposes them to vectors of potentially deadly diseases such as malaria (Barua et al., 2013). Additionally, this practice has been linked to increased alcohol consumption (Jadhav & Barua, 2012), sleep deprivation and mental health illness (Hoare, 2000).

The death or disability of a household breadwinner due to carnivore attacks increases the workload of other household members (Ogra, 2008); family members of victims also show increased rates of post-traumatic stress disorder, depression and suicidal tendencies (Barua et al., 2013). School children in rural communities are often used to herd livestock and help protect them from predators, thus limiting their ability to engage in school activities. This jeopardizes learning and literacy (Norton-Griffiths & Southey, 1995; Barua et al., 2013), and causes low class attendance and poor performance (Sieff, 1997).

The adoption of livestock protection measures such as predator-proof fences also imposes extra, and often prohibitive, expenditures to livestock owners (Thirgood et al., 2005). In Namibia, electrified fences to prevent depredation cost approximately US \$781/km to install and an additional \$952/km per year to maintain (Schumann et al., 2006). In South Africa, installing a predator-proof mesh fence costs between US \$5,250

- US \$7,250/km with an additional prohibitive maintenance cost of approximately US \$320 km/year (Lindsey et al., 2012a). In Tanzania, constructing a predator-proof livestock enclosure costs an average of US \$500 per household (Dickman, *pers. comm.*), which equates to approximately 82% of the estimated US \$609 annual income of rural families in the country (The World Bank, 2013).

1.3.4. *Impacts of HCC on carnivores*

In order to decrease or avoid carnivore predation upon humans and livestock, people will often persecute and kill the animal perceived to be inflicting the damage (Kissui, 2008). 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 & Packer, 2004).

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; Maclellan et al., 2009). Although lions later recolonised the area from adjacent communal lands, the population is again in decline 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 (Ogutu et al., 2005; Frank et al., 2006a). 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 current steep decline in the local hyaena population.

Persecution contributed to the African wild dog (*Lycaon pictus*) population decline (Woodroffe & Ginsberg, 1999), restricting the species to 7% of its original range

(Woodroffe, 2011) and to a wild population of less than 7,000 individuals (Woodroffe & Sillero-Zubiri, 2012). Between 1945 and 1959, a total of 4,995 wild dogs were killed by wild dog vermin control operations carried out in Zambia (Buk, 1995), where the population was of approximately 500 individuals in 1995 (Woodroffe & Ginsberg, 1999).

In most extreme cases, retaliatory killing has led to the extinction of carnivore species, as was the case of the Falkland wolf (*Dusicyon australis*), which became extinct in 1876 as a result of both pest control and the fur trade (Sillero-Zubiri et al., 2004).

In summary, HCC often incurs debilitating costs on the livelihoods of people living in close proximity to carnivores (Dickman et al., 2011), and exposes some of the most iconic species of large carnivores to unnaturally high mortality rates (Loveridge et al., 2010a) which threatens their long term persistence (Woodroffe et al., 2005b). Hence, given the current scenario of increasing rates of HCC (Dar et al., 2009) and declining populations of large carnivores (Woodroffe, 2000; Woodroffe, 2001), a better understanding of the main drivers of HCC is crucial in order to develop targeted strategies to prevent and mitigate conflict, and to promote large carnivore conservation (Thirgood et al., 2005; Dar et al., 2009).

1.4. Contextualizing HCC in Tanzania's Ruaha landscape

Investigating the drivers of HCC has been highlighted as a conservation priority for large carnivores in Africa (Woodroffe et al., 2005b), but such studies are still limited to few key study sites, such as around the Serengeti in Northern Tanzania (Holmern et al., 2007), and around reserves and parks in Botswana (Gusset et al., 2009), Kenya (Hazzah

et al., 2009), Zimbabwe (Loveridge et al., 2010b) and South Africa (Lagendijk & Gusset, 2008).

One particularly important but understudied area for large carnivore conservation is the Ruaha landscape of southern Tanzania. This 45,000km² landscape is centred around Ruaha National Park, which at 20,226km² is the largest Park in Tanzania (Kendall, 2011). However, it also encompasses adjacent Game Reserves, the Pawaga-Idodi Wildlife Management Area (PIWMA) and village lands, which are inhabited by *ca.* 40,000 people (MBOMIPA, 2006). The landscape represents one of the four remaining lion strongholds in East Africa (Riggio et al., 2012), and harbours significant populations of leopards, spotted hyaenas, African wild dogs (Mills et al., 2001; Ray et al., 2005), and cheetahs (*Acinonyx jubatus*) (Gros, 2002) (Additional information provided on Chapter 2).

However, this relative abundance of large carnivores has led to significant levels of HCC being reported on village lands around Ruaha National Park (Dickman, 2008), particular involving lions, spotted hyaenas and leopards. Dickman's study (Dickman, 2008) showed that, even though depredation was responsible for only 0.32% of monthly livestock losses (compared to 4.4% to diseases), depredation still incited significant hostility towards large carnivores and led to retaliatory killing. Research in this area revealed a very high rate of lion killing, with at least 27 lions killed in just three of the 21 villages close to Ruaha National Park between January 2011 and May 2012 (Dickman, *pers. comm.*). These killings were mainly retaliatory, and happened in response to the predation of domestic stock by large carnivore such as, spotted hyaenas, lions or leopards (Dickman, 2008).

The intensity and socio-economic drivers of conflict around Ruaha have been examined (Dickman, 2008; Dickman et al., 2014) but to date there has been no assessment of the landscape-level/bioclimate features that are associated with either the distribution of these carnivores across the landscape, or with hotspots of conflict. In addition, even though previous studies found that poor husbandry practices was a major factor related to increased depredation risk (Dickman, 2008), no research has so far assessed the relative influence of husbandry practices and landscape features on predation risk in this globally important area. To address this gap, this study uses species distribution models (SDMs) to examine the key ecogeographical features affecting large carnivore occurrence and the incidence of depredation across the Ruaha landscape.

1.5. Applications of species distribution models (SDMs) in carnivore conservation and conflict mitigation

Ecogeographical variables (EGVs) such as resource availability, vegetation cover, and temperature affect habitat quality and suitability, influencing carnivore behaviour and habitat use (Kolowski & Holekamp, 2009; Davidson et al., 2011). For example, increased habitat suitability for lions has been linked to proximity to water sources, with better hunting and reproductive success in areas close to water (Mosser et al., 2009). In spotted hyaenas, increased habitat suitability has been related to temperature stability (isothermality) (Varela et al., 2009), whereas variation in rainfall apparently predisposes the species to increased conflict with humans due to perturbations in prey availability (Cooper et al., 1999).

Recently, ecogeographical variables have been incorporated into species distribution models (SDMs) aiming to predict carnivore distribution across the landscape (Rosas-

Rosas, 2006; Rodríguez-Soto et al., 2011) and potentially identify areas with increased risk for HCC (Zarco-González et al., 2013). These models compare EGVs from a species presence point (or attack point, in the case of modelling conflict) with those found across the landscape, and use algorithms to predict areas with increased likelihood of species presence or attack based on estimated habitat suitability (Guisan & Zimmermann, 2000). Such outputs are important for conservation initiatives as they depict potential hotspots of carnivore occurrence (Rodríguez-Soto et al., 2011; Tôrres et al., 2012), and enable the predictions of areas with increased HCC where mitigation efforts should be prioritised (Zarco-González et al., 2013). 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, SDMs revealed that landscape-level variables such as vegetation cover classes and altitude were associated with an increased risk of livestock depredation by jaguar and mountain lion (*Puma concolor*) in Mexico, enabling the prediction of high-risk areas for conflict (Zarco-González et al., 2013). Such detailed ground-level information provides valuable support to the development of contextualized and applied strategies for conflict mitigation (Zarco-González et al., 2013) and the development of pre-emptive conservation planning (Elith et al., 2006).

Predictive modelling algorithms such as Maxent (Phillips et al., 2006), Ecological Niche Factor Analysis (ENFA) (Hirzel et al., 2002) and Support Vector Machines (SVMs) (Cortes & Vapnik, 1995) are some of the specific algorithms that can be used to study the spatial ecology of large carnivores (Zimmermann, 2004; Zarco-González et al., 2012). These particular algorithms have 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 (Papes & Gaubert, 2007). The ability of these algorithms to perform well using presence-only data is an advantage when compared to those relying on presence-absence information, 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 (Gu & Swihart, 2004). This is important as the use of unreliable absence records in predictive modelling leads to unrealistic species probability of occupancy 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.

In the context of the Ruaha landscape, there has been little data collected on the ecology or distribution of its critically important large carnivore populations, and this lack of information is hindering the development of effective conservation and management plans. Existing information about lions, spotted hyaenas and leopards is largely still limited to the core areas of the National Park, preventing an in-depth understanding of the landscape ecology of these species around Ruaha. Furthermore, although there is intense and patchily-distributed conflict across this landscape, no modelling has been done on which EGVs might be linked to that conflict, and therefore form predictions on where conflict mitigation efforts could best be targeted. SDMs are a potentially useful tool to assess the influence of various EGVs on the distribution of species presence and conflict across the landscape, and this modelling is likely to provide valuable baseline information for further conservation planning and local conflict mitigation strategies.

1.6. Importance of the present study

The present study will address two key issues in the Ruaha landscape. Firstly, it will determine the spatial features associated with the occurrence of lions, leopards and spotted hyaenas across the landscape. This will provide the first map of likely carnivore distribution across the Ruaha landscape – both within and beyond the National Park – thereby identifying priority areas for future conservation planning. Secondly, using a combination of SDMs and generalized linear models (GLM), the research will identify the EGVs related to livestock depredation events and build a predictive model of likely depredation hotspots on village land around Ruaha. Whilst the predictive SDMs on depredation will include landscape features, the GLM will incorporate both landscape and husbandry practices, which will provide much-needed information on the respective importance of habitat and husbandry in terms of depredation risk. This will help guide future conflict mitigation strategies – if husbandry practices emerge as more important predictors of risk than landscape features, then mitigation measures should focus upon those. However, if husbandry proves relatively unimportant compared to spatial features (such as vegetation cover), then mitigation should focus more on issues such as avoiding likely conflict hotspots while grazing vulnerable stock. The SDMs will allow the identification of high-risk areas so that conflict mitigation efforts can be implemented proactively, before there is a high level of depredation and retaliatory killing of large carnivores.

1.7. Aims and objectives

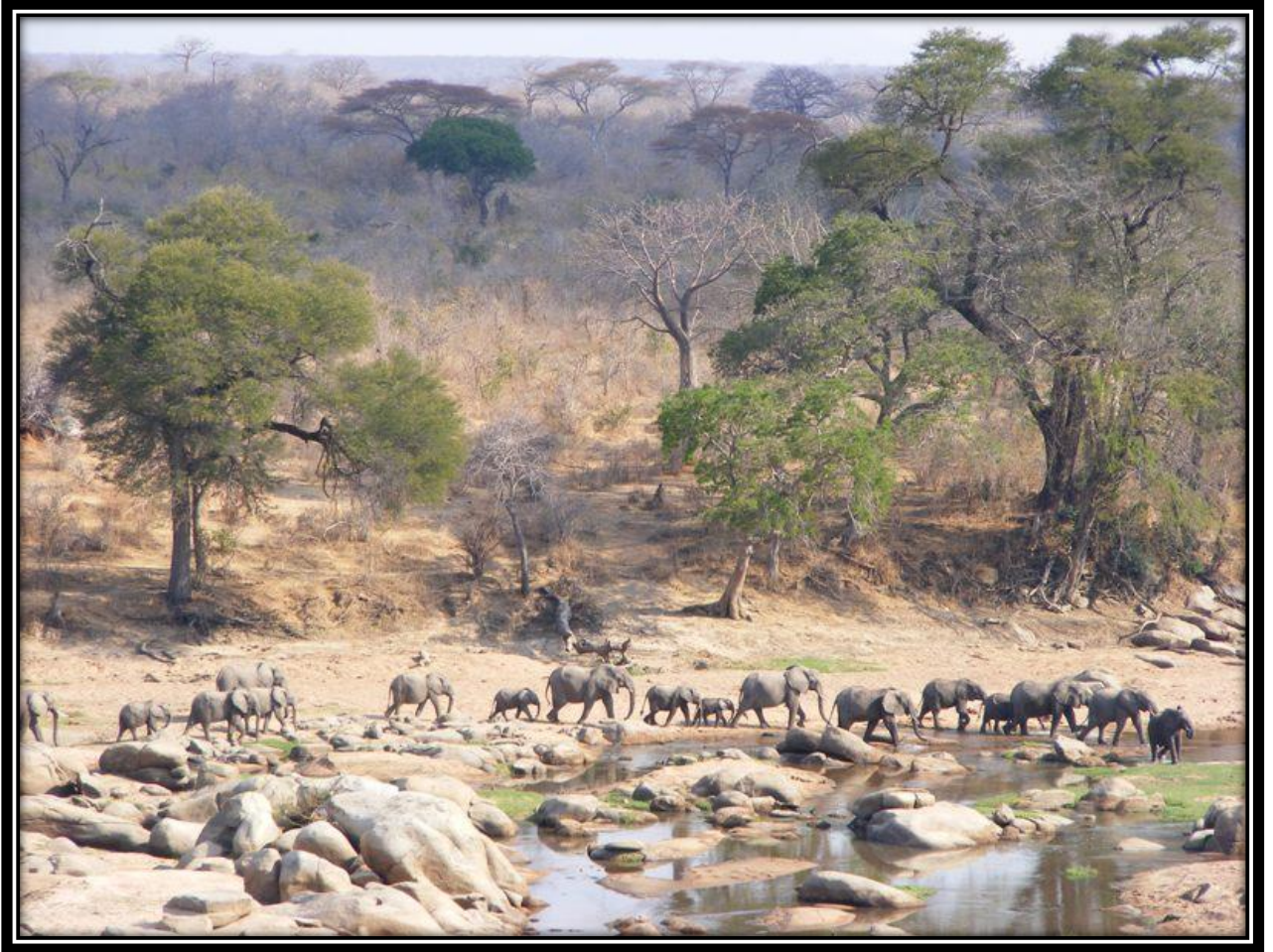
The present study aims to increase the understanding of the underlying environmental and bioclimatic features influencing both carnivore distribution and depredation risk in

the Ruaha landscape, Tanzania. The two objectives are as follows:

(1) To combine presence data from camera-trapping, direct sightings events and scats to model the potential distribution of lions, leopards and spotted hyaenas across the Ruaha landscape and identify high-priority areas for carnivore conservation;

(2) To map out lion, leopard and spotted hyaena depredation events, assess which spatial features and husbandry practices are correlated with a high risk of depredation, and build a predictive map of depredation risk for village land.

Chapter 2



Study Area

2.1. Study site

2.1.1. An overview of the Ruaha landscape

The study area is located in the Rungwa-Ruaha region of Tanzania, which spans more than 45,000km². This landscape includes Ruaha National Park (RNP), adjacent Game Reserves, the Pawaga-Idodi Wildlife Management Area (PIWMA), and adjoining village land, between 6°15'00" to 8°20'00" S and 33°45'00" to 35°50'00" E (Figure 1). The region is considered to be one of the most biologically valuable ecoregions in the world (Olson & Dinerstein, 1998). The study was focused in the RNP and adjoining village land.

The Rungwa-Ruaha area still supports an intact guild of large carnivores, harbouring an estimate population of 3,779 lions, representing one of the four lion strongholds in East Africa (Riggio et al., 2012), a significant population of leopards and spotted hyaenas, the third largest population of the endangered African wild dog (*Lycaon pictus*) in the world (IUCN, 2007), and one of the only four Eastern African cheetah populations supporting 200 adults or more (IUCN, 2007). Due to its importance for carnivores, particularly threatened large carnivores, this area has been considered a priority for African carnivore conservation (Mills et al., 2001). At the heart of the Rungwa-Ruaha region is the Ruaha National Park (RNP), which at 20,226km² is the largest park in Tanzania (Kendall, 2011). It was created in 1964, expanded in 2009, and is listed as category II by the IUCN (2009). Large parks such as Ruaha are designed to protect a functioning ecosystem and the large-scale ecological processes that would disappear from small protected areas. These protected areas also play an important role as key stepping-stones of biodiversity connectivity, protecting wide-ranging and migratory species which could not be conserved in isolated and smaller areas (IUCN, 2009).

2.1.2. *Biophysical aspects of the Ruaha landscape*

The climate of the region is semi-arid to arid, with rainfall peaks occurring between December to January and March to April, and an average annual rainfall of 500mm (Walsh, 2000). The temperature ranges from 15 to 35°C (Darch, 1996). The altitude ranges from 696 to 2,171m (ESA, 2009).

The vegetation cover is a mosaic of typical East African semi-arid savannah and northerly Zambesian *miombo* woodland (Sosovele & Ngwale, 2002), dominated by *Acacia* sp., *Combretum* sp. and *Commiphora* sp. Land-use varies from woodland to grassland and cultivated landscapes, with at least 17 different types of vegetation classes (ESA, 2009). The Ruaha River is the main water supply in the study area, providing key resources for wildlife, attracting species towards the park borders with the PIWMA and village land. During the driest periods of the year, the river becomes the most important water source for wildlife and livestock in this landscape (Dickman, 2008).

2.1.3. *Human dimensions of the Ruaha landscape*

The PIWMA and village land are located on the south-eastern borders of RNP, as part of the Iringa district. The area is inhabited by approximately 40,000 people distributed across 21 villages (MBOMIPA, 2006), with at least 35 different ethnic groups represented in the area (Williams, 2005). These ethnic groups include various pastoralist groups, such as the Maasai and Barabaig, which are traditionally oriented towards cattle herding, whereas groups such as the Hehe, Sukuma and Bena rely on agro-pastoral activities (Dickman, 2008).

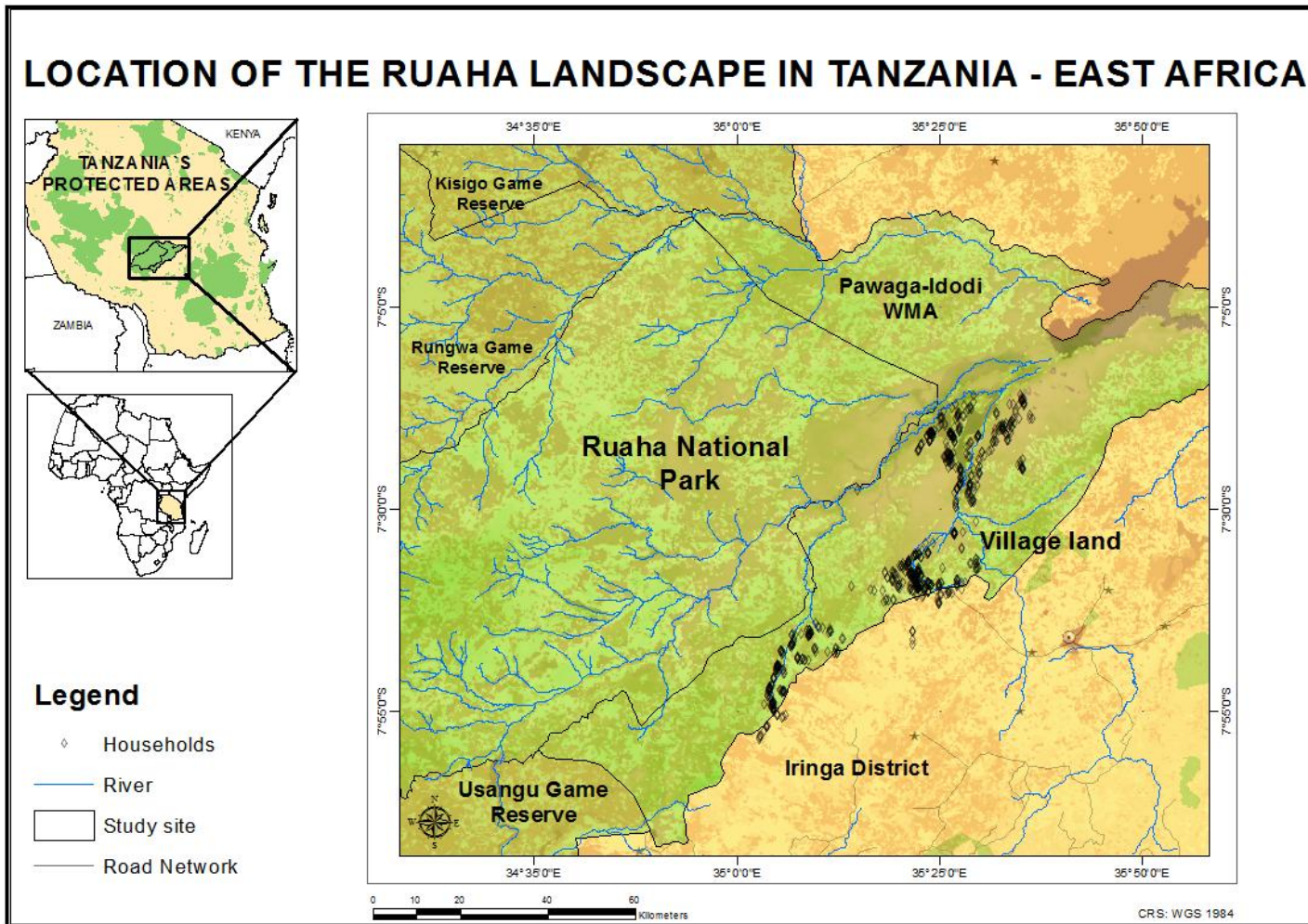


Figure 1. Location of the Ruaha landscape, southern Tanzania, East Africa, composed of the Ruaha National Park, Pawaga-Idodi Wildlife Management Area, adjacent game reserves and village land.

The major ethnic group inhabiting the region is the Hehe, but since 1939, the area has been increasingly occupied by other ethnic groups, especially the Barabaig, Maasai and Bena. The number of livestock owned apparently doubled between 1990 and 1995, accompanying the increase in human occupation (Arnold, 2001). This rapid human population increase, combined with illegal hunting for bushmeat, has been proposed as the main reason for the decline in wildlife in some areas surrounding RNP (Arnold, 2001). Overall, the livelihood of all the ethnic groups rely largely on livestock, which represented the main source of income for 71.3% (n=179) of households assessed (n=268) in the study site (Dickman, 2008). These groups share close cultural similarities, though they retain distinct traditions in terms of their lifestyle, perceptions of and interactions with wildlife, and particularly, tolerance towards large carnivores (Dickman, 2008). Dickman (Dickman et al., 2014) found that pastoralists were less tolerant towards large carnivores than agro-pastoralists, considering lions, spotted hyaenas and leopards as the most conflict-causing in the study site, respectively. Ethnicity has been reported as a significant factor contributing to HCC in Ruaha (Dickman et al., 2014) as it is related to distinct practices of livestock husbandry (Dickman, 2005), which has directly influenced livestock risk to predation by large carnivores (Dickman, 2008). Detailed information on the role of husbandry practices in terms of predation risk will be provided in later sections.

2.1.4. *HCC in the Ruaha landscape*

Previous studies conducted by Dickman (2005; 2008) in the study site characterized the general patterns of livestock predation by lions, leopards and spotted hyaenas. The following two sections will briefly provide information on the links between husbandry practices and stock vulnerability to attacks, and describe the most important factors

related to livestock predation risk so far identified in the study area. This information will serve as a baseline for the main analyses conducted during the present study.

2.1.4.1. Characterization of livestock husbandry practices and their relationship to predation risk

The stock in the region is mainly composed of small stock (goats and sheep), which Dickman (2008) found were owned by 91.4% (n=245) households and accounted for 52.6% of the overall stock kept in the area. Cattle were also extremely important, owned by 90.7% (n=243) of respondents and accounting for 42.6% of stock owned, while donkeys were owned by 28.7% (n=77) but only represented 1.2% of stock owned (Dickman, 2008).

During the day, herds are generally let out to graze, reportedly under the surveillance of herders and untrained guarding dogs. Grazing generally occurs near villages, between early morning and sunset; however, some livestock are illegally grazed within the nearby National Park. Use of human herders is a common form of livestock guarding, reportedly used by all 268 households visited by Dickman (2008), and may involve more than one person at a time, ranging from children to elders. Even though commonly reported, herding did not seem to be effective in decreasing livestock risk to predation, given that in 97.1% (n=190) of the reported predatory attacks that occurred during the day, the herds were supposedly under surveillance (Dickman, 2008). This result may be a consequence of herders leaving the stocks grazing alone in the bush or exhibiting low attentiveness. The use of dogs is also commonly reported as a strategy to prevent predation, with dogs supposedly safeguarding 86.5% of the overall stock owned in the region. The presence of dogs has been shown to substantially decrease livestock

risks to predation, with attacks more common on herds lacking the presence of a guarding dog (Dickman, 2008).

At night, the stock is usually accommodated in thornbush enclosures called bomas. Reportedly, cattle are always accommodated in bomas at night (Dickman, 2008), usually separately from the small stock, which are enclosed in smaller thornbush bomas (94%, n=231 households) or huts. The structure of the boma may vary among households (e.g. height, number of rooms, etc), as well as the raw material used to build it (thorny bushes, branches or poles), which influences its overall quality. The quality of the enclosure has shown to influence livestock risk to predation at night (Dickman, 2005). For example, bomas constructed using branches or bushes were more vulnerable to predation, suffering more attacks by spotted hyaenas, lions, and leopards than those constructed with better raw material such as poles (Dickman, 2005; Dickman, 2008). The use of alternative anti-predator devices, such as scarecrows, torches or fire is relatively rare in the area.

2.1.4.2. An overview of the characteristics of depredation events in the study site

Almost half of households assessed in the study site (44.9%, n=268) reported attacks in their bomas by large carnivores (overall n. attacks=467). Spotted hyaenas and lions were reportedly the main perceived culprits (35%; 28% respectively), followed by leopards (15%). In general, most depredation events caused by lions and spotted hyaenas reportedly occurred in bomas at night (>75%; >95% respectively, n=467), while diurnal attacks were most likely to be caused by leopards, cheetahs and wild dogs, and more likely to happen in the bush than in the bomas. Reportedly, lions showed a preference for preying on cattle (> 70% predation events, n= 469), whereas spotted hyaenas tended to selectively attack small stock (> 80% predation events).

Seasonality seemed to slightly influence livestock predation risk, given that 56.7% of the attacks (n=365) were reported to occur during the wet season. The number of predation events seemed to be higher during the wet season for both hyaenas and lions, whereas predation events caused by leopards were slightly more common during the dry season (Dickman, 2008). Finally, the first analyses of environmental features at a small scale around the bomas influencing livestock vulnerability to attacks suggest that vegetation cover does not have a major influence upon boma depredation risk (Dickman, 2008).

Even though previous studies provided an insight on the carnivore patterns of predation and landscape aspects of predation sites, there is still a paucity of in-depth understanding on the broader role of environmental and landscape features influencing livestock vulnerability to attacks by predators in this area. Variables such as net primary productivity, elevation and patterns of precipitation, among other variables are significant factors influencing livestock risk to depredation (Zarco-González et al., 2012; Zarco-González et al., 2013), but their roles have not hitherto been assessed in the context of the study site. The present study will assess the role of these potential variables in livestock predation risk around Ruaha National Park, which will enable the development of depredation risk maps and therefore the identification of areas at most risk of HCC. Further details of each variable considered for the models of predation risk will be provided in the next chapters.

Chapter 3



RCP Archive

**Using landscape and bioclimatic features to predict the
distribution of lions, leopards and spotted hyaenas in Tanzania's**

Ruaha landscape

Abstract

Tanzania's Ruaha landscape is an international priority area for large carnivore conservation, supporting over 10% of the world's lions, and important populations of leopards and spotted hyaenas. However, a lack of ecological data on large carnivore distribution and habitat use hinders the development of effective conservation strategies for these species in this critical landscape. Therefore, the study aimed to: (i) identify the most significant ecogeographical variables (EGVs) influencing the individual and collective distribution of lions, leopards and spotted hyaenas across the Ruaha landscape; (ii) estimate the portion of the landscape with highest suitability for harbouring those species; and (iii) use species distribution models (SDMs) to map areas of conservation importance for large carnivores. Habitat suitability was strongly influenced by water availability, with highly suitable areas for leopards, lions and spotted hyaenas those that were relatively close to rivers and experienced higher annual precipitation. Net primary productivity and tree cover also exerted some influence on habitat suitability. All three species showed relatively narrow niche breadth and low tolerance to changes in their habitat characteristics. In total, 95.4% (1,624km²) of the area deemed highly suitable for the occurrence of at least one of the carnivores was located within 30km of Park-village border, raising concerns about human-carnivore conflict. This was of particular concern for spotted hyaenas, with highly suitable areas for that species located significantly closer to the Park boundary than for lions and leopards. This study provides the first map of likely carnivore distribution across the globally important Ruaha landscape, but also demonstrates that SDMs can be an effective technique for understanding large carnivore ecology in areas where sampling is limited, and would be relevant in many other important wildlife areas which only have haphazard presence-only records, but which nevertheless urgently require strategic conservation planning.

3.1. Introduction

Apex predators such as lions, leopards and spotted hyaenas play an important role in the regulation of ecological interactions and ecosystem health, substantially influencing lower trophic levels (Ritchie & Johnson, 2009; Pitman et al., 2012). As keystone species (Power et al., 1996; Elbroch & Wittmer, 2012; Kunkel et al., 2012), they affect the density of mesopredators and natural prey (Krebs et al., 2001; Elbroch & Wittmer, 2012), and influence plant communities (Augustine & McNaughton, 1998) by suppressing the effects of large ungulates on vegetation (Messier, 1994; Hobbs, 1996; Bowyer et al., 2005). Their removal from the ecosystem unleashes trophic cascades (Beschta & Ripple, 2009), which ultimately results in alteration of top-down regulations of the ecosystem (Terborgh et al., 2001; Bowyer et al., 2005) and can lower biodiversity and species richness (Terborgh et al., 2001; Ripple & Beschta, 2006). However, large carnivores have experienced dramatic reductions in both population size and geographic range over the past century, necessitating urgent conservation planning for these species (Ray et al., 2005).

In Africa, high levels of human-induced carnivore mortality have been shown to be the most important factor leading to local extinction of large carnivores (Balme et al., 2009; Hazzah et al., 2009; Watts & Holekamp, 2009). Reserve-adjacent areas often experience particularly high human-carnivore conflict (HCC) and carnivore killing, acting as significant population sinks (Woodroffe & Frank, 2005; Balme et al., 2010; Loveridge et al., 2010a). It is therefore vital to develop effective large carnivore conservation strategies both within and beyond the boundaries of protected areas. However, developing such strategies across an entire landscape requires an understanding of the eco-geographical preferences and therefore distribution of the

target taxon (Rodríguez-Soto et al., 2011). Large carnivore distribution and habitat selection is largely determined by prey availability (Hayward et al., 2009; Valeix et al., 2010), which in turn is affected by factors such as vegetation cover, water availability and elevation (Schadt et al., 2002; Pita et al., 2009; Valeix et al., 2010). However, in many priority wildlife areas, researchers lack the time and resources needed to collect systematic presence-absence data on prey and carnivore distributions at the landscape level. They often rely upon opportunistic detections of species occurrence, but this presence-only data might not be well-suited to commonly-used techniques such as occupancy modelling (Brotons et al., 2004; but see Royle et al., 2012).

This issue is vividly illustrated by Tanzania's Ruaha landscape, which is a priority area for African carnivore conservation (Mills et al., 2001). This landscape supports over a tenth of the world's lions (Riggio et al., 2012), one of only four cheetah (*Acinonyx jubatus*) populations in East Africa numbering 200 adults or more (Chardonnet, 2002), the world's third largest population of the endangered African wild dog (*Lycaon pictus*) (IUCN, 2007) and globally important populations of leopards and spotted hyaenas (IUCN, 2007; TAWIRI, 2009). However, despite this global significance, the Ruaha landscape has received very little research attention and there are no published studies on large carnivore distribution and spatial ecology in this area, preventing the development of informed carnivore conservation plans. Such planning is particularly urgently needed given the extremely high level of human-carnivore conflict around Ruaha, which is mainly driven by lion, leopard and spotted hyaena depredation upon livestock (Dickman et al., 2014). As in many important wildlife areas, researchers in Ruaha have limited presence-only data on carnivore locations from across the landscape, and there is an urgent need to use this information as fully as possible, in order to predict wider patterns of carnivore presence and conflict with humans.

Recently, predictive algorithms such as Maxent (Phillips et al., 2006), Ecological Niche Factor Analysis (ENFA) (Hirzel et al., 2002) and Support Vector Machines (SVMs) (Cortes & Vapnik, 1995) have been used in species distribution models (SDMs), as they are potentially useful for determining species habitat suitability and distribution patterns from presence-only data. Moreover, they are able to deal with limited sample size and biased sampling (detailed explanation provided on the next section) (Hirzel et al., 2002a; Drake et al., 2006; Phillips et al., 2006), which are common problems in large carnivore research. These SDMs incorporate an array of eco-geographic factors to predict species distribution based on habitat suitability (Zaniewski et al., 2002; Zarco-González et al., 2012), and generate data which can be converted to maps of likely species distribution, helping researchers to identify areas of particular conservation importance and to inform future conservation planning strategies (Cabeza et al., 2004; Zarco-González et al., 2012). Furthermore, identification of areas where people and carnivores are likely to overlap (e.g. if highly suitable habitat is located close to a Park boundary) will help identify potential hotspots of human-carnivore conflict. These data could be used to help target pre-emptive conflict mitigation strategies in high-risk areas, therefore reducing the conservation threat posed by conflict and retaliatory carnivore killing.

Therefore, this study aims to evaluate the potential distribution of three key large carnivores - the lion, leopard and spotted hyaena - across the Ruaha landscape, based upon key environmental and bioclimatic features likely to influence carnivore habitat suitability in this ecosystem. An ensemble modelling technique, derived from predictive models generated by Maxent, ENFA and SVMs, was used to (i) identify the most significant environmental and bioclimatic factors influencing the distribution of each species and the overall assemblage of large carnivores; (ii) estimate the portion of the

study site with highest suitability for harbouring large carnivores; and (iii) map out areas of conservation importance for these species. The study is the first to investigate the key factors affecting large carnivore distribution in the poorly known Ruaha region and to generate maps of likely presence, which also highlight risky zones for human-carnivore conflict. This ensemble modelling approach could usefully be employed in other priority wildlife areas which have opportunistically collected presence-only data and require urgent conservation planning.

3.2. Methods

3.2.1. Study area

The study site is comprised of the Ruaha National Park, Pawaga-Idodi Wildlife Management Area and village land, covering approximately 21,050km². Detailed information about the area is provided in Chapter 2.

3.2.2. Species distribution data

Georeferenced presence-only points of carnivore locations were collected from 2010 to 2013 using direct observation, camera-trapping data and scat identification within the National Park, village land and an adjacent Wildlife Management Area (WMA). A Global Moran's I test was performed to assess the distribution pattern of presence points registered across the study area, and investigate for pseudoreplication between location records (Millar & Anderson, 2004). For leopard and spotted hyaena, no spatial buffering of point selection was necessary due to the low spatial autocorrelation among points. For lions, only single presence points located at least 3km apart were considered, in order to minimize spatial autocorrelation. In total, 122 presence points

were considered for leopards (118 points from direct observations; 2 from scat identification; 2 from camera-trapping), 93 for spotted hyaenas (88 from direct observation; 5 from camera-trapping) and 59 for lions (52 from direct observation; 7 from camera-trapping). The majority of carnivore location points considered for the models were collected within RNP, with a total of 96% (n =117) of the leopard points collected in RNP, 97.9% (n=91) of the locations for spotted hyaenas, and 88.1% (n=52) for lions, with the remainder collected in the village lands and WMA. Although few location points were collected outside the protected area, they helped the model to incorporate landscape heterogeneity, especially regarding information on carnivore occurrence in relation to close proximity to human households.

3.2.3. Ecogeographical variables

The ecogeographical variables (EGVs) were selected according to their potential influence on the distribution of each species (Ogutu & Dublin, 2002; Packer et al., 2005a; Gavashelishvili & Lukarevskiy, 2008; Varela et al., 2009; Hunter et al., 2013), and were divided among landscape, bioclimatic and human disturbance features (Table 1). Prior to running the models, the set of EGVs was first submitted to a Pearson correlation test, to avoid issues of multicollinearity among variables. Guisan et al. (2002) showed that highly correlated covariates could be considered as non-significant by the model, even significantly contributing for the model output when considered individually. Therefore, the selected predictors were those minimally correlated ($< \pm 0.85$ (Elith et al., 2006)). Elevation data were extracted from the Shuttle Radar Topographic Mission (USGS, 2000), and rainfall was downloaded from the WorldClim database v. 1.04 (<http://www.worldclim.org/current>). The ‘distance to water bodies’ and ‘distance to human households’ rasters were generated using the Euclidean Distance

function in ArcGIS 10.1 based on the presence of water bodies in the study site (original data from FAO Africover, 2004), and the location of households mapped by WildCRU's Ruaha Carnivore Project (RCP) in the study site. The variable distance to roads was not included in the final model due to the high correlation with elevation. Due to a scarcity of data on the local distribution of wild prey such as ungulates and other herbivores, a Normalized Difference Vegetation Index (NDVI) layer was considered. NDVI is related to photosynthesis and vegetation productivity (Levin et al., 2007; Bradley & Fleishman, 2008), and has been incorporated into models (Gavashelishvili & Lukarevskiy, 2008) as a proxy to identify potential landscape patches with increased biomass of ungulates and herbivores (Loe et al., 2005; Pettorelli et al., 2005).

Table 1. Set of ecogeographical variables (EGVs) used for modelling the potential distribution of lions, leopards and spotted hyaenas in Tanzania’s Ruaha landscape.

Ecogeographical features	Source	Original Resolution
Bioclimatic variables		
Annual precipitation	WorldClim database, v. 1.04. http://www.worldclim.org/current	30 arc-seconds (~1 km)
Landscape features		
Digital elevation model	Shuttle Radar Topography Mission. http://www.landcover.org/data/srtm/	3 arc-seconds (90 metres)*
Slope	Derived from digital elevation model	-
Normalized Difference Vegetation Index – NDVI	MODIS Terra - MOD13A. http://glovis.usgs.gov/	500 metres*
Vegetation Continuous Fields - VCF	ftp://ftp.glcfc.umd.edu/modis/vcf/collection_5/	250 metres*
Geology - Cation Exchange Capacity	http://www.isric.org/data/soil-property-maps-africa-1-km Derived from FAO.	1km
Distance to water bodies	http://www.africover.org/system/area.php?place=7	-
Human Disturbance		
Distance to human households	Derived from Ruaha Carnivore Project Data	-

* Raster files converted to ~ 1km x 1km cell size

The NDVI raster incorporated into the models was derived from a compilation and processing of NDVI rasters from Terra (EOS AM) satellite images generated between March 2011 and December 2012. Information on vegetation cover (vegetation continuous fields - VCF) was also considered. VCF depicts the landscape surface as gradations of three components of ground cover, (1) percent tree cover, (2) percent of non-tree vegetation, and (3) bare soil (Townshend et al., 2011). A raster containing information on the cation exchange capacity of the soil was incorporated as it is also related to vegetation cover and primary net productivity. Higher cation exchange capacity is related to increased soil capacity to retain nutrients, which contributes to soil

fertility and plant productivity (Clark et al., 2007), and positively influences large ungulate biomass and lion distribution (Loveridge & Canney, 2009; Packer et al., 2013).

The raster files were converted in habitat-grid cells of approximately 1km x 1km resolution according to their original resolution size (Table 1, Figure 2a-b). Spatial data preparation and raster analyses were conducted in ArcGIS (Esri, 2012) and IDRISI Selva (Eastman, 2012), and the statistical analyses in R v. 2.15.1 (R Core Team, 2012). ENFA modelling was conducted in Biomapper v. 4.0.7.373, Maxent in Maxent v. 3.3.3e and SVMs in openModeller Desktop v. 1.1.0.

3.2.4. Building the predictive models

Prior to spatial modelling, the presence-only location points related to each species were randomized and then divided into training (70%) and testing (30%) data to allow *post hoc* validation of the resulting models. The output models generated by ENFA, SVMs and Maxent were used to build the final ensemble model (Araújo & New, 2007; Marmion et al., 2009) to determine the potential distribution of lions, leopards and spotted hyaenas across the Ruaha landscape. A grouped model encompassing all large carnivore species together was also considered in order to compare the potential influence of the EGVs on the distribution of the overall assemblage of large carnivores. The predictive algorithms were selected based on their high predictive power, and especially due to their capabilities of performing well relying solely on presence-only data (Hirzel et al., 2002; Phillips et al., 2006; Elith et al., 2011). This is relevant as often, distribution models have to rely on data from species surveys, which cannot identify areas of total absence of occurrence for a particular species within its distribution range, especially for large carnivores (Gu & Swihart, 2004). Therefore, the

capacity to use presence-only points obviates the risk that models incorporate unreliable absence records (which could lead to unrealistic and misleading scenarios of species probability of occupancy and distribution (Gu & Swihart, 2004; Jiménez-Valverde et al., 2008)).

The ENFA algorithm is based on Hutchinson's ecological niche concept (Hutchinson, 1957; Hirzel et al., 2002), which is described as a multidimensional space in a hypervolume comprising ecological variables that allows an organism to survive and reproduce (Hutchinson, 1957; Pulliam, 2000; Hirzel et al., 2002). ENFA calculations are similar to a component analysis, and summarize the species preference for habitat types in two distinct components or factors, marginality and specialisation, which measure the habitat used from the overall habitat available (Basille et al., 2009). The first factor represents species global Marginality (M), comparing the deviation of all the environmental conditions where the species occurs (species distribution) to those found in the study area (global distribution) (Basille et al., 2009). In other words, the global Marginality describes the position of the species habitat within the environment, taking into account the contribution of all EGVs considered, and ranges from 0 to 1, with higher values indicating that the species inhabits a very particular habitat type in relation to the reference habitat (Hirzel et al., 2002). ENFA also enables the identification of species preferences for particular EGVs, as it calculates a 'marginality coefficient' relating the degree of correlation between each variable to the global marginality factor.

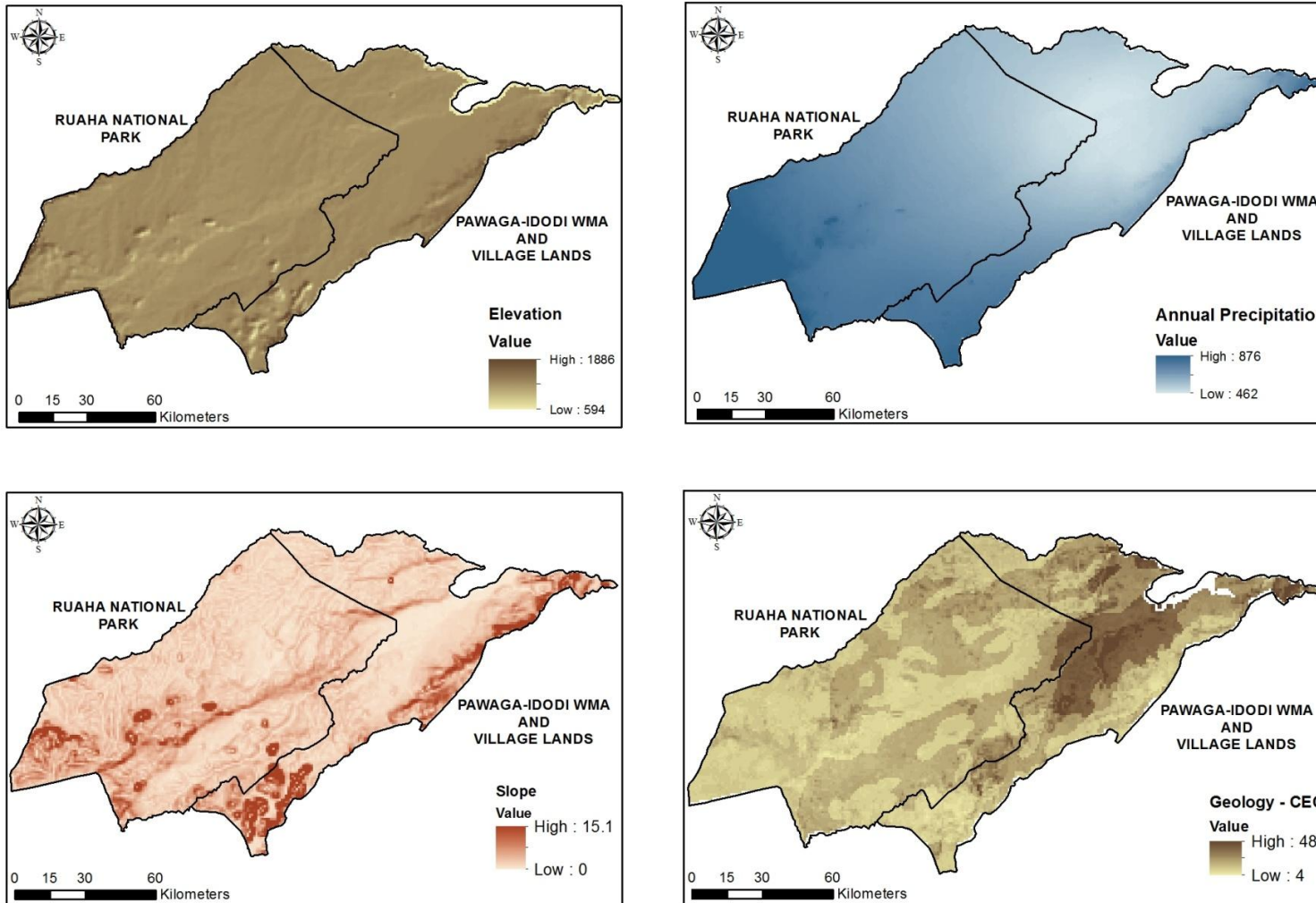


Figure 2a. Representation of the raster files used for the predictive modelling of the distribution of lions, leopards and spotted hyaenas in the Ruaha landscape. Elevation (m), Annual Precipitation (mm), Slope (degrees) and Geology – cation exchange capacity.

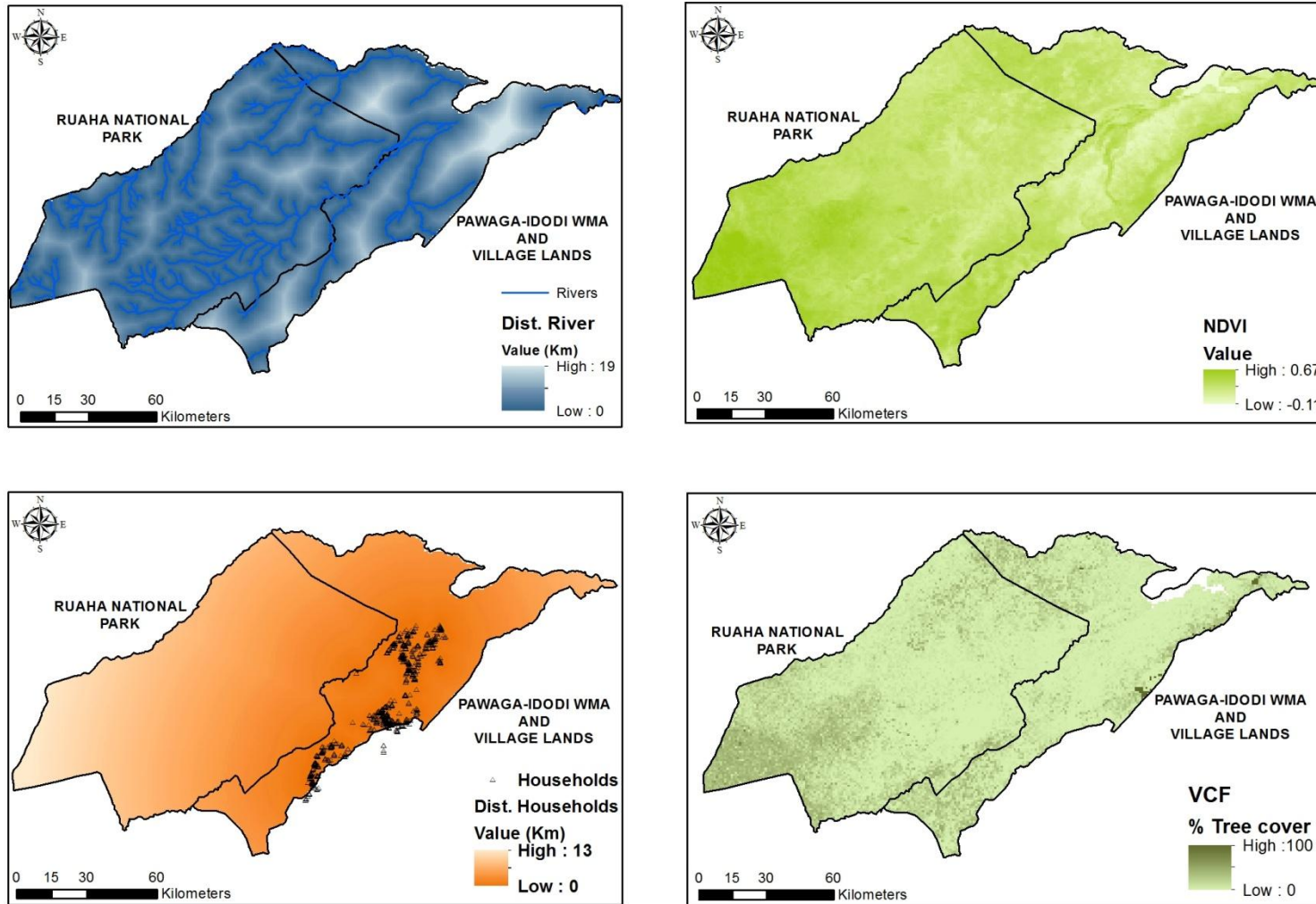


Figure 2b. Representation of the raster files used for the predictive modelling of the distribution of lions, leopards and spotted hyaenas in the Ruaha landscape. Distance to rivers (km), NDVI, Distance to households (km) and VCF (% Tree cover).

High absolute marginality value of a coefficient indicates that the species favours that particular EGV more than the mean value available in the habitat for that particular variable, and the more it contributes to the global marginality. A negative marginality coefficient indicates that the species favours lower-than-mean values of a particular EGV than those found in the habitat (Xuezhi et al., 2008). The second component represents species global Specialisation (S), which is a measure of the ratio of the variance in global distribution to that observed in the species distribution (Hirzel et al., 2002). Global Specialisation depicts a species' niche restrictiveness (Leverette & Metaxas, 2005), with values above 1 indicating a certain level of specialisation by the species (Hirzel et al., 2002). As global Specialisation values might be difficult to interpret as it varies from 1 to infinity, ENFA provides an overall index of species tolerance (global Tolerance, $1/S$) which varies from 0 to 1, with values close to 1 indicating that the species tolerates large variations from its optimum conditions (Simard et al., 2009), is widely distributed in the study site (Xuezhi et al., 2008), and show broader niche breadth (Braunisch et al., 2008). To facilitate interpretation of the results generated by ENFA, the mid-point of the Global Marginality and Global Tolerance indices (i.e. 0.5) was used as a threshold, with values above the threshold for (M) indicating species preference for particular habitat types, and those for ($1/S$) indicating low niche restrictiveness and broader niche breadth. No threshold was defined for (S) as the values vary from 1 to infinity. The influence of each EGV was also based on a threshold choice, with the absolute value of the marginality coefficients above the mid-point (i.e. > 0.5) indicating stronger preference for a particular EGV.

Support vector machines (SVMs) algorithms have recently become adopted in the field of spatial modelling of species distribution in order to assess niche suitability (Drake et al., 2006; Drake & Bossenbroek, 2009; Pouteau et al., 2012; Zarco-González et al.,

2013). SVMs is a powerful tool to deal with data uncertainty, sampling autocorrelation and presence-only datasets (Drake et al., 2006), dealing well with problems commonly related to ecological studies such as small sample size and incidentally-collected (haphazard) data. The algorithm is part of a non-probabilistic pattern recognition classifier (Drake & Bossenbroek, 2009). It relies on a kernel-based function (Cortes & Vapnik, 1995) to classify objects in a multidimensional optimal hyperplane, i.e. one with maximized margin of separation between two data clusters (Karatzoglou et al., 2006; Yu et al., 2010). SVM was run using the default settings, using 1 replicate, 10,000 background points, one-class SVM, and the radial-basis function. Although a robust predictive method, it can be challenging if used in isolation as it does not tabulate the potential contribution of each variable as Maxent and ENFA do, thereby limiting identification of key features associated with greater habitat suitability (Zarco-González et al., 2013).

Maxent is a machine learning method used to estimate probability of distribution, based on the principle of maximum entropy (Phillips et al., 2006). Maxent will predict the probability of species distribution under the most dispersed scenario assuming all the environment constraints affecting species presence were taken into consideration during the calculations (Phillips et al., 2006; Elith et al., 2011). The Maxent models were run using the settings defined by Phillips *et al.* (2006), using 10 replicates, bootstrap, 500 iterations, and 10,000 background points. As in the ENFA algorithm, a threshold above the mid-point of variable contribution (i.e. above 0.5) was chosen to determine those variables strongly influencing species habitat suitability and therefore, probability of occurrence.

It is noteworthy that due to distinct processing of each algorithm, and the idiosyncratic responses of each species to landscape features, no direct comparisons between the different modelling outputs were performed. Therefore, the present study assessed the distribution of each species independently, intending to depict general patterns of species distributions across the landscape.

3.2.5. *Model validation*

The performance of each independent model was evaluated by calculating the area under the receiver operating characteristic (ROC) curve, abbreviated to Area Under the Curve (AUC) (Hanley & McNeil, 1982; Jiménez-Valverde et al., 2008) in IDRISI Selva. The ROC curve is calculated based on values of sensitivity (correct discrimination of true positive location points) and specificity (correct discrimination of true negative absence points) of the model. The AUC ranges from 0.5 (random) to 1.0 (perfect discrimination), providing reliable estimation of model fitness as it compares the likelihood of occurrence with the true presence data used as reference (Thuiller et al., 2005; but see Lobo et al., 2008). Models showing AUC values > 0.7 are considered fair and those with scores > 0.9 are considered highly accurate (Pearce & Ferrier, 2000; Manel et al., 2001). The AUC internal (training data) and external (testing data) was calculated overlaying the previously randomized set of presence-points with the output models generated by each algorithm. This step enables to check the model accuracy, as it fits the model to the data used for training the model (AUC internal), and its ability to extrapolate based on the testing data (AUC external).

Each modelling approach has limitations and potential errors inherent to their algorithms and may show different levels of efficacy and performance while predicting species distribution (Segurado & Araújo, 2004; Araújo & New, 2007; Marmion et al.,

2009). Developing consensus models is a good strategy for overcoming model uncertainties and increasing the reliability of predictions, since the final output incorporates areas of consistent prediction from all models (Araújo & New, 2007; Zarco-González et al., 2013). Here, a consensus model (ensemble model) was calculated using the weighted average of the resulting internal AUC values of each model, as described in Marmion *et al.* (2009), and used by Rodríguez-Soto *et al.* (2011) to predict the distribution of jaguars in Mexico. The performance of the ensemble model was also assessed according to the resulting weighted AUC value. The following formula was used to calculate the resulting ensemble model in the IDRISI calculator:

$$\text{Ensemble model} = \frac{[(\text{Image Algorithm 1} * \text{AUCi}) + (\text{Image Algorithm 2} * \text{AUCi}) + (\text{Image Algorithm 3} * \text{AUCi})]}{[\text{AUCi Algorithm 1} + \text{AUCi Algorithm 2} + \text{AUCi algorithm 3}]},$$

where AUCi corresponds to the internal AUC, resulting from model fitting of the training data.

Finally, the ensemble model outputs were converted into maps of habitat suitability for species occurrence. These maps depict a gradient of suitability across the landscape, in which each grid cell of the map has an associated value of habitat suitability, and therefore probability of species occurrence, varying from 0 to 100, with highly suitable grids cells closer to 100. To allow identification of the most important areas for species occurrence and therefore conservation planning, ‘highly suitable’ grid cells were defined as those with values above the species’ median suitability, considering the median value of the location points used to train the models (Liu et al., 2005; Rodríguez-Soto et al., 2011; Zarco-González et al., 2013). According to Liu *et. al* (2005), the median is a meaningful threshold choice as it does not assume a symmetric distribution (i.e. normal distribution) for habitat suitability across the landscape. A linear model was used to assess the distribution patterns of highly suitable cells for each

carnivore species. In addition, the distance of these grid cells to village lands was calculated, highlighting zones of potential overlap between large carnivores and human activities which are likely to be human-carnivore conflict hotspots.

3.3. Results

3.3.1. Model performances

Overall, the SDMs performed well in terms of predicting the distribution of all the large carnivores across the study area, with all models showing AUC values above 0.7 (Table 2). Maxent outperformed ENFA and SVMs in predicting large carnivore distribution, both for individual species and when the three were grouped together (Table 2). ENFA was the lowest-performing algorithm for both individual carnivores and the grouped model, while the ensemble model performed well, with AUC values only slightly lower than from Maxent alone.

3.3.2. Grouped model

The ENFA analysis suggested that, if assessed as an assemblage (i.e. no discrimination among species), the large carnivores had a global Marginality value ($M = 0.446$; Table 3) which was slightly below the pre-defined threshold of 0.5, suggesting that they did not select for an overly narrow set of ecogeographical traits. The global Tolerance value ($1/S = 0.414$; Table 3) suggested they showed low relative ecological flexibility to variations in the optimal environmental conditions available in the study area. The ENFA algorithm suggested that habitat suitability for the assemblage of large carnivores increased mostly with proximity to water bodies (Table 4). NDVI, VCF and altitude showed some contribution to species marginality and habitat suitability, but did

not strongly influence large carnivore distribution (Table 4). Maxent modelling identified annual precipitation as the most important variable influencing large carnivore habitat suitability, followed by increased distance to human settlements and proximity to rivers. However, none of the predictors showed % contribution values above the pre-defined threshold of 0.5 (Table 4). From the overall potential distribution of large carnivores across the Ruaha landscape, a total of 2.18% (442km²; median suitability > 67% habitat suitability) of the study area was estimated as highly suitable according to the ensemble model, when no differentiation was considered among large carnivore species (Table 5, Figure 3).

Table 2. Performance of algorithms used to predict the distribution of leopards, lions and spotted hyaenas across Tanzania's Ruaha landscape. Significant models showing AUC > 0.7.

Algorithm	Species	Training AUC	Testing AUC
<i>ENFA</i>	Grouped	0.753	0.765
	Leopards	0.756	0.822
	Lions	0.750	0.622
	Spotted Hyaenas	0.822	0.848
<i>Support Vector Machines</i>	Grouped	0.892	0.883
	Leopards	0.905	0.902
	Lions	0.863	0.701
	Spotted Hyaenas	0.886	0.904
<i>Maxent</i>	Grouped	0.947	0.921
	Leopards	0.949	0.957
	Lions	0.873	0.753
	Spotted Hyaenas	0.944	0.960
<i>Ensemble</i>	Grouped	0.907	0.900
	Leopards	0.921	0.934
	Lions	0.852	0.706
	Spotted Hyaenas	0.921	0.942

Table 3. Indices for species niche global marginality and tolerance according to Ecological Niche Factor Analysis (ENFA). *Indicates values above the mid-point threshold (0.5).

Species	Marginality (M)	Specialisation (S)	Tolerance (1/S)
Grouped	0.446	2.416	0.414
Leopards	0.492	3.045	0.328
Lions	0.436	2.463	0.406
Spotted hyaenas	0.578*	3.471	0.288

Table 4. Estimated marginality and specialisation coefficients according to ecogeographical variables by Ecological Niche Factor Analysis (ENFA) and % variables contribution to species distribution according to Maxent. Negative signs indicate preference towards lower values of a particular EGV (Hirzel et al., 2002). *Indicates features associated with greater habitat suitability (i.e. > 0.5).

Species	Variables	ENFA		Maxent
		Marginality Coefficient	Specialisation Coefficient	(%) Contribution
<i>Grouped</i>	Dist. River	-0.68*	-0.25	13.1
	NDVI	-0.36	-0.20	5.8
	VCF	-0.35	0.63	4.2
	Altitude	-0.35	0.42	12.1
	Slope	-0.27	0.01	1.4
	Geology	-0.22	-0.12	3.6
	Annual Precipitation	0.17	0.40	44
	Dist. Settlements	-0.09	-0.39	15.8
<i>Leopards</i>	Dist. River	-0.62*	0.28	12.7
	NDVI	-0.47	0.12	2.4
	VCF	-0.37	-0.38	2.1
	Altitude	-0.36	-0.58	13.8
	Slope	-0.25	-0.01	1.2
	Geology	-0.20	0.15	4.5
	Annual Precipitation	0.14	-0.39	49.7
	Dist. Settlements	-0.08	-0.50	13.7
<i>Lions</i>	Dist. River	-0.74*	0.19	30.1
	NDVI	-0.22	0.01	1.1
	VCF	-0.32	0.84	6.8
	Altitude	-0.36	-0.27	17.2
	Slope	-0.27	-0.32	3
	Geology	-0.12	0.15	2.9
	Annual Precipitation	0.29	-0.06	30.4
	Dist. Settlements	-0.10	0.21	8.5
<i>Spotted hyaenas</i>	Dist. River	-0.59*	-0.21	14.6
	NDVI	-0.49	-0.07	1.6
	VCF	-0.33	0.24	21.5
	Altitude	-0.35	0.57	9.8
	Slope	-0.30	0.08	2.7
	Geology	-0.26	-0.16	0.6
	Annual Precipitation	0.03	0.38	32.2
	Dist. Settlements	-0.16	-0.62	17.1

3.3.3. *Leopards*

The ENFA results suggested that leopards showed certain selectivity for specific habitat types within the study area, but were slightly below the pre-defined marginality threshold and, overall, did not select for a particularly narrow set of habitat conditions ($M = 0.492$). The species also showed limited tolerance for large variations in the optimal conditions of EGV available in the landscape ($1/S = 0.328$) (Table 3). According to the algorithm, habitat suitability for leopards was associated with proximity to rivers (Table 4). Areas of relatively low primary net productivity, open canopy and lower altitudes also contributed to habitat suitability, but not as strongly as distance to water bodies (Table 4). The Maxent results suggested that leopard distribution in Ruaha was influenced by a positive index of annual precipitation, with that variable alone contributing almost 50% to the probability of species occurrence. Even though the distribution of leopards seemed to be spread widely across the landscape in terms of the overall habitat suitability for the species (Figure 3), the ensemble model estimated that only approximately 2.4% (510.1km²) of the study site was highly suitable for leopard occurrence (Table 5).

3.3.4. *Lions*

The ENFA algorithm suggested that lions did not show a strong preference for particular habitat conditions ($M = 0.436$), although they had relatively low tolerance to changes in the environmental conditions composing the habitat (Table 3). ENFA also suggested that, in the Ruaha landscape, habitat suitability for lions was strongly influenced by proximity to water sources, while lower elevation, and open canopy, also made a slight contribution to habitat suitability (Table 4). The Maxent algorithm related habitat suitability for lions to annual precipitation and proximity to water sources (Table

4). Based on the median suitability threshold approach, 4.8% of the study area (1,010.4km²) was predicted to be highly suitable for lions (Table 5).

3.3.5. *Spotted hyaenas*

The ENFA algorithm suggested that spotted hyaena probability of occurrence was related to certain habitat types ($M = 0.578$), and that the species showed limited tolerance to large deviations in environmental features, and narrow niche breadth ($1/S = 0.288$). They exhibited lower tolerance than any other carnivore examined. In addition, the ENFA results suggested that spotted hyaena habitat suitability was strongly influenced by distance to rivers (Table 4). Areas of decreased net productivity, low altitude and vegetation cover also had higher habitat suitability for the species (Table 4). The Maxent modelling linked an increased probability of hyaena occurrence with higher annual precipitation, with little influence of vegetation cover, and distance to settlements (Table 4). The species showed the most limited distribution among all the large carnivores based on the amount of highly suitable cells estimated by the ensemble model, with highly suitable areas covering only 0.8% of the study area (181.7km², Table 5). This limited distribution is likely to reflect the elevated median for habitat suitability for species occurrence used in the analysis (h.s. > 76% species median suitability and probability of occurrence).

Potential distribution of large carnivores across the Ruaha Landscape

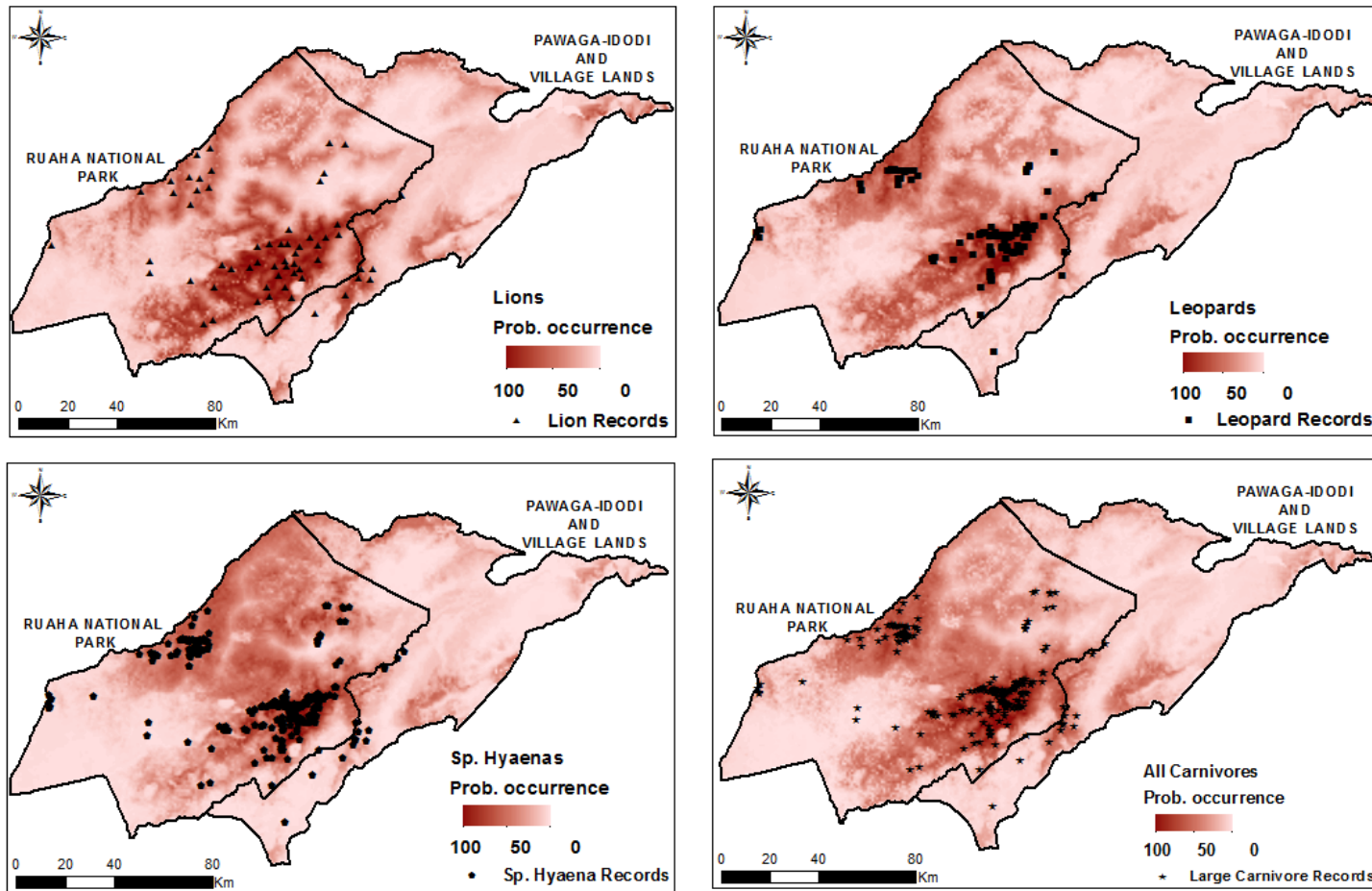


Figure 3. Map of potential distribution of large carnivores across Tanzania’s Ruaha landscape. The maps were generated using ensemble modelling approach based on the outputs of Maxent, ENFA and SVMs.

Table 5. Total estimated habitat suitability area/species according to the ensemble model output. Highly suitable grid cells with increased probability of species occurrence were defined as those with values above the species median suitability and probability of occurrence (h.s. > median). Total area study site: 21,050km².

Species (h.s. > median)	Suitable Area km² (% of Study Site)
<i>Grouped (h.s.> 67)</i>	442 (2.1)
<i>Leopards (h.s > 63)</i>	510.1 (2.4)
<i>Lions (h. s.>67)</i>	1, 010.4 (4.8)
<i>Spotted hyaenas (h.s.>76)</i>	181.7 (0.8)

3.3.6. Distribution of highly suitable patches

The sum of the grid cells identified as highly suitable for each species depicted that, in total, 1,702km² (8% of the study area) emerged as highly suitable for the occurrence of at least one of the carnivore species. Of this area, 95.4% (1,624km²) was located within 30km of the border between the Park and village land (Figure 4), which accounts for approximately 27.1% (5,717km²) of the overall study area (21,050km²). According to the results of the linear model, the distribution of highly suitable cells varied significantly according to each large carnivore species, with areas of high suitability for spotted hyaenas occurring closer to the park boundaries than for lions and leopards (p<0.001) (Figure 4). The proximity of highly suitable grid cells to village land is a cause for conservation concern as it suggests that large carnivores in Ruaha, especially lions and spotted hyaenas, are likely to occur in areas located close to human-dominated land. This increases both the risk of HCC and the likelihood that retaliatory killing will also impact carnivores within the Park. The results also suggested that highly suitable

habitats for leopards were patchier and more widely distributed across the study area than those for lions and spotted hyaenas (Figure 4).

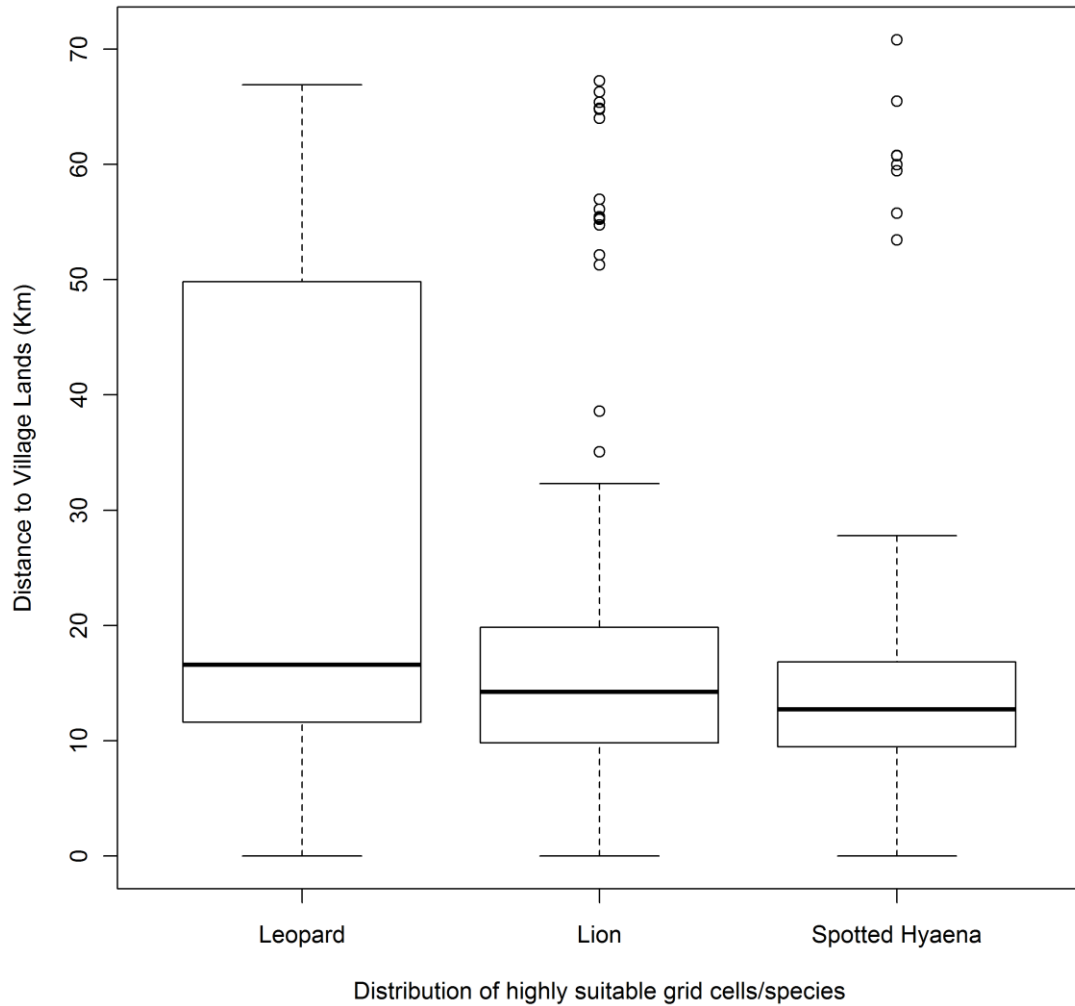


Figure 4. Distribution of grid cells deemed highly suitable for large carnivores in relation to proximity to village land.

3.4. Discussion

Species distribution modelling proved effective at using the opportunistically-collected data from Ruaha to provide the first data on carnivore habitat preferences and likely distributions across the wider landscape. This modelling showed that lions, leopards and spotted hyaenas all showed intermediate to high levels of specialisation, relatively narrow niche breadth and low ecological tolerance for large deviations from optimal environmental conditions available. Interestingly, the lion was the most tolerant species to changes in the environmental conditions composing the species habitat, and showed greater niche breadth than the other carnivores, followed by leopard and spotted hyaena. The most common features influencing the probability of occurrence of large carnivores in the Ruaha landscape were proximity to water bodies and positive index of annual precipitation for all the species assessed, corroborating previous studies which related habitat suitability of lions (Valeix et al., 2009; Valeix et al., 2010), leopards (Balme et al., 2013) and spotted hyaenas (Kolowski & Holekamp, 2009) to areas of increased proximity to rivers and water bodies.

3.4.1. Leopards

Increased habitat suitability for leopards has been related to proximity to water sources (Simcharoen et al., 2008; Steyn & Funston, 2009), areas covered by thick bushes and forest types (Hayward et al., 2006; Pitman et al., 2012), and with positive NDVI (Gavashelishvili & Lukarevskiy, 2008). This study corroborates the importance of water availability in terms of habitat suitability for leopards, though in the Ruaha landscape the species avoided areas of increased net productivity, instead favouring habitat types with less vegetation cover. This pattern was also reported in Phinda Reserve, South Africa (Balme et al., 2007), with leopards favouring habitats of open-to-

intermediate vegetation cover. These habitat types provide enough cover for hunting without interfering with prey detection, increasing hunting success (Balme et al., 2007). Even though elevation has been suggested as a factor influencing habitat selection by leopards (Pitman et al., 2012), enabling them to avoid competition with lions, our results suggest an overlap between all three large carnivores, as lions and spotted hyaenas also favoured lower altitudes. This pattern is potentially related to the increased distribution of wild prey around perennial water sources in lower elevation ranges. The influence of rainfall in habitat suitability supports previous studies which linked high precipitation to increased vegetation cover (i.e. grazing fields) and biomass of key leopard prey (Marker & Dickman, 2005; Balme et al., 2007), resulting in high hunting success, cub survival rates and reproductive success (Balme et al., 2013).

3.4.2. Lions

Lion potential distribution was largely influenced by proximity to rivers, which, as with leopards, is likely linked to the increased presence of water-dependent prey species in the surroundings of water bodies (Hayward & Kerley, 2005; Hayward & Kerley, 2008), as reported in Hwange National Park in Zimbabwe (Valeix et al., 2009) and Serengeti National Park in Tanzania (Hopcraft et al., 2005). Increased habitat quality for lions is known to be determined by proximity to water sources and seasonal rainfall (Mosser et al., 2009), as these areas harbour higher availability of wild prey which increases lion hunting success, reproductive success and cub survival, characterizing these sites as population sources (Mosser et al., 2009). The results of this study corroborate those from Davidson *et al.* (2013) which described surface water as a passive trap for prey, strongly influencing lion distribution. The influence of positive rainfall on habitat suitability is unsurprising as precipitation increases net primary productivity and water

availability, affecting the distribution and availability of ungulates (Ogutu et al., 2008) and therefore lions (Valeix et al., 2012; Davidson et al., 2013).

3.4.3. *Spotted hyaenas*

Hyaenas are commonly portrayed as highly adaptable, showing relatively high plasticity to habitat disturbances (Boydston et al., 2003; Yirga et al., 2013). However, our findings suggest that hyaenas selected for particular habitat types, showed intermediate levels of ecological flexibility, and, even though the species does not require extreme niche conditions, it had relatively low tolerance for large deviations from its optimal environmental conditions.

As for lions and leopards, the preference of spotted hyaenas for areas close to water is probably due to higher prey availability and preferential denning sites in those locations (Kolowski & Holekamp, 2009). The avoidance of highly productive areas found in the present study was also observed in spotted hyaenas from Kenya's Maasai Mara Game Reserve, Kenya, where they preferred shrublands and areas of intermediate vegetation cover over forest (Kolowski & Holekamp, 2009). The preference for habitats exposed to intermediate precipitation rates instead of extreme rainfall is corroborated by previous studies, which found the species absent from areas such as deserts or pluvial forests (Varela et al., 2009). Rainfall can significantly affect habitat suitability and population trends, as it influences hyaenas' feeding behaviour, demography, recruitment and intensity of conflict with humans. Cooper *et al.* (1999) observed that oscillation in rainfall affected prey availability and led to immediate changes in hyaenas feeding behaviour, especially due to interference in the dynamics of ungulates migration. High precipitation was also related to low recruitment, due to increased

juvenile mortality and high human-carnivore conflict induced by fluctuations in prey availability (Watts & Holekamp, 2009).

3.4.4. Distribution of highly suitable habitat patches

The small portion of the study site classed as highly suitable habitat for the large carnivore species is probably due to the high median values used as thresholds for selection of highly suitable habitats. Even though generating a more conservative distribution, threshold decisions based on predicted probability/suitability, as the median suitability adopted in this study, can provide more reliable cut-off point to determine habitat suitability than arbitrary selection of 50% of probability of occurrence (Liu et al., 2005; Rodríguez-Soto et al., 2011; but see Liu et al., 2013), as the later surmises a biased normalized distribution of habitat suitability scores (Liu et al., 2005).

3.4.5. Influence of human disturbance on species distribution

The low influence of human density on carnivore habitat suitability in this study must be regarded with caution since it might reflect sampling bias in data collection. The majority (95.6%) of carnivore location points used for modelling were collected within the National Park, with few collected in areas of high human density. This lack of representation of carnivore presence points from village lands could prevent the model from accurately assessing the influence of human disturbance on habitat suitability for each species. Therefore, further sampling of carnivore presence in village lands would produce a better assessment of the influence of human disturbance on large carnivore habitat suitability in this area.

3.5. Conclusions

According to the present study, the habitat suitability and distribution of leopards, lions and spotted hyaenas in the Ruaha landscape were strongly influenced by proximity to rivers and positive index of annual precipitation. All the species assessed showed relatively narrow niche breadth and low tolerance to changes in the environmental conditions composing their habitat. Highly suitable habitats were limited in distribution regarding the overall size of the study site, but this result might reflect the use of the median suitability as threshold. It is therefore suggested that for future studies, other threshold choices should be compared and tested to assess the distribution patterns of high suitability for species occurrence. This study shows that predictive algorithms using opportunistically-collected presence-only points can provide valuable landscape-level insights into carnivore spatial ecology and species distribution and identify potential areas of increased risk of HCC. This ensemble modelling approach could therefore be a valuable tool in other priority areas which lack systematic presence-absence data on carnivores, but where maps of likely carnivore distribution and habitat use would help inform much needed carnivore management and conservation strategies.

Chapter 4



**Assessing the relative importance of landscape and husbandry
factors in livestock predation risk by large carnivores in
Tanzania's Ruaha landscape**

Abstract

Tanzania's Ruaha landscape is a top-priority area for large carnivore conservation, harbouring significant populations of lions, leopards, and spotted hyaenas, but these large carnivore populations are threatened by intense conflict with local people, mainly due to livestock depredation. The intense human-carnivore conflict (HCC) reported in the village land around Ruaha National Park (RNP), southern Tanzania, has contributed to severe retaliatory carnivore killing, with at least 27 large carnivores killed in just 3 of the 21 villages surrounding RNP within 18 months. Further understanding of the potential relationship between ecogeographical variables (EGVs) and husbandry practices in terms of predation risk is required to best target future conflict mitigation strategies, and therefore reduce depredation and carnivore killing. This study intended to (1) assess which, if any, EGVs are associated with depredation risk for grazing livestock on village land around RNP, whilst generating a predictive map of predation risk by large carnivores, based on species distribution modelling algorithms (SDMs); and (2) investigate the relative influence of husbandry practices and EGVs on depredation risk of enclosed stock to large carnivores, based on a generalized linear model. While grazing, livestock predation risk was higher in areas which were close to rivers, and had lower elevation and lower vegetation cover, and approximately 41% of the study area was mapped as high-risk. The GLM results did not find discernible influence of current husbandry practices on predation risk, which suggests that traditional husbandry adopted in bomas were insufficient to outweigh the innate risks of some areas of the landscape for carnivore predation. Therefore, using new husbandry methods, such as specialised breeds of guarding dogs and reinforcing bomas with chainlink fencing, could be valuable for reducing depredation, human-carnivore conflict and the killing of carnivores in the Ruaha landscape.

4.1. Introduction

Wilderness is being lost or degraded by conversion to agriculture, livestock-keeping, human settlements and industry (Goodland, 1997; Turner et al., 2007). Consequently, people and carnivores increasingly impinge upon each other (Lindell et al., 2005; Woodroffe et al., 2005b; Schuette et al., 2013), provoking widespread and often intense human-carnivore conflict (HCC) (Inskip & Zimmermann, 2009; Nyhus & Tilson, 2010). One of the key drivers of this conflict is depredation of livestock by large predators such as lions, leopards and spotted hyaenas (Ogutu et al., 2005; Kissui, 2008; Gusset et al., 2009; Loveridge et al., 2010a). Such depredation can impose severe economic costs and compromise the economic security of entire households (Ogada et al., 2003; Gusset et al., 2009). It also reduces local tolerance for carnivore predator presence (Graham et al., 2005a; Gusset et al., 2009), and often leads to pre-emptive or retaliatory carnivore killing (Baker et al., 2008; Hemson et al., 2009). Conflict-related killings have contributed to population declines and local extirpations for cheetahs (Marker et al., 2003b), lions (Patterson et al., 2004; Hemson et al., 2009), spotted hyaenas (Ogada et al., 2003; Kissui, 2008; Yirga & Bauer, 2010) and endangered African wild dogs (Woodroffe et al., 2007b; Kissui, 2008). Once depredation has occurred, negative attitudes and actions towards carnivores persist for a long time (Marker et al., 2003a), so it is far more effective to prevent conflict from occurring than trying to reduce it afterwards. Therefore, understanding which factors are associated with ‘conflict hotspots’ is crucial for targeting pre-emptive conflict mitigation strategies to reduce depredation and retaliatory killing of carnivores.

Various factors affect livestock depredation and therefore conflict risk, such as predator-prey densities (Graham, 2003; Loveridge et al., 2010a), the spatial distribution

of carnivores and livestock (Treves et al., 2004; Kolowski & Holekamp, 2006; Valeix et al., 2012) and the quality of livestock husbandry (Ogada et al., 2003; Ogutu et al., 2005; Woodroffe et al., 2007a). In Northern Tanzania, distance to protected area influenced livestock vulnerability to lion attack, with attacks occurring mainly in properties within three kilometres from the protected area boundary (Holmern et al., 2007), whereas in Kenya, spotted hyaena depredations were associated with increased vegetation cover (Kolowski & Holekamp, 2006). Understanding the ecogeographical factors associated with a depredation risk is very valuable in areas where HCC poses a significant threat to both local communities and large carnivores.

One such area is Tanzania's Ruaha landscape, which has a high level of HCC, mainly due to livestock depredation (Dickman et al., 2014). This compromises the economic security of local villagers, and has led to significant carnivore killing, with at least 27 large carnivores killed in 18 months, in just three of the 21 villages close to Ruaha National Park (RNP) (Dickman, *in prep.*). Previous studies conducted in this area (Dickman et al., 2014) investigated the influence of husbandry on livestock risk to predation, but did not assess the influence of ecogeographical variables (EGVs) such as precipitation and vegetation cover on attack risk. These EGVs have been used in predictive modelling for species distribution (Rosa-Rosa, 2007; Rodriguez, 2010), and can potentially identify areas with increased risk for HCC (Murphy, 2010; Murphy & Macdonald, 2010). However, to date, few studies have actually applied the concepts of species distribution modelling to predicting the distribution of carnivore depredation and estimating depredation risk at a landscape level (Zarco-González et al., 2012; Zarco-González et al., 2013).

Here, two distinct but complementary approaches are used to further understanding of the dynamics of large carnivore depredation in the Ruaha landscape. Firstly, ensemble modelling, based on species distribution modelling algorithms (SDMs) such as Maxent, Ecological Niche Factor Analysis (ENFA) and support vector machines (SVMs), is used to examine how well depredation risk in the bush around RNP can be predicted from EGVs. The null hypothesis will be that the EGVs considered here, based on those identified as the most influential to carnivore distribution in the study site (Abade et al., 2014), have no significant predictive value for bush depredation risk, with such events occurring randomly. The models will enable the generation of the first depredation risk map for the Ruaha landscape, which can be used to inform the targeting of conflict mitigation approaches.

One common conflict mitigation approach is improving livestock husbandry, as many studies have focused upon the importance of husbandry practices such as the presence of guarding dogs (Marker et al., 2005) and herders (Woodroffe et al., 2007a), the use of livestock enclosures at night (Ogada et al., 2003; Gusset et al., 2009), and the characteristics of those enclosures (Ogada et al., 2003; Patterson et al., 2004; Woodroffe et al., 2007a). However, few studies have examined the relative importance of husbandry practices compared to the inherent geographic risk associated with local landscape features such as thick vegetation cover and topography (Kissling et al., 2009). In the second part of the analysis performed in this study, data on the location, husbandry quality and depredation history of livestock enclosures (bomas) was combined into a generalized linear model (GLM) to determine whether the reported traditional livestock husbandry methods used played a more important role in alleviating depredation risk than EGVs, with the null hypothesis that husbandry practices would have no significant influence. This analysis was not possible on the

bush dataset as the GLM requires a binomial response (i.e. attack or non-attack), which was only available for livestock enclosures. The results of this study will be important in making recommendations for future conflict mitigation approaches around Ruaha. If livestock husbandry variables prove significant, then this would suggest that villagers can keep their stock even in risky areas as long as they implement certain practices, whereas if they do not, then the recommendations would focus upon avoiding risky areas regardless of husbandry. Furthermore, this approach could have widespread applicability for testing the efficacy of local husbandry practices and guiding conflict mitigation strategies in the many other areas where HCC poses a significant threat to both communities and large carnivores.

4.2. Methods

4.2.1. Study area

The study area was the village land surrounding Ruaha National Park, and more information about the characteristics of the landscape is provided in Chapter 2.

4.2.2. Social aspects and livestock husbandry practices

Further information on human aspects of the landscape, as well as the characterization of livestock husbandry and large carnivore attack patterns on livestock is provided in Chapter 2.

4.2.3. Depredation data

Georeferenced points of carnivore attacks on livestock were determined from monthly records of household stock loss, which were collected from 2010 to 2012 on village

lands surrounding RNP. The predation data was divided in two distinct groups, for large carnivore attacks in the boma and for attacks in the bush. The data on ‘boma depredation events’ comprised 129 presence and 139 absence points of predation events which occurred while livestock was enclosed in bomas, while the ‘bush depredation events’ comprised 53 presence-only points for attacks while the livestock was ranging freely in the landscape. The veracity of the depredation event was confirmed by trained members of WildCRU’s RCP staff after visiting the location and interviewing the livestock owner reporting the loss. In most of the cases, identification of the specific large carnivore species responsible was not possible since most of the losses were reported more than 24 hours after the actual killing, and the carcass was already eaten by scavengers or had disappeared. Therefore, this analysis is based upon the reported species seen or tracked by the livestock owner. Only attacks attributed to lions, leopards or spotted hyaenas were included in the dataset as these were the most common predators associated with local depredation. However, the lack of individual species identification meant that no discrimination was made between the species involved in the predation events – they were collectively viewed as large carnivore depredation events.

4.2.4. Ecogeographical variables

The explanatory spatial variables used on the predictive models were selected based on their potential influence on the distribution of large carnivores across the Ruaha landscape (Abade et al., 2014), and were divided among landscape, bioclimatic and human disturbance features (Table 6). Information on elevation and slope were extracted from the Shuttle Radar Topographic Mission (USGS, 2000). The information on distance to rivers was generated using the Euclidean Distance function in ArcGIS v.

10.1 (Esri, 2012) based on the presence of water bodies in the study site. A Normalized Difference Vegetation Index (NDVI) image, derived from a compilation and processing of NDVI rasters from Terra (EOS AM) satellite images generated between March 2011 and December 2012, was considered as a proxy for wild prey availability. In addition, a vegetation continuous field (VCF) image was used to assess influence of percentage of tree cover in vulnerability to attack (See further explanation about NDVI and VCF in Chapter 3).

EGVs were converted in a 1km x 1km habitat-grid cells raster file according to their original resolution size (Table 6). The spatial data preparation and raster analyses were implemented in ArcGIS v. 10.1 (Esri, 2012) and IDRISI Selva (Eastman, 2012).

Table 6. Ecogeographical variables considered to potentially influence livestock risk to predation in SDMs.

Attack Class	Ecogeographical variables*
	Annual Precipitation
<i>Bush</i>	Elevation
<i>depredation</i>	Slope
<i>events</i>	Dist. River
	NDVI
	VCF

*Information on the original source of each variable can be found in the previous chapter (Chapter 3, Section 3.2.3).

4.2.5. Bush depredation events - Predictive modelling algorithms

Predictive modelling was used to analyze the attacks occurring in the bush, as this technique copes well with presence-only datasets. Predictive modelling works by comparing the EGVs from a presence record with those found across the landscape, and by using predictive algorithms and mathematical processes (Guisan & Zimmermann, 2000) to produce an output model, which identifies potential areas with increased likelihood for occurrence based on their similarities to the original training record. Before running the SDMs, the presence-only bush attack dataset was divided into training and testing data (70%; 30% of attack points respectively) to allow *post hoc* model validation (Marino et al., 2011). This predictive model considered the whole extension of the village land around RNP, and no mask was used for limiting the potential distribution of attacks around known areas used for grazing (non-masked model). An additional model using a 4km buffer distance around the households located within village land (masked model), which was calculated based on the average distance walked by herds on the study area, was used to delimit the potential area available for livestock grazing and therefore those likely areas for carnivore attacks on the free-grazing livestock. The outputs derived from ENFA, SVMs and Maxent were used to build the final ensemble models (Araújo & New, 2007; Marmion et al., 2009) to predict the distribution of bush depredation (detailed information on the ensemble modelling approach is provided on the previous chapter). In predictive modelling for species distribution, the output of the ensemble model is a probability map of occurrence with scores ranging from 0 to 100, with higher scores indicating increased probability of occurrence. In the present study, the probability of occurrence output can be understood as a map of predation risk (Zarco-González et al., 2013), with high scores indicating higher risk of a carnivore attack in the bush in that location. To

facilitate the interpretation of the final map outputs for the non-masked and masked models, the ‘high-risk’ areas were defined as those habitat-grid cells in which the probability value calculated by the ensemble model exceeded the lowest probability value found among the attack points used for training the models (Zarco-González, *pers. comm.*).

ENFA was conducted using Biomapper v. 4.0.7.373, Maxent using Maxent v. 3.3.3e and SVM using openModeller Desktop v. 1.1.0. Additional information on the aspects of each algorithm used and on the ensemble modelling technique is provided in the previous chapter (Chapter 3, Section 3.2.4).

4.2.6. Boma depredation events - Generalized linear model

In order to identify the most important predictors influencing depredation risk for livestock enclosed within bomas, information on husbandry practices and EGVs related to the presence and absence record of each boma predation event was extracted, and then used to generate the GLM. The quality of boma husbandry practice adopted by each household was calculated based upon the following metrics: height and width of the boma walls, number of entrances, visibility of the enclosed stock, positioning of the thornbush stems (if they face out they facilitate carnivore access to the boma). The presence of guarding dogs, number of livestock owned, and the density of people in each household was also considered as potential predictors. The *a priori* expectation was that good quality bomas would show higher and wider boma walls, fewer entrances, lower visibility, stems facing inwards, as well as more livestock, dogs and people in the household. For the GLM, two distinct approaches were considered: the first approach used the standardized scores (Z score) of each boma characteristic, in

addition to the associated EGV values as the predictors for boma predation risk; the second approach used the contribution scores of the first three axes of a principal component analysis (PCA), which was implemented using the values of each boma characteristic and associated EGVs, as the main predictors for predation risk. The set of potential husbandry variables influencing the vulnerability to boma predation and the EGVS considered in the GLM is summarized below (Table 7). All the statistical analyzes were performed in R v. 2.15.1.

Table 7. Husbandry and ecogeographical variables considered in the generalized linear model (GLM) for livestock risk to predation.

Attack Class	Husbandry Variables	Ecogeographical variables*
<i>Boma depredation events</i>	Height of boma wall	
	Width of boma wall	Annual Precipitation
	Number of entrances	Elevation
	Presence of stems out	Slope
	Visibility of stock	Dist. River
	Number of livestock	NDVI
	Number of guarding dogs	VCF
	Density of people in the household	

*Information on the original source of each variable can be found in the previous chapter (Chapter 3, Section 3.2.3).

4.3. Results

4.3.1. Bush depredation events - Predictive modeling

In general, all the algorithms used in the non-masked model exhibited good performance in predicting the potential distribution of bush depredation incidents

around RNP based upon EGVs, with AUC values exceeding 0.7 (Table 8). The ensemble model performed better than any other predictive algorithm, although it was closely followed by Maxent (Table 8).

The predictive modelling outputs led to the rejection of the null hypothesis, suggesting that EGVs did exert an influence on the patterns of large carnivore depredation, and identified areas closer to rivers, with lower slope and vegetation cover as those with increased predation risk for grazing livestock. The ENFA and Maxent algorithms results concurred in suggesting that proximity to rivers was the main feature contributing to the risk of a bush depredation event (Table 9). The ENFA results also suggested that low slope slightly influenced depredation risk, whereas Maxent showed that areas with a low percentage of tree cover were associated with increased risk (Table 9). Proximity to rivers was also identified as the most important EGV influencing habitat suitability for large carnivores according to ENFA in the previous chapter, which suggests that risk factor for predations in the bush is likely related to those areas with greater suitability for large carnivores.

According to the ensemble non-masked model, approximately 41% (2,835 km²) of the village land examined around RNP was defined as ‘high-risk’ for livestock grazing (Figure 5). The ensemble masked model identified 59% (565 km²; 8% of the village land) of the area calculated to encompass the known grazing fields in the village land (944 km²; 13% of the village land) as high-risk.

The predictive algorithms for the masked model showed a low performance when compared to the non-masked model, and only Maxent generated AUC values exceeding 0.7 (Table 8). No ensemble modelling was calculated due to the low performances of ENFA and SVM algorithms (Table 8). The Maxent output was used to

generate the final map for livestock risk to predation. Maxent identified proximity to rivers as the most important factor associated with high predation risk for grazing livestock, contributing to 45.6% of predation risk (Table 9).

Table 8. Performance of algorithms used to predict the distribution of large carnivore predation on livestock around Ruaha National Park. Significant models showing AUC > 0.7.

Attack Class	Algorithm	Training AUC	Testing AUC
<i>Bush depredation events non-masked model</i>	ENFA	0.831	0.858
	Maxent	0.894	0.854
	SVM	0.889	0.846
	Ensemble	0.908	0.885
<i>Bush depredation events masked model</i>	ENFA	0.610	0.528
	Maxent	0.759	0.722
	SVM	0.623	0.596

MAP OF LIVESTOCK PREDATION RISK BY LARGE CARNIVORES AROUND RUAHA NATIONAL PARK, TANZANIA

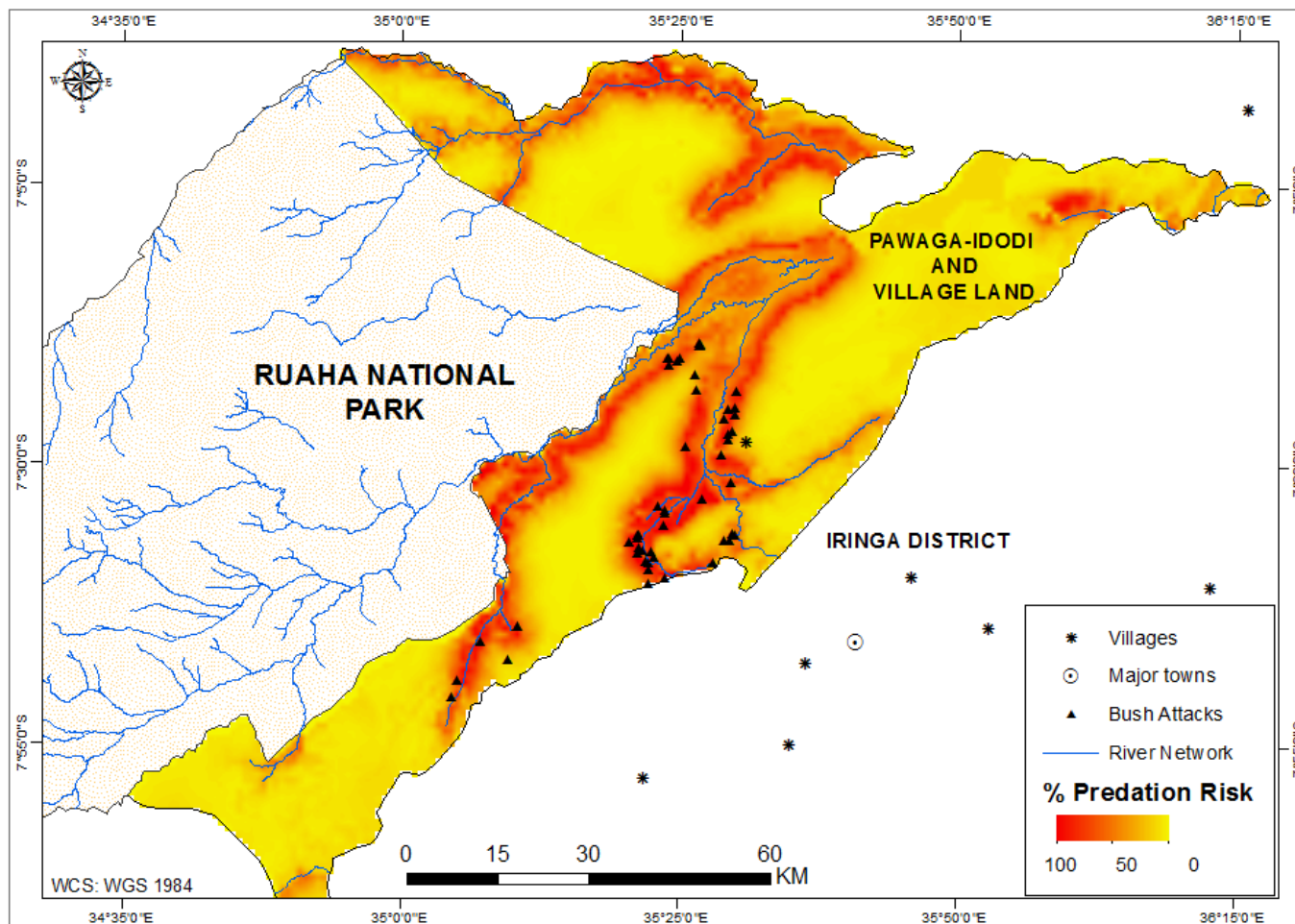


Figure 5. Non-masked predictive map of livestock predation risk by large carnivores on village land surrounding Ruaha National Park, southern Tanzania. The colour gradient indicates probability of predation risk, with warmer areas representing the areas in which attacks are most likely to occur.

MAP OF LIVESTOCK PREDATION RISK BY LARGE CARNIVORES AROUND RUAHA NATIONAL PARK, TANZANIA

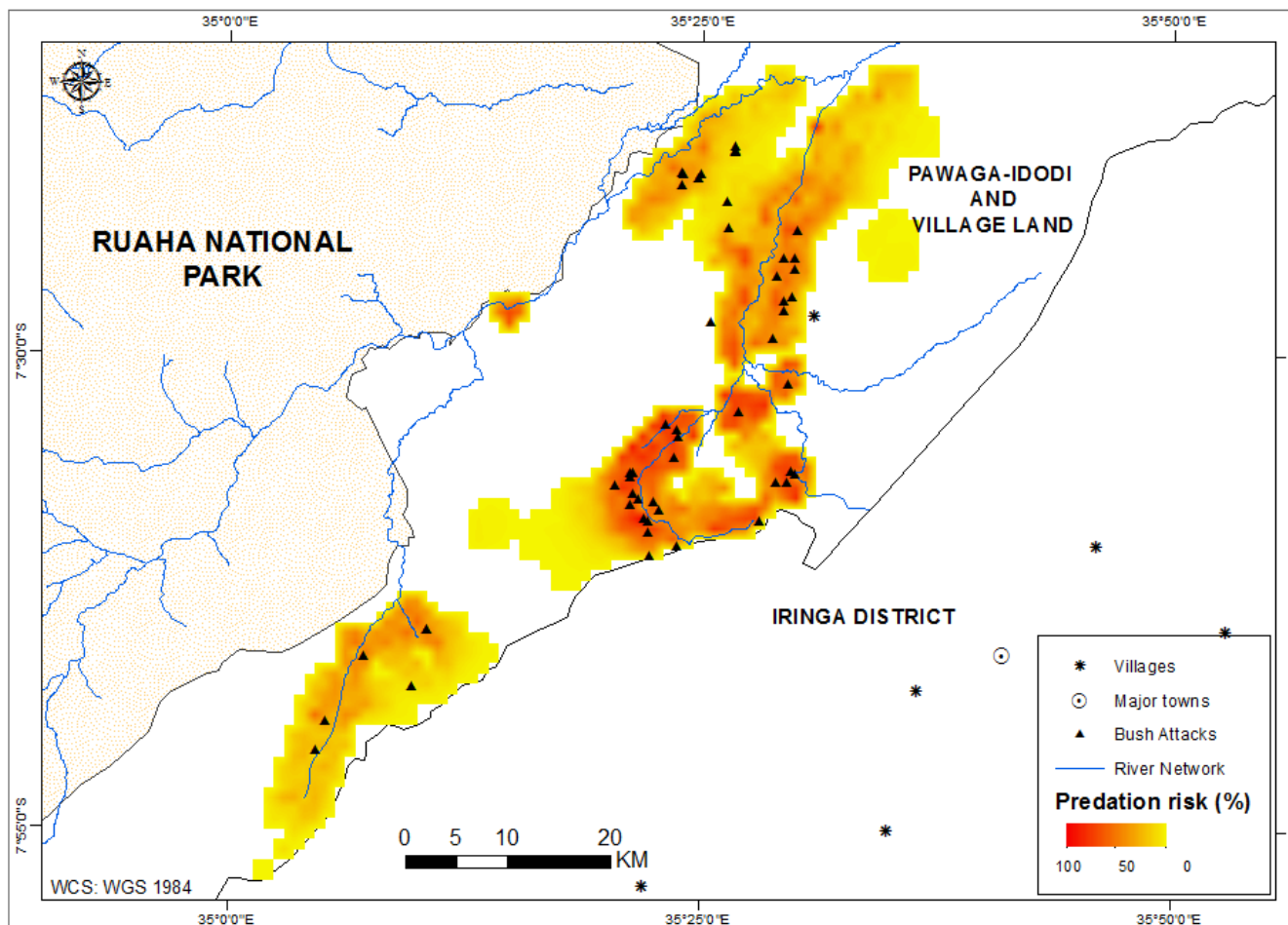


Figure 6. Masked predictive map of livestock predation risk by large carnivores on village land surrounding Ruaha National Park, southern Tanzania. The colour gradient indicates probability of predation risk, with warmer areas representing the areas in which attacks are most likely to occur.

Table 9. Estimated marginality and specialisation according to ecogeographical variables by Ecological Niche Factor Analysis (ENFA) and % variables contribution to livestock predation risk according to Maxent. Negative signs indicate preference towards lower values of a particular EGV (Hirzel et al., 2002). *Indicates values above the mid-threshold (i.e. 0.5) – more information on threshold selection is provided in the previous chapter.

Attack Class	Variables	ENFA		Maxent
		Marginality	Specialisation	(%) Contribution
<i>Bush depredation events – non-masked model</i>	Dist. River	-0.88*	-0.22	54.8*
	Slope	-0.31	-0.02	5.1
	Altitude	-0.27	0.14	1.9
	VCF	-0.24	0.97	15.4
	Annual Precipitation	-0.04	0.01	9
	NDVI	0.01	0	13.7
<i>Bush depredation event – masked model</i>	Dist. River	-	-	45.6
	Slope	-	-	7.7
	Altitude	-	-	7.7
	VCF	-	-	5
	Annual Precipitation	-	-	16.8
	NDVI	-	-	17.2

4.3.2. Boma depredation events - Generalized linear model

The GLM results for boma depredation based on the standardized scores of boma characteristics and EGVs suggested that neither landscape features nor the husbandry practices adopted by livestock owners in the study site significantly influenced predation risk ($p > 0.05$) (Table 10), corroborating the null hypothesis. Boma height showed a slight influence on boma predation risk, which was just at the level of statistical significance ($p = 0.05$), with taller bomas less susceptible to predation. For the second approach, the PCA failed to summarise a useful quantity of variability in the predictors of boma risk to predation, and no significance was found in the GLM ($p >$

0.05). The lack of influence of husbandry quality and EGVs in boma predation, suggests that in this landscape, attacks of large carnivores on bomas are likely occurring randomly, and that traditional husbandry is not sufficient to alleviate the predation risk posed by the presence of large carnivores.

Table 10. Level of significance of each predictor used in the in the generalized linear model (GLM) for boma vulnerability to predation (*p*-significance < 0.05); *z* = z-score).

Predictors	<i>p</i> value
(z) Boma height	0.059
(z) Boma width	0.217
(z) No. entrances	0.735
(z) Stems-out	0.976
(z) Visibility of stock	0.329
(z) No. livestock	0.945
(z) No. dogs	0.256
(z) Density people	0.622
Annual precipitation	0.360
Elevation	0.358
Slope	0.565
Dist. River	0.625
NDVI	0.905
VCF	0.120

4.4. Discussion

This study suggests that the combined use of SDMs and GLM enables an in-depth understanding of risk factors associated with large carnivore predation events, whilst the predictive modelling enabled high-risk areas for livestock grazing to be mapped out.

4.4.1. Bush depredation events - Predictive modelling

The SDMs suggested that proximity to rivers was the main factor influencing bush depredation risk, with low slope and low percentage of tree cover showing some contribution to predation risk. The increased predation risk closer to river network is associated to the findings of the previous chapter (Chapter 3), which identified areas closer to rivers as highly-suitable for large carnivores in the study site, suggesting that, as would be expected, the likely suitability of an area for large carnivores could make it as high risk area for livestock grazing. Areas surrounding water sources tend to concentrate assemblages of natural prey, making them attractive to large carnivores given the availability of food supply (de Boer et al., 2010; Valeix et al., 2012). In areas where water availability is the main landscape feature influencing distribution of prey and carnivores, as it seems the case in Ruaha – at least for large carnivores (Abade et al., 2014), lions favoured hunting and preying mostly within 2km of water sources (Davidson et al., 2013), which would explain the increased predation risk around rivers. Moreover, in the Ruaha area, herders tend to rely on natural water sources for grazing their livestock, and these areas are often shared with large carnivores, which increases livestock risk. The concurrence of these results reinforce that, in Ruaha, availability of water sources is likely the most important force driving habitat use and spatial distribution of large carnivores, whilst contributing to predation risk of grazing livestock herds.

Even though the current results differed from others reported in other parts of Africa in suggesting little influence of vegetation cover on predation risk, it is recommended that herders around Ruaha should still attentively guard stock while in proximity to dense vegetation, as it provides coverage for large carnivores to stalk and ambush livestock (Thorn et al., 2012; Thorn et al., 2013).

It is important to highlight that the SDMs for predation risk used similar predictors as those incorporated in the models assessing large carnivore distribution in the previous chapter, therefore, the identification of equivalent EGVs influencing carnivore habitat suitability and predation risk might simply reflect large carnivore distribution pattern. However, if compared to the map of carnivore distribution, the predictive map of predation risk identified high risk areas which were not necessarily depicted as highly suitable for large carnivores, suggesting that livestock grazing can also be risky even in areas which are less favoured by large carnivores. Therefore, predictive maps of large carnivore presence *per se* are likely to be insufficient for identifying high risk areas for attacks, and it is recommended that predictive modelling based on predation events should be used to help identify areas with increased high risk of HCC.

Given the relatively high risk of grazing livestock around Ruaha, the combined use of predator-deterrent strategies such as trained guarding shepherd dogs, and cheap devices such as livestock bells and noise-makers (Shivik & Martin, 2000), in addition to intensive surveillance and attentiveness by the herders, could substantially help to protect the stock and decrease predations in the bush. Whenever possible, livestock grazing should be avoided in those areas identified as a high-risk, especially close to water bodies.

4.4.2. *Boma depredation events - Generalized linear model*

The GLM results showed that overall, neither ecogeographical features nor traditional husbandry practices or boma characteristics played an important role in alleviating boma predation risk, with only boma height slightly contributing to decrease predation risk. Regarding boma characteristics, our results corroborate those presented by Ikanda & Parker (Ikanda & Packer, 2008), which did not find any relation between boma visibility, wall thickness, presence of dogs, and number of livestock on boma vulnerability to predation by lions. However, the previous study solely focused on predations performed by lion, whilst the present study also incorporated predations events by hyaenas and leopards. Conversely, the results of this study differ from others performed across in Africa, which found positive correlation between presence of dogs (Woodroffe et al., 2007a), boma quality and intense human activity in the areas surrounding the boma (Ogada et al., 2003), and low vulnerability to predation by carnivores. These previous studies classified depredation events according to the carnivore species performing the attack, which was not possible in the present study, and this could explain such disparity in results. Different species adopt different hunting strategies; for instance, hyaenas and lions are more likely to break through the boma walls, whilst leopards tend to jump over the fences for attacking the stock (Kissui, 2008), and the presence of dogs might decrease lion predation on small stock (Ogada et al., 2003), therefore classifying attacks by species could help further understanding of the role of particular boma characteristics on deterring carnivore predation according to species. The fact that husbandry practices did not significantly influence boma predation risk raises questions about how effective traditional boma husbandry practices are at deterring predation in risky landscapes. Even the ‘good’ practices here are only good relative to a low average standard (Dickman, *pers.obs.*), as bomas are often weakly constructed, the guarding dogs are small, underfed and sickly, and the herders

are inattentive to the stock even when they are present. Therefore, the local relatively ‘good’ husbandry techniques reportedly implemented still appear insufficient to substantially decrease the inherent risk of predation in the landscape. Thus, for bomas located in a high-risk area, the adoption of new and improved husbandry strategies, such as the use of specialised breeds of livestock guarding dogs, reinforced wired bomas, and incentive schemes to improve herder attentiveness, should be considered to prevent further livestock losses to carnivores. In Namibian farmlands, for example, almost 70% of farmers that adopted specialised Anatolian shepherd guarding dogs to protect domestic stock reported a complete cessation in livestock loss by large carnivores (Marker et al., 2005). Similarly, reinforcing traditional bomas with poles and chain-link fencing has been shown to completely prevent boma depredation events in study households around Ruaha (Dickman, *in prep*). Even though the adoption of such strategies may impose extra expenditures to livestock-keepers, their long-term efficacy it is a worthwhile investment for avoiding further costly depredation events, and should therefore be considered for long-term conflict mitigation.

It is noteworthy that other factors different from those assessed by the study could be influencing carnivore predation in bomas, therefore further studies should consider assessing the potential influence of other variables such as carnivore density and wild prey availability on predation risk, as this has been linked to increased rates of carnivore predation on livestock (Graham et al., 2005b).

4.5. Conclusions

The present study showed that a combination of SDMs and GLM is a good approach to further understanding of the dynamics of large carnivore predation on livestock, as they enabled investigating the contributory role of husbandry and landscape features on predation risk, and mapping areas of increased risk for livestock grazing around RNP. The study findings suggest that traditional husbandry practices adopted in bomas are insufficient to outweigh the innate risks of some areas of the landscape. Therefore, new livestock protection methods, such as the use of specialised breeds of guarding dogs and reinforcement of existing bomas with poles and wires, should be considered in order to help reduce depredation and conflict. Given the high proportion of the study area identified as high-risk for livestock grazing based on the non-masked model output, especially in areas closer to rivers, extra anti-predator methods such as specialised guarding shepherd dogs, noise makers, and increased surveillance should be considered in order to lessen depredation risk. The predictive modelling is suggested as a reliable tool to map areas of increased predation risk, and could be easily adopted by future studies investigating the dynamics of carnivore predation on livestock in other areas. This will enable pre-emptive identification of likely ‘conflict hotspots’ with high risk of depredation, where mitigation strategies should be targeted in order to reduce livestock losses and retaliatory killing of large carnivores.

Chapter 5



RCP Archive

General Discussion

5.1. Synthesis

Environmental and bioclimatic factors significantly influence large carnivores distribution and habitat use (Carroll, 2007; Valeix et al., 2010), with direct implications for likely locations of human-carnivore conflict (Zarco-González et al., 2013). Therefore, improving knowledge about the most important ecogeographical variables and their role on carnivore distribution is key to better understanding large carnivore ecology, and, most importantly, to help inform action plans and the development of contextualized conservation strategies for carnivore conservation (Rodríguez-Soto et al., 2011). The present study aimed to increase the understanding of the contributory role of ecogeographical variables on the distribution of lions, leopards and spotted hyaenas in the Ruaha landscape, and to further the understanding of the relative influence of environmental features and husbandry practices in the dynamics of carnivore attack on livestock on village land around Ruaha National Park. Chapter 3 aimed to identify the main environmental features associated with habitat suitability for lions, leopards and spotted hyaenas across the Ruaha landscape, using ensemble modelling, which was based on the results of predictive modelling generated by Maxent, ENFA and SVMs algorithms. Highly suitable areas for species occurrence were mapped across the Ruaha landscape, a critical area for large carnivore conservation in southern Tanzania, providing the first information about carnivore spatial ecology in this very important but understudied region. Chapter 4 aimed to deepen understanding of the relative contributory role of landscape and husbandry practices to livestock predation risk by lions, leopards and spotted hyaenas in the village land surrounding RNP. The predation risk for livestock in the bush was determined by SDMs based on environmental aspects, whereas for the enclosed livestock, the predation risk was determined assessing the influence of environmental features and

husbandry practices using a GLM. This approach allowed in-depth understanding of the environmental and husbandry practices associated with livestock vulnerability to predation in the study site, in order to help inform future conflict mitigation approaches.

5.1.2 Distribution of large carnivores across Tanzania's Ruaha landscape

In the Ruaha landscape, large carnivore distribution was mainly influenced by proximity to rivers and annual precipitation, with some influence of areas of low primary productivity and vegetation cover. This link between carnivore presence and water availability in this ecosystem is probably because of the increased availability of large ungulates and smaller prey around any water sources (Valeix et al., 2009). Areas of increased suitability for lions, leopards and spotted hyaenas, with increased cub survival and reproductive success, have been attributed to regions proximate to rivers (Mosser et al., 2009; Yirga & Bauer, 2010; Balme et al., 2013), which is corroborated by the current findings. The inferred preference for areas with low vegetational coverage and productivity is potentially related to the hunting strategies adopted by the carnivores in the study area. Low vegetation areas have been related to increased hunting success and prey catchability (Balme et al., 2007), as well as favouring species of grazer-type herbivores (Valeix et al., 2009), which constitute substantial part of the diet of large carnivores (Hayward & Kerley, 2005; Hayward et al., 2006; Hayward & Kerley, 2008).

The use of ensemble modelling approach to predict the distribution of large carnivore species showed good performance and is recommended for studies aiming to study carnivore distribution and which rely on presence-only data, limited sample size, and haphazard data collection. However, the relatively small percentage of the study area identified as highly suitable for the occurrence of large carnivore species requires

careful interpretation. The use of the median as the threshold for habitat suitability influenced the final output, and it is suggested that, depending on the aim of the study, different threshold choices should be considered. In the context of the present study, the objective was to identify core areas with particular ecogeographical variables more suitable for species occurrence, however, if further studies are interested, for example, on identifying new areas harbouring unprotected populations of large carnivores, lower thresholds should be considered, as suggested by Liu *et al.* (Liu et al., 2005; Liu et al., 2013).

The findings of this study provide valuable and much needed information on the spatial ecology of large carnivores in this priority landscape for African carnivore conservation. They provide a baseline for the understanding on how lions, leopards and spotted hyaenas are using the Ruaha landscape, and which are the main ecogeographical characteristics associated with their presence in this area.

5.1.3. Landscape, husbandry techniques, and their relative influence on livestock predation risk

River network was the most important factor influencing predation risk for grazing livestock, corroborating previous findings which described surface water as live traps for large carnivore prey (Davidson et al., 2013). In addition, the increased predation risk in these areas is likely reflecting the increased habitat suitability for large carnivores around rivers. This seemed also true for the influence of low vegetation cover on predation risk, which suggests that, in the study area, predation risk is related to habitat characteristics favouring habitat suitability for large carnivores. However, it is important to note that, even though areas of predation risk were often those deemed highly suitable for carnivores, certain areas identified as less suitable for carnivores still

showed high predation risk. This suggests that predation risk is associated with a particular set of EGVs, which are strongly linked to high habitat suitability for carnivores but not solely determined by that. Given the high proportion of the study area identified as high-risk for livestock grazing, especially in areas closer to rivers, extra anti-predator methods such as specialised guarding shepherd dogs, noise makers, and increased surveillance should be considered in those areas in order to lessen depredation risk

The traditional livestock husbandry reportedly used in the study bomas appeared non-significant to prevent carnivore predation on bomas, which was an important finding for guiding conflict mitigation strategies. These results suggest that rather than relying on existing approaches, livestock husbandry strategies should be improved considerably and new techniques attempted if depredation and human-carnivore conflict is to be significantly reduced in the Ruaha landscape. This study has identified areas of particular risk for depredation where such techniques should be prioritised, which could help guide the targeting of future conflict mitigation efforts.

5.2. Project follow-up and recommendations for future studies

The majority of the carnivore presence points used in this study was obtained from within Ruaha National Park, which limited how well the models could predict carnivore occurrence outside the borders of the Park, particularly in areas such as Game Reserves which were not sampled in this study. Reserve-adjacent areas often constitute an important portion of large carnivore home ranges, but also have high rates of conflict and anthropogenic carnivore mortality (Dickman et al., *submitted*), contributing to higher risks of local extirpation (Woodroffe & Ginsberg, 1998; Loveridge et al., 2010a).

These areas are therefore priorities for large carnivore conservation, and it would be valuable to conduct more sampling across the village land, Game Reserves and other Wildlife Management Areas around Ruaha in order to better comprehending the overall population dynamics and spatial ecology of large carnivores across the wider Ruaha landscape. This would help provide the first good data on the potential influence of human activities and landscape structure on landscape permeability to carnivore movements across the landscape, their selection of habitat patches for dispersal and colonization, habitat connectivity between populations, and carnivore survival in village lands. Thus, broadening the scope of the research to the overall landscape surrounding RNP, including village land and adjacent game reserves is recommended, and would be fundamental to (i) better understand the population dynamics and spatial ecology of large carnivores in areas exposed to different levels of human disturbance; and (ii) provide data that will underpin the development of targeted carnivore conservation strategies and management plans in human-dominated areas. In a practical approach, this broader focus would help the understanding of landscape structure on movement patterns of large carnivores across village lands, the source-sink dynamics of large carnivore metapopulations in the study area (Chetkiewicz & Boyce, 2009), the animal dispersal patterns (LaRue & Nielsen, 2008), identification of potential corridors of connectivity between protected areas and gene flow among mating areas (Ferrerias, 2001; Rabinowitz & Zeller, 2010), and barriers for carnivores occupation and use of habitat (Singleton et al., 2002). In addition, understanding of the movement patterns of these large carnivores in the village land could provide further information about potential areas with increased risk for HCC, providing further guidance for the development of conflict mitigation strategies (Adriaensen et al., 2003).

This study has provided the first baseline data on the likely distribution of both large carnivores and depredation risk across the Ruaha landscape. These data will be shared with local and national authorities, with the aim of helping inform carnivore conservation strategies and conflict mitigation approaches in the globally important Ruaha landscape.

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