Aspects of the ecology of spotted hyena (*Crocuta crocuta*) in relation to prey availability, land use changes and conflict with humans in western Zimbabwe

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ABSTRACT

Patch selection by carnivores is affected by various factors including availability of prey and denning areas, extent of vegetation cover, competition from sympatric large carnivores and anthropogenic habitat change among other variables. Understanding the influence of such factors is fundamental in the management of the carnivores. The study investigated spotted (i) hyena occupancy and (ii) co-occurrence with mesocarnivores in Zambezi National Park, Matetsi Safari (hunting) Area and Dimbangombe Ranch (mixed livestock and wildlife) in western Zimbabwe during the dry and wet seasons of 2014 and 2015 using camera traps. First, habitat characteristics, potential major prey and possible disturbance factors were modelled using the occupancy modelling approach to quantify habitat occupancy of the spotted hyena. It was found that the spotted hyena mean site occupancy was high ($\psi = 0.617$, SE = 0.147 and $\psi = 0.502$, SE = 0.107 for wet and dry seasons respectively). Furthermore, spotted hyena habitat occupancy increased in clayey soil and grasslands in the national park and hunting area, a behaviour attributed to denning preferences and possibly prey movement. Management priorities should focus on improving habitats for wild prey outside protected areas while preserving clayey areas for enhanced productivity of the spotted hyena inside protected areas. Secondly, it was predicted that mesocarnivores would avoid habitats occupied by the spotted hyena resulting in seasonal variation in temporal overlap between the spotted hyena and mesocarnivores. The study found that the detection probability of the mesocarnivores varied in the presence of the spotted hyena as a function of the detection of the leopard, presence of rocky and mixed vegetation habitats and road network. The high temporal coefficients of overlap for all pairs of species implied high chances of co-detection at the same sites. It was recommended that land management and top predator introductions should consider how optimal use of the habitat by small carnivores is affected. In addition, the study (iii) determined spotted hyena prey selection by comparing differences in frequency of occurrence of prey remains in their scats from a hunting area (117 scats) and a national park (137 scats). Small, medium and large-sized mammalian prey contributed 19.8 %, 41.9 % and 19.8 % to the diet of the spotted hyena in the safari area, compared with 34.3 %, 24.0 % and 35.9 % in the national park, inclusive of domestic stock (10.3 % in the safari area; 12.0 % in the national park). The difference in diet composition of the spotted hyena between the two land-uses was attributed to the ability of the species to shift between prey species in relation to the availability. Furthermore, a questionnaire survey was done (iv) to assess the attitudes and perceptions towards the spotted hyena of people (n = 353 households) in communities living at various distance categories within 0 - 20 km from the protected area boundary. It was found that livelihood source and extent of livestock loss had an influence on perceptions about the spotted hyena. The study recommended development of a modified incentive driven model that will encourage human-wildlife coexistence. Bushmeat harvesting is thought to affect prey distribution for the carnivores and a questionnaire survey was done on 355 households (v) to determine the factors driving bushmeat activities in the area in relation to conservation efforts. Bushmeat availability was highly influenced by scarcity of protein sources and season (dry). The dry season peak in bushmeat availability was attributed to increased demand that coincided with a period of low protein availability in the villages. The hunting zone (distance from protected area boundary) was the most influential predictor of how communities viewed illegal bushmeat harvesting in relation to conservation efforts. Mitigating illegal activities would likely be effective when started in settlements that are inside wildlife zones. Insights on community perceptions towards conservation may help in managing edge effects around PAs.

PREFACE

The data described in this thesis were collected in Hwange District, Republic of Zimbabwe from October 2014 to January 2016 with various chapter objectives being investigated in different months of this period. Fieldwork was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof. C. T. Downs and Dr. T. Ramesh.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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Mlamuleli Mhlanga

December 2017

I certify that the above statement is correct and as the candidate's supervisor, I have approved this thesis for submission.

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Professor Colleen T. Downs

Supervisor

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DECLARATION 1 - PLAGIARISM

I, Mlamuleli Mhlanga, declare that

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3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

Detail of contribution to publications that form part and/or include research presented in this thesis:

Publication 1- in review

Mhlanga M, T Ramesh, R Kalle, TH Madiri & CT Downs. Spotted hyena (*Crocuta crocuta*) habitat use across a conservation land-use gradient in western Zimbabwe.

Author contributions:

MM conceived paper. MM collected data and analysed with TR and RK. MM wrote the paper. TR, RK, HTM, and CTD contributed valuable comments to the manuscript.

Publication 2- in review

M Mhlanga, T Ramesh, R Kalle, T H Madiri & CT Downs. Spotted hyena co-occurrence with mesocarnivores across a wildlife management gradient (Ranch, Hunting Area and National Park) in western Zimbabwe

Author contributions:

MM conceived paper. MM collected and analysed data with TR and RK. MM wrote the paper. TR, THM and CTD contributed valuable comments to the manuscript.

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Author contributions:

MM conceived paper. MM collected and analysed data with TR, RK & EN. MM wrote the paper. TR, RK and CTD contributed valuable comments to the manuscript.

Publication 4- in review

M Mhlanga, F Muranda, T Ramesh, R Kalle & CT Downs. Incentives matter: the influence of settlement type and land-use on public attitudes towards the spotted hyena (*Crocuta crocuta*) in Zimbabwe.

Author contributions:

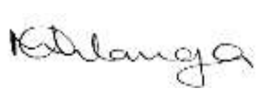
MM conceived paper. MM and FM collected data. MM analysed the data with TR and RK. MM wrote the paper. TR, FM, RK and CTD contributed valuable comments to the manuscript.

Publication 5- in review

M Mhlanga, T Ramesh, R Kalle & CT Downs. Perceptions on bushmeat demand and its effect on conservation in western Zimbabwe.

Author contributions:

MM conceived paper. MM collected the data. MM analysed the data with TR and RK. MM wrote the paper. TR, RK and CTD contributed valuable comments to the manuscript.



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Mhlanga Mlamuleli

December 2017

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CHAPTER 1

1.0 Introduction

Large carnivore management involves decision-making processes that either improve or destroy the contribution of carnivores to the ecosystem which consequently affect prey species (Honer et al., 2005; Packer et al., 2009; Treves, 2009). Various ecological and anthropogenic aspects affecting large carnivore conservation need to be monitored continuously to avoid deviance from the desired (Woodroffe & Ginsberg, 1998; Kolowski & Holekamp, 2009). Such monitoring activities employ various techniques that enable accounting for the species in various ecosystems (Smallwood & Schonewald, 1998; Rosenblatt *et al*., 2014; Boydston et al., 2006; Watts & Holekamp, 2007; Cozzi et al., 2013). This chapter discusses various land management systems, and threats that affect spotted hyena (*Crocuta crocuta*) ecology in a tropical ecosystem and the consequences in declines of spotted hyena populations as well as aims and objectives of the study.

1.1 The spotted hyena

1.1.1 Species description and behaviour

The spotted hyena is a large terrestrial carnivore (Holekamp & Dloniak, 2010) with light brown or greyish brown coats that have dark brown spots all over the body and upper half of the limbs. They have raised forequarters that have a strong neck and forelegs while the hindquarters are generally lower because of short hind legs (Spoor & Badoux, 1988). Spotted hyenas stand at approximately 85 cm shoulder height with an average weight of 63 kg and 53 kg for females and males respectively. The species is conspicuous of being very vocal (laugh) and for being territorial (Hofer & East, 1993). Distinguishable sexual dimorphism and behaviour is lacking in this species except the body size in which females are larger than males (Muller & Wrangham, 2002; Szykman et al., 2003). The female clitoris is similar to the male penis and distinguishing between the sexes is difficult (Muller & Wrangham, 2002; Holekamp & Dloniak, 2010), because phenotypically, the female is masculinised (Holekamp & Dloniak, 2010). Breeding occurs throughout the year (Holekamp et al., 2012) with a gestation period of 110 days (Holekamp & Dloniak, 2010) resulting in an average of one or two cubs (Holekamp et al., 2012) that are weaned between 12-18 months (East et al., 2009; Watts et al., 2009; Holekamp et al., 2012).

Spotted hyenas are nocturnal social carnivores with a defined matriarchal hierarchy within the group (Frank, 1986a; Holekamp & Smale, 1993; Engh et al., 2000). This social hierarchy is influenced by various factors including genetics, sex, age, body size, tenure and politics within the group (Engh et al., 2000) as well as inheritance of maternal traits (Holekamp & Smale, 1993; East et al., 2009). The species is gregarious (Wahaj et al., 2001; Szykman et al., 2003; Van Horn et al., 2004) and groups may range from 11 to 30 individuals (Holekamp et al., 1997a; Szykman et al., 2003) in which males are submissive to the matriarch females (Szykman et al., 2003). However, access to food after a kill and general protection from within clan conflicts depends on the rank and maternal lineage of an individual (Holekamp et al., 1997a, b; Engh et al., 2000). Females spend their entire life with the same clan unlike males that leave the clan at an average age of two to three years (Holekamp et al., 1997a, b). The species however, has a 'fission-fusion' kind of lifestyle characterised by immigration and emigration between groups of the same clan and commuting behaviour in response to prey migration (Hofer & East, 1993). However, adult females tend to associate more closely with their mature female kin than with unrelated grown females (Holekamp et al., 1997b). In addition, it has been shown that there is a stronger relationship between females from high ranking matrilines (Holekamp et al., 1997b). This species recognises third party relationships, making their social system complex (Engh et al., 2005). These traits can be recognised in scenarios where a clan member or group attacks an opponent and its relatives (Engh et al., 2005). Males also show aggression towards females during conception although more research still needs to be done on such behaviour (Szykman et al., 2003). However, often males will be submissive especially to matriline members. Once they grow as sub-adults, males disperse to join nomadic males before they settle in a new clan (Frank, 1986b).

1.1.2 Species distribution in Africa

The species is widely distributed throughout Africa, but highly concentrated in southern Africa where it has been classified as "Least Concern" (Mills & Hofer, 1998; Holekamp & Dloniak, 2010; Fig. 1.1) by the International Union for the Conservation of Nature (IUCN) but is still conservation dependant. It is found in a variety of habitats including the semi-desert, arid savannah (Holekamp & Dloniak, 2010), open woodlands, bushveld, pans, thorn veld, thick woodland and mountains (Mills & Hofer, 1998; Holekamp & Dloniak, 2010), grasslands and communal areas as well as ranches. In Zimbabwe, the species is highly concentrated in the western part of the country mostly in protected and surrounding areas. However, recent reports from national parks indicate that the species is displacing fast into areas where it was less common. This includes southern Zimbabwe and Bulawayo peri-urban where it has increasingly been in conflict with livestock farmers (Mhlanga pers. obs.). Like any other carnivore, the species requires optimum conditions with respect to habitat quality and thus a greater proportion of the metapopulation lives inside protected areas or zones of low human density with sufficient numbers of suitable prey (Mills & Hofer, 1998). The species does not survive well in rain forests (Holekamp & Dloniak, 2010) but has a well-established population in the drier regions of western Zimbabwe.

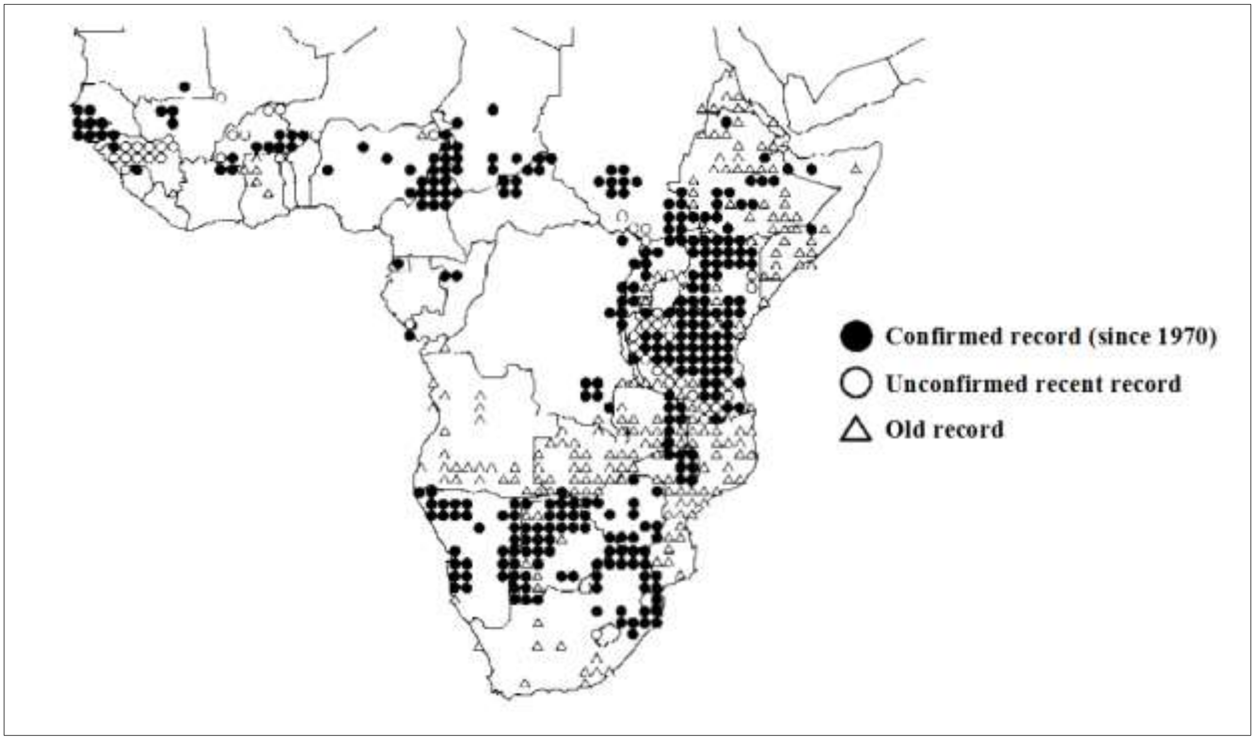

Fig. 1.1 Distribution of the spotted hyena. Source: Mills & Hofer (1998).

1.1.3 Population status

Population estimates of wildlife inside and outside of protected areas are crucial for large carnivore management (Smallwood & Schonewald, 1998; Jenks et al., 2011; Kalle et al., 2011; Holekamp et al., 2012). Population estimates are useful in making informed management decisions that determine the continued existence of various species (Silveira et al., 2003; Balme et al., 2009; Jenks et al., 2011). These estimates are crucial because they are used as empirical data (Kalle et al., 2011) used in wildlife management (Gros et al., 1996; Treves and Karanth, 2003). In addition, population estimates enable determination off-take (hunting quota) where trophy is permitted. (Packer et al., 2009; Treves, 2009; Gandiwa et al., 2013).

Various techniques are employed to estimate the population of nocturnal species like the hyena. These techniques include baiting (Cozzi et al., 2013; Rosenblatt et al., 2014), telemetry (Kolowski

& Holekamp, 2009), camera traps (Ramesh et al., 2012; Rovero et al., 2013; Brassine & Parker 2015), call-back tapes, den observation (Boydston et al., 2006; Watts & Holekamp, 2007) and spoor counts among other methods (Smallwood & Schonewald, 1998; Silveira et al., 2003). Before the 21st century, population estimates for carnivores relied on call back tapes, spoor counts, water hole counts, radio telemetry and ranger or tourist sightings (Gros et al., 1996; Smallwood & Schonewald, 1998; Stander, 1998). In the past decade, camera traps have become popular (Silveira et al., 2003; Silver et al., 2004; Rovero and Marshall, 2009; Jenks et al., 2011; Foster and Harmsen, 2012; Yu et al., 2013; Ramesh et al., 2016). Camera traps are less invasive to the animals than other methods like telemetry and call-back tapes. In addition, camera traps are a good tool in identifying individual animals (Jenks et al., 2011) for certain species, hence making it possible to differentiate between individuals of the same group as well as the population size of that species.

Population dynamics, feeding and reproductive performance of the spotted hyena has been estimated in various studies inside protected areas (Mills and Hofer, 1998; Salnicki et al., 2001). Densities (individuals/km^2) of the species have been recorded at 0.02 in Etosha National Park in Namibia (Trinkel and Kastberger, 2005) and 0 - 1.25 in Hluhluwe-iMfolozi National Park in South Africa (Graf et al., 2009). In Hwange National Park, the spotted hyena density was estimated at 0.07 individuals/km^2 (Holekamp and Dloniak, 2010). However, not much research has been done on the species inside and outside of protected areas.

The spotted hyena has attracted relatively little interest from the research community in southern Africa. Most research on the spotted hyena has been conducted on populations in the Serengeti, Maasai Mara and Ngorongoro Crater National Parks in East Africa (Kolowski & Holekamp, 2006) but relatively little published work exists in southern Africa (Mills & Hofer, 1998). Management of hyenas requires extensive research, which involves tracking clans of various sub-populations. That is crucial in influencing policy on the management of the species. As such, there is urgent need to exhaust various techniques that would provide a holistic explanation to changes in population size, survival rates, sex and age ratios among other variables. That would enable implementation of urgent measures, which enable protection of the species from persecution and possible extinction in the near future (Rosenblatt et al., 2014).

The spotted hyena often occurs sympatric with other large carnivores like the African lion *Panthera leo* (Periquet et al., 2016). As a result, the spotted hyena competes for prey and in situations where it is competitively excluded by the African lion, there could be long-term population reduction of the spotted hyena. In addition, the major competitors are endangered, that is lion, African wild dog *Lycaon pictus*, cheetah *Acinonyx jubatus* and leopard *Panthera pardus* and most research and conservation efforts focus on these while relatively little attention is given to the spotted hyena.

1.2 Threats to spotted hyenas

1.2.1 Land-use types, changes and the Zimbabwe land reform programme.

Zimbabwe introduced land reform programmes in the early 80s (Kinsey, 1999) and subsequently in the early 2000s (Goebel, 2005) and there have been some changes in the management of protected areas (Wolmer et al., 2004). These changes mainly involved subdivision of vast wildlife farms to allocate numerous settlers in need of land. The government's interest in the land reform programme was to spearhead development which included maximising livestock and crop production, native empowerment and equity, wildlife conservation and harvesting and promotion of public-private engagements (Kinsey, 1999; Moyo, 2000; Hellum & Derman, 2004; Wolmer et al., 2004). Therefore, the land reform programme introduced a change in land-use in which large-scale commercial wildlife farms were converted to A1 (small-scale) and A2 (commercial wildlife farming) models (Wolmer et al., 2004). A1 model is mainly community-based resources management combining human settlements, wildlife, crops and livestock production for community development (Wolmer et al., 2004). However, with the active involvement of the Zimbabwe Parks and Wildlife Management Authority, resettled farmers have excelled in wildlife management (Mhlanga, pers. obs.), especially in areas where there is collective (block) management in which wildlife freely moves across farm boundaries. The challenge however, exists in combating destruction of wildlife habitat caused by fragmentation due to infrastructure development. This is further confounded by the increasing demand for cropping and grazing land caused by a continually increasing in human population. There is also a need to empower the attitudes of the resettled farmers so that they can coexist harmoniously with wildlife amid human-wildlife interactions (Kuiper et al., 2015).

As a result of the land reform programme, this study classifies land-use options for wildlife conservation under six categories (Bruce et al., 1993), that is, national parks, safari areas (government and private run hunting areas) and conservancies, forestland, Environmental Conservation Areas (ECAs, resettled wildlife farms) and communal areas (Wolmer et al., 2004). This classification does not deviate from that of the Parks and Wildlife Act [Chapter 20:14 of 1975] which is the main instrument used in the management of wildlife resources in Zimbabwe (Parks & Wildlife Act, 1975). National parks are characterised by intensive wildlife conservation with non-consumptive use of wildlife (Parks & Wildlife Act, 1975; Gandiwa 2013) and are run by the state through the Zimbabwe Parks and Wildlife Management Authority (ZPWMA). The safari (hunting) area has similar characteristics to the national park and the major difference is consumptive use of wildlife in in the former (Loveridge et al., 2007; Ndaimani et al., 2013). Forest land has similar characteristics with national parks, the marked difference is that former are run by the state through the Forest Commission under the Forest Act [Chapter 19:05] and allows wildlife harvesting (Bruce et al., 1993), although the major objective is indigenous floral species conservation and sustainable use (Campbell et al., 2000). Conservancies are intensive wildlife conservation areas managed by a number of independent wildlife farmers or groups, each owning some portion in the conservancy under the A2 model of the land reform programme (Wolmer et al., 2004). As a result, conservancies and forestland act as buffer zones between national parks and communal areas (formerly Tribal Trust Lands). Communal areas were set aside for human settlement wherein natural resources and other resources are common property and no individual has exclusive rights to assets like water sources, grazing land, forests and other resources. In addition, communal areas are characterised by uncontrolled establishment of new households every year. In this land-use type, trophy hunting is permitted through appropriate authority granted to Rural District Councils (RDCs) under the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) (Alexander & McGregor, 2000, Frost and Bond 2008, Gandiwa et al., 2013). The other settlement areas are Environment Conservation Areas (ECAs) in which wildlife and land-use are managed by the settlers themselves (Wolmer et al., 2004). These are a combination of model A1 and A2 wildlife farmers. However, it is crucial to note that ECAs differ in mode of wildlife management from communal areas because in the latter wildlife is managed through CAMPFIRE while in the former communities manage their own wildlife resource and revenue (Gandiwa et al., 2013).

As such, the change in land ownership, and hence differences in the management of the subdivisions influence the status of various predators and prey. Fences have always been a good model for containing wildlife within conservancies, hence reducing human-wildlife conflicts.

However, continued creation of barriers in small land holdings that contain large carnivores like the spotted hyena can have negative impacts not only on restricting escape options for prey species but also on genetic diversity of animals inside the fences (Mills & Hofer, 1998). Fences reduce genetic diversity leading to a bottleneck due to inbreeding within the subpopulation (Woodroffe & Ginsberg, 1998). Although fencing is strongly discouraged in Zimbabwe, such a wildlife-farming practise seems to be booming in southern Africa, especially in small private farms. Consequently, the subdivisions could be affecting the status and ecological adaptations of spotted hyena inside and outside protected areas. As such, understanding how land-use change has influenced some aspects of the ecology of this large carnivore will shed more light on present and future management of the spotted hyena and other large carnivores.

Western Zimbabwe has people from various tribal backgrounds including the Dombe, Tonga, Lozwi, Nambya, Nyanja and Ndebele (Zimbabwe National Statistics Agency, 2012). They have coexisted with wildlife for approximately more than a century. The protected areas were designated when some of their ancestors had settled in those areas (western Zimbabwe) and have thus adapted to living near wildlife zones. Historically, these settlers were hunters but their activities were affected by the introduction of legislation that prohibits unlicensed harvesting of wild animals.

Table 1.2 Surface area of land-use types available for the conservation of the spotted hyenas in western Zimbabwe.

Land-use type	**Purpose**	**Estimated size (km^2)**
National Parks	Non- consumptive conservation	15548
Recreational Parks	Public recreation	0.56
Safari Areas	Sport hunting	3465
Forest Land	Indigenous forest conservation	6675
Matetsi ECAs	Community-based conservation and harvesting; human settlement	654

Communities living adjacent to protected areas are incentivised through community based natural resources management programmes, for example, the CAMPFIRE in Zimbabwe (Alexander & McGregor, 2000; Shackleton et al., 2002; Frost & Bond 2008). Unfortunately, misappropriation of funds by the appropriate authorities has been recorded (Wolmer et al., 2004), leading to mistrust of Rural District Councils by communities thereby further catalysing negative attitudes towards wildlife. Although CAMPFIRE is a noble program, people thus view it as a source of income for the participating Rural District Councils at the expense of the communities (Wolmer et al., 2004).

1.2.2 Prey abundance, optimal foraging and edge effects

Fortunately, most protected areas in Zimbabwe and elsewhere do not have boundary fences and hence do not restrict spotted hyena movement inside and outside the protected areas.

Unfortunately, this simultaneously allows illegal entry of humans into protected areas leading to poaching (Gandiwa, 2011) which is a serious threat to wildlife. Most poaching activities use fire to distract park manager. Regrettably, this method used by poachers, results in destruction of large tracks of vegetation, which consequently affects availability of food and cover in a habitat. Once such basic habitat requirements are eliminated from the habitat, various species will abandon the area for better habitats offering optimal foraging opportunities. Unfortunately, accelerated prey loss or emigration from protected areas has a strong impact on the food chain involving the spotted hyena. As such, diet selection of the spotted hyena can be influenced by land-use type. For example, human interference can affect the type and abundance of prey (Abay et al., 2011) found in a landscape, thereby affecting prey choice of the spotted hyena.

As more habitats are lost inside protected areas and the abundance of prey decreases, the spotted hyena expands its home range by commuting to habitats that are outside protected areas. This eventually overlaps with human dominated landscapes including pastureland and settlement areas. Regrettably, that catalyses livestock predation by the spotted hyena leading to the accelerated human-spotted hyena conflict and negative attitudes towards the species (Packer et al., 2009).

The human-hyena conflict has intensified over the last two decades (Treves & Karanth, 2003). The species has been reported in almost every district in western and south-western Zimbabwe, including ranges common to the brown hyena *Hyaena brunnea*. The situation fuelled speculation that the population of the spotted hyena is in excess and needs to be culled. Such attitudes can lead to retaliatory killing and consequent reduction of the spotted hyena population. Unfortunately, no published data exist on the extent of the conflict in Zimbabwe, although such behaviour has been reported elsewhere (Packer et al., 2009).

Furthermore, illegal activities within protected areas destabilise prey and hyenas (Loibooki et al., 2002). On one hand, such illegal activities lead to prosecution (Gandiwa et al., 2014) and that has engendered conflicts between communities and protected area managers (Gandiwa et al., 2014). On the other hand, increased human-wildlife conflicts (Treves & Karanth, 2003) amidst failure by conservation science to consider social obligations of to those communities (Alexander & McGregor, 2000; Brashares et al., 2004; Dickman et al., 2011) has also fuelled negative attitudes towards wildlife leading to increased poaching and retaliatory killing (Gandiwa et al., 2013; Constant et al., 2015).

Besides having a large home range (ca 30-45 km^2), the spotted hyena is a social and commuting species (Pereira, et al., 2014). It follows migratory species and often would venture into communal areas. As such, when prey availability dwindles inside protected areas, the spotted hyenas are expected to commute (Honer et al., 2005) and forage outside where they are consequently killed through wire snaring, poisoning or shooting (Kolowski & Holekamp, 2006). Farmers often poison livestock carcasses to kill spotted hyenas, consequently killing various other scavengers like vultures (Ogada, 2014)

Major threats to the spotted hyena are in the form of habitat fragmentation and destruction caused by fires set by poachers. Furthermore, increased illegal poaching and bushmeat trade (Gandiwa, 2011), and mining activities in protected areas are a serious threat to prey and eventually predators. In recent years, there has been an increase in elephant poisoning in Zimbabwe. That raises concerns to conservationists because the spotted hyena is susceptible to poison attack as they scavenge on elephant carcasses. Increased trophy hunting affects foraging of the spotted hyena due to disruption of prey distribution (Honer et al., 2005; Watts & Holekamp, 2009).

The spotted hyena is associated with myths about witchcraft (Gould, 1981; Gottlieb, 1989). Such myths make the conservation of this large carnivore difficult because of persecution associated with the beliefs and 'misconceptions' (Dart, 1956; Gould, 1981). This causes people to kill any spotted hyena that dens near their villages. Consequently, that affects the population of the spotted hyena resulting in the species being dependent on protected areas for continued existence (Bohm & Honer, 2015).

1.3. Consequences of spotted hyena declines

Large carnivore populations are in a rapid global decline (Rosenblatt et al., 2014). Their loss implies a loss in genetic heterogeneity in the ecosystem. In addition, it will lead to a loss in top down and bottom up influences that the species has on the range in which it is distributed (Carbone et al., 1997; Linnell & Strand, 2000). The species play a crucial role in regulating populations of various herbivores to align to the carrying capacities of a landscape. It also influences numbers of competing meso-carnivore species to sustainable ecosystem levels. Furthermore, as a scavenger, the species is crucial in sanitising the landscape of carrion from dead animals and waste disposed by humans.

1.4 Statement of the problem

Although the spotted hyena has been classified as 'least concern' by the IUCN, the species is conservation dependent (Bohm & Honer, 2015). Numerous studies have been conducted on the ecology and habitat use of the spotted hyena using clan observations (Hofer & East, 1993c), collared individuals (Kolowski & Holekamp, 2009), audio call-back tapes (Cozzi et al., 2013; Rosenblatt et al., 2014) and den observations (Boydston et al., 2006; Watts & Holekamp, 2007).

However, the last two decades experienced a decline in the study of the spotted hyena in protected areas. Remarkable land-use changes and habitat destruction have occurred over the last two decades, especially in Zimbabwe where the agrarian land redistribution programme created a different management approach through land ownership changes. Furthermore, increased human-hyena conflicts have occurred over the years resulting in retaliatory killing of the species to prevent further damage to livestock in communal and commercial farms around the country. Amid these constraints, very little research is done on the species, particularly on how it has adapted to increased disturbances in and outside protected areas. Further, relatively few studies have attempted to use camera traps to study the spotted hyena and other large carnivores (Stein et al., 2008) in southern Africa particularly Zimbabwe (Brassine & Parker 2015). Yet camera traps have become an important but less invasive method in understanding population dynamics and habitat use of various elusive species compared to earlier methods like telemetry. Western Zimbabwe has vast forestland, national parks, private wildlife farms and safari areas (Forest Act, 1949; Parks & Wildlife Act, 1975), which provide habitat for substantial subpopulations of hyenas. Reports on human-hyena conflicts have increased on the peripheries of these conservation areas thereby making the region a suitable area for the study. Hence, the study aimed at understanding some ecological aspects of the hyena amidst increased changes in land-use, and its interaction with other carnivores inside and outside protected areas. The study assessed the attitudes of people living adjacent to protected areas towards the spotted hyena. Furthermore, the study investigated perceptions of these communities on illegal bushmeat harvesting which reduces prey species for the spotted hyena. The study aimed at contributing towards effective management of the spotted hyena in and outside protected areas while also shedding light on the human-spotted hyena conflict and mitigation in the region.

The study was carried out in four locations within the northwestern tip of Zimbabwe (Fig 1.2). These included Zambezi National Park, Matetsi Safari Area, Dimbangombe Ranch, Matetsi Environmental Conservation Areas (ECAs-resettlement) and Jambezi Communal lands.

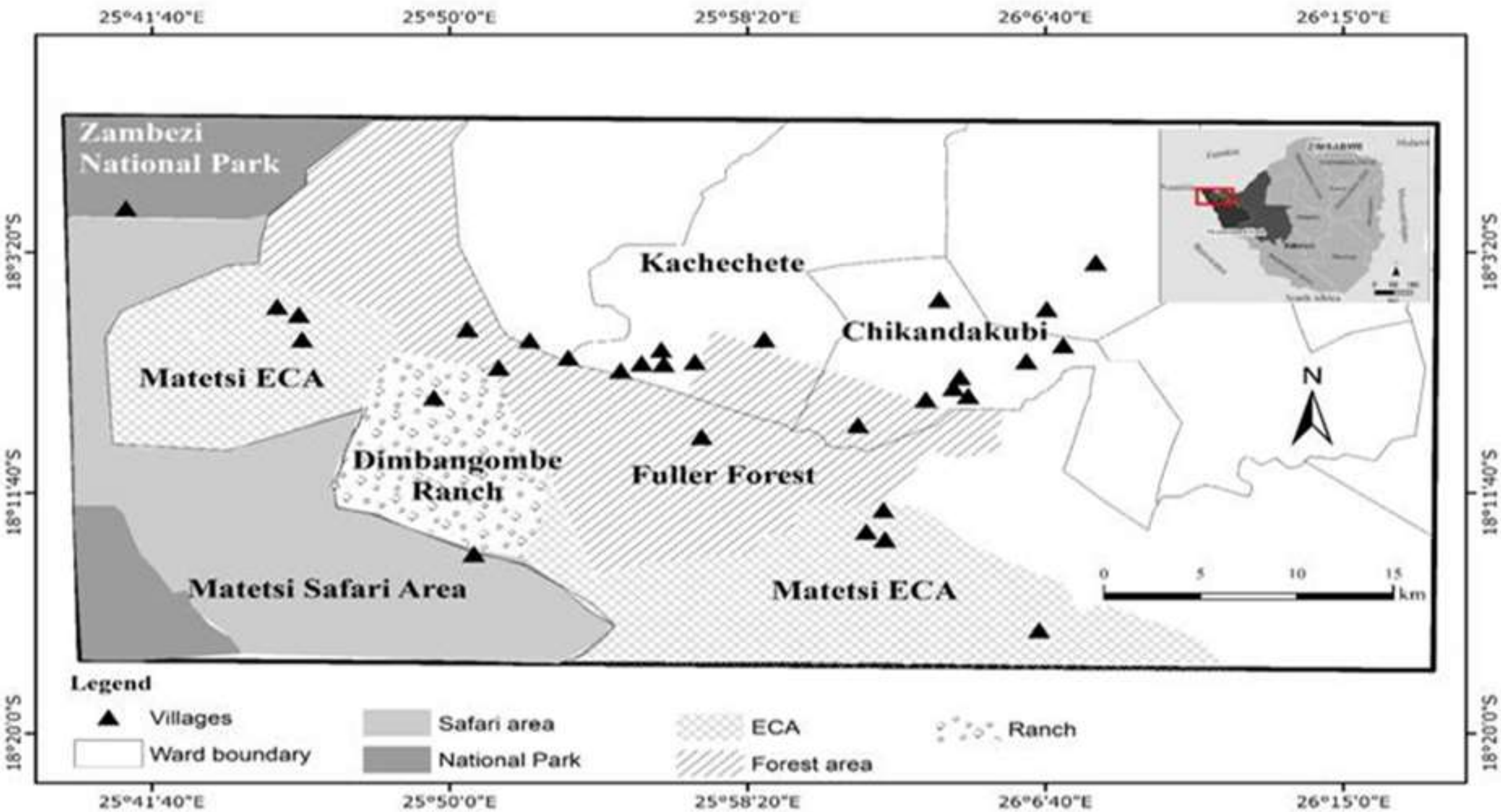

Fig. 1.2. Location of the study area in western Zimbabwe with varying conservation land-use: Communal areas (Kachechete and Chikandakubi wards), Environmental Conservation Areas (Matetsi ECAs), Protected Area (Zambezi National Park), Hunting Area (Matetsi Safari Area) and Ranch (Dimbangombe).

1.5 Aims and objectives

The main aim of the study was to investigate the ecology of the spotted hyena under changing land-uses and to assess the extent of the impact of human-hyena conflict on the attitudes towards the species with the idea of contributing to effective management of this carnivore in and outside PAs in Western Zimbabwe. The study thus had the following specific objectives:

1. To investigate habitat use by the spotted hyena along a conservation land-use gradient in Zambezi National Park, Matetsi Safari Area (hunting) and Dimbangombe Ranch
    a. To determine whether spotted hyena habitat use (occupancy) increased with soil type and higher prey species detection since soil type can influence denning behaviour.
    b. To ascertain whether different land management systems with varying levels of human interferences affect prey abundance that lead to change in habitat use and detection probability of the species.
    c. To investigate whether habitat use of hyena would increase with higher detection of domestic prey due to the higher variation in distribution or lower abundance of wild prey in the disturbed habitats.
    d. To investigate the effect of season on habitat use and detection probability of the spotted hyena in Western Zimbabwe.
2. To assess co-occurrence of the spotted hyena with other carnivores along a conservation land-use gradient in Zambezi National Park, Matetsi Safari Area and Dimbangombe Ranch.
    a. To investigate the influence of land-use type on spotted hyena co-occurrence with small carnivores in and outside protected areas in Western Zimbabwe.
    b. To investigate the effect of season on spotted hyena co-occurrence with small carnivores in Western Zimbabwe.

3. To determine diet composition of the spotted hyena in Zambezi National Park and Matetsi Safari Area (hunting).
    a. To assess prey preferences by the spotted hyena in varying land-use types in Western Zimbabwe.
    b. To investigate the effect of season on spotted hyena prey choice in and outside protected areas in Western Zimbabwe.
4. To determine the impact of conservation and human-wildlife conflict on people's attitudes towards the spotted hyena in areas surrounding Zambezi National Park.
    a. To investigate the attitude of local people towards the spotted hyena in Jambezi communal areas and Matetsi Environmental Conservation Areas (ECAs).
    b. To determine the effect of settlement type and distance of homesteads from protected area boundary on livestock losses and attitudes of people towards the spotted hyena in Western Zimbabwe.
    c. To assess whether incentives influence attitudes of people towards the spotted hyena in communities living adjacent to protected areas.
5. To assess the status of bushmeat trade and its impacts on conservation efforts in western Zimbabwe
    a. Investigate the extent of illegal bushmeat activities in the Jambesi communal areas and Matetsi ECAs surrounding PAs and conservation areas in Western Zimbabwe.
    b. To determine factors contributing towards increased illegal bushmeat trade in areas surrounding PAs and conservation areas in Western Zimbabwe.
    c. Assess if there is a seasonal trend in illegal bushmeat harvesting in the Jambesi communal areas and Matetsi ECAs surrounding PAs and conservation areas in Western Zimbabwe.
    d. Determine local people's perception on the effect of illegal bushmeat harvesting on conservation efforts in Western Zimbabwe.

1.6 Study outline

The thesis is comprised of seven chapters, of which five are arranged as data chapters prepared for publication in relevant international peer-reviewed journals, and thus some repetition in the chapters was inevitable. The hypotheses and predictions are presented in the respective chapters. The chapters are arranged in the following manner:

The current chapter, Chapter 1, serves as an overview to the research, study area, the study organism and the methodology of the study.

Chapter 2 Spotted hyena (*Crocuta crocuta*) habitat use across a conservation land-use gradient in western Zimbabwe

Chapter 3 Spotted hyena co-occurrence with mesocarnivores across a wildlife management gradient (Ranch, Hunting Area and National Park) in Western Zimbabwe

Chapter 4 Comparison of spotted hyena (*Crocuta crocuta*) prey in two protected wildlife land–use types, a hunting area and a non-hunting area, in western Zimbabwe

Chapter 5 Incentives matter: the influence of settlement type and land-use on public attitudes towards the spotted hyena (*Crocuta crocuta*) in Zimbabwe

Chapter 6 Perceptions of bushmeat supply and its effect on conservation in western Zimbabwe.

Chapter 7 Conclusions. Chapters 2 to 4 dwelt on key ecological aspects of the spotted hyena while chapter 5 and 6 focused on public perceptions. The implications of all chapters are discussed in the concluding chapter that summarises the findings of the study.

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CHAPTER 2

Spotted hyena (*Crocuta crocuta*) habitat occupancy in a national park, hunting area, and private ranch in western Zimbabwe

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Running title: Spotted hyena occupancy across a land-use gradient

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2.0 Abstract

The management of large carnivores faces numerous challenges including habitat disturbance and loss inside and outside protected areas. This affects how a species uses a habitat as it measures the risks and benefits associated with inhabiting such a disturbed ecosystem. Estimating habitat occupancy of a species is one of the methods used in assessing how well a species utilises its environment, thereby enabling conservationists to make informed decisions in the management of wildlife. The spotted hyena *Crocuta crocuta*, is one such carnivore facing anthropogenic disturbance in various land-uses. We thus modelled habitat occupancy of the spotted hyena in western Zimbabwe using sixty camera stations in a national park, hunting area, and a private ranch. Spotted hyena mean occupancy was $\psi = 0.617$, SE = 0.147 and $\psi = 0.502$, SE = 0.107 during the wet and dry seasons respectively. Occupancy increased in clayey soils and grasslands in the national park and the safari area, a behaviour attributed to denning site preferences and possibly prey movement. Therefore, with changing land-use, the spotted hyenas are likely to inhabit areas outside the national park as they search for food while restricting their dens to areas along grasslands that have clayey soils.

Key words: Camera trap, detection, large carnivore, protected area, land-use, habitat occupancy, hyena

2.1 Introduction

The spotted hyena *Crocuta crocuta* is a common large carnivore in Africa (Holekamp & Dloniak 2010; Watts *et al*., 2010). The species exists in substantial populations (Holekamp & Dloniak 2010) and partially monopolizes the landscape due to lower numbers of competing large carnivores like the African lion *Panthera leo*, African wild dog *Lycaon pictus*, cheetah *Acinonyx jubatus* and leopard *Panthera pardus* (Loveridge *et al*., 2007; Pettorelli *et al*., 2010; Palazy *et al*., 2012; Berghe *et al*., 2012). Numerous factors are important in the survival of the spotted hyena (Boydston *et al*., 2003a; Watts & Holekamp, 2009; Pangle & Holekamp, 2010). Selection of habitats with suitable soils imply suitable dens (Holekamp & Dloniak, 2010) for communal and social development (Hofer & East, 1993b), rearing young (Hofer & East, 1993d), escape from predators and harsh environmental conditions (Pokines & Peterhans, 2007). Prey also play a major role in influencing clan and territory size (Holekamp, Sakai & Lundrigan, 2007) in the survival of hyenas. A diversity of vegetation types generally support a variety of prey guilds and are thus considered an important component of habitat use by the spotted hyena. Although spotted hyenas prefer open landscapes, they occasionally hunt in densely vegetated habitats (Kolowski & Holekamp, 2010). Unfortunately, anthropogenic activities are increasingly disturbing the habitats of spotted hyenas particularly near human settlements (Woodroffe 2000), road networks and other land-use types like newly ranches (Cozzi *et al*., 2015; Cozzi *et al*., 2013). Competition and interference from other large carnivores due to niche overlap also influences habitat choice and success of the spotted hyena (Periquet *et al*., 2016).

Although the species has been classified as ‘least concern’ by the International Union for Conservation of Nature (IUCN), it remains conservation dependent (Bohm & Höner, 2015), requiring active human action through habitat management in rangelands where it occurs. Management of hyenas and other large carnivores inside and outside of protected areas is a difficult task for conservation managers because of increased environmental change induced by anthropogenic human activity (Pettorelli *et al*., 2010). These include encroachment of humans into protected and other conservation areas (Ramesh *et al*., 2012; Ramesh & Downs, 2013; White, 2013). For example, safari areas are hotspots for trophy hunting, thus, disturbance and possible reduction of some prey species by hunters affects the carnivores. Thus, the spotted hyenas is negatively affected both inside and outside of protected areas (Woodroffe 2000; Williams *et al*., 2016). Therefore, human actions force hyenas to expand the size of their home range thereby venturing out of protected areas and foraging in settlements leading to conflicts with humans. As such, several factors affect the extent of habitat occupancy by the spotted hyena (Carbutt & Goodman, 2013; Périquet *et al*., 2016).

Therefore, it is fundamental to understand the spatial and temporal characteristics of habitat occupancy of spotted hyenas. Obtaining such information for such an elusive species is difficult (Pettorell *et al*., 2010; Efford & Dawson 2012; Rosenblatt *et al*., 2014). There is therefore a need for empirical ecological data that permits current and future management of such elusive animals under diverse anthropogenic disturbance pressures (Trinkel *et al*., 2006). Habitat occupancy is one such significant ecological attribute that enables relative understanding of species occurrences in a habitat (Efford & Dawson, 2012; Carbutt & Goodman, 2013; Ramesh *et al*., 2016) and enables acquisition of valid evidence of species-environment interactions under diverse land-use management systems.

Numerous studies have been conducted on the ecology and habitat use of the spotted hyena using clan observations (Hofer & East, 1993c), collared individuals (Kolowski & Holekamp, 2009), audio call-back tapes (Cozzi *et al*., 2013; Rosenblatt *et al*., 2014), and den observations (Boydston, Kapheim & Holekamp, 2006; Watts & Holekamp, 2007). However, relatively few studies have used camera traps to study spotted hyenas and other large carnivores (Stein *et al*., 2008; Brassine & Parker, 2015) in southern Africa, particularly Zimbabwe. Unlike other survey methods (Stein *et al*., 2008; Rovero *et al*., 2013; Rosenblatt *et al*., 2014), camera trapping has become an important, effective and less invasive tool used to study habitat occupancy of nocturnal species (Ramesh *et al*., 2012; Rovero *et al*., 2013; Brassine & Parker, 2015) with minimum disturbance to animals. This technique employs the mark-recapture method, allowing for large robust and empirical data to be collected over larger areas (Rovero *et al*., 2013). Camera trapping thus becomes an effective method because spotted hyenas disperse widely across diverse land-uses in the landscape (Holekamp and Dloniak, 2010) in response to various factors including prey dispersal (Trinkel *et al*., 2004; Trinkel *et al*., 2006; Cozzi *et al*., 2015). As such, there is need to understand specific covariates influencing the presence or absence of the spotted hyenas in an area as these are the determinants of habitat occupancy (Valeix *et al*., 2010; Ramesh *et al*., 2012) of the species.

As such, we conducted a study to determine seasonal occupancy of spotted hyenas across three conservation land-use types (protected area, safari area-conservancy with trophy hunting, and a ranch combining domestic stock and wildlife farming). Different land management systems were assumed to have varying levels of human interference and would therefore affect habitat characteristics and consequently alter habitat occupancy by the spotted hyenas. Therefore, our objectives were to determine variables influencing seasonal habitat occupancy of spotted hyenas through a selection of explanatory models (Kalle *et al*., 2014; Rovero *et al*., 2014) across the three conservation land-use management systems. We hypothesised that the spotted hyena would show variation in habitat occupancy in different land-use types due to differences in management. We further hypothesized that habitat characteristics would influence spotted hyena occupancy in different land-use types.

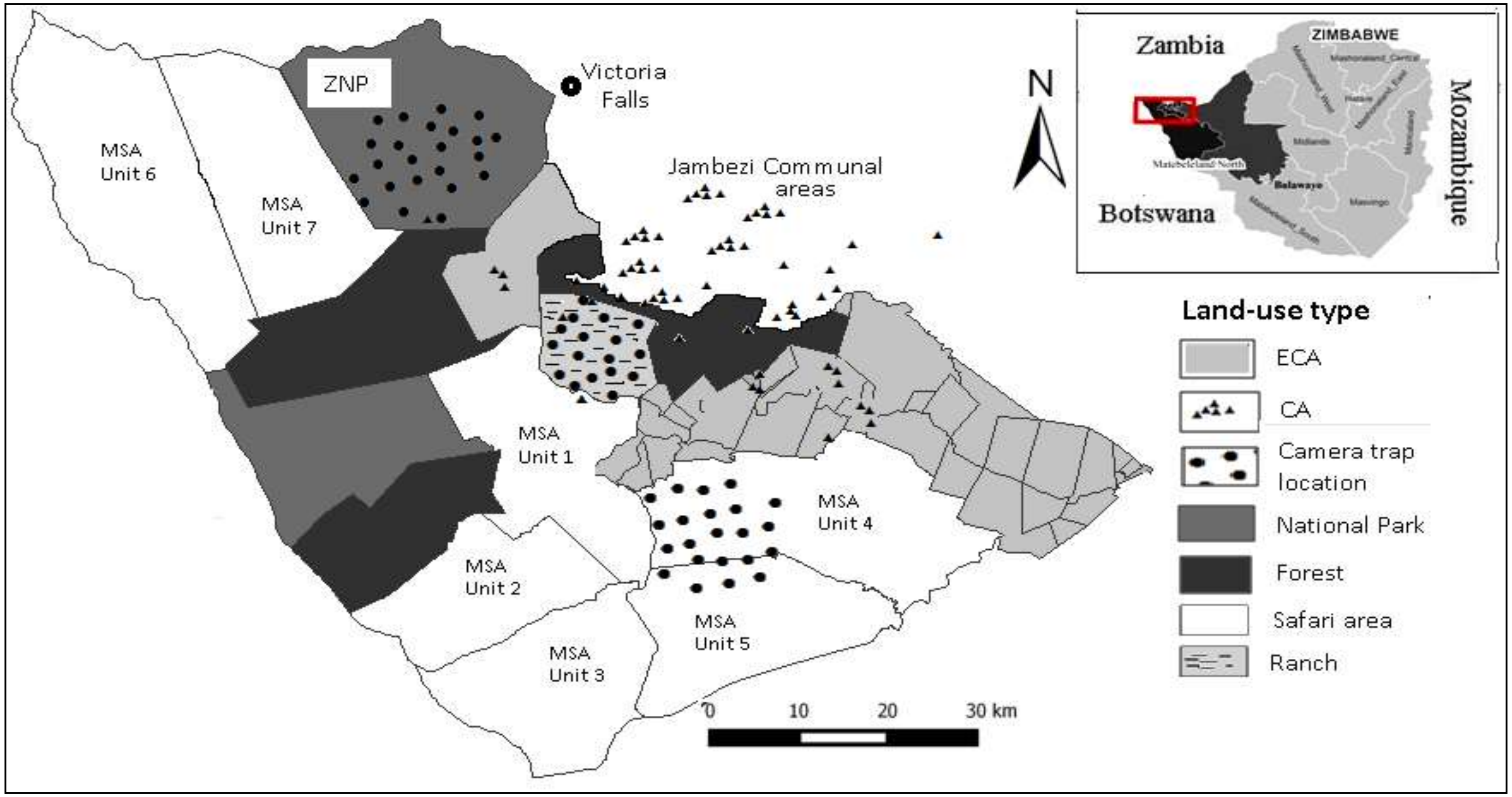

Fig. 2.1 Camera trap locations at Dimbangombe Ranch, Matetsi Safari Area and Zambezi National Park (ZNP) in western Zimbabwe during both the wet and dry seasons of 2014-2015. (ECA- Environmental Conservation Areas: Self-sufficient settlement type practicing community based natural resources management in farms characterised by a fixed number of households, conservation of wildlife, farming or crops and rearing of domestic stock. CA-Communal Areas: Settlement type with no restricted number of households and the rural district council manages natural resources including wildlife on behalf of the community).

2.2 Methods

Study sites

The study was carried out in three conservation land-use management units in western Zimbabwe, namely Dimbangombe Ranch, Matetsi Safari Area, and the Zambezi National Park. The study sites differed in management and that was assumed to have an impact on the spotted hyena habitat occupancy.

Zambezi National Park

Zambezi National Park (17° 57.341' S 25° 41.399' E) stretches along the Zambezi River and was designated as a non-hunting protected area (~560.1 km^2) although illegal harvesting by poachers may occur. It is bordered by Victoria Falls town to the north, as well as communal rural areas, protected forestlands and numerous private and government owned hunting concessions. The soils are mainly deep Kalahari sands (regosols) with few patches of a rocky terrain (Muposhi *et al*., 2016) and some clayey areas (lithosols) near the Zambezi River floodplain. The study focused on Chamabondo, which is on the southern part of the national park.

Matetsi Safari Area

Matetsi Safari Area (18° 22.760' S, 25° 52.353' E) is a relatively large protected area that promotes trophy hunting (~ 3000 km^2) and was established in the early 1970s for trophy hunting (Crosmary *et al*., 2013; Muposhi *et al*., 2016) and photography. It is sub-divided into blocks called units. Units 1-6 are for selective legal trophy hunting and Unit 7 is a photographic concession. However, the study concentrated on Unit 4 (358 km^2) and Unit 5 (364 km^2) which were under management of the Parks and Wildlife Management Authority (Muposhi *et al*., 2016) while other sections were leased to private safari operators. It is bordered by Hwange

National Park to the south, human resettlements to the northeast, and Dimbangombe Ranch to the northwest.

Dimbangombe Ranch

Dimbangombe Ranch (18° 11.202' S, 25° 52.500' E) spans 32 km^2 and is characterised by cattle ranching as well as trophy hunting and habitat reclamation activities (Savory & Parsons, 1980). The ranch also utilised a portion within neighbouring Fuller Forest for holistic research and domestic stock grazing (Savory & Parsons, 1980). As such, that section of the forest was included as part of the ranch for the purposes of effective camera deployment to increase detection of spotted hyenas and prey species resulting in an area of approximately 68 km^2. This area is bounded by Matetsi Unit 1 to the southeast and part of Matetsi Environmental Conservation Area (ECA) to the west. Matetsi ECA is a community-based natural resources management scheme comprised of families resettled in wildlife farms. The communities manage wildlife through a hunting quota approved by the Parks and Wildlife Management Authority.

The ranch lies ~34 km southeast of Victoria Falls town. It had a resident mixed large herd of cattle, sheep and goats managed through a planned holistic rotational grazing system in unfenced paddocks with transferrable night corrals. This involves the rotational grazing of grouped domestic stock, which incorporates use of herd effect for land restoration (Savory & Parsons, 1980; Morris, 2017). Livestock herding is employed all year round to minimise losses to predators although in nearby communities domestic animals are allowed to free range during the dry season (Kuiper *et al*., 2015).

Common characteristics of the study sites

These three study sites fall under the Natural Region IV of the Zimbabwe Agro-ecological Zones, and are characterised by low rainfall (< 650 mm pa) with recurrent droughts (Ndaimani *et al*., 2013). The dry season is long (May to November), characterised by extremes of cold (May to July) and hot (August to October) months with highest mean monthly temperatures of 32° C in October. The sites are not fenced and have a variety of predators and prey species (Table 2.1) (Crosmary *et al*., 2013; Ndaimani *et al*., 2014). Omnivores present include warthog *Phacochoerus africanus* while herbivores include African elephant *Loxodonta africana*, Cape buffalo *Syncerus cafer*, sable antelope *Hippotragus niger*, greater kudu *Tragelaphus strepsiceros*, and roan antelope *Hippotragus equinus*, common duiker *Sylvicapra grimmia*, bushbuck *Tragelaphus sylvaticus*, waterbuck *Kobus ellipsiprymnus*, and impala *Aepyceros melampus*. Large carnivores present include lions, cheetah, wild dog and leopard (Muposhi *et al*., 2016).

Data collection

Moultrie M880 (Trail Campro LLC, Springfield, USA) and Ltl Acorn 6210MC, (Shenzhen Ltl Acorn Electronics Ltd, Guangdong, China) passive infrared detector camera traps were deployed at 60 camera locations in the three study sites (Fig. 1). The study covered Unit 4 and Unit 5 in Matetsi Safari Area, as well as Dimbangombe Ranch and the southern part of Zambezi National Park.

A preliminary assessment of spotted hyena activity in the study sites employed signs like scats, spoors, individual sightings and information from the resident ecologist and rangers. The study site map was divided into 9 km^2 grids using ArcMap Version 10.3 (Esri Redlands, CA, USA). Grids for camera locations were identified and marked resulting in at least two/three sampling locations within a spotted hyena home range assumed to be between 30 and 60 km^2 (Holekamp *et al*., 1997; Woodroffe & Ginsberg, 1998). The geographic coordinates of the central point of each camera location were marked and loaded in a global positioning system (GPS) pending deployment of the cameras. Camera stations positioned at these systematically determined regular points (Brassine & Parker, 2015) resulted in 16, 22 and 22 sites at Dimbangombe Ranch, Matetsi Safari Area and Zambezi National Park respectively. To increase the detection of spotted hyena, placement of camera traps at highly probable locations, like along animal trails, were considered (Brassine & Parker, 2015; Cusack *et al*., 2015).

Cameras were secured in metal casing attached to trees (Brassine & Parker, 2015) at ~45 cm above the ground in order to capture images of spotted hyenas and other animals (Ramesh *et al*., 2012). Cameras were active 24 h day^{-1}, with a 30 s delay between consecutive photographs, and the sensitivity of the motion sensor was set to high. On deployment, we allowed an inter-camera distance of 3 ± 0.2 km considering that large carnivores like spotted hyenas move longer distances and can be captured at several camera trapping locations (Rovero *et al*., 2013). Cameras were left for 30 days per site per season resulting in 3600 trap days. No attractants were used since occupancy is a function of natural behaviour although the actual positioning of the camera was based on animal movement and activity.

Data for fourteen site specific covariates were collected at each camera location and used in regression models. Site-specific covariates recorded within 30 m radius around every camera location were: dominant vegetation types (Zambezi teak *Baikiaea plurijuga*, mopane *Colophospermum mopane*, mixed vegetation and grassland), soil type (clay, sand and rock), fire incidence, and canopy cover (open or closed). We also recorded distance to nearest water source, distance to nearest human settlement, and distance to nearest frequently used major road using geographic locations of the camera from pre-marked points with a global positioning system (GPS, eTrex 30; Garmin, Olathe, KS, USA). Levels within the variables were treated as independent covariates in the data matrix, for example, vegetation type had three levels, but each operated as a covariate in the analysis. We also used land-use levels as covariates, that is, national park (park), hunting area (safari) and private farm (ranch).

Data analyses

We recorded whether the camera was placed within the park, ranch or safari as a binary variable (0/1) in the data matrix in which land-use was treated as a site covariate. We created a matrix for the spotted hyena detection spanning 24 h survey (00:00 – 23:59) in columns and rows consisting of camera numbers. We developed detection histories of spotted hyena as '1', '0' or '-' for each observation where '1' indicated one or multiple occurrences within the particular 24 h period, '0' indicated no record, and '-' indicated malfunction of the camera. Six trap days were merged to improve spotted hyena detection, resulting effectively in five surveys. Therefore, we created a 6-day detection history of the species from a 30-day survey, wherein six days constituted a survey (Boitani *et al*., 2012). These variable measurements and spotted hyena detection history were generated separately for each season.

Site covariates such as distance to road, settlement and water were standardized to *z*-scores. To avoid multi-collinearity, we tested for correlations among site covariates (Graham 2003), and retained the least correlated variables in the models. Subsequently we removed the variable 'sand soil' as this variable was highly correlated to other covariates. Further, we determined animal species richness in the three land-uses (Table 2.1), which we considered important for existence of the carnivore under study. However, these animals were not considered in estimating occupancy in this study.

Detection histories were pooled from the three study sites and analysed in a single-species, single-season occupancy model (MacKenzie *et al*., 2004; 2006; Lesmeister, *et al*., 2015) using program PRESENCE 8.3 (Hines, 2006) to predict habitat occupancy of the spotted hyena in western Zimbabwe. Potential covariates for occupancy were allowed to vary, individually or in combination and models with all potential occupancy (*ψ*-probability) covariates and detection probabilities (p) were produced (Burnham & Anderson, 2002; Ramesh *et al*., 2012). We selected the best models from the candidate models following the framework of Burnham & Anderson (2002). The best models with lowest Akaike Information Criterion (AIC) value (≤2 ΔAIC) and highest Akaike weight were used to estimate occupancy parameters and the model fitness test was verified by estimating the mean dispersion parameter C-hat (ĉ) using 10 000 parametric bootstraps (Burnham & Anderson, 2002). Only models with ˆc between 0.9 and 1.1 were selected since the best model should have a value of ĉ = 1.

2.3 Results

Thirty days of camera trapping from 60 sites (n = 1800 trap nights per season) yielded 131 (national park = 32; safari area = 44, ranch = 55), and 225 (national park = 94; safari area = 71, ranch = 60) independent photographs of the spotted hyena for the wet and dry seasons respectively. Mean herbivore species richness for Matetsi Safari Area, Zambezi National Park and the ranch was 11.5, 9.5 and 10.5 respectively (Table 2.1).

During the wet season, spotted hyena were captured at 48 % (n = 29) of camera stations. The mean estimated spotted hyena site occupancy probability in the wet season was ψ = 0.617, SE = 0.147. The best models with ≤2AIC (Table 2.2) suggested that occupancy of the spotted hyena was negatively influenced by the national park (β = -1.431, SE = 0.814) and open grassland patches (β = -2.181, SE = 1.598) while being positively influenced by clayey soil (β = 1.957, SE = 1.591) (Fig 2.2). The probability of site occupancy was low in the national park (ψ = 0.476, SE = 0.135) but increased in the ranch (ψ = 0.686, SE = 0.152) and the safari area (ψ = 0.708, SE = 0.158). The naïve occupancy estimate was ψ = 0.483. The bootstrap estimate of standard error for overall occupancy was SE = 0.104.

During the dry season, there was a 2 % increase in spotted hyenas captured at camera stations (50 %, n = 30) compared with the wet season. The mean probability of site occupancy was high (ψ = 0.502, SE = 0.107).

Table 2.1 Variation in prey species richness detected at Dimbangombe Ranch (DR), Matetsi Safari Area (MSA), and Zambezi National Park (ZNP) during the wet and dry seasons.

	Wet season			**Dry season**		
	DR	**MSA**	**ZNP**	**DR**	**MSA**	**ZNP**
Herbivores	9	14	7	12	9	12
Large carnivores	3	4	2	3	3	4
Mesocarnivores	7	7	5	9	5	5
Domestic stock	2	-	-	4	-	-

The best model with ≤2AIC (Table 2.3) showed that the spotted hyena occupancy increased with occurrence of clayey soil (β = 1.170, SE= 0.585) and open grasslands (β = 1.233, SE = 0.880) while negatively increasing with occurrence of teak (β = -0.997, SE = 0.633) (Fig 2.3). Similar to the wet season, the dry season probability of occupancy of the spotted hyena was high in the safari area (ψ = 0.573, SE = 0.107) compared to the ranch (ψ = 0.534, SE = 0.107) and the national park (ψ = 0.407, SE = 0.106). The naïve occupancy was 0.483 while the bootstrap estimate of standard error for overall occupancy was SE = 0.068.

Table 2.2 Summary of model selection procedure for variables influencing habitat use of spotted hyena during the wet season in the Dimbangombe Ranch, Matetsi Safari Area and Zambezi National Park, Zimbabwe. **ΔAIC** = the difference in AIC values between each model and the model with the lowest AIC; $\boldsymbol{W_i}$ = the model AIC weight; **ψ** = probability of habitat use (psi); **p** = probability of detection; **Model Likelihood** = Probability of encounter histories; no. Par. = Number of parameters in the model; **-2*LogLike** = Twice the negative log-likelihood.

Model	AIC_c	ΔAIC	W_i	Model Likelihood	No. Par.	-2*LogLik
ψ(clay + grass), p(.)	262.39	0.00	0.40	1.00	4	254.39
ψ(park + grass), p(.)	262.91	0.52	0.31	0.77	4	254.91
ψ(.), p(.)	264.34	1.95	0.15	0.38	2	260.34
ψ(grass + road), p(.)	266.12	3.73	0.06	0.15	4	258.12
ψ(teak), p(water)	267.35	4.96	0.03	0.08	4	259.35
ψ(canopy + road), p(.)	268.07	5.68	0.02	0.06	4	260.07
ψ(mopane + rock), p(.)	268.11	5.72	0.02	0.06	4	260.11

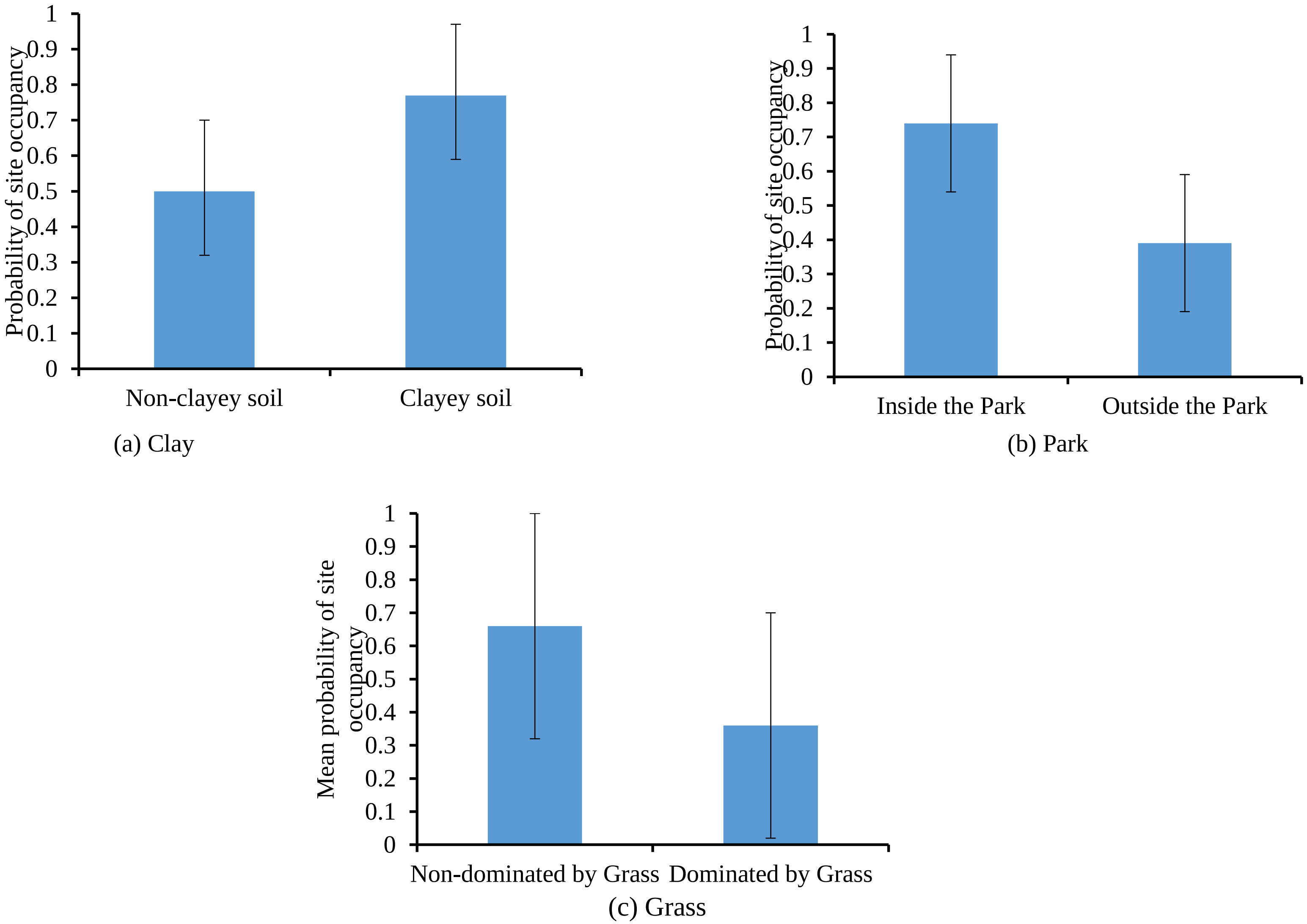

Fig. 2.2 Mean probability of site occupancy of the spotted hyena as influenced by (a) soil type (clayey), (b) landuse (park) and (c) vegetation type (grass) in the wet season. Present- hyena detected in the camera site; absent- hyena not detected in the camera site.

Table 2.3 Summary of model selection procedure for variables influencing habitat use of spotted hyena during the dry season in the Dimbangombe Ranch, Matetsi Safari Area and Zambezi National Park, Zimbabwe. **ΔAIC** = the difference in AIC values between each model and the model with the lowest AIC; ***W*i** = the model AIC weight; **Model Likelihood** = Probability of encounter histories; **ψ** = probability of habitat use (psi); **p** = probability of detection; **no. Par.** = Number of parameters in the model; **-2*LogLike** = Twice the negative log-likelihood.

Model	AIC_c	ΔAIC	W_i	Model Likelihood	No. Par.	-2*LogLik
ψ(grass + clay), p(.)	283.67	0	0.3698	1	4	275.67
ψ(teak), p(.)	285.66	1.99	0.1367	0.3697	3	279.66
ψ(.), p(water)	285.71	2.04	0.1333	0.3606	3	279.71
ψ(.), p(.)	286.26	2.59	0.1013	0.2739	2	282.26
ψ(rock), p(.)	286.88	3.21	0.0743	0.2009	3	280.88
ψ(canopy), p(.)	286.99	3.32	0.0703	0.1901	3	280.99
ψ(park), p(.)	288.14	4.47	0.0396	0.107	3	282.14

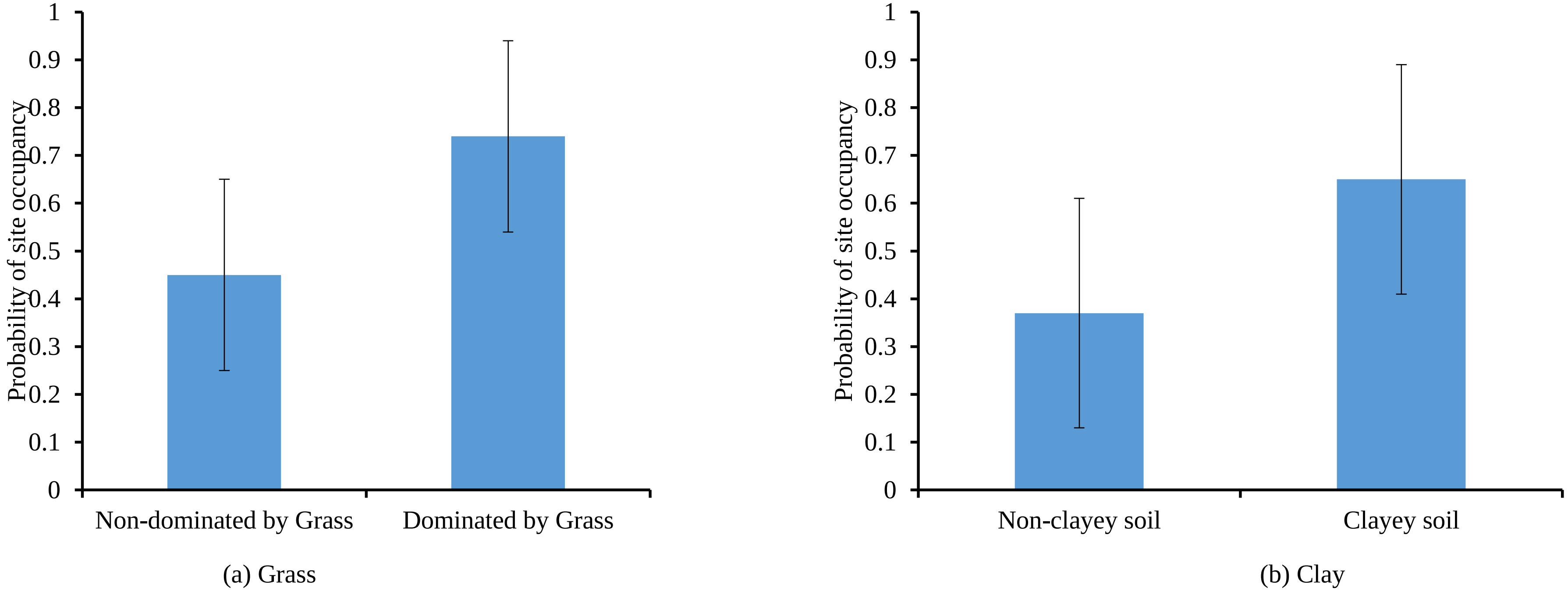

Fig. 2.3 Mean probability of site occupancy of the spotted hyena as influenced by (a) vegetation type (grass) and (b) soil type (clayey) in the dry season. Present- hyena detected in the camera site; absent- hyena not detected in the camera site.

2.4 Discussion

We found that soil type, land-use type and vegetation type determined site occupancy of spotted hyena. During both seasons, spotted hyena occupancy was higher in the safari area and ranch compared with the national park. During the wet season, it was also possibly due to prey dispersion caused by availability of water throughout the landscape (Honer *et al.*, 2005; pers. obs.). In the dry season, there could have been the effect of sport hunting in the safari and ranch, which increased food availability for spotted hyenas through carcass remains from sport hunting. That could have further been catalysed by the baiting method used in hunting large carnivores by first luring them to prey carcasses (Bischof, *et al*., 2008), thereby increasing occurrence of the spotted hyenas in areas outside the national park. Prey dispersal and other factors affecting food availability in a hyena clan's home range triggered behavioural shifts in foraging tactics, which encouraged commuting behaviour in hyenas (Hofer & East, 1993b; Trinkel *et al*., 2004). As a result, the spotted hyena occupied areas with optimal foraging returns (Honer *et al.*, 2005). Earlier studies (Hofer & East, 1993c; Honer *et al*., 2005), showed that spotted hyenas forage outside their clan territory when prey densities are low and are not excluded by other clans whose territories have high prey densities (Honer *et al*., 2005). Such behaviour is more typical of less dominant females within the clan (Hofer & East, 1993a; Honer *et al*., 2005). Consequently, this likely explained the behaviour shown in the occupancy by the spotted hyena in the current study. Although protected areas still play a pivotal role in long-term survival of the spotted hyenas, the behavioural plasticity of the species enables it to occupy disturbed ecosystems as shown by this study. That behaviour could further be enhanced by the species' ability to commute to areas with prey as reported by earlier studies (Valeix *et al*., 2010; Thaker *et al.*, 2011; Crosmary *et al*., 2012). The combination of these characteristics which are crucial for habitat occupancy will enable them to be persistent in various landscapes amid anthropogenic challenges (Boydston *et al*., 2003b).

Spotted hyenas are a denning species (Boydston, *et al*., 2006; Watts & Holekamp, 2007; Periquet *et al*., 2016) that use burrows excavated by other animals, including aardvark *Orycteropus afer* (Pokines & Peterhans, 2007). They modify these burrows to suit their needs; mainly rearing of their young, escaping predators like lions, and as refugia against harsh weather. In our study, occupancy was positively influenced by clayey soil during both seasons. This was attributed to burrow denning preferences in clayey soils which hyenas favoured compared with sandy and rocky sections of the available habitat (Holekamp & Dloniak, 2010; Pokines & Peterhans, 2007). This was confirmed by the numerous dens we observed along the clayey patches particularly in grasslands in the national park and safari area. Hence, denning of spotted hyenas in the three land-use types was common in patches with clayey soil, although they are recorded to den in different habitat types (Holekamp & Dloniak, 2010; Pokines & Peterhans, 2007) and other favourable areas of the landscape. Generally, clay burrows are less likely to collapse than those in sandy soils (pers. obs.).

Spotted hyenas are generally known to prefer open landscapes where they hunt, but they are occasionally found in densely vegetated patches as they search for prey (Kolowski & Holekamp, 2009) and cover. Prey availability is important for survival of a carnivorous species like the spotted hyena (Trinkel *et al*., 2004; Honer *et al*., 2005; Owen-Smith, & Mills 2008). Thus, carnivore management greatly emphasises habitat organisation that promotes an increase in food availability within the home range.

2.5 Conclusions

Various factors, including disturbances by humans through spatial and temporal use of various landscapes, influences prey distribution and habitat selection by spotted hyenas. As such, studies focusing on the basic ecological requirements in terms of habitat occupancy are essential for better management of a conflict-prone carnivore such as the spotted hyena. In summary we found that soil type, land-use type and vegetation determined site occupancy of spotted hyena. Their occupancy was generally determined by soil type for denning sites. Our study is a precursor to more in-depth studies of behavioural flexibility and modifications, and spatiotemporal habitat preferences of this large carnivore in disturbed habitat, particularly in relation to degree of anthropogenic disturbance in a range of conservation land-use areas, and outside protected areas in southern Africa and elsewhere.

2.6 Acknowledgements

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CHAPTER 3

Spotted hyena co-occurrence with mesocarnivores across a wildlife management gradient (ranch, hunting area and national park) in western Zimbabwe

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Running header: Spotted hyena co-occurrence with mesocarnivores

3.0 Abstract

Anthropogenic habitat change generally affects the behaviour of wildlife. We used camera-traps to investigate the spatial habitat use and co-occurrence of spotted hyena C*rocuta crocuta* with serval *Leptailurus serval,* black-backed jackal *Canis mesomelas* and African civet *Civettictis civetta* along an anthropogenic disturbance gradient of three wildlife management land-use types (safari (hunting) area, ranch and national park) in western Zimbabwe, during respective wet and dry seasons. We predicted that mesocarnivores would avoid habitat patches with spotted hyenas in the three land-use types and that there would be seasonal variation in temporal overlap between spotted hyena and mesocarnivores. We used single-season two-species detection models to test co-occurrence between pairs of species. We found that the detection probability of serval increased with presence of spotted hyenas on the ranch as a function of low leopard detection. Serval and black-backed jackal showed high detection probabilities in the safari area during the wet (n = 13; 53) and dry (n = 22; 63) seasons respectively. Detection probability of African civet increased in the presence of spotted hyena in the safari area (n = 19) during the wet season and on the ranch (n = 45) during the dry season as a function of rocky habitats and mixed vegetation. Detection of black-backed jackal varied negatively where spotted hyena were detected as a function of road network in the park, but increased on the ranch. Temporal coefficients of overlap were high for all pairs of species implying that they were more likely to be co-detected at the same sites. Although mesocarnivores increased activity in the more anthropogenically disturbed land-use types (hunting area and ranch), changes in land management and top predator introductions should consider how optimal use of the habitat by small carnivores is affected.

Keywords Prey; Camera-trap; detection; Coexistence; Competitive exclusion

3.1 Introduction

Natural habitat use by spotted hyena *Crocuta crocuta* is a function of various factors including land-use type, vegetation type, presence of other animals and anthropogenic disturbances within the landscape among other variables (Haswell et al. 2016; Rota et al. 2016). Land-use type generally influences the level of disturbance and hence affects species assemblages. (Woodroffe and Ginsberg 1998; Boydston et al. 2003; Kolowski and Holekamp 2009). For example, in Zimbabwe, the extent of disturbance aligns with the land-use type, increasing respectively from protected area to safari area and ranch.

Generally, occurrence of large carnivores in a habitat patch depends largely on prey (Holekamp et al. 1997; MacKenzie et al. 2002a). Top predator management is a crucial component of wildlife conservation as they play top-down influences on various herbivores and mesocarnivores (Letnic et al. 2012; Yarnell et al. 2013; Ferreira and Funston 2016). Spotted hyena interaction with the environment is of paramount importance as that affects the species' long-term population dynamics (Ferreira and Funston 2016) and that of its conspecifics as well as mesocarnivores (Hayward and Kerley 2008; Rota et al. 2016) and prey. The utilisation of the resources is not as random as it would be in the absence of competition or predation (Palomares and Caro 1999; Letnic et al. 2012; Yarnell et al. 2013). Animals of the same size and niche tend to show a similar pattern in habitat use (Farris et al. 2015) and similar or different temporal activity (Farris et al. 2015) due to individual species' preferences. Such temporal variation is crucial in avoiding competition and confrontation. Hence, understanding inter-specific interactions is prioritised (Palomares et al. 1995; Letnicet al. 2012) in the management of the spotted hyena (Palomares et al. 1995; Ferreira and Funston 2016).

Significant efforts have been made in researching on the coexistence of spotted hyena and lions *Panthera leo* in various tropical ecosystems (Hayward and Kerley 2008; Watts and Holekamp 2009) but more research still needs to be done on its interaction with small carnivores (Ramesh et al. 2017a,b). Managing the habitat to enhance survival of a single species may have adverse effects on other species within the habitat (Zipkin et al. 2010). Since habitat use is a response to resource availability, some species may occur within a habitat and may be preyed on, fought out of the habitat or fear the hyena because of small body size (Damon et al. 2015; Wang et al. 2015). Body size has been recorded to have an effect in the interaction of carnivore guilds (Damon et al. 2015). The smaller species fear the large ones thereby affecting resource use by the inferior species (Rota et al., 2016) resulting in top-down effects on the weaker competitor. Some species on the other hand can be found in a habitat because of facilitation by another species (Wang et al. 2015) and can influence the detection of both species in that particular habitat patch. In studying species co-occurrence, environmental factors, presence or absence of interacting species and other variables are key to understanding species interaction (Rota et al. 2016). However, failure to understand such interspecific interactions may lead to biased presumptions and decision making in the modelling and management of ecosystem dynamics (Rota et al. 2016). Furthermore, seasonal variations in environmental attributes may lead to changes in behavioural responses of various species with respect to habitat use. This may incorporate migration of one species (mostly prey) which may trigger the other species (mainly predator) to change feeding and habitat use strategies. This could result in the predator following prey, leading to decreased detection of both, or it may result in the predator shifting to alternative prey. Such a change in the feeding strategy triggers interference from other predators that mainly feed on that alternative prey. It may also result in varied temporal use of the habitat by the inferior species thereby explaining existence of complex interactions involving a balance between risk and the need to forage (Wang et al. 2015).

Mesopredators show variation in their adaptation to a mosaic of habitats with large predators (Schuette et al. 2013; Wang et al. 2015) and human development (Chen and Koprowski 2015; Wang, Allen and Wilmers 2015), however, such adjustments are species specific (Yarnell et al. 2013). Some species may not be detected when present in an ecosystem, especially when using methods like radio telemetry or den observations (MacKenzie et al. 2002b). Failure to detect them indicates avoidance of certain habitat patches by the species due to presence of large carnivores like the spotted hyena within the ecosystem (Ramesh et al. 2017). It may also be due to inefficiencies of the techniques used in attempting to detect the species (Driessen et al. 2017). Recently, camera-traps have been a useful tool for studying elusive species (Ramesh and Downs 2013; Cusack et al. 2015; McShea et al. 2015; Driessen et al. 2017), and some have been detected in ranges where they were considered absent. However, although effective, camera-traps may fail to detect all species present because they depend on the targeted species passing within the infrared sensor detection range (Pease et al. 2016; Driessen et al. 2017). Furthermore, as land-use change continues to increase and habitats fragment, it is important to document the behavioural responses of mesocarnivores in the presence of large carnivores (Boydston et al. 2003; Haswell et al. 2016) and human disturbance (Wang et al. 2015).

Relatively little published information exists on the impact of and investigate the spatial habitat use and co-occurrence of spotted hyena with serval *Leptailurus serval*, black-backed jackal *Canis mesomelas* and African civet *Civettictis civetta* along an anthropogenic disturbance gradient of three wildlife management land-use types (safari (hunting) area, ranch and national park) in western Zimbabwe, during respective wet and dry seasons. We predicted that mesocarnivores would avoid habitat patches with spotted hyenas in the three land-use types and that there would be seasonal variation in temporal overlap between spotted hyena and mesocarnivores coexistence (Schuette et al. 2013; Ramesh et al. 2017b). In addition, literature is available on spotted hyena ecology but little is known about serval, black-backed jackal and African civet interactions with spotted hyena. Therefore, the aim of our study was to determine spotted hyena co-occurrence with mesocarnivores along an anthropogenic disturbance gradient of three wildlife management land-use types (safari (hunting) area, ranch (wildlife and cattle farming) and national park) in western Zimbabwe during respective wet and dry seasons. We predicted that mesocarnivores avoid habitat patches with spotted hyenas in the three land-use types. We further predicted that there would be seasonal variation in co-occurrence and temporal overlap between spotted hyena and mesocarnivores as well as among mesocarnivores in the study area.

3.2 Methods

Study sites

The study was carried out in three protected areas (Fig. 3.1) that differed in conservation land-use management in western Zimbabwe, namely Dimbangombe Ranch (DR, mixed wildlife and cattle farming, 18^0 11.202' S, 25^0 52.500' E), Matetsi Safari (hunting) Area (MSA, (18^0 22.760' S, 25^0 52.353' E) and Zambezi National Park (ZNP, 17^0 57.341' S 25^0 41.399' E). These sites were perceived to have an impact on habitat use by mesocarnivores and large carnivores because of the different management practices. ZNP is situated near Victoria Falls and stretches along the Zambezi River (Crosmary et al., 2013). MSA bounds it to the southeast and Victoria Falls town to the North. It covers approximately 560.1 km^2.

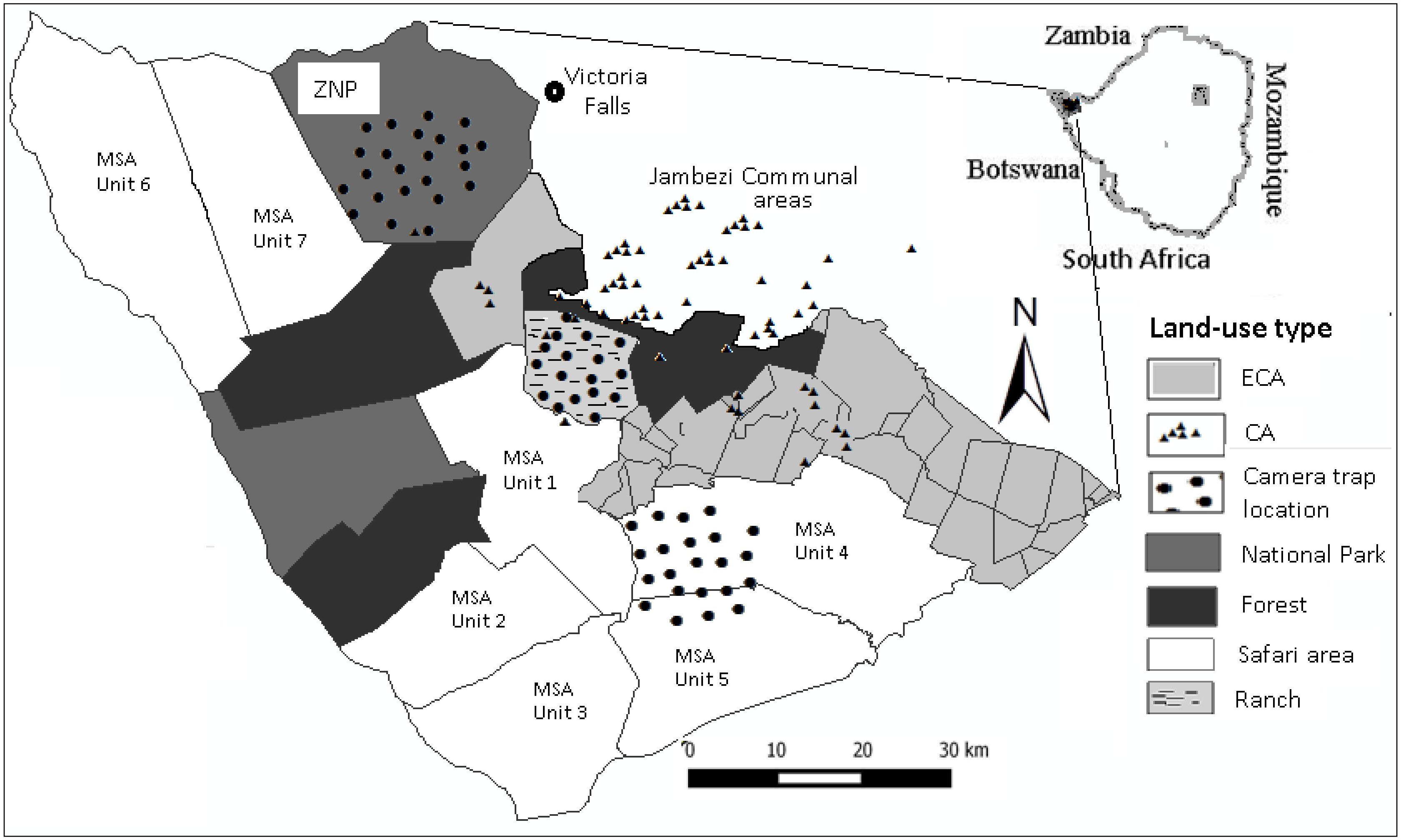


Fig 3.1 Camera-trap locations at Dimbangombe Ranch (DR), Matetsi Safari Area (MSA) and Zambezi National Park (ZNP) during the wet and dry seasons. (ECA - Environmental Conservation Areas-resettlement areas for community-based natural resources management with fixed number of households, CA - communal areas – human settlements with no fixed number of households. ECA and CA are villages in or around the conservation areas).

The greatest part of ZNP is mainly Kalahari sands with patches of rocky terrain (Ndaimani et al. 2014) and clayey portions especially northwards to the Zambezi River flood plain, to which the landscape slopes.. The study focused on Chamabondo, which is the southern part of the park. There is no hunting in the park (Parks-and-Wildlife-Act 1975, Ndaimani et al. 2014). MSA, established in the early 1970s, is a vast area comprised of six hunting units and one photographic concession (Crosmary et al. 2013). The area is bounded by Hwange National Park to the south, resettlements to the northeast and DR to the northwest. MSA is Zimbabwe's oldest hunting safari area covering approximately 3000 km^2. The study concentrated on Unit 4 (470 km^2) and Unit 5 (370 km^2) which were readily accessible through a permit from Parks and Wildlife Management Authority while other sections were leased to private safari operators. DR lies 34 km southeast of Victoria Falls town and spans 32 km^2. MSA Unit 1 borders it to the southeast, Fuller Forest to the north and part of Matetsi Environmental Conservation Area (ECA) to the west. However, the adjacent part of the nearby forest utilised by the ranch was also included in this study resulting in an effective 68 km^2 area for the ranch. The ranch has a resident mixed large herd of cattle, sheep and goats managed through a planned holistic rotational grazing system in unfenced paddocks with transferrable night corals (Savory and Parsons 1980). Livestock guarding is all year round to minimise losses to predators although in nearby communities domestic animals are allowed to free range during the dry season (Kuiper et al. 2015).

The study sites lie in a dry region characterised by low rainfall (below 650mm p.a.) with recurrent droughts (Ndaimani et al. 2013) and a relatively long dry season stretching from May to November while the wet season starts in December ending in April. The mean monthly temperature is 32° C in October and 25° C in July (Ndaimani et al. 2014). Herbivores include impala *Aepyceros melampus*, sable antelope *Hippotragus niger*, and greater kudu *Tragelaphus* *strepsiceros* among others. Large carnivore species present include lions, cheetah *Acinonyx jubatus*, African wild dog *Lycaon pictus* and leopard *Panthera pardus* (Crosmary et al. 2013, Ndaimani et al. 2014). Some of the mesocarnivores include serval, black-backed jackal and African civet.

Data collection

We conducted a non-invasive survey using passive infrared Moultrie M880 Trail Campro LLC (Springfield, USA) and Ltl Arcon 6210MC (China) motion detector camera-traps that were deployed at 60 locations in the three study sites (Fig 3.1). These were established using ArcMap Version 10.3 (ESRI Redlands, CA, USA) based on the central points of predetermined 9 km^2 grids overlaid on the study site map and at least to have two/ three sampling points within an individual hyena home range (ca. 30-45 km^2). We mainly placed each camera-trap within 500 m radius from the predetermined central point of the individual grid wherever higher evidence of hyena were recorded during the carnivore sign survey. Data on other species were by-catch information from camera-traps and were found useful in attempting to explain spotted hyena coexistence with mesocarnivores in the area. Camera-traps were active 24 h/day, with a 60 s delay between consecutive photographs, and the sensitivity of the motion sensor was set to high. Inter-camera distance was 3 ± 0.2 km with 22, 16 and 22 sites at MSA, DR and ZNP respectively. To increase detection probability of spotted hyena, placement of camera-traps at highly probable locations like along animal trails were considered. Camera-traps were tied on trees at 45 cm above the ground in order to increase quality of pictures (Ramesh et al. 2012). Camera-traps were left for 30 days per site per season (wet and dry respectively) resulting in 3600 trap nights. Co-occurrence of species is a function of natural behaviour hence we did not use attractants at our camera-trap stations. We assumed that occurrence of smaller species was dependent on the occurrence of a spotted hyena, but the presence of the hyena was independent of the small species. Fifteen site and two sample specific covariates were used in the regression model. We characterized microhabitat at each camera-trap location within a 15 m radius and covariates thought to influence detection probabilities were dominant vegetation types teak *Baikiaea plurijuga*, mopane *Colophospermum mopane*, mixed vegetation, grassland, soil types (clayey, sand and rocky), fire incidence and canopy cover (open or closed). In addition, we recorded distance to nearest water sources, distance to nearest human settlement, distance to nearest frequently used road by vehicles at each camera-trap location using geographic locations of the camera-trap from pre-marked points on a global positioning system (GPS eTrex 30; Garmin, Olathe, KS, USA). We recorded whether the camera-trap was placed within park, ranch or safari as a binary variable (0/1). We created matrices for each species spanning a 24 h survey (00:00 – 23:59) in columns and rows consisting of camera-trap numbers. We developed detection histories of prey and spotted hyena as ̔1', '0' or '.' for each observation where '1' indicated one or multiple occurrences within the particular 24 h period, '0' indicated no record, and '.' meant malfunction of the camera-trap. We used mesocarnivore species, i.e., African civet, serval and black-backed jackal, as sampling covariates. These variable measurements and species detection histories were generated separately for each season.

Data analyses

To avoid multi-collinearity, we tested for correlations among site covariates (Graham 2003) and retained the least correlated variables in the models. Subsequently we removed the variable 'sand soil' as this variable was highly correlated other covariates. Detection histories were pooled from the three study sites and analysed in a single-season two-species occupancy model (MacKenzie

Bailey and Nichols 2004) for each season to explain species interactions. Thus, three days were pooled to be one survey to increase detections thus resulting in ten surveys for each season (wet and dry seasons respectively). Land-use variation and other covariates were thought to influence co-occurrence of black-backed jackal, serval and African civet in relation to spotted hyena detection.

Data on detection of African lion and leopard were insufficient and were thus included in the regression as sampling covariates but could not be used to assess the complete carnivore guild in the area. As such, only data for occurrence of the spotted hyena and the three mesocarnivores was used in this study. Only data with at least 30 % presence per individual species were considered for the regression. Although interspecific interactions occur in different ways between numerous species (Rota et al., 2016), we used single season two-species occupancy models to assess whether the presence of a species affected the detection probability of another co-occurring species at camera-trap sites (MacKenzie et al. 2004) in Program PRESENCE 8.3 (Hines 2006) w.r.t. co-occurrence of the spotted hyena with other species in western Zimbabwe. We restricted our analyses to detection probabilities of species because spacing between camera-trap sites were insufficient to provide spatial independence within a spotted hyena home range (Boydston et al. 2005), which was the dominant species. Potential covariates for species co-occurrence were allowed to vary individually, or in combination, and models with all potential detection probabilities were produced (Burnham and Anderson 2002; Ramesh et al. 2012). A more detailed description about model parameters is explained in Table 3.1. We selected the best models from the candidate models following the framework of Burnham and Anderson (2002). The best model with the lowest AIC value ($\leq 2\Delta$AIC) and high Akaike weights was selected to estimate detection probability parameters. We used delta parameterization option and considered detection of species interaction factor (SIF) values <1 to indicate that camera-traps were less likely to detect the spotted hyena during a 24 h period provided that any of the mesocarnivore species were detected during the same period. The SIF values >1 were considered to indicate that the species were more likely to co-occur in the same 24 h period. SIF = 1 indicated that the two species occurred independently without avoidance (Richmond et al. 2010; Ramesh et al. 2017b).

We further investigated temporal activity of the carnivore species by analysing the effect of spotted hyena activity on mesocarnivores during the respective wet and dry seasons in the three land-use types. We converted time from the 24 h format to radians and used that to determine fitted kernel densities of animal activity using the package 'Overlap' (Meredith and Ridout, 2017) in Program R version 2.1 (R Core Team 2015). We measured the kernel density estimates of temporal overlap of activity patterns between pairs of species using the coefficient of overlapping (Ridout and Linkie 2009; Meredith and Ridout 2017). Overlaps were plotted for pairs of species and compared season wise.

3.3 Results

We recorded 31 species of mammals from the 3600 camera-trap nights. Spotted hyena were detected more on the ranch during the wet season (n = 55) while they were highly detected in the park during the dry season (n = 94). Serval and black-backed jackal showed high detection in the safari area during the wet (n = 13; 53) and dry (n = 22; 63) seasons respectively. African civet were detected more in the safari area (n = 19) during the wet season and on the ranch (n = 45) during the dry season. Overall, the spotted hyenas were detected more than the mesocarnivores at all the stations during both the wet (48.3 %) and dry seasons (83.3%) (Table 3.2).

Table 3.1 Occupancy model parameters for detection as defined and used in this study.

Parameter with description
PsiA -probability of site occupancy for species A, regardless of occupancy status of species B
PsiB - probability of site occupancy for species B, regardless of occupancy status of species A
pA - probability of detection for species A, given species B is absent
pB - probability of detection for species B, given species A is absent
rA - probability of detection for species A, given species A and B are present
rB - probability of detection for species B, given species A and B are present
An expression of whether two species co-occur independently at survey sites $\boldsymbol{Phi = \frac{Psi\ AB}{PsiA\ X\ PsiB}}$ **Where, PsiAB is the probability of both species being present.**
An expression of whether two species are detected independently at survey sites, and termed a ‘detection species interaction factor’ (SIF); is defined by the following equation: $\boldsymbol{Delta = \frac{rAB}{rA\, rB}}$ **Where, rAB is the probability of detecting both species,**

Wet season

Spotted hyena and serval: The top ranking model within ≤2ΔAIC indicated that spotted hyena had a high probability of detection compared with the serval (Table 3.3). Overall, the detection probabilities of spotted hyena were lower in the absence ($p^{spotted\ hyena}$ = 0.075, SE = 0.038) than in the presence ($r^{spotted\ hyena}$ = 0.266, SE = 0.036) of serval. The detection probabilities of serval were lower in the absence (p^{serval} = 0.077, SE = 0.047) than in the presence (r^{serval} = 0.167, SE = 0.039) of spotted hyena. The probabilities of detecting serval at camera-trap locations where spotted hyenas were detected, were lower (r^{serval} = 0.114, SE = 0.029) in the park and safari area, and increased on the ranch (r^{serval} = 0.300, SE = 0.063). There were high probabilities of detecting serval in the absence of spotted hyena where leopard detection was high (β = 1.154, SE = 0.963) in the national park (r^{serval} = 0.102, SE = 0.047) compared with the safari area (r^{serval} = 0.085, SE = 0.045) and the ranch (r^{serval} = 0.030, SE = 0.013). The delta value was 1.642 (SE = 0.289). In general, the possibility of detecting the species together was higher than detecting them in the absence of one another. Both species showed more nocturnal activity and the mean kernel density temporal overlap coefficient estimate (Dhat4) with 10,000 smoothed bootstrap was high (0.78). Peak activity for both species was observed around the midnight hours with the serval showing less avoidance of the spotted hyena within the 24-h period (Fig. 3.2).

Spotted hyena and African civet: The top ranked model within ≤2ΔAIC indicated that African civet had an overall low site detection compared with spotted hyena. Detection of spotted hyena was less in the absence ($p^{spotted\ hyena}$ = 0.0314, SE = 0.031) than presence ($r^{spotted\ hyena}$ = 0.228, SE = 0.033) of African civet. Similarly, the detection probabilities of African civet independent of spotted hyena were less (p^{civet} = 0.030, SE = 0.026) compared with camera-trap locations where spotted hyena were detected (r^{civet} = 0.108, SE = 0.036).

In areas where spotted hyena were detected (r^{civet} = 0.108, SE = 0.036), the African civet were strongly likely to be detected in rocky habitats (β = 1.726, SE= 0.724) or in mixed vegetation (β = 1.249, SE = 0.745). African civet activities were limited to the dark hours making it predominantly nocturnal and the mean kernel density temporal overlap coefficient estimate (Dhat4) was high (0.77).

Table 3.2 Detection level of spotted hyena and mesocarnivores at Dimbangombe Ranch, Matetsi Safari Area and Zambezi National Park in western Zimbabwe

Season	Species	Number of independent photos			Percentage of stations detecting species
		Park	Safari	Ranch	
Wet	Spotted hyena	32	44	55	48.3 % (n = 29)
	Serval	1	13	9	38.3 % (n = 23)
	Black-backed jackal	4	53	28	26.7 % (n = 16)
	Civet	5	19	15	36.7 % (n = 22)
Dry	Spotted hyena	94	71	60	83.3 % (n= 50)
	Serval	9	22	11	53.3 % (n = 32)
	Black-backed jackal	9	63	40	26.7 % (n = 16)
	Civet	7	9	45	38.3 % (n = 23)

Spotted hyena and black-backed jackal: Spotted hyena had an overall high site detection compared with black-backed jackal. Detection probabilities of spotted hyena at camera-trap locations were independent of black-backed jackal ($p^{spotted\ hyena}$ = 0.074, SE = 0.0.038), and were less than in locations where black-backed jackal were detected ($r^{spotted\ hyena}$ = 0.257, SE = 0.037). Detection probability of black-backed jackal at camera-trap locations where spotted hyena were not detected (p^{jackal} = 0.078, SE = 0.0.036) were less than at locations where spotted hyena were detected (r^{jackal} = 0.138, SE = 0.042). The detection probabilities of black-backed jackal in the presence of spotted hyena were negatively influenced by the road network (β = -0.541, SE = 0.233), especially in the national park (β = -1.261, SE = 0.650). In addition, detection probabilities of black-backed jackal in the presence of spotted hyena were higher on the ranch (r^{jackal} = 0.216, SE = 0.048) and in the safari area (r^{jackal} = 0.159, SE = 0.040) than the national park (r^{jackal} = 0.062, SE = 0.038). The delta estimate for the top supported model was 1.761 (SE = 0.304). Spotted hyena and black-backed jackal showed nocturnal activity and the mean kernel density temporal overlap coefficient estimate (Dhat4) was high (0.88).

Dry season

Spotted hyena and serval: Overall site detection probabilities of spotted hyena and serval varied in the dry season. Detection probabilities of spotted hyena in the absence ($p^{spotted\ hyena}$ = 0.073, SE = 0.038) and presence ($r^{spotted\ hyena}$ = 0.265, SE = 0.036) of serval varied greatly.

Table 3.3 Top ranking models (2≤AIC) on wet season co-occurrence of spotted hyena with mesocarnivores at Matetsi Safari Area, Dimbangombe Ranch and Zambezi National Park.

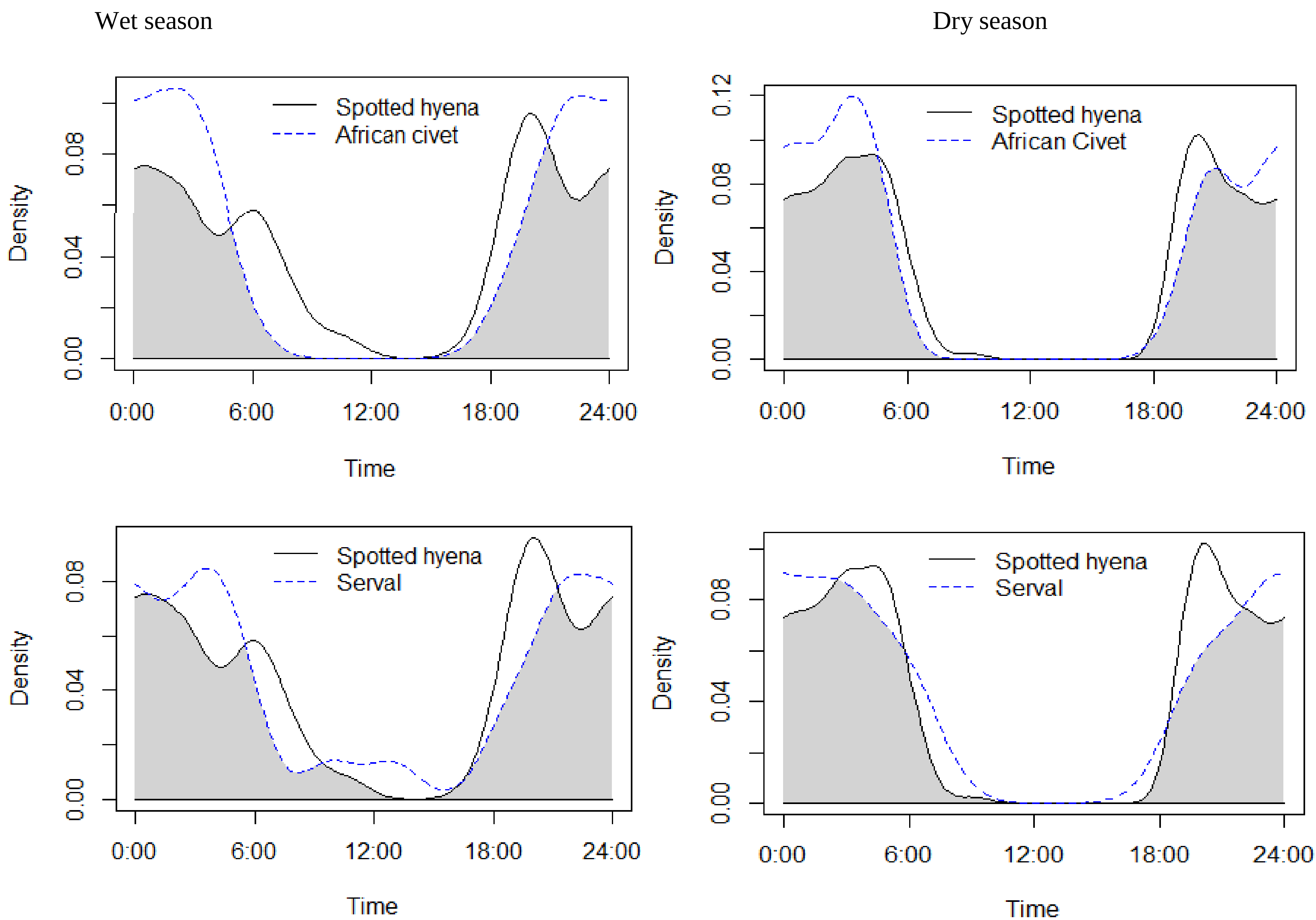
	Model	**AIC**	**ΔAIC**	**AIC wgt**	**Model Likeli-hood**	**No. Par.**	**-2Log Like**
Hyena-serval	psiA, psiB, phi, pA, pB(ranch + leopard), rA, rB(ranch), delta	675.59	0.00	0.42	1.00	11	653.59
Hyena-serval	psiA, psiB, phi, pA(ranch + lion), pB, rA, rB(ranched + mixed), delta	676.85	1.26	0.23	0.53	13	650.85
Hyena-civet	psiA, psiB, phi, pA, pB, rA, rB(rock + mixed), delta	609.17	0.00	0.67	1.00	10	589.17
Hyena-jackal	psiA, psiB, phi, pA, pB, rA, rB(road + park), delta	676.69	0.00	0.43	1.00	10	656.69
Hyena-jackal	psiA, psiB, phi, pA(lion), pB, rA, rB, delta	678.43	1.74	0.19	0.42	9	660.43

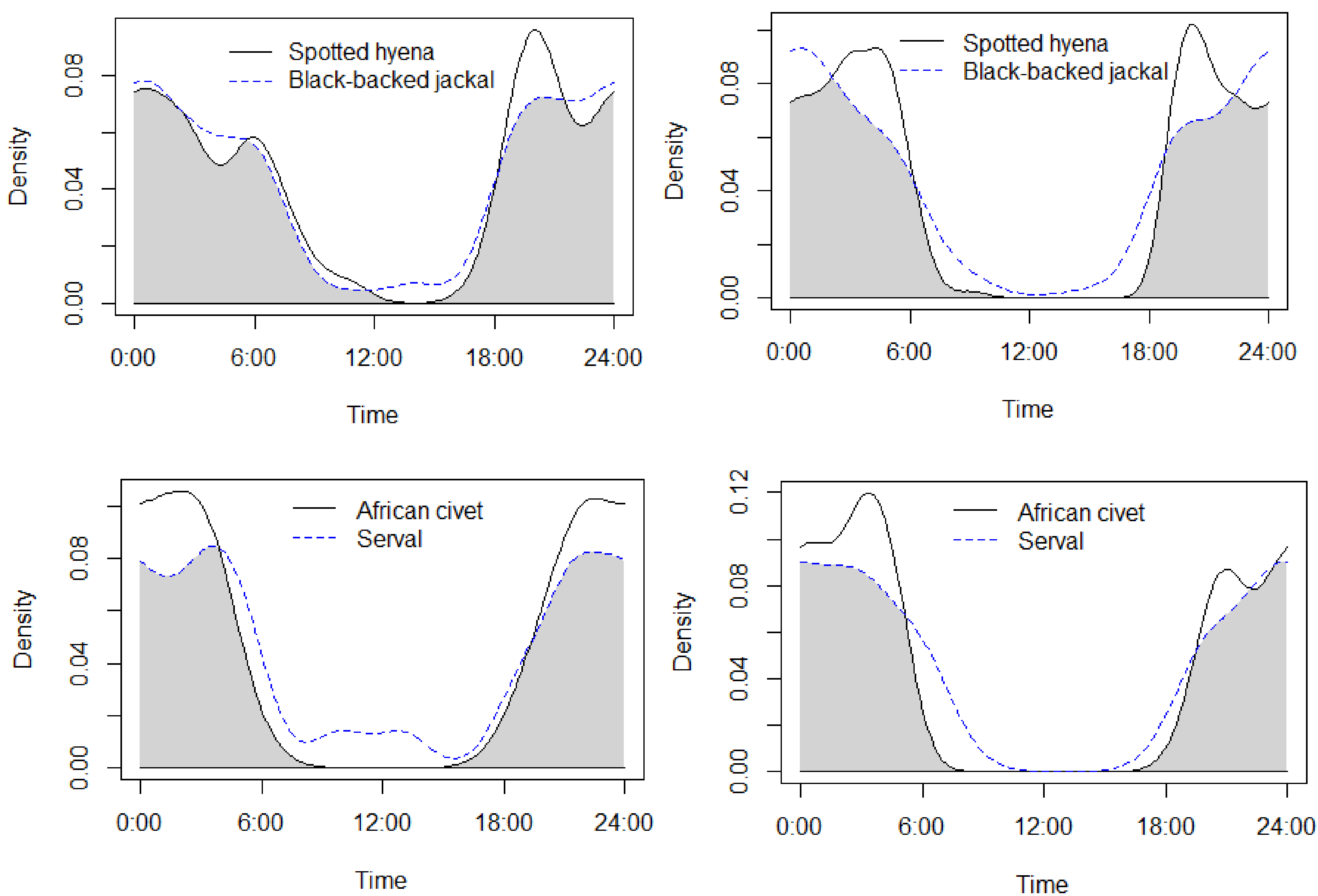
Delta AIC = the difference in AIC values between each model and the model with the lowest AIC; AIC wgt = the model weight; Model Likelihood = Probability of encounter histories; no. Par. = Number of parameters in the model; -2*LogLike = Twice the negative log-likelihood

Table 3.4 Top ranking models (2≤AIC) on dry season co-occurrence of spotted hyena with mesocarnivores at Matetsi Safari Area, Dimbangombe Ranch and Zambezi National Park.

	Model	**AIC**	**ΔAIC**	**AIC wgt**	**Model Likelihood**	**No. Par.**	**-2Log Like**
Hyena-serval	psiA, psiB, phi, pA, pB(leopard), rA, rB(ranch), delta	674.43	0.00	0.57	1	10	654.43
Hyena-civet	psiA, psiB, Phi, pA(grass), pB, rA, rB, delta	790.55	0.00	0.43	1.00	9	772.55
Hyena-civet	psiA, PsiB, Phi, pA(park), pB, rA, rB, delta	791.05	0.48	0.34	0.78	9	773.03
Hyena-jackal	psiA, psiB, phi, pA, pB, rA(park), rB, delta	851.35	0.00	0.56	1.00	9	833.35
Hyena-jackal	psiA, psiB, phi, pA, pB, rA(park + rock), rB, delta	852.23	0.88	0.36	0.64	10	832.23

Delta AIC = the difference in AIC values between each model and the model with the lowest AIC; AIC wgt = the model weight; Model Likelihood = Probability of encounter histories; no. Par. = Number of parameters in the model; -2*LogLike = Twice the negative log-likelihood


Wet season
Dry season
Spotted hyena
African civet
Spotted hyena
African Civet
Spotted hyena
Serval
Spotted hyena
Serval
Density
Time
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00


Spotted hyena
Black-backed jackal
Density
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Time
Spotted hyena
Black-backed jackal
Density
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Time
African civet
Serval
Density
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Time
African civet
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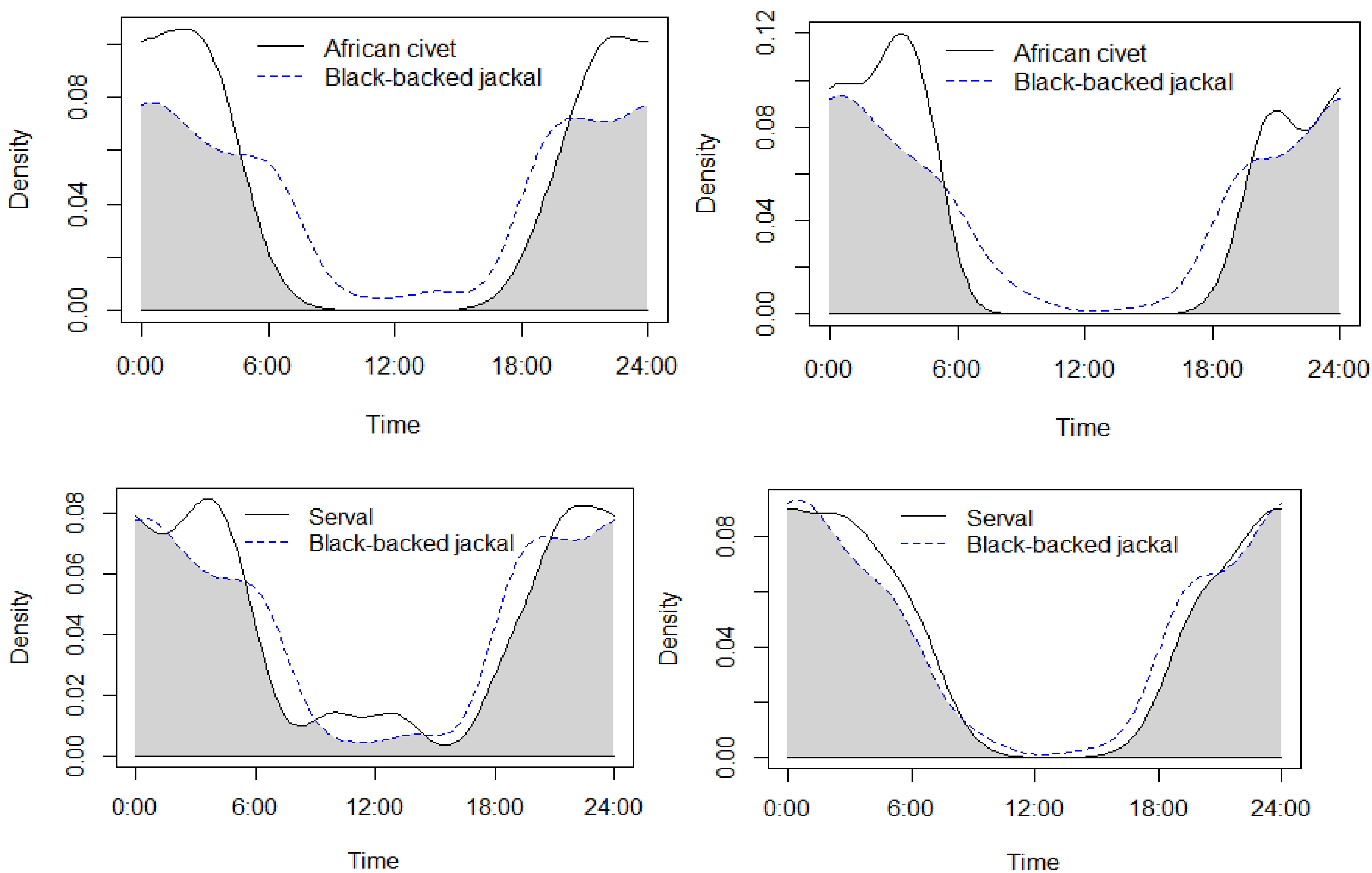

Fig 3.2 Temporal overlap activity of the spotted hyena and mesocarnivores during the wet and dry seasons in western Zimbabwe. The coefficient of overlapping equals the area (shaded) below both curves.

Detection probabilities of serval in the absence (p^{serval} = 0.081, SE =0.046) and presence (r^{serval} = 0.167, SE = 0.039) of spotted hyena varied and these were a function of leopard presence (β = 1.319, SE = 0.973, Table 3.4). Detection of serval on the ranch (β = 1.268, SE = 0.412) was more in the presence of the spotted hyena. The delta estimate for the top supported model was 1.641 (SE = 0.160.289). Both spotted hyena and serval were nocturnal during the dry season (Fig. 3.2) and the mean kernel density temporal overlap coefficient estimate (Dhat4) was high (0.83).

Spotted hyena and African civet: The top model within ≤2ΔAIC indicated that overall site detection of spotted hyena was higher than civet during the dry season. Detection probabilities of spotted hyenas differed little at camera-trap locations not occupied by African civet ($p^{spotted\ hyena}$ = 0.307, SE = 0.060) from those at occupied locations (r^{hyena} = 0.299, SE = 0.035). Probabilities of detecting African civet in the absence (p^{civet} = 0.037, SE = 0.014) of spotted hyena were lower than in the presence (r^{civet} = 0.297, SE = 0.037) of spotted hyena. Detection probabilities of spotted hyena in the absence of African civet were higher in grassland (β = 1.668, SE = 0.561), particularly on the ranch ($p^{Spotted\ hyena}$ = 0.339, SE = 0.061) than the other land-use types. The delta estimate for the top supported model was 1.481 (SE = 0.185). Both species exhibited nocturnal activity (Fig. 3.2) and the mean kernel density temporal overlap coefficient estimate (Dhat4) was high (0.86).

Spotted hyena and black-backed jackal: The top model within ≤2ΔAIC indicated that spotted hyena had an overall high detection compared with blacked-backed jackal. Detection probabilities of spotted hyena in the absence of black-backed jackal were lower ($p^{spotted\ hyena}$ = 0.108, SE = 0.040) than when present ($r^{spotted\ hyena}$ = 0.195, SE = 0.034). Detection probabilities of black-backed jackal in the absence of the spotted hyena (p^{jackal} = 0.074 SE = 0.044) were lower than in the presence (r^{jackal} = 0.357, SE = 0.031) of spotted hyena. Detection probabilities of spotted hyena in the presence of black-backed jackal were high, and similar on the ranch and safari area ($r^{spotted\ hyena}$ =0.255, SE = 0.037) but were lower in the national park ($r^{spotted\ hyena}$ = 0.0196, SE = 0.030; β = -1.221, SE = 0.401). The delta estimate for the top supported model was 1.179 (SE = 0.173). Overall, both species exhibited nocturnal activity during the dry season (Fig. 3.2) and the mean kernel density temporal overlap coefficient estimate (Dhat4) was high (0.85).

Although interaction detection probabilities among mesocarnivores were not assessed in this study, mean kernel density temporal overlap coefficient estimate (Dhat4) was high for the wet and dry seasons respectively for all pairs of species: African civet and serval (0.77; 0.82), African civet and black-backed jackal (0.78; 0.82), as well as serval and black-backed jackal (0.79; 0.85). Activity patterns of serval and black-backed jackal were similar during the dry season and varied slightly during the wet season (Fig. 3.2).

3.4 Discussion

Mesocarnivores often forage under the fear of top-predators (Erik and Russell 2009; Ramesh et al. 2017b), hence their populations and habitat use are largely dependent on the occurrence of large carnivores present in the area (Letnic et al. 2012; Damon et al. 2015; Ramesh et al. 2017a,b). It is therefore appropriate for mesocarnivores to optimise foraging while reducing high-risk habitats where large carnivores occur (Ritchie and Johnson 2009). Through site-specific presence/absence data, we explored interactions between the spotted hyena and three highly detected mesocarnivores in Matetsi Safari Area, Dimbangombe Ranch and Zambezi National Park in western Zimbabwe to explain top-down influences of large carnivores (Ritchie and Johnson 2009; Letnic et al. 2012) under varying land-use types. The influence of large carnivores on mesocarnivores employs the fear factor (Roemer et al. 2009; Suraci et al. 2016; Ramesh et al. 2017b), often in terms of body mass, which results in restricted access to resources within the landscape (Palomares et al. 1995). Such an interaction results in adaptive behavioural changes in the mesocarnivore to enhance their survival. However, since prey distribution is often the major determining factor in spatial selection of habitat by predators (Bell et al. 2009), differences in prey preference allows for coexistence of the carnivores, albeit the smaller species also avoiding the large carnivores. Overall, we observed that hyena and mesocarnivores most likely were co-detected at the same sites within a 24 h period although increase/decrease in detection probability of mesocarnivores was influenced by land-use type, leopard detection, and habitat features.

The structural complexity of the landscape, however, reduced the magnitude of spotted hyena impact on serval. For example, during the dry season, serval detection probability was high in the presence of spotted hyena in the park compared with the other land-use types, and especially in the presence of the leopard. However, detection was high on the ranch during the dry season which was attributed to the likely avoidance between leopard and hyena (Ramesh et al. 2017b), with serval probably taking opportunities to use the habitat effectively when spotted hyenas were not detected (Watts et al. 2010; Ramesh et al. 2017b), so likely less of a deterrent influence on serval.

Furthermore, increased detection of serval on the ranch compared with the other land-use types could be due to increased adaptation of this mesocarnivore to anthropic areas, which become refuge sites from predation risk by large top hunting carnivores (Schuette et al. 2013; Ramesh et al. 2017a). Since larger carnivores are hunted as trophies on the ranch, that could have had an influence on their presence and detection, which then affected the interaction of serval and these top predators. Consequently, high activity of the serval in the absence of spotted hyena is an indicator of possible avoidance of direct contact with larger carnivores.

African civet and serval feed predominately on small mammals while the spotted hyena feeds on medium-sized prey especially various sizes of ungulates (Holekamp et al. 1997; Kolowski et al. 2007; Ramesh and Downs 2015). Mesocarnivores may reduce or abandon foraging in certain habitat patches in order to avoiding direct contact with large carnivores like the spotted hyena (Caro and Stoner 2003; Succari et al. 2016: Ramesh et al. 2017b). Although the spotted hyena does not compete directly for prey with African civet, black-backed jackal or serval, the small overlap of small prey and habitat preference (for example rocky areas and mixed vegetation) may create fear leading to spatial avoidance for mesocarnivore when they are detected with large species in the same area.

During the wet season, serval were more active on the ranch compared with the safari area and national park, but in both land-use types it reduced activity when spotted hyena were present. Serval had high detection probability on the ranch during both wet and dry seasons while black-backed jackal had high detection probability in the safari area during the wet season and on the ranch during the dry season. The behaviour of serval showed that it varies temporal site use in the presence of the large carnivores similar to Ramesh et al. (2017b). However, detection of African civet within a 24 h period was not affected by the presence of the spotted hyena during the wet season. This behaviour in the African civet could be attributed to temporal variation in space use within the same 24 h period. Thus, African civet probably effectively avoided direct contact with spotted hyena and optimised foraging even in habitats where spotted hyena were detected (Schuette et al. 2013; Wang et al. 2015). Although overall detections of African civet were higher in the safari area and ranch during both the wet and dry seasons respectively, top models revealed that there was no influence of land-use type on the detection probabilities of African civet in the presence or absence of spotted hyena during the wet season. African civet preferred rocky patches intercropped with grasslands (Admasu et al., 2004) hence detection probabilities increased in that habitat type (Gerber et al. 2012), and similar habitat effects on interactions were recorded by Ramesh et al. (2017b). In the dry season, African civet were detected more frequently when spotted hyena were absent compared with the wet season. Such behaviour was attributed to change in vegetation cover and thus the species restricted itself to habitats that optimised survival in terms of foraging while reducing predation risk (Suraci et al. 2016). Spotted hyena somehow affects the African civet because detection of the latter decreased considerably when spotted hyena were present as in other studies (Roemer et al. 2009; Suraci et al. 2016). The interaction between the two species suppresses the full potential of African civets to exploit habitats (Palomares and Caro 1999). Land-use type had an influence on detection probability of African civets and they were more likely to be detected more in the park even when spotted hyena were present suggesting preference for less disturbed habitats.

Black-backed jackals utilised the habitat more or less the same as spotted hyenas when the latter were not detected. This was attributed to low predation risk but the risk increased in areas where spotted hyena were detected resulting in lower detection of black-backed jackals as in other studies (Kamler et al. 2013). There is probably a prey overlap between black-backed jackal and spotted hyena hence the former is the inferior species with respect to body size (Durant et al. 2010). A weight disparity of factor two or more (Loveridge and Macdonald 2002) allows canids to coexist. As such, black-backed jackals avoided direct contact with the spotted hyena on the ranch and safari area. Thus, low detection of black-backed jackal where spotted hyena were present could be attributed to exclusion of the smaller species by the larger one (Palomares and Caro 1999, Loveridge and Macdonald 2002, Humphries et al. 2016). The park influenced co-occurrence between spotted hyena and black-backed jackal. Furthermore, a negative effect of road network on black-backed jackal activity was observed. Generally, carnivores may prefer small roads, paths and trails (pers. obs.). In the wet season, black-backed jackal took advantage of the presence of lions in habitats where spotted hyena were not detected (Palomares and Caro 1999). Lion were superior to the hyena, leading to the exclusion of the latter (Vanak et al. 2013). There is a strong prey overlap between lion and spotted hyena (Hayward and Kerley 2008; Watts et al. 2010) hence a possible exclusion of spotted hyena by lion enhanced detection of black-backed jackal in the same habitat (Palomares and Caro 1999). The delta values in our study revealed that the probability of detecting both hyena and serval, back-backed jackal or African civet within the same 24 h period were more likely than the probability of detecting either species alone. Nevertheless, the high variation (increase or decrease) in detection probability of mesocarnivores with the presence of spotted hyena as a function of leopard, land-use type and habitats, implied that mesocarnivores would not necessarily avoid spotted hyena completely in the study area. As such, they utilised opportunities availed by the absence and/or low occurrence of large carnivores (Yarnell et al. 2013; Ramesh et al. 2017b). However, mesocarnivores would risk foraging in the presence of spotted hyena in the landscapes within the same 24 h period but avoided direct contact as shown by high mesocarnivore temporal overlap with spotted hyena, and among each other were high in the study area. This implied that the mesocarnivores did not totally avoid spotted hyena but utilised opportunities in its low detection period more so as a function of leopard presence. Temporal overlap clearly indicated that spotted hyena and mesocarnivores utilised the habitat simultaneously although the latter capitalised on the low detections of the former and the findings were consistent with our prediction that mesocarnivores can avoid large carnivores selectively.

3.5 Conclusions

Significant activity of mesocarnivores in the safari area and ranch showed that smaller carnivorous species adapt to anthropic activity. The co-occurrence of spotted hyena and mesocarnivores in the study areas is important to prevent mesocarnivore release (Watts and Holekamp 2009). Structural complexity of habitats (mixed vegetation and rocky habitats) may reduce the likelihood of negative interactions between predators, thereby creating an opportunity for mesocarnivores to utilise the same patch amid fear of the top predator. As such, anthropogenic wildlife land-use management must be conscious of possible negative impacts of large carnivore introductions on mesocarnivores in similar habitats. Furthermore, land managers should discourage increased land disturbance by humans to enhance habitat suitability for mesocarnivores since this will enable the small predators to use the diverse habitats optimally.

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CHAPTER 4

Comparison of spotted hyena (*Crocuta crocuta*) prey in two protected wildlife land–use types, a hunting area and a non-hunting area, in western Zimbabwe

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4.0 Abstract

Changing land-use practices affect the feeding ecology of large carnivores. We determined whether the spotted hyena *Crocuta crocuta* show feeding behavioural plasticity with a shift in prey selection under varying land-use. We determined their prey selection by comparing differences in frequency of occurrence of prey remains in their scats from two wildlife land-use types in western Zimbabwe; a hunting area (Matetsi Safari Area) and a protected area, Zambezi National Park (NP). Between 2014 and 2015, we collected 117 and 137 scats from Matetsi Safari Area and Zambezi NP respectively. Small, medium and large-sized mammalian prey contributed 19.8 %, 41.9 % and 19.8 % to their diet in the Safari Area, compared with 34.3 %, 24.0 % and 35.9 % in Zambezi NP, inclusive of domestic stock. Despite being in wildlife areas, we found a relatively high percentage of domestic stock occurrence in spotted hyena scats (10.3 % Safari Area; 12.0 % Zambezi NP). Impala *Aepyceros melampus* was the most consumed prey in both land-uses. Overall diet composition differed significantly between the two land-uses. Large-sized mammalian prey was consumed more in Zambezi NP, while medium-sized prey in the Safari Area. This was attributed to the ability of the spotted hyena to shift to prey species, possibly, in relation to the availability and/or proximity to human habitations. Therefore, it is suggested that management minimises habitat anthropogenic disturbance to foster a broad prey guild for spotted hyena and so reduce their potential livestock attacks in neighbouring local communities.

Key words: hyena, human-wildlife interaction, land-use, prey selection, scat analysis

4.1 Introduction

Feeding strategies and behaviour of large carnivores vary because of differences in land-use practices and habitat characteristics (Trinkel *et al.*, 2006). One carnivore species reportedly showing behavioural plasticity in feeding behaviour is the spotted hyena *Crocuta crocuta*, which is widely distributed in most protected areas (PAs) in southern Africa (Bohm & Honer, 2015).

Unfortunately, changing land-use and habitat modification affect the distribution of spotted hyena prey (Trinkel, Fleischmann & Kastberger, 2006). Knowledge of spotted hyena diet is important in determining the extent of resource utilisation (Kolowski *et al*., 2007). They are efficient hunters whose diet consists of various sizes of ungulates (Holekamp *et al.*, 1997) but would occasionally prey on domestic animals resulting in retaliatory killing. Scavenging and kleptoparasitism occur when opportunities arise. In view of continued habitat change and varied management practices, we determined whether spotted hyenas showed a shift in prey selection according to land-use type by assessing their behavioural plasticity in feeding. We determined the impact of land-use on spotted hyena prey selection by comparing differences in frequency of occurrence of prey remains in their scats in two wildlife land-use types in western Zimbabwe; Zambezi National Park (NP), and Matetsi Safari Area (trophy hunting). Sport hunting is known to influence the distribution of hunted species (Ndaimani, Murwira & Kativu, 2014) but little is known on whether spotted hyenas show behavioural flexibility in prey type in response to the effects of trophy hunting on their prey base. In addition, large-sized prey species are generally sensitive to habitat disturbance. Therefore, we predicted that spotted hyena diet would vary according to prey body size between the two PAs differing in land-use management.

4.2 Materials and methods

Zambezi NP (17° 57.341' S 25° 41.399' E) and Matetsi Safari Area (18° 22.760' S, 25° 52.353' E) cover 560 km^2 and 3000 km^2, respectively (Fig. 4.1). Both areas are state lands managed by the Zimbabwe Parks and Wildlife Management Authority. Although both are protected, they differ in the predominant land-use. Zambezi NP is used exclusively for photographic tourism, whereas the majority of management units at Matetsi Safari Area (including Units 4 and 5 sampled for this study) are used for trophy hunting (Muposhi *et al*., 2016). The two areas are inhabited by various species of ungulates and large carnivores (Muposhi *et al*., 2016). Fuller and Kazuma Forests, various private wildlife farms, and human settlements (both communal and Environmental Conservation Areas, (ECA)) surround the two study areas. The Matetsi ECAs are community-based wildlife conservation farms that have partially overlapping grazing land with wild animals. These ECAs share the boundary with the Safari Area in the southeast and Zambezi NP on the western side. Records indicate that the spotted hyena densities in the landscape range from 0.055 to 0.113 individuals per km^2 (Holekamp and Dloniak, 2010) while their key competitors, the African lion *Panthera leo*, are about 0.026 individuals km^2 (Loveridge *et al*., 2007).

Spotted hyena scats were collected (n = 254) along 16 trails in the Matetsi Safari Area and 22 trails in Zambezi NP (each trail was 2.5 km long) resulting in a total of ~40 km and ~55 km of traversed distance, respectively, between 2014 and 2015. Trails covered riparian systems and access roads, and scats were identified by their conspicuous white colour and size. Scat collection and analyses followed Mbizah *et al*. (2012), Ramesh and Downs (2015) and Boast *et al.* (2016). Scats older than two weeks were not collected. Scats were sun-dried (when fresh), packaged in brown envelopes and stored for further analyses.

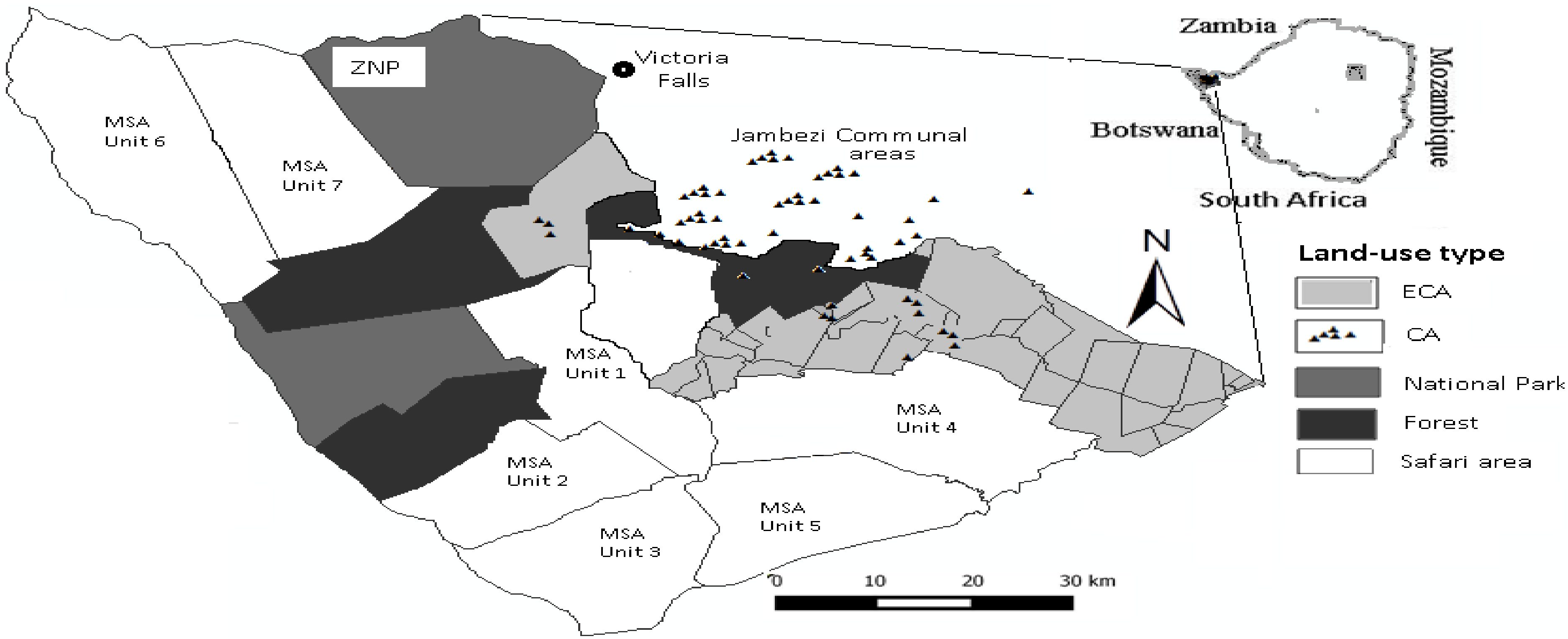

Fig. 4.1 Sites for scat collection at Matetsi Safari Area (Unit 4 and 5) and Zambezi National Park during 2014 and 2015 in western Zimbabwe. Land-use around the sampled sites involve human settlements and forest and other safari (hunting) areas

Table 4.1 Spotted hyena prey consumption and frequency of occurrence in Matetsi Safari Area and Zambezi National Park (NP), western Zimbabwe. (FO - frequency of occurrence; PO -percentage occurrence).

		Matetsi Safari Area		Zambezi NP	
Prey category	**Prey species**	**FO**	**PO (%)**	**FO**	**PO (%)**
Small (0.5 - 25 kg)	Bat-eared fox *Otocyon megalotis*	-	-	3	2.4
	Common duiker *Sylvicapra grimmia*	10	9.7	22	17.7
	Domestic dog *Canis familiaris*	1	1.0	4	3.2
	Scrub hare *Lepus saxatilis*	7	6.8	-	-
	Springhare *Pedetes capensis*	3	2.9	-	-
	Steenbok *Raphicerus campestris*	4	3.9	12	9.7
Total small		**25**	24.3	**41**	33.1
Medium (25 - 100 kg)	Bushbuck *Tragelaphus sylvaticus*	3	2.9	4	3.2
	Bush-pig *Potamochoerus larvatus*	-	-	2	1.6
	Goat *Capra aegagrus*	5	4.9	-	-
	Impala *Aepyceros melampus*	36	35.0	24	19.4
	Warthog *Phacochoerus africanus*	9	8.7	6	4.8
Total medium		**53**	51.5	**36**	29.0
Large (>100 kg)	Buffalo *Syncerus caffer*	2	1.9	3	2.4
	Blue wildebeest *Connochaetes taurinus*	-	-	4	3.2
	Cattle *Bos taurus*	2	1.9	1	0.8

	Donkey *Equus asinus*	6	5.8	14	11.3
	Greater kudu *Tragelaphus strepsiceros*	8	7.8	19	15.3
	Roan antelope *Hippotragus equinus*	1	1.0	-	-
	Sable *Hippotragus niger*	-	-	4	3.2
	Waterbuck *Kobus ellipsiprymnus*	2	1.9	2	1.6
	Zebra *Equus quagga*	4	3.9	-	-
Total large		**25**	24.3	**47**	37.9

We soaked dry scats in water until soft and then washed them with running water through a 1 mm sieve. Hairs were then separated, washed in acetone, dehydrated in 98% ethanol and dried on filter paper followed by microscopic (magnification *60 - 100) cuticular scale imprint and hair cross section examination (Yirga *et al.*, 2015; Boast *et al.*, 2016). Prey species were identified to species level based on undigested hairs. Hair of prey species generally remain undigested in carnivore scats and therefore hair identification is useful in determining the prey species in the diet of carnivores (Ramesh *et al.*, 2012). Therefore, we used a combination of hair characteristics, including hair width, medullary and cuticular structure, to identify spotted hyena prey. These were observed microscopically and compared with reference hairs of potential prey species collected from carnivore kill sites, trophy animals, and a taxidermy in Bulawayo, Zimbabwe. We then only identified species for which hair remains were most prevalent in each scat sample. We also recorded two prey species in some of the scat samples. We randomised the original order of scat samples (1000 iterations) and the rarefaction and extrapolation curve was used to ascertain the adequacy of scat samples (Appendix 4.1) to assess species richness (Chao *et al*., 2014).

We classified the size of the major mammalian prey species of the spotted hyena into small (0.5–25 kg), medium (26–100 kg), and large (>100 kg) body mass categories based on their documented body mass (Mbizah *et al*., 2012). We calculated the percentage of occurrence (number of occurrences of a food category/total number of occurrence of all food categories $\times$ 100) and the relative frequency of occurrence (number of occurrences of a food category/total number of scats with hairs $\times$ 100) of each prey item, to provide measures of how often spotted hyenas fed on the various types of prey and as a measure of importance of the respective prey types in their diet (Loveridge and Macdonald, 2003). We used the Pearson's Chi-square test at ≤ 0.05 in Program R (R Core Team, 2015) to determine whether there was significant variation in diet composition (small, medium and large prey) between the two land-use areas.

4.3 Results

Mammalian prey consumed by spotted hyena were identified from 89.4 % of the 254 scat samples collected (Zambezi NP, n = 124; Matetsi Safari Area, n = 103). About 10.6 % (n = 27) of total scats collected had no identifiable hairs and were thus excluded from further analyses. The total mammalian prey species in the spotted hyena diet was 18 for Matetsi Safari Area and 16 for Zambezi NP. Sample coverage against increasing number of samples indicated that adequate scat samples were achieved in both study areas (Appendix 4.1). Diet composition of spotted hyenas differed significantly between the two land-use types ($\chi 2$ = 12,008, d.f. = 2, p = 0.003).

Total percentage occurrence of prey species in spotted hyena scats showed domestic stock occurrence as 13.6 % for Matetsi Safari Area and 15.3 % for Zambezi NP. Total percentage occurrence of small, medium and large-sized mammalian prey was 24.3 %, 51.5 % and 24.3 % respectively for the Matetsi Safari Area, while 33.1 %, 29.0 % and 37.9 % respectively for Zambezi NP. Spotted hyenas also fed on rodents, particularly the springhare *Pedetes capensis* in the Safari Area (Table 4.1). Common duikers *Sylvicapra grimmia* were preyed on more in Zambezi NP (17.7 %) than the Safari Area (9.7 %). Zebras *Equus quagga* (3.9 %) were consumed in the Safari Area but not in Zambezi NP, while blue wildebeest *Connochaetes taurinus* (3.2 %) occurred in scats from Zambezi NP only. In both areas, the frequently consumed small-sized, medium-sized and large-sized mammalian prey were common duiker, impala *Aepyceros melampus* and greater kudu *Tragelaphus strepsiceros,* respectively. Overall, impala was the most consumed prey in both the Matetsi Safari Area (35.0 %) and Zambezi NP (19.4 %) (Table 4.1).

4.4 Discussion

Total mammalian prey species in the spotted hyena diet was similar for Matetsi Safari Area (18) and Zambezi NP (16). However, their diet composition differed significantly between the two land-use types. Total percentage occurrence of the respective prey of spotted hyena varied between the two land-use types. This was attributed to their ability to shift to alternative prey during lean periods (Holekamp & Dloniak, 2010). In the current study, their diet comprised small to large-sized mammals similar to spotted hyenas in Save Valley Conservancy, Zimbabwe (Mbizah *et al.*, 2012). They frequently consumed small-and large-sized mammalian prey in Zambezi NP compared with the safari/hunting area where medium-sized mammalian prey were consumed. This prey body size variation was attributed to availability of prey, the heterogeneity of habitats across the two land-use types and proximity to human settlements, resulting in the varying percentage occurrence of prey species in the scats of spotted hyenas in the two land-use types. Impala was the most consumed prey in both the Matetsi Safari Area and Zambezi NP. Occurrence of large-sized mammalian prey consumed in scats from Zambezi NP was possible due to higher availability of such prey. In the absence or low abundance of large-sized prey species in the Safari Area, spotted hyenas might consume medium-sized prey species more (Mbizah et al., 2012). Their diet in the two land-uses further differed with zebras being present in the diet in the safari/hunting area while wildebeest were present in the diet in Zambezi NP. Zebras were sighted in both land-uses (Mhlanga, pers. obs.) and their frequency of occurrence in spotted hyena diet from the Safari Area was attributed to scavenging or kleptoparasitism.

Domestic stock was consumed by spotted hyenas in both wildlife land-use types despite a variation in disturbance level. Occurrence of domestic stock in the spotted hyena’s diet in both land-use types was possible due to substantiated existence of human-wildlife interaction (Peterson *et al*., 2010; pers. obs.). Spotted hyenas in the Safari Area preyed more on cattle *Bos* *taurus* and goats *Capra aegagrus* while those in Zambezi NP preyed on domestic dogs and donkeys *Equus asinus*. This is an indication that hyenas can shift their diets and adapt to the availability of different prey species (Periquet *et al*., 2015), other predators and/or the presence of people. However, the ability of spotted hyenas to move relatively long distances in search of prey, possibly allows the species to forage in human settlements that in or near the PAs, especially if domestic stock are unprotected (Kuiper *et al*., 2015).

In conclusion, spotted hyena showed a shift in prey selection under the two varying land-uses showing behavioural plasticity in their feeding. This facilitates its ability to occupy disturbed landscapes including areas with high human densities, and makes it adaptable to anthropogenic pressures and changing land-use. Variation in size and type of prey species consumed was aligned to land-use type and the ability to adapt foraging strategies resulting in dietary shifts in relation to likely availability. Our study demonstrates how land-use affects hyena diets. Therefore, wildlife managers should take cognisance of the way land use influences ecological processes, such as predation, at higher trophic levels, which may contribute to stock losses in neighbouring communities.

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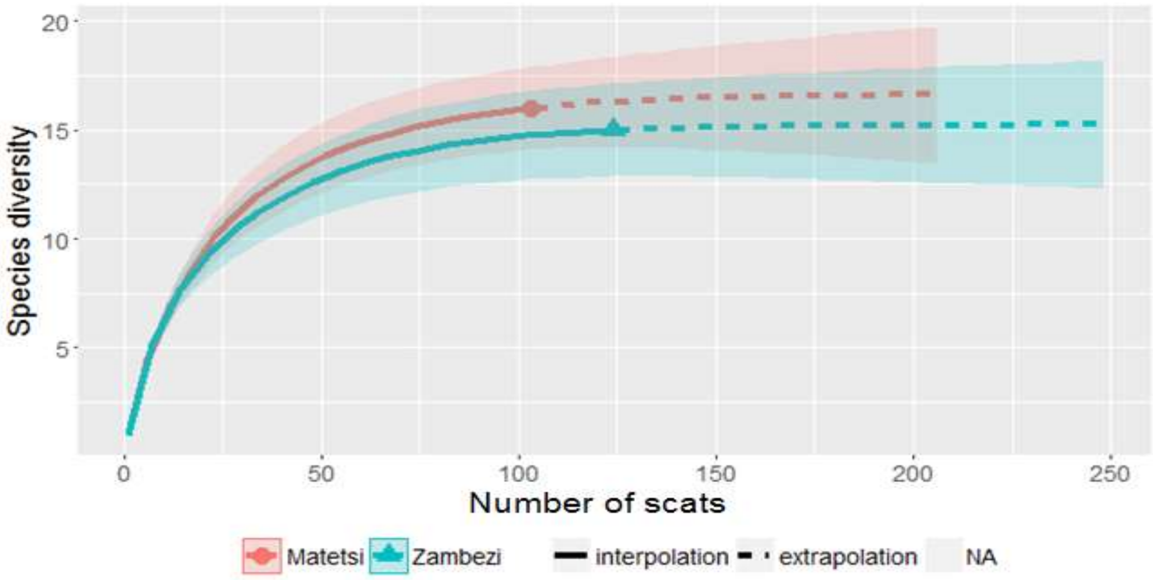
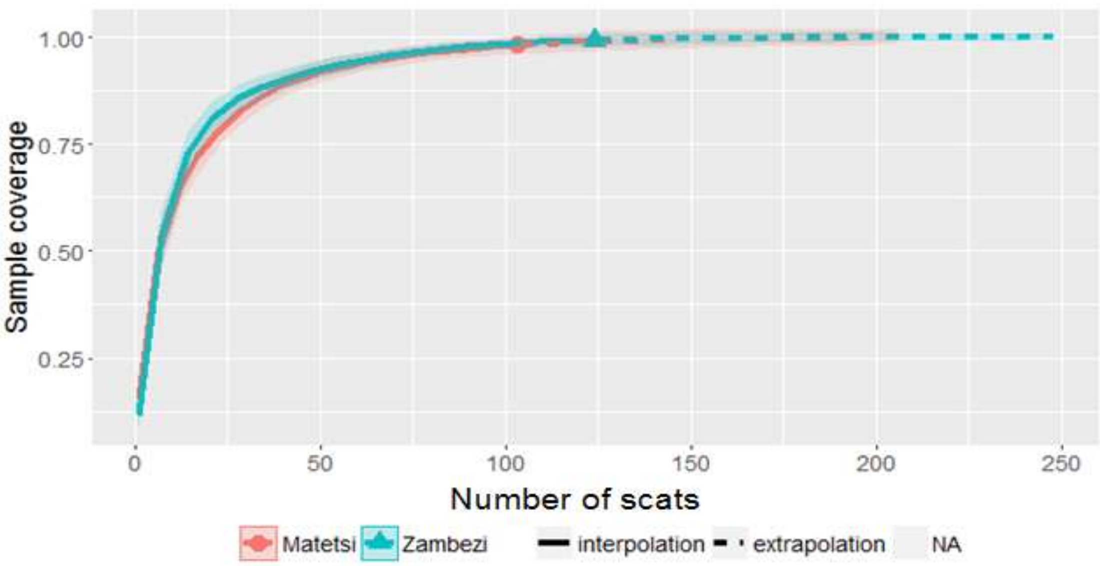
Appendix 4.1: Supplementary material

a.



b.



Supplementary material Fig. 4.2: Spotted hyena (a) prey species diversity, and (b) sample coverage in Matetsi Safari Area and Zambezi NP in the current study.

CHAPTER 5

Influence of settlement type and land-use on public attitudes towards the spotted hyena (*Crocuta crocuta*) in Zimbabwe

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Running header: Public attitudes towards spotted hyena

5.0 Abstract

Perceptions of people towards spotted hyenas *Crocuta crocuta* outside of protected areas are central to the management programs targeted to conserve this species. We conducted structured questionnaire surveys to assess the attitudes and perceptions of people (n = 353) towards the spotted hyena in western Zimbabwe from October 2014 to February 2015. The study area was split into Environmental Conservation Areas (ECAs) and communal areas based on their distance from the protected area boundary. People's perceptions and attitudes were analysed using multinomial logistic regression. Top model ranking showed that distance from protected area, livelihood source and extent of livestock loss had an influence on villagers' perceptions about the spotted hyena. Furthermore, it was noted that incentives would play a pivotal role in moderating the human-spotted hyena conflict. It is recommended that a modified incentive driven ECA model should be embraced in communal areas to promote and encourage positive attitudes towards the spotted hyena and other wildlife.

Key words: Carnivore, Conservation, Human-wildlife Conflict, Attitudes

5.1 INTRODUCTION

Biodiversity is at a great risk due to habitat loss, overexploitation and poor management of protected and conservation areas, as well as conflicts that exist between humans and wildlife (Gusset *et al*., 2009). Without mitigation of these problems, rare and endangered species will go extinct while conservation dependent species will likely be endangered in the near future. Human-wildlife conflicts on the fringes of protected areas have evolved over the years, in which humans were generally blamed for intruding into wildlife zones through agriculture, resettlement and development as well as subsistence poaching (Bajracharya *et al*., 2006) with the blame now also being directed to large carnivores for attacks on livestock inside enclosures (Miller, Jhala & Schmitz, 2016).

Predator monitoring is an important subject in wildlife management amid concerns of declining and threatened carnivore populations. Several threats have been identified chiefly habitat destruction and fragmentation (Karanth & Chellam, 2009; Mantyka-Pringle, Martin & Rhodes, 2012), interspecific interactions (Dröge *et al.*, 2016; Lehmann *et al*. 2017) and persecution (Kuiper *et al*., 2015; Belton, 2017) on farmlands and communal areas. Negative attitudes ensue due to undesirable impact of wildlife predation of livestock (Kansky & Knight, 2014; Miller, 2015), disease transmission (Mlilo *et al*., 2015) and human maiming (Yirga & Bauer, 2010), hence lethal control measures are generally perceived as the immediate solution to eradicate problem animals. Unfortunately, non-offending individuals are not spared, hence a decline in populations generally outside protected areas. Attitudes are not only catalysed by damage but also emanate from culture (Page-Nicholson *et al*., 2017), traditional beliefs, myths and folklore that includes music and stories (Kansky *et al*., 2014; Mbaegbu, 2015). As such, some negative attitudes towards carnivores develop early in life depending on upbringing (Page-Nicholson, 2017).

Generally, society has a number of myths and unproven beliefs about the spotted hyena (*Crocuta crocuta*), which are linked to witchcraft in many communities (Bothma, 2013). Furthermore, there is generally a relatively low demand for the species by sport hunters because it is considered as unattractive (Bohn & Honer, 2015), a factor that further portrays the spotted hyena negatively. Moreover, considerable evidence exists that points to the spotted hyena as one of the problem animals in landscapes where it is distributed (Yirga & Bauer, 2010; Stuart & Stuart, 2014; Girmay *et al*., 2015). In fact, it has been claimed to have the highest impact in terms of livestock losses in some areas (Trinkel, 2009; Schuette *et al*., 2013).

Due to increased competition for resources in the already small and fragmented habitats caused by human encroachment, spotted hyenas sometimes extend their home ranges into human settlement areas (Inskip & Zimmermann, 2009; Kolowski & Holekamp, 2009). In contrast, several communities near protected areas often advocate these wildlife zones as they benefits through forest and non-forest products like firewood, timber, thatch grass and grazing land (Frost & Bond, 2008; Dickman *et al*., 2011; Harihar *et al*., 2015). When communities are denied the benefits, generally negative attitudes ensue (Kideghesho, 2007). Various countries worldwide have proposed or attempted implementing compensation schemes (Sangay & Vernes, 2008) but these have often not provided the intended long-term mitigation (Inskip & Zimmermann, 2009; Taylor, 2009; Yirga & Bauer, 2010; Wegge *et al*., 2012). In addition, the compensation schemes were often too rigorous for the aggrieved villagers to pursue (Sangay & Vernes, 2008), or corrupt members of society adulterated them (Alexander and McGregor 2000). What makes human-carnivore conflict more complex is that the protectionist style of wildlife management generally fails to consider social, cultural, and political issues affecting communities on the fringes of protected areas (Graham *et al*., 2005). As such, Community-Based Natural Resources Management (CBNRM) programmes have been implemented to 'sooth' the impacts of these conflicts by providing incentives (Mishra *et al*., 2003; Taylor, 2009). In Zimbabwe for example, the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) programme was introduced in the 1980s (Frost & Bond, 2008; Taylor, 2009) to alleviate poverty, and change attitudes and increase tolerance (Gandiwa *et al*. 2013) of people towards wildlife. Unfortunately, CAMPFIRE has not functioned as expected due to misappropriation of funds (Frost & Bond, 2008; Taylor, 2009).

Unfortunately, although numerous studies have examined various human-wildlife conflicts worldwide (Yirga & Bauer, 2010; Ogada 2014; Girmay *et al*., 2015), published information generalises on various species of large carnivores. Furthermore, relatively little published information exists that explains the attitudes of local people towards the spotted hyena in particular (Romañach *et al*., 2007; Miller, 2015), yet it is one of the most targeted predators in communities affected by livestock depredation where spotted hyenas are present (Kissui, 2008). Relatively little research has compared the attitudes of people living in rural areas with different wildlife management regimes in southern Africa (Mutanga *et* al. 2015; Thorn *et al*. 2015). Therefore, we conducted structured questionnaire surveys to assess the attitudes and perceptions of people towards the spotted hyena in western Zimbabwe. We predicted that though CBNRM programmes are implemented, positive attitudes of people towards the spotted hyena are dependent on incentivised programmes. Furthermore, we predicted that settlement type (hence land-use) and distance of homesteads from protected areas strongly influence livestock losses and hence attitudes of people towards the spotted hyena in western Zimbabwe.

5.2 STUDY AREA

This study was conducted in Jambezi Communal Lands and Matetsi resettlement areas of Hwange District, Western Zimbabwe. It was centred at 18° 6.350'S and 25° 58.949'E (Fig. 5.1). Three administrative wards were covered, namely Chikandakubi, Kachechete, and Matetsi Wards. The area is bordered by Fuller Forest to the south, Binga District to the north, Zambezi National Park and Victoria Falls to the west (Fig. 5.1). The predominant soil type is mainly the Kalahari sands and a near rugged hilly terrain with regosols (Ndaimani, 2014) and the vegetation is primarily savanna, largely miombo woodland mixed with shrubland and grasslands (Childes & Walker, 1987). Common large carnivores include the African lion (*Panthera leo*), spotted hyena, leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*) while prey species include the buffalo (*Syncerus caffer*), zebra (*Equus quagga*), impala (*Aepyceros* *melampus*) and greater kudu (*Tragelaphus strepsiceros*) (Muposhi *et al*. 2016; Mhlanga *et al.* 2018).

Settlement type is mainly communal and resettlement, implying that most natural resources are common properties. Environmental Conservation Areas (ECAs) are concentrated in Matetsi Ward (Breakfast Farm, Isla Farm and Masuwe Village, which are mainly resettlements) and comprise resettled villagers who manage wildlife but also keep domestic stock and practice cropping. However, household landholding does not increase unlike in communal areas where there is less control in the establishment of new households. ECA and communal areas were differentiated by their approach to wildlife management. Communal areas wildlife is managed using the CAMPFIRE model where wildlife is managed by the Rural District Council (RDC) for the government and also for rural communities (Frost & Bond, 2008).

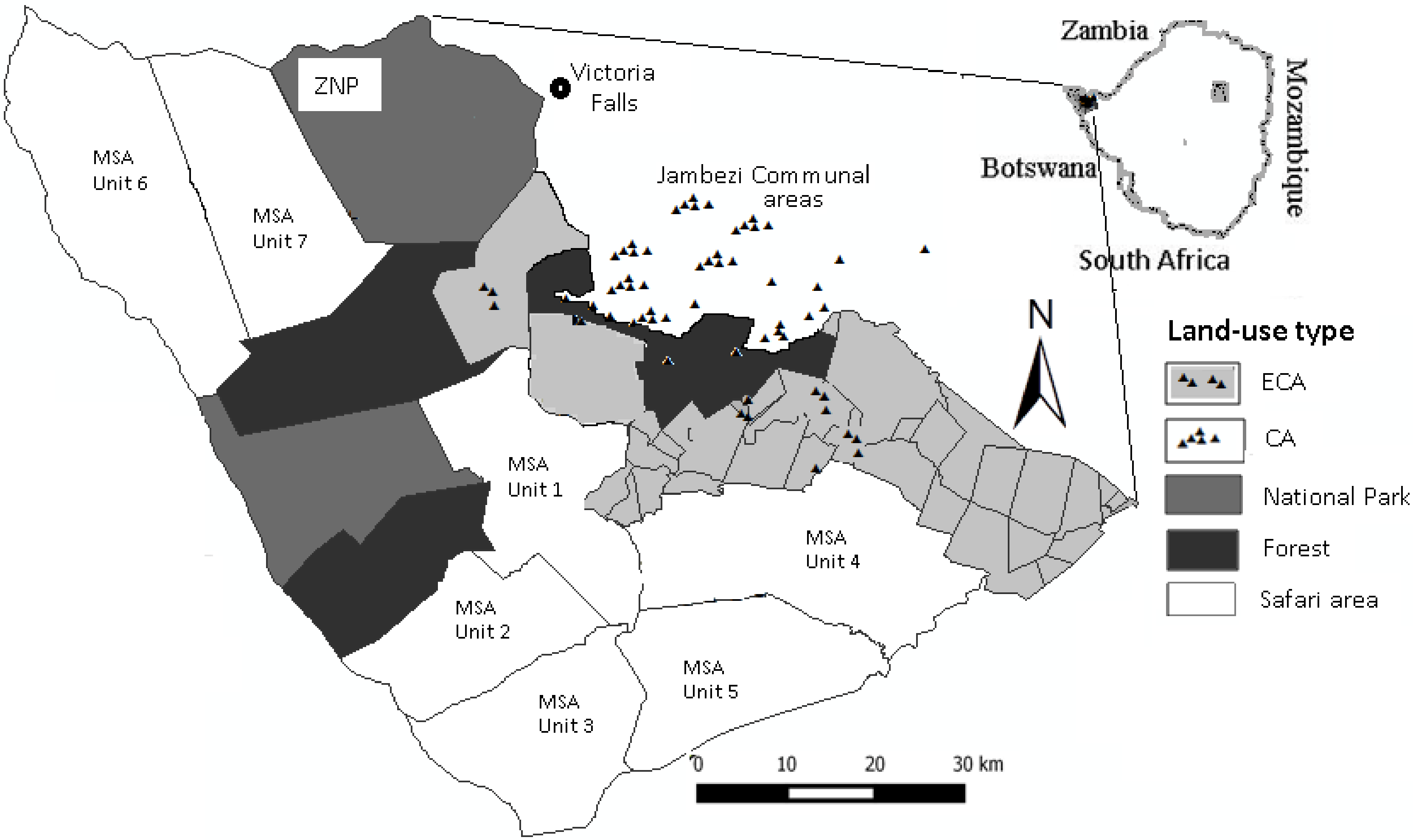


Fig. 5.1. Distribution map of villages within the three wards in Jambezi communal lands and Matetsi area, Zimbabwe, where the questionnaires were administered. MSA refers to Matetsi Safari Area.

The RDC also markets the quota to a hunting operator on behalf of the community and shares revenue with the community on an agreed percentage. Often, the RDC manages the community funds by running various projects that are beneficial to most people like construction of halls, schools and clinics. In ECAs, wildlife is strictly managed by the community and all the revenue is used within the area. The major difference between ECAs and communal areas is that in the former RDCs do not interfere with decision making and revenue management. The power of wildlife management has been devolved completely to the local community (Frost & Bond, 2008).

In the study areas households are generally distributed along the main roads or haphazardly around an area of high activity like shops, schools or chiefs' homestead (pers. obs.). Communities in this region rely on subsistence agriculture as a source of livelihood although the area has intermittent and relatively low rainfall averaging 650 mm p.a. (Loveridge *et al*., 2007) characterised by recurrent long dry spells even in the wet season which is about four months (Kuiper *et al*., 2015). The seasons are divided into a hot wet season (December-April), a cold dry season (May-August) and a hot dry season (Sept-November). The sandy soils are not suitable for crop farming while some patches of clay and loamy clay provide the alternative fertile land. Where cropping is significant, only early maturing and drought resistant crop varieties of sorghum (*Sorghum bicolor*), millet (*Pennisetum glaucum*) and to some extent maize (*Zea mays*) are grown (Kuiper *et al*., 2015) because of the low rainfall and highly leached nutrient deficient Kalahari sands. The district has a rural population of ~62670 (Zimbabwe National Statistics Agency 2012), and the total population for the sampled area was ~4038 with ~976 households and a mean family size of ~4.1 members (Zimbabwe National Statistics Agency 2012). The livelihoods are mainly agro-pastoral in which livestock is herded through the day during the wet season and corralled at night. However, livestock free range during the day in the dry season but are corralled at night. Domestic dogs guarding the homesteads at night generally guard the nearby corral as well (pers. obs.).

5.3 METHODS

The study used a stratified design using distance of household from the protected area. Two strata were established, that is, ECA (wildlife zone) which mainly included resettlements inside wildlife farms and communal area with homesteads outside the protected area. The area outside the protected area was further split into four distance categories (0 - 5 km, 6 - 10 km, 11 - 15 km and 15 - 20 km) from the protected area boundary. Although conscious that hyenas move long distances, we were cautious not to increase the distance of the categories because we perceived that increased human presence in somewhat reduced cover in the area hence deterrent free movement of the spotted hyena. As such, we supposed that 5 km intervals would have differences in terms of spotted hyena movement thereby resulting in differences in exposure of communities in these distance categories to the species as well as livestock predation. Consequently, we expected respondents in the 5 km distance categories to have different perceptions and attitudes towards the species. Every fourth homestead with a functional livestock corral (kraal) was sampled for administration of the questionnaire. If there was no person above 18 years of age in the selected homestead, or he or she was not interested in taking part in the survey, the interviewer sampled the next homestead that suited the sampling criterion. Prior to sampling, permission was sought from the local chiefs and village heads. The interviewer targeted the household heads, or any family representative if the household head was absent. The study sampled 353 households, at least 70 in each distance category. Ethical clearance was obtained from the University of KwaZulu-Natal.

Prior to the interview, the interviewee was informed that the data collected were mainly for academic reasons and there were no direct monetary or non-monetary benefits associated with taking part in the survey. The interviewees' current livestock holding and other sources of livelihood were assessed to determine household economic status and to link that with their attitude towards spotted hyenas. We also inquired about species of livestock lost and their economic value. Average market prices of all livestock species killed through depredation were used to estimate the economic loss in monetary terms. Middlemen (buyers) and villagers (sellers) provided livestock purchase price. Young livestock were treated as mature (opportunity cost) since juvenile and adults were often attacked while calves less than four months are usually left to graze around the homestead when the rest of the herd feeds in the pastures (pers. obs.). The period considered was the past 12 months because rural villagers generally do not keep records. Their attitudes towards the spotted hyena were determined by asking questions about their feelings towards them. For example, they were asked on how they feel about spotted hyenas, to which they would choose from (i) very positive, (ii) quite positive, (iii) indifferent, (iv) quite negative, and (v) very negative. Data on attitude towards the spotted hyena were subjected to multinomial logistic regression in which attitude (feeling) was the response variable while distance from the protected area, livestock loss, livelihood source, livelihood threat, gender, and time in the area were predictor variables.

Information about management of natural resources, including wildlife in the area, were sought from CAMPFIRE and ECA offices and the information obtained was explained in the description of the study site above. Cross tabulations of data on attitudes towards the spotted hyena were produced. Attitudes towards the spotted hyena were determined by questions, which addressed the following: how they felt about the presence of the spotted hyena in the area and frequency of bothering by the spotted hyena in the area. Perceptions about the spotted hyena were determined by questions, which included what they expected to happen to population size of spotted hyenas in the area; and whether the community was willing to coexist with the spotted hyena; (Appendix 5A). In this study, perception mainly focused on the intellectual viewpoints of the respondents particularly the analytical responses from interpretation of their interaction with wildlife and the possibility of coexistence. On the other hand, attitude focused on their standpoint of respondents based on their interaction with the species in the study area.

Furthermore, multinomial logistic regressions were computed using AICcmodavg (Mazerolle, 2015), reshape2 (Wickham, 2007), foreign (R Core Team, 2015a), nnet (Venables & Ripley, 2002), MASS (Venables & Ripley, 2002), MuMln (Barton, 2016) and rJava (Urbanek, 2016) in Program R version 2.1 (R Core Team, 2015b). The best-fit candidate models with few predictors were generated following the framework of Burnham and Anderson (2002). Best models that strongly influenced attitude were selected based on their Akaike's Information Criterion value ($\Delta AIC \leq 2$) (Burnham & Anderson, 2002). We summed the model weights from all the candidate models containing the particular covariate to conclude the relative importance of each covariate on attitude towards the spotted hyena.

5.4 RESULTS

Of the sampled households, 39% were female headed. Families that depended on livestock as the major source of livelihood comprised 74% (n = 261), while those which depended on crop farming as a major activity comprised 22% (n = 76), and 4% mainly relied on other sources of income. Of the total livestock loss incidents reported 71% (n = 204) were cattle, 11% (n = 33) were donkeys, and 18% (n = 52) were goats. Respondents showed a strong and significant negative feeling towards the spotted hyena ($\beta = 2.211$; SE = 0.353; $P < 0.01$). Although respondents were negative about spotted hyena ($P < 0.01$), they were somehow indifferent to the species' presence in the area. Distance from the protected area boundary had no significant effect on the respondents in communities inside ECAs who showed negative attitudes but on the contrary wished the population of the spotted hyena to increase. On the contrary, negative attitudes and perceptions towards the spotted hyena increased with increased distance from the protected area boundary (Table 5.1). That is, areas outside ECAs were negative about the spotted hyena (Fig. 5.2). Overall, of all the respondents who were positive about the spotted hyena, 93% were in the ECA, while the other 7% were mainly from within 5 km of the boundary from the protected area boundary. In general, the majority of villagers desired that the spotted hyena numbers should decrease in their area (Fig. 5.2).

Five predictor variables in various candidate models influenced the attitudes of the people towards the spotted hyena. Top two models with $\leq 2\Delta AIC$ were selected for their strong influence on attitudes (Table 5.2).

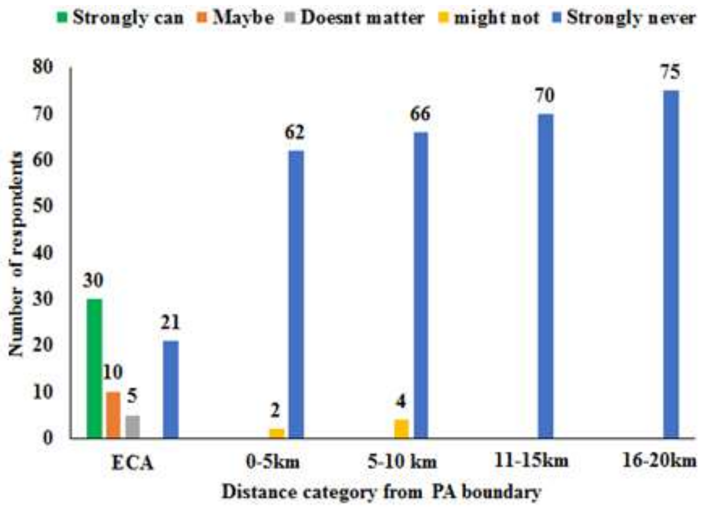
The selected models showed that distance from protected area ($\beta = 4.93$, SE = 1.62, relative importance = 1 and $P = 0.001$), livestock loss ($\beta = 0.0007$, SE = 0.00032, relative importance = 0.92 and $P = 0.03$), and livelihood source ($\beta = 1.55$, SE = 1.21, relative importance = 0.69 and $P = 0.001$) strongly influenced people's attitude towards the spotted hyena.

Table 5.1. Respondent's perceptions (%) on coexistence with the spotted hyena in their area.

	Can you co-exist with spotted hyenas in this area?				
Distance from protected area Boundary	**Strongly can**	**Maybe**	**Does not matter**	**Might not**	**Strongly never**
ECAs	44	15	7	0	34
0-5 km	0	0	0	4	96
6 – 10 km	0	0	0	6	94
11-15 km	0	0	0	0	100
15-20 km	0	0	0	0	100

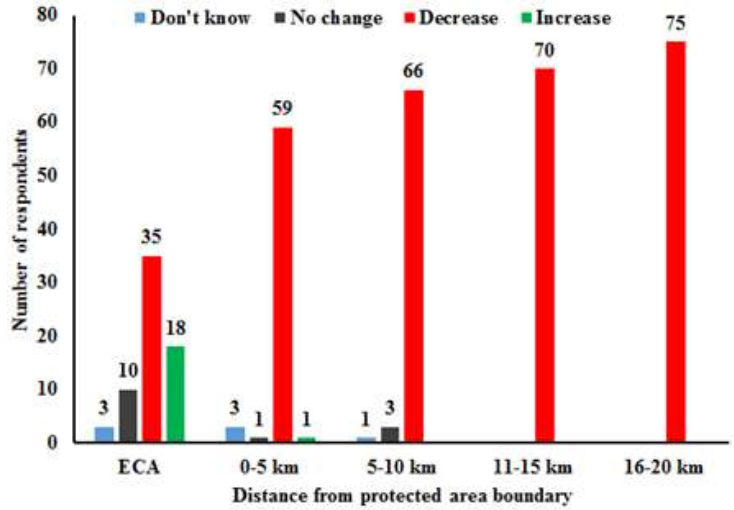
Table 5.2. Component model results for multinomial logistic regression examining the attitudes of humans towards the spotted hyena grouped by distance category.

Variables	df	logLik	AIC	ΔAIC	weight
Distance + livelihood +Livestock loss	20	-167.88	378.28	0.00	0.44
Distance+ Livestock loss	12	-176.98	378.87	0.59	0.33
Distance+ Livelihood	16	-173.67	380.95	2.67	0.12
Distance + Livelihood + Livestock loss +Time in area	32	-155.58	381.76	3.48	0.08
Gender + Distance + Livelihood + Livestock loss	24	-166.45	384.56	6.28	0.02
Gender + Distance +Livestock loss	16	-176.43	386.48	8.19	0.01
Gender + Distance + Livelihood	20	-172.19	386.91	8.63	0.01
Distance + Livelihood threat+ livestock loss+ Time in area	36	-154.76	389.95	11.67	0.00
Distance + Livelihood + Livelihood threat+ Livestock loss	32	-162.25	395.10	16.82	0.00
Distance + livelihood + livelihood threat	28	-167.89	396.80	18.52	0.00



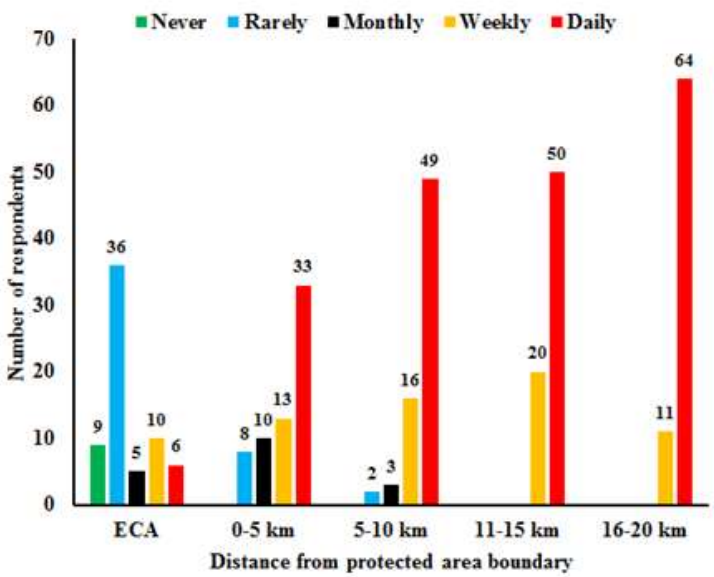
Strongly can
Maybe
Doesnt matter
might not
Strongly never
Number of respondents
80
70
60
50
40
30
20
10
0
30
10
5
21
62
2
66
4
70
75
ECA
0-5km
5-10 km
11-15km
16-20km
Distance category from PA boundary

(a)



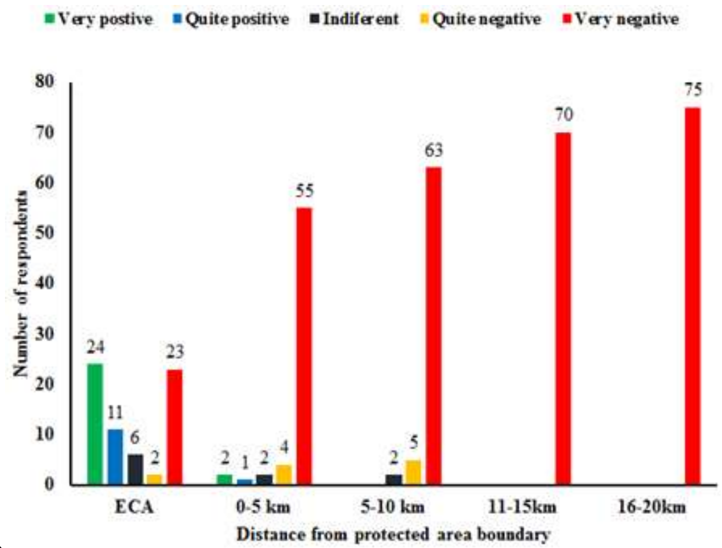
Don't know
No change
Decrease
Increase
Number of respondents
80
70
60
50
40
30
20
10
0
3
10
35
18
3
1
59
1
1
3
66
70
75
ECA
0-5 km
5-10 km
11-15 km
16-20 km
Distance from protected area boundary

(b)



Never
Rarely
Monthly
Weekly
Daily
Number of respondents
70
60
50
40
30
20
10
0
9
36
5
10
6
8
10
13
33
2
3
16
49
20
50
11
64
ECA
0-5 km
5-10 km
11-15 km
16-20 km
Distance from protected area boundary

(c)



Very postive
Quite positive
Indiferent
Quite negative
Very negative
Number of respondents
80
70
60
50
40
30
20
10
0
24
11
6
2
23
2
1
2
4
55
2
5
63
70
75
ECA
0-5 km
5-10 km
11-15km
16-20km
Distance from protected area boundary

(d)

Fig. 5.2. Effect of distance from protected area boundary on respondents' attitude towards the spotted hyena; (a) perception on possible coexistence with spotted hyenas, (b) perception on what respondents expected to happen to the spotted hyena population in their area, (c) perception on frequency of bothering by the spotted hyena in the area, and (d) respondents' feeling about presence of spotted hyenas in their area. Distance was categorised, i.e. ECA where areas within wildlife farms which are protected private properties for the community in the resettlement scheme, between, between 0 -5 km; 5-10 km, 11 – 15 km and 16-20km; from protected area boundary.

As expected, when the households in communal areas were grouped to reduce the number of distance categories, it was observed that villagers farther away from the protected area witnessed lower monetary losses through livestock predation. Average economic losses through depredation was $759, $876 and $438 per household p.a. for ECAs, ≤ 10 km and ≥11 km categories respectively. Respondents who lived inside ECAs showed some positive attitudes towards the spotted hyena compared with their counterparts in the communal areas (Fig. 5.2).

Of the respondents > 10 km away from the protected area who lost livestock, 60 % (n = 50) lost their animals either in pastures or in the cropping land in which animals fed during the dry season when there were no crops. In that distance category, 40% of livestock was killed either near the home or inside the coral.

5.5 DISCUSSION

The majority of respondents were negative about the spotted hyena presence in the human settlement areas and wanted their numbers reduced or the species exterminated from the area. A negative attitude was least expected in communities away from protected areas because of perceived low incidences of losses. However, respondents in homesteads that were further away from the protected areas seemed against conservation of spotted hyenas because they also experienced livestock losses to the spotted hyenas. In Jambezi communal lands, there are patches of community forests that probably provide refuge to spotted hyenas (Mhlanga, pers. obs.). This, coupled with likely laxity in husbandry practices and possibly wild herbivores that stray to areas near human settlement, could have made livestock within that locality susceptible to predation (Sangay & Vernes, 2008; Kuiper *et al*. 2015), especially in dry seasons. Villages further away from the protected areas (>10 km) lost more of the livestock in the grazing areas, contrary to Kolowski and Holekamp (2006), who found that spotted hyenas attacked livestock in a more or less the same pattern regardless of distance from park boundary. The spotted hyenas in the study area were claimed to patrol the villages as far closer to the homestead as possible thereby attacking livestock either near the home or inside the corral. Our results are in agreement with Kolowski and Holekamp (2006), who found that 58% of attacks occurred inside corrals in Kenya. Often, although some villagers keep their livestock in enclosures at night for safety, the type of enclosures were not secure enough to safeguard livestock from spotted hyenas or other predators (Mhlanga pers. obs.) as recorded in other studies (Kolowski & Holekamp, 2006). Livestock predation could also be attributed to possibly low prey availability on the edges of protected areas (Yirga & Bauer, 2010; Pereira *et al*., 2014), or from increased competition for wild prey with other large carnivores in protected areas (Watts *et al*., 2010). As such, poor husbandry practices were costly to villagers because spotted hyenas predation of livestock negatively affected their livelihoods. Furthermore, poor management of revenue from wildlife by the RDCs was one of the concerns raised during interviews, leading to increased negative attitudes (Dickson, 2011). Mudzuzo (1995) argued that there are various factors other than stock depredation, which increase negative attitudes toward wildlife. Based on our knowledge of the study area, the misappropriation of revenue in CBNRM programmes could be one of the major causes of intolerance coupled with poor relations between the communities and extension services of the protected areas.

The negative attitudes observed, indicated strongly that communities were aware of incentives from the wildlife proceeds that they were supposed to receive, but the funds were supposedly not benefiting the community. This is in agreement with Gusset et al, (2009), where communities showed negative attitudes towards wild dogs (*Lycaon pictus*) in Botswana, despite presence of compensation schemes. The spotted hyena was a possible liability rather than an asset to the villagers as shown by unwillingness to coexist with the species in the area. It was clear that exclusion of communities from the full benefits from wildlife resources caused people not to embrace conservation efforts as in other studies. Our study further supports previous studies (Frost & Bond, 2008; Wegge *et al*., 2012; Gandiwa *et al*., 2013; Constant *et al*., 2015) where incentives played a pivotal role in changing the attitudes of communities towards wildlife.

Woodroffe *et al*. (2005) argued that incentives, mainly from sport hunting, could encourage a strong zeal to conserve a species that is generally in conflict with humans because the benefits are tangible. In Zimbabwe, a similar study concluded that protected areas which fail to meet the social needs of neighbouring communities cultivated negative attitudes towards conservation (Mutanga *et al*., 2015). Thus, the proper management of revenue from wildlife resources at community to household level is crucial for the creation of a variety of incentives that meet part of the social needs of the affected people. For example, ECAs mentioned school construction, tap water provision to every household, formation of hunting companies at local level that generate income for the community and dam construction as key projects in their livelihood and development. Furthermore, locals are employed as scouts, and representatives consult the community before any developmental projects are implemented. As such, protected area managers who have exclusive rights to land inhabited by the spotted hyena should consider the social needs of neighbouring local communities to reduce the negative attitudes caused by human-wildlife interactions.

In order to protect the spotted hyena from persecution, communities must see the real benefits of keeping wildlife. Dickman *et al*. (2011) clearly highlighted that the magnified value of a species at a global scale is usually a direct opposite at a local scale because of the economic costs experienced by villagers on the fringes of protected areas. Pastoralists invest significant energy and money in securing and maintaining a herd of livestock but large carnivores like spotted hyenas can reduce or impact such investments overnight leaving the farmer susceptible to poverty (Dickman *et al*., 2011). In a bid to protect their investment, villagers will retaliate by killing any large carnivores that roam within their villages (Pangle and Holekamp 2010; Ogada 2014; Kuiper *et al*. 2015). If such behaviours and attitudes continue, populations of large carnivores outside of protected areas will decline rapidly. On the contrary, pressure groups and conservationists advocate for non-lethal control methods in areas affected by human-carnivore conflicts (Woodroffe, 2005) and lethal control techniques can only be used when all other efforts would have failed.

The majority of villagers with strongly negative attitudes were those whose livelihoods were dependent on livestock rearing rather than crop farming or other sources for survival. As expected, it was justified for pastoralists to disagree with the presence of spotted hyenas in their areas because of the losses they incur. Although with high losses per household per annum (US$759), respondents in ECAs showed a generally positive attitude towards the species. This was contrary to findings by Gusset *et al*. (2009) of attitudes towards wild dogs in northern Botswana where they found that negative attitudes decreased with increase in distance from the protected area. Matetsi Ward comprises farmers resettled inside wildlife farms and their positive attitudes were again explained by presence of tangible incentives. Communities in ECAs strongly benefited from wildlife revenue through various projects that were developed and run at local level. For example, the communities now enjoy piped tap water in their homesteads, a project that was implemented using hunting quota revenue. Such incentives have also been recorded elsewhere with positive outcomes (Bajracharya, 2006). The reason they experienced such tangible benefits was attributed to being resettled on wildlife farms. Again, there were fewer homesteads in ECAs than in communal areas. Discussions with ECA respondents revealed that they refused to be under CAMPFIRE, which they belonged to before being resettled in wildlife farms. As such, the government allowed them to manage their natural resources using the ECA model in which there was participatory decision making, hence more benefits that were tangible. On the contrary, villagers outside protected areas have been in the area for many years (some greater than 40 years) and CAMPFIRE was not perceived contributing to their livelihoods. Instead, they felt wildlife made their lives more miserable because of their susceptibility to poverty due to livestock losses by spotted hyenas and other carnivores. Although overall respondents in this distance category experienced lower economic losses, their attitude showed potentially dangerous intolerance with respect to spotted hyena conservation.

As we advocate for the protection of spotted hyenas and of their habitat, neglect of social needs of adjacent communities makes most of these conservation efforts ineffective. The apparent best methods for attitude changes and tolerance to wildlife are co-existence through revenue generation that simultaneously achieves community development and conservation goals not only of scientists/conservationists but also supported by the local community (Woodroffe *et al*., 2005).

5.6 Conclusions and management recommendations

Communities adjacent to protected areas generally experience more human-wildlife conflicts and hence would likely show a negative attitude towards wildlife in general. Contrary to our expectation, this study revealed that villages within wildlife areas (ECA) had a higher proportion of respondents who were positive about having spotted hyenas in their areas. The same communities wanted the population of the spotted hyena to increase. This was attributed to tangible incentives that the villages have accrued through revenues and developmental projects from wildlife harvesting. Benefits included boreholes and portable water provided to households, well-managed gravel roads and a coordinated system coupled by famers' close ties with the Parks and Wildlife Management Authority in terms of community liaison. On the other hand, communal areas under the CAMPFIRE mode of CBNRM did not realise the benefits of conserving the spotted hyena and other wildlife and hence had negative attitudes towards the species. As suggested by other studies (Frost and Bond, 2008; Hemson *et al*., 2009; Taylor, 2009), community based management of natural resources is beneficial when managed properly because it provides tangible incentives to villagers thereby negating negative attitudes caused by livestock depredating carnivores. The findings indicated that the ECA mode of wildlife management outside protected areas must be implemented for the benefit of large spotted hyenas. It is suggested that government should remodel CAMPFIRE and strictly monitor its management in a way that it imitates ECAs that seem to be democratic in participatory decision making in relation to revenue distribution. Thus, distance of settlement from protected area boundary would have little effect on the attitudes of people living on their fringes. It is clear that villagers have greater tolerance of carnivores when incentives reach the community (Manoa & Mwaura, 2016). Therefore, attitudes of communities affected by edge effects of protected areas are a pointer to management problems and solutions associated with spotted hyena conservation.

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APPENDIX 5.A. Questionnaire used in the present study.

[All instructions to interviewer are given within square brackets]

Interviewer name: ________________________ Date of interview: ________________________

SECTION 1: Personal information

1a.What is your name? ____

1b. What is your position in the household? ____

1c. What is your age? ____

1d. Level of education [None, Primary, Secondary, Tertiary]__________________________

1e. How long have you lived in the area?________________

1f. What is your first language________________________

1g. Are you employed?

1. Employed	2. Self employed	3.Unemployed	4. Other (Specify)

2. How many people are in your household?

Position in household	Age	Sex	Living at home? (Y/N)
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			

3a. How many of the children attend school? ______________________________________

3b. How many meals do you eat per day?______________________

3c. How often do you eat meat? (tick applicable)

4.

1.Daily	2.twice a week	3.once a week	4.fortnightly	5.bi monthly	6.monthly	7.rarely	8.never

What are the household's sources of livelihood? Please list all, giving the largest/most important first.

[List responses in code, using key below]

____

1 = Livestock 2 = farming of crops	5 = Arts and crafts 6 = Other small business (please specify) 7 = hunting	9 = money sent home from abroad

3 = Regular employment (please specify) 4 = Casual labour (please specify)	8 = photographic tourism	10 = Other (please specify)

5a.What do you think is the greatest threat to your livelihood? ___________________________
[code using key below]

1 = Crop raiding 2 = Predators killing livestock 3 = Disease of livestock 4 = Natural deaths of livestock	5 = Accidental deaths of livestock 6 = Drought 7 = Lack of government assistance 8 = Theft of livestock	9 = Malnutrition of family 10 = Disease of family 11 = Other (specify)

SECTION 2: Crop husbandry
[ignore this section if crops not listed as source of income in question 4]

6a. Which crops do you grow?
[List all in the table below, using key below]

1 = Maize 2 = Cotton	3 = Millet 4 = Vegetables (specify which)	5 = Other (specify)

6b. What quantities of each crop did you harvest in the past 3 years? [use information to complete table below]
7. What measures do you take to protect each crop?
[List all in the table below, using key below]

1 = Fences 2 = Children guarding	3 = Adults guarding 4 = Repellents (specify)	5 = Other (specify)

Response grid

a. Crop	b. Amount (bags)	c. When harvest	d. Steps to protect	Comments

8a. How do you till your land?

Tractor		Hand hoe		Plough		Other (specify):	

- own		- own		- own		- own	
- hire		- hire		- hire		-hire	

8b. Do you experience droughts in this area? 1. Yes 2. No

8c. If yes, how do you survive when there is crop failure? (What do you do to survive?)

1.	2.	3.	4.	5.	6.	7.	8.
batter exchange	Buy using cash	Borrow money from banks to buy grain	sell livestock	Sell bushmeat	Get government support	Get N.G.O. support	Other specify

SECTION 3: Livestock husbandry

[ignore this section if livestock not listed as source of income in question 4]

9. What livestock does your household own? (indicate numbers in the space provided)

Cattle: ________ Oxen: ________ Donkeys: _________ Goats: ________ Sheep: _________

Poultry: _________ Dogs: ________Other (specify): ________________________________

10. What livestock has the household acquired in the last 12 months, and how was it acquired?

	Bought	Born	Traded	Gifts	Other (specify)
Cattle					
Oxen					
Donkeys					
Goats					
Sheep					
Dogs					
Poultry					
Other (specify):					

11a. What do you do to protect your livestock? [encourage respondent to list all measures]

____

11b. Where do livestock drink? [include distance from homestead] ________________________

12a. How do your livestock usually graze: [use code below to record response for each type of livestock kept]

Cattle		Goats		Oxen		Donkeys		Sheep		Poultry		Other (specify):	

1 = Unattended 2 = Herded by children (go to Q12b)
3 = Herded by adults (go to Q12b) 4 = Guarded by dogs (go to Q12c)

12b. Are the herders armed in any way? [circle answer] 1. Yes 2. No
If yes, what are they armed with ___________________________________
12c. If guarded by dogs, how many? ____
13. Do you have a boma? No (go to Q17) Yes (go to Q14)

14a. What livestock do you put into your boma? [circle all that apply]
1 = Cattle 2 = Oxen 3 = Donkeys 4 = Goats
5 = Sheep 6 = Dogs 7 = Other (specify)___________________________
14b. What are the reasons for using your boma in the wet season? [list all reasons in order of importance

____
____

14c. What are the reasons for using your boma in the dry season? [list all reasons in order of importance]____
____

15a. Do you use your boma more: [circle appropriate answer]

1= in the wet season than in the dry season	2= in the dry season than in the wet season	3= use same amount in wet and dry season

15b. How often do you put your livestock into your boma in the wet season? [circle appropriate answer]

1. Never	2. Rarely	3. < a week	4. > a week	5 = Every night (Go to Q16)

15c. How often do you put your livestock into your boma in the dry season? [circle appropriate answer]

1. Never	2. Rarely	3. < a week	4. > a week	5 = Every night (Go to Q16)

16. Can we see the boma?
[Inspect boma and complete all sections of Q16 – do not ask respondent]

16a. What is the distance to the nearest human habitation in meters? ___________________

16b. Where is the boma situated in relation to village? _________________________________

16c. What is the boma made of?

1 = Poles 2 = Thorn bushes 3 = Piles of sticks

4 = Wire 5 = Other (specify)____

16d. Write a brief description of the boma, detailing how it is constructed and mentioning the complexity of the design. ____

16j. What is the visibility through boma? [circle closest answer]

1. No visibility	2. 25%	3. 50%	4. 75%	5. 75%+

16k. Which of the descriptions below best matches the construction of the boma?

1 = Small hedge	2 = Small branches	3. Medium branches	4 = Thick branches	5 = Strong poles

16l. If constructed of wire, please specify construction:

1 = Diamond mesh on poles

2 = Barbed wire (specify number of strands)____

3 = Other (please specify) ____

17. What is the furthest distance from your homestead that you graze the following livestock in the wet season? (km)

Cattle		Oxen		Goats		Donkeys		Sheep		Poultry		Other (specify):	

18. What is the furthest distance you graze the following livestock in the dry season? (km)

Cattle ____________Oxen ______________Donkeys _______________ Goats ________________

Sheep ____________Other (specify) ____

19a. Do you graze your livestock in wildlife areas?

1. Yes 2. No

19b. If yes, which livestock? ____

In what months? ____

And, where and how far? [distance from homestead] ___________________________

20. What husbandry activities listed below do you do?[tick applicable]
1. Dipping____ 2. vaccination______ 3. dosing_____________ 4. None____

21a. Do any of your livestock wear bells? 1. Yes 2. No /
21b. If yes, what livestock and how many? ____

SECTION 4: Wildlife in the area
22. Please tell me all of the wild animals found in this area that you remember:

1	2	3	4	5
6	7	8	9	10
11	12	13	14	15

23. Can you can co-exist with the following animals, and why?

Species	5 = strongly can	4 = Maybe	3 = doesn't matter	2 = might not	1 = strongly never	Why?
Hyena						
Elephant						
Lion						
Leopard						
Baboon						
Bushpig						
Genet						
Serval						
Caracal						
Python						
Wild dog						
Jackal						
Cheetah						
Kudu						
Buffalo						
Vervet						
Porcupine						

24. What would you like to see happen to the numbers of the following animals in the area around your village, and why?

Species	Increase	Decrease	Stay the same	Don't know	Why?
Hyena					
Elephant					
Lion					
Leopard					
Baboon					
Bushpig					
Genet					
Serval					
Caracal					
Python					
Wild dog					
Jackal					
Cheetah					
Kudu					
Buffalo					

25. How important do you think it is to protect wildlife in parks?

5 = very important	4 = quite important	3 = neither important or unimportant	2 = quite unimportant	1 = very unimportant

26. How important do you think it is to protect wildlife in the communal lands?

5 = very important	4 = quite important	3 = neither impt or unimpt	2 = quite unimportant	1 = very unimportant

27. How do you feel about having hyenas in your area?

5 = very positive	4 = quite positive	3 = indifferent	2 = quite negative	1 = very negative

28. Why do you feel this way?____

29. How often are you bothered by each of the following?

29a. When was the last time you were bothered by each of the following?

Species	1=Daily	2=Weekly	3=Monthly	4 = Rarely	5= Never	Last bothered
Hyena						
Elephant						
Lion						
Leopard						
Baboon						
Bushpig						
Genet						
Serval						
Caracal						
Python						
Wild dog						
Jackal						
Cheetah						
Kudu						
Buffalo						

29b. Can you tell me all the ways that each animal bothers you? [record answers in table below]
29c. Is the problem better in the wet season or dry season? [record answers in table below]

Species	Destroys crops	Kills livestock	Disrupts humans	Scavenges food	Damages property	Injures humans	Other (specify)	Wet vs Dry
Hyena								
Elephant								
Lion								
Leopard								
Baboon								
Bushpig								
Genet								
Serval								
Caracal								
Python								
Wild dog								
Jackal								
Cheetah								
Kudu								

Buffalo								

SECTION 5: Livestock losses

30a. How many livestock have you lost to each of the following causes in the last 12 months? [for each loss reported, please record which month loss occurred]

Species	Cattle	Oxen	Donkeys	Goats	Sheep	Dogs	Poultry	Month(s)
Predators								
Disease								
Natural deaths								
Accidental deaths								
Slaughter								
Sold								
Used in transaction								
Stolen								
Given as gift								
Other (specify								

30b. Can you tell me a bit about the animals you lost to predators in the last 12 months? [please complete table below – one row for each animal lost to a predator:]

Animal lost	Number lost	Age of animal	Sex of animal	Predator	Month of loss	GPS of incident
1						
2						
3						

31. Do you think that killing of livestock by predators has increased, decreased or stayed the same over the past 12 months? (tick applicable)

Increased	Decreased	Stayed the same

32. Who do you think is responsible for your losses to predation, and why?

____

____

33. How do you think livestock can be better protected against predation?

____

____

34. What action do you think should be taken after livestock predation has occurred? Who do you think should take such action?

____

Section 7: Human injury

42. Has anyone in your household ever been attacked by a wild animal? 1. Yes 2. No

If yes, please give details.

[please try to record the following information: name of person attacked, age of person attacked, when and where the attack happened, what the person was doing at the time, nature of the injury, type of predator, what happened to the predator]

____

43. Do you think that attacks of humans by wild animals has increased, decreased or stayed the same over the past 5 years? (tick applicable)

Increased		Decreased		Stayed the same	

SECTION 8: Conservation & CAMPFIRE

44a. Are you aware of the existence of National Park, Sikumi Forest & Fuller Forest in the region? 1. Yes 2. No

44b. If yes, how do you like it?

5=Strongly like		4=quite like		3=neither like nor dislike		2=quite dislike		1=strongly dislike	

44b. Why? ____

44c. What do you think is the purpose of Matetsi Safari area, Zambezi National Park and Fuller Forests? Why does it exist?____

44d. Have you ever had someone from National Parks or Fuller forests come and talk to you about the Park?

1. Yes 2.No

44d. If yes, describe the encounter: ____

45a. Do you benefit from the presence of National Parks and nearby forests? 1. Yes 2. No /

45b. If yes, how? ____

46. Have you heard of the CAMPFIRE scheme? 1.Yes 2. No

47. What is the function of this scheme?

____

48a. Have you ever benefited from the CAMPFIRE scheme? 1. Yes 2. No

48b If yes, when/how often: ____

How: [select from options below]

	Amount	When? [Year]	Where?
Financial (specify when & amount)			
Meat (specify when & amount)			
Building schools (When? Where?)			
Building roads (When? Where?)			
Drilling boreholes (When? Where?)			
Other (specify, include amount, when & where)			

49a. Have you ever received compensation for the loss of livestock from CAMFIRE/ECA or any programme? 1. Yes 2. No

49b. If yes, from whom?: ____

From Whom	When	How much (US$)	For What loss

50. How much compensation (in US $) do you think is appropriate for the loss of a:

Cattle	Oxen	Donkey	Goat	Sheep	Dog	Poultry (Hen/Cock)	

51a. In your opinion, are there any positive aspects of having wild animals in your area? 1. Yes 2. No

51b.If yes, what? ____

52a. In your opinion, are there any positive aspects of having wild animals in your area?

Yes 2. No

52b. If yes, what?

____

53a. Do you feel the benefits of having predators in your area outweigh the negative aspects?

Yes 2. No

53b. Why?

____

54a. Do you think it is necessary to control the predation of livestock by wild animals?
Yes 2. No
54b. If yes, which of the following methods do you think are appropriate?
[if more than one, please rank your choices, 1 for the most preferred and so on]

Method	Rank
Improving methods for protecting livestock	
Avoiding areas with high risks	
Financial compensation	
Removing problem animals	
Eradication of predators	
Fencing the Park	
Other (specify):	

55a. Do people in this household ever need to take action to control wild animals?
1. Yes 2. No
55b. If yes, what action? ___________________________________
How often? ____
55c. If no, why not? _______________________________________

[Thank the respondent and give information about how and when he will know the results of the study – refer to separate notes]

CHAPTER 6

Perceptions of bushmeat supply and its effect on conservation in western Zimbabwe

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6.0 Abstract

To successfully manage wildlife populations and mitigate illegal wildlife trade, an understanding of how local communities perceive their role in such trade and how it affects conservation efforts around Protected Areas is warranted. We investigated the perceptions of communities living adjacent to Protected Areas on illegal bushmeat harvesting and supply in relation to ongoing conservation efforts using structured household interviews (n = 355) in western Zimbabwe from October 2014 to February 2015. We applied ordinal logistic regression methods to understand the perceptions on factors driving illegal bushmeat harvesting and supply and the possible impacts of this on conservation efforts in the area. The high bushmeat demand was influenced by scarcity of the meat, dry season, killing method (snare and gun) and poachers. The peak in the dry season was attributed to increased demand that coincided with a period of low protein availability in the villages. The effect of bushmeat harvesting on conservation perceptions was highly influenced by those communities residing in wildlife zones and within 10 km, hunting activities both inside and outside Protected Areas and being unemployed, self-employed or a pensioner. Hunting zone was the most influential predictor of how communities viewed illegal bushmeat harvesting in relation to conservation efforts. Mitigating illegal activities would likely be effective when begun with communities in wildlife zones and within 10 km from the National Park boundary because they were highly likely to agree that illegal bushmeat activities were not good for conservation. Such insights on communities' perceptions may help in managing edge effects around Protected Areas.

Keywords Community perceptions, Bushmeat demand, Livelihood, Poaching, Snare

6.1 Introduction

Wildlife has always been legally harvested by various societies worldwide as part of tradition in the supply of food and other values like medicines (Duffy et al. 2015; Gandiwa 2011; Santos-Fita et al. 2012). Most historical hunting was for subsistence and cultural activities (Duffy et al. 2015). However, recent decades brought a double faceted shift where commercial hunting has increased (Bi et al. 2016; Nielsen and Meilby 2015), and traditional norms have become 'illegal' activities according to wildlife conservation laws. The transformation was spearheaded by those who wanted to protect sport hunting (Duffy et al. 2015). Unfortunately, very little communication and awareness was done to make society aware of the transformation hence some communities continued to harvest wildlife using their traditional norms and values (León and Montiel 2008; Santos-Fita et al. 2012; Swift et al. 2007). Regrettably, those found illegally hunting were arrested and prosecuted. Subsistence bushmeat harvesting has been a part of African societies since ancient times and it represents an important complementary source of animal protein (Grey et al. 2010) in the diet of most communal people, and in some instances urban communities (Lindsey et al. 2011a; 2013; Mbete et al. 2011). This further points out that those communities adjacent to Protected Areas (PA) disagree with criminalising subsistence wildlife harvesting. As such, their unwillingness to embrace the criminalisation of subsistence bushmeat harvesting catalyses continued arrests of community members thereby engendering negative attitudes especially in societies where there are numerous human wildlife-conflict incidences. Communities that do not benefit from conservation of wildlife are less likely to accept the criminalisation of bushmeat harvesting and trade (Nasi et al. 2008). Instead, they use other crude means of illegal harvesting such as wire snares to get bushmeat while also reducing the number of possible wild animals that threaten their livelihood in their villages (Gandiwa 2011). This is usually achieved by setting numerous snares in areas with relatively high wildlife presence. The snare is non-selective (Wadley 2010), and although the poacher eventually collects one or two of the carcasses, numerous others killed by the snares remain for scavengers like spotted hyenas (*Crocuta crocuta*) and vultures.

In recent years the bushmeat trade at both subsistence and commercial level has increased (Bi et al. 2016; Wright and Priston 2010) posing a great risk to species conservation and spread of zoonotic diseases not only within a country but across continents (Bair-Brake 2014). Studies conducted in central Africa showed that illegal hunting occurs mostly in the dry season when large herds of migratory herbivores arrive near communal settlements (Martin et al. 2012), although one study showed no specific seasonal effect in Tanzania (Martin et al. 2012). However, non-migratory species like primates are also hunted for bushmeat in some Protected Areas in central Africa (Wright and Priston 2010). Various methods have been employed in hunting wild animals in different parts of the world. It is usually conducted with dogs (Wright and Priston 2010), wire snares (Pangau-Adam et al. 2012; Wright and Priston 2010), pit falls, poisons (Schulte-Herbrüggen et al. 2013), and spears or bows (Pangau-Adam et al. 2012). Unfortunately, bushmeat trade and illegal hunting cause reductions in populations of various hunted species, especially ungulates, and non-target species (Martin et al. 2012; Wright and Priston 2010) thereby threatening the sustainability of wildlife-based land-uses (Lindsey et al. 2011a) and also threatening the biological stability of some ecosystems (Nasi et al. 2008). Consequently, there is a need to control illegal hunting and bushmeat trade. However, little knowledge is available on the extent of bushmeat trade and illegal hunting, particularly in southern Africa (Grey et al. 2010), hence attempts to manage the problem are currently difficult.

Earlier studies revealed numerous drivers of increased illegal hunting and bushmeat trade in Africa which include poverty (Duffy et al. 2015; Kümpel et al. 2010; Robinson and Bennett 2002), unemployment (Lindsey et al. 2011b), food shortages and droughts. In Zimbabwe, non-performing Community-based Natural Resource Management (CBNRM) programmes, absence of affordable protein sources other than illegally sourced bushmeat, poor and inadequate investment in anti-poaching and weak penalties (Mancini et al. 2011; Nielsen et al. 2014) on offenders that do not deter potential illegal bushmeat hunters (Lindsey et al. 2011b) are some of the additional variables fuelling illegal harvesting.

Scavengers such as spotted hyenas benefit from the illegal snaring of numerous ungulates in Protected Areas (Pangau-Adam et al. 2012; Williams et al. 2016). They feed on the carrion and bones thereby sanitising the area of rotting carcasses (Abay et al. 2011). Wire snares that would not have caught prey accidentally kill such scavengers (Wadley 2010) as spotted hyenas as they attempt to get to the ensnared carcasses. However, in other instances, snares are deliberately deployed to catch both ungulates for bushmeat and spotted hyenas and other carnivores that are perceived destructive to the livelihoods of communities on the fringes of Protected Areas. Furthermore, scavengers sometimes consume prey caught in snares before poachers retrieve catches, thereby creating further negativity towards the species. Consequently removal of the prey base by poachers (Williams et al. 2016) has a negative effect on the carnivore population in Protected Areas. This causes the spotted hyenas to expand their home range out of Protected Areas (Williams et al. 2016) to search for alternative prey, which is unfortunately livestock if there are communities living adjacent to the Protected Areas. Thus, any spotted hyena dens near the communities or in the PA sections where illegal hunting activities occur are likely to be destroyed or any spotted hyenas killed (Williams et al. 2016) to protect livestock. Such unfortunate behaviour leads to reduced spotted hyena numbers (Williams et al. 2016), thus threatening the species' population in and outside Protected Areas.

In some studies authors lamented that controlling illegal bushmeat trade is not feasible if there is no political and economic stability, or will (Lindsey et al. 2011b; Stiles 2011). Another challenge in controlling bushmeat trade is that it is usually spearheaded by known poachers in communal areas (CAs) but would never be exposed because some community members also buy bushmeat from them (Nasi et al. 2008). Due to the aforementioned concerns pertaining to the conservation of threatened wildlife species, we undertook a structured questionnaire survey to assess illegal bushmeat harvesting activities and community perceptions about such illegal activity on ongoing conservation efforts. We predicted that bushmeat supply was influenced by challenges in accessing the meat, hunter origins (local or external people), killing methods used and hunting season. We further predicted that household distance from PA boundary, employment status, preferred hunting season, hunting zone (inside or outside Protected Areas), and target species were likely to influence perceptions about ongoing conservation efforts in relation to bushmeat harvesting in the area. This study is important in influencing policy on illegal bushmeat harvesting and trade in communities adjacent to Protected Areas. It also ‘sheds some light’ on possible drivers of large carnivore population declines.

6.2 Methods

Study site

Our study was conducted in Chikandakubi, Kachechete, and Matetsi Wards of Jambezi Communal Lands and Matetsi resettlement areas in Hwange District, Western Zimbabwe. It was centred at 18° 6.350'S and 25° 58.949'E (Fig. 6.1).The study area has two models of CBNRM, namely the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) and Environmental Conservation Areas (ECAs) (Frost and Bond 2008). Environmental Conservation Areas (ECAs) are concentrated in Matetsi Ward (Breakfast Farm, Isla Farm and Masuwe Village) which are mainly resettlement areas. Settlement types are mainly communal and resettlement.

Households are distributed either linearly along the main road or haphazardly around an area of high human activity like a business centre or school. Communities in this region rely on subsistence agriculture (agro-pastoral) as a source of livelihood although there is very little cropping which is characterised by early maturing and drought resistant crop varieties like sorghum (*Sorghum bicolor*) and millet (*Pennisetum glaucum*) (Kuiper et al. 2015). The region receives delayed, sporadic and low rainfalls averaging 650 mm p.a. (Loveridge et al. 2007). The seasons are divided into a hot-wet season (December-April), a cold-dry season (May-August), and a hot-dry season (Sept-November). The district has a rural population of ~62670 (Zimbabwe National Statistics Agency 2012), and the total population for the sampled area was ~4038 with ~976 households and a mean family size of 4.2 members (Zimbabwe National Statistics Agency 2012).

The study area is bordered by Fuller Forest to the South, Binga district to the North, Zambezi National Park and Victoria Falls to the West. The predominant vegetation is primarily savanna, largely miombo woodland mixed with shrubland with a smaller part being grassland (Périquet et al. 2016) on Kalahari sands. Major prey species found in the study area include the greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*) and warthog (*Phacochoerus africanus*) and impala (*Aepyceros melampus*) (Mills and Hofer 1998).

Data collection and analysis

In Zimbabwe, The Parks and Wildlife Act Chapter 20:14 (1975) prohibits hunting of wildlife without a hunting permit. We applied a stratified sampling design using distance of household from the PA. Two strata were established i.e. wildlife zone which mainly involved resettlements under the ECAs and homesteads outside the PA (Fuller Forest). The area outside the PA was split into three distance categories i.e., ≤5 km, 6-10 km and above 10 km from the Fuller Forest boundary. Households within each stratum were systematically selected for structured interviews and, every fourth homestead was sampled. If there was no person above 18 years of age in the selected homestead or he or she was not interested in taking part in the survey, the interviewer sampled the next homestead that suited the sampling criterion.

Prior to sampling, we obtained ethical clearance from the University of Kwa-Zulu-Natal and permission was sought from the local chiefs and village heads. The interviewer targeted household heads or any family representative if the household head was absent. The study sampled 355 households, at least 70 from each distance category, targeting illegal bushmeat hunters and bush meat consumers in the study site. Prior to the interview, the interviewee was informed that the data collected were mainly for academic reasons and there were no direct monetary or non-monetary benefits associated with taking part in the survey. The interviewees' current livestock holding and other sources of livelihood were assessed.

Two response variables were used to assess illegal bushmeat harvesting activities and community perceptions about wildlife conservation in the area. In the first response variable, interviewees were asked whether bushmeat demand was high in the area and 13 predictive variables were considered to influence this response variable (Table 6.1). These were bushmeat consumption by the respondent, why they considered bushmeat demand as (not) high, source of bushmeat in the area; type (sex and age) of active bushmeat hunters; modes of communicating availability of bushmeat for sale; challenges they faced in accessing bushmeat; whether hunters were locals or people from other villages; hunting zone; killing methods used; preferred hunting season by poachers; and ethnic background of poachers in the area, and quantity of bushmeat bought per household per week.

In the second response variable, we measured respondents' perceptions based on how they viewed bushmeat harvesting in relation to conservation of wildlife in the area. That is, whether they considered illegal bushmeat harvesting positive or negative for conservation efforts in the area. We used thirteen predictor variables considered to influence illegal bushmeat harvesting as being positive or negative for conservation (Table 6.1). These were bushmeat consumption by the respondent; type (sex and age) of active bushmeat hunter; distance of household from PA boundary; level of education; employment status of the respondent; bushmeat source; preferred hunting season by poachers; hunting zone; sources of livelihood; the most hunted species; preferred killing method; tribe of bushmeat supplier; and length of time the responded had lived in the area.

Data were then subjected to ordered logistic regression in Program R version 3.2.5 (R Core Team 2015b) using supportable packages: ordinal (Christensen 2015), AICcmodavg (Mazerolle 2015), Hmisc (Frank et al. 2016), reshape2 (Wickham 2007), foreign (R CoreTeam 2015a), nnet (Venables and Ripley 2002a), MASS (Venables and Ripley 2002b), and MuMln (Barton 2016). The best-fit candidate models with few predictors were generated following the framework of Burnham and Anderson (2002). Best models that strongly influenced perception were selected based on the Akaike's Information Criterion value ($\Delta AIC \leq 2$) (Burnham and Anderson 2002). We summed the model weights from all the candidate models containing the particular covariate to conclude the relative importance of each covariate on perceptions about illegal bushmeat harvesting.

Limitations

Although sport hunting is legal with a permit, the law does not permit subsistence hunting of any animal. Considering the legal implications of those involved in illegal bushmeat harvesting, there were limitations in the way responses were provided. Persons found with evidence of illegal harvesting of bushmeat shall be guilty of an offence and liable to a fine (Parks and Wildlife Act 1975). Hence, the majority of respondents were hesitant to release information opting for the "Not willing to disclose (NWTD)" option is their response.

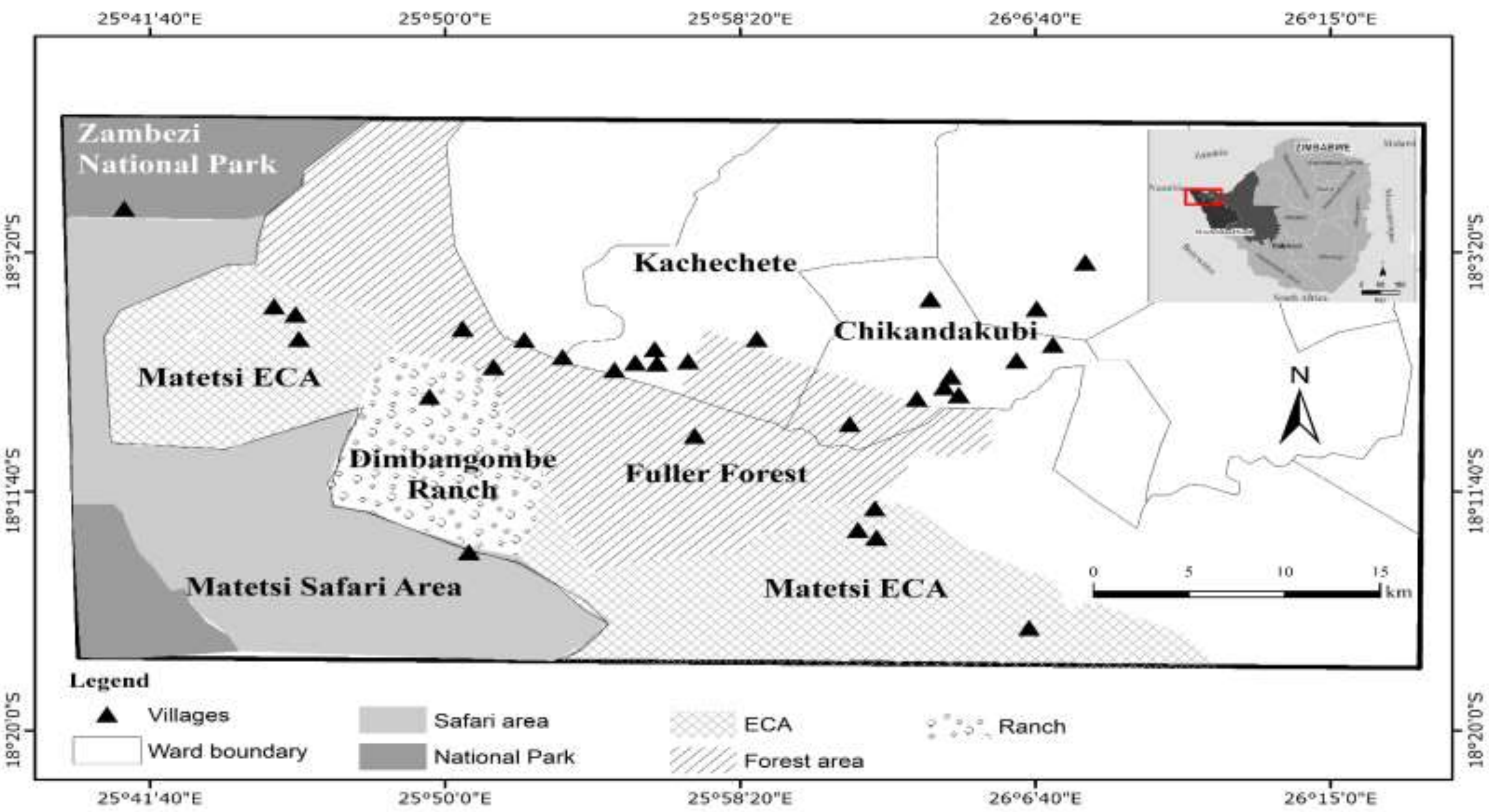


Fig. 6.1 Distribution of studied villages in Matetsi ECAs and Jambezi CAs, Zimbabwe, where the interviews were conducted (Villages covered were Baobab, Dunu, Elsa, Masikili , Siyazama and Jabulani (wildlife zones, Matetsi Ward), Batanani, Chishanga, Mbizha, Mithimitema and Ndimakule (communal areas, Chinkandakubi ward) and Misenyika, Siamwele, Ndlovu, Mvutu, Lupinyu, Cheumba, Mpumelelo, BH 24, BH25, and

BH26 (communal areas, Kachechete ward). The protected areas near the villages include Fuller Forest, Mvutu Forest, Dimbangombe Ranch and Matetsi Safari Area).

Table 6.1 Predictors and response questions used in interviews to determine perceptions of bushmeat activities in western Zimbabwe.

Predictors	**Levels**		**Response (Perception)**	
			Demand	Conservation
1. What is your main source of livelihood?	• Livestock • Other	• Crop Farming		√
2. What is the distance to the nearest protected area boundary?	• Wildlife zone • Above 10km	• Within 10km •		√
3. How long have you lived in this area?	• ≤10years • > 20 years	• 11-20years		√
4. What is your level of education?	• None • Secondary	• Primary • Tertiary		√
5. To which tribe do you belong?	• Nambya • Other	• Ndebele	√	

6. What is your employment status?	• Employed Pensioner	• Self-employed • Unemployed		√
7. Do you eat bushmeat?	• Yes	• No	√	√
8. If yes to (7) where do you source it?	• Poachers • NWTD	• PAC/Quota	√	√
9. What method was used to kill the hunted animals?	• Gun • Combination	• Wire snare • NWTD	√	√
10. What challenges do you face in accessing bushmeat?	• Not licenced • NWTD	• b/meat scarcity • None	√	
11. Why do you say demand for bushmeat is (not) high?	• Alternative protein • NWTD	• Do not know	√	
12. Are hunters local or external?	• Local • Both	• External • NWTD	√	
13. How is bushmeat availability communicated within the village?	• Word of mouth • NWTD	• Poachers sell around	√	

14. Which species is hunted most for bushmeat (Priority species 1)	-	-	√	√
15. What quantities do you buy per week?	• Up to 1 kg	• 2-4 kg	√	
	• >4 kg	• NWTD		
16. Who are the active bushmeat hunters the village?	• Young men	• Adult males	√	√
	• Both	• NWTD		
17. Do poachers hunt inside or outside protected areas?	• Inside	• Outside	√	√
	• Both	• NWTD		
18. From which tribe does your bushmeat supplier belong?	• Nambya	• Ndebele		√
	• Other	• NWTD		
19. When is bushmeat hunting most preferred?	• Dry season	• Wet season	√	√
	• Both	• NWTD		

Table 6.2 Multi-model selection results of ordered ordinal logistic regression showing the variables influencing perceptions of the demand of and illegal harvesting of bushmeat in western Zimbabwe.

Model	**d.f**	**LogLikelihood**	**AIC**	**ΔAIC**	**Weight**
Challenges + Hunters(L/E) + Killing method + Hunting season + bushmeat source	18,00	-163.88	365.79	0.00	0.49
Challenges + Hunters(L/E) + Killing method + Bushmeat source	15,00	-167.78	366.97	1.17	0.27
Challenges + Hunters(L/E) + bushmeat source + Target species	16,00	-167.45	368.50	2.71	0.13
Challenges + Communication method + Hunters(L/E) + Killing method + Source	17,00	-167.70	371.21	5.42	0.03
Challenges + Hunters(L/E) + Killing method + Source + Target species	19,00	-165.54	371.34	5.54	0.03
Challenges + Hunters(L/E) + Source	12,00	-173.25	371.41	5.62	0.03
Challenges + Hunters(L/E) + Hunting zone + Source	15,00	-171.63	374.67	8.87	0.01
Challenges + Hunters(L/E) + Hunting zone + Season + Source	18,00	-169.09	376.21	10.41	0.00

6.3 Results

Eighty-two percent (n = 94) of those who were willing to disclose information considered bushmeat demand to be high in the area, while 15% (n = 17) perceived it not to be high. Only 3% (n = 3) did not know if bushmeat demand was high or not. Of those who were willing to disclose, 36% (n = 19) thought illegal bushmeat harvesting does not affect conservation while 64% (n = 34) perceived it to be negative. Overall, the majority of respondents were not willing to disclose information about illegal bushmeat trade in the area.

In the first response variable, top two models with strong predictors were selected for their strong influence on perceptions based on ≤2ΔAIC values (Table 6.2). Five predictors, that is, bushmeat sourced from poachers or Problem Animal Control (PAC), scarcity, hunters' origins (local or external people), season (dry season) and hunting method (use of snares for killing animals) were influential variable on how the community viewed trends in bushmeat supply in the study area (Table 6.3). Supply sourced from PAC or sport-hunting (quota) carcasses significantly influenced the demand for bushmeat ($\beta = 38.9251$, SE = 3.7413, $P = 0.0012$). Based on the estimated top model coefficients, availability of bushmeat was high during the dry season ($\beta = 4.21$, SE = 1.61).

In the second response variable (bushmeat versus conservation), the top model with the strong predictors was selected for its strong influence on perceptions based on ≤2ΔAIC values (Table 6.4). Four predictors, that is, settlements in wildlife zones ($\beta = -2.41$, SE = 0.86, $P = 0.00$), hunting inside Protected Areas ($\beta = 20.02$, SE =1.52, $P = 0.00$), hunting in the dry season ($\beta = 3.90$, SE = 2.07, $P = 0.00$) and employment status (pensioners) were more influential on the community's perception on illegal bushmeat harvesting in relation to conservation of wildlife (Table 6.5). Communities inside wildlife zones (ECAs) were highly likely to influence the thinking that illegal bushmeat activities were negative for conservation. Illegal bushmeat harvesting activities were high in the dry season compared with the wet season. Predicted probabilities for the influence of the distance effect on perception on conservation versus illegal bushmeat harvesting showed that communities in wildlife zones and within 10 km to PA boundary discouraged poaching (Fig. 6.3). Challenges in accessing bushmeat (scarcity), source of the bushmeat (PAC or quota and poachers), prey killing method (snares), hunting season (dry) and hunter origins (local and external poachers) had relative importance of 1, 1, 0.83, 0.5 and 1 respectively, in influencing bushmeat demand. Variables influencing perceptions on ongoing conservation efforts, that is, hunting season (dry), household distance from PA (inside wildlife zones), employment status (self-employed, employed and pensioners), and hunting zone (inside Protected Areas) had relative importance of 1, 0.99, 0.9 and 0.87 respectively.

Table 6.3 Top model coefficient (β) estimates and standard errors (SE) and probabilities of significant predictor variables.

Predictor (level)	**B**	**S.E**	**t-value**	**P value**
Hunters (both)	21.83	20.39	1.07	0.28
Hunters (external)	24.04	20.42	1.18	0.24
Hunters (local)	23.31	20.41	1.14	0.25
Hunters (NWTD)	20.90	20.42	1.02	0.31
Killing method (combined)	-1.73	1.31	-1.32	0.19
Killing method (gun)	0.58	1.47	0.39	0.70
Killing method (NWTD)	1.48	1.25	1.18	0.24
Challenge (none)	-9.51	11.52	-0.83	0.41
Challenge (not licenced)	-6.06	11.50	-0.53	0.60
Challenge (NWTD)	-9.08	11.49	-0.79	0.43
Source (from poachers)	0.97	0.64	1.52	0.13
Source (NWTD)	-1.20	0.39	-3.04	0.00*
Source (PAC/Quota)	38.92	3.74	10.36	0.00*
Season (Both wet & dry)	11.05	51.00	0.22	0.83
Season (dry)	4.21	1.61	2.61	0.01*
Season (NWTD)	3.19	1.57	2.03	0.04*
|No	4.46	9.43	0.47	0.64
No | NWTD	12.79	16.74	0.76	0.44
NWTD | Yes	18.14	16.74	1.08	0.28

* Indicates significant values

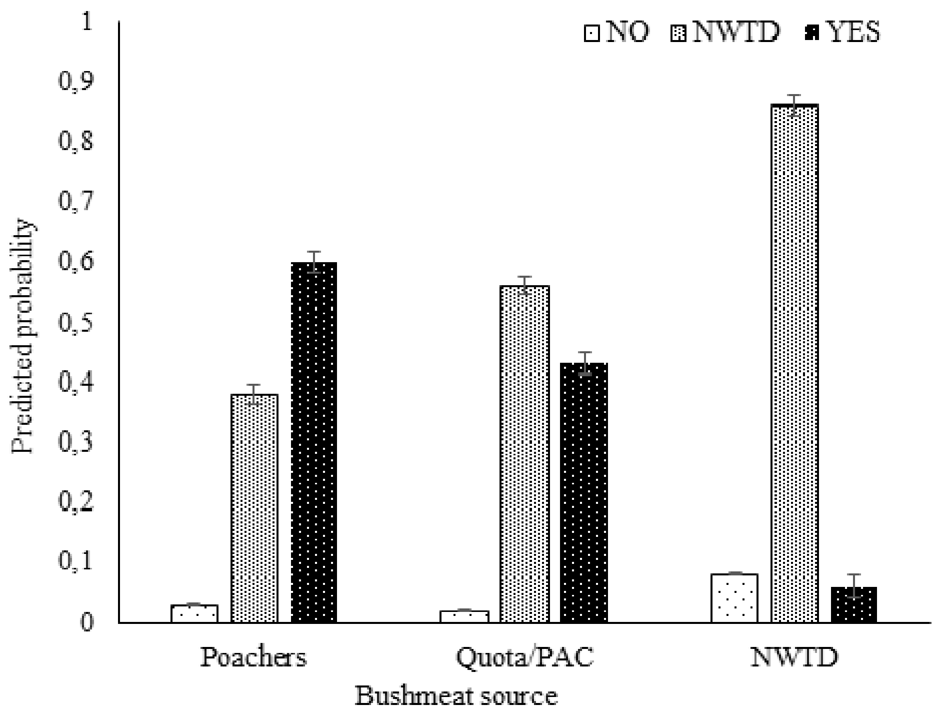
Table 6.4 Multi-model selection results of ordered ordinal logistic regression on perceptions of the community of illegal bushmeat activity and its conservation efforts.

Model	**d.f**	**LogLikelihood**	**AIC**	**ΔAIC**	**Weight**
Distance + Employment status + Hunting season + Hunting zone	13	-97.22	221.50	0.00	0.81
Distance + Eat bushmeat + Employment status + Hunting season	12	-100.12	225.16	3.65	0.13
Distance + Hunting season + Hunting zone + Target species	15	-98.29	228.00	6.49	0.03
Distance + Hunting season + Hunting zone	10	-104.57	229.79	8.28	0.01
Employment status + Hunting season + Hunting zone	11	-103.86	230.50	8.99	0.01
Distance + Hunting season	7	-110.20	234.73	13.23	0.00

Table 6.5 Estimated coefficient (β), standard error (SE) and probability (P) values for the top model variables influencing conservation perceptions in relation to illegal bushmeat activities

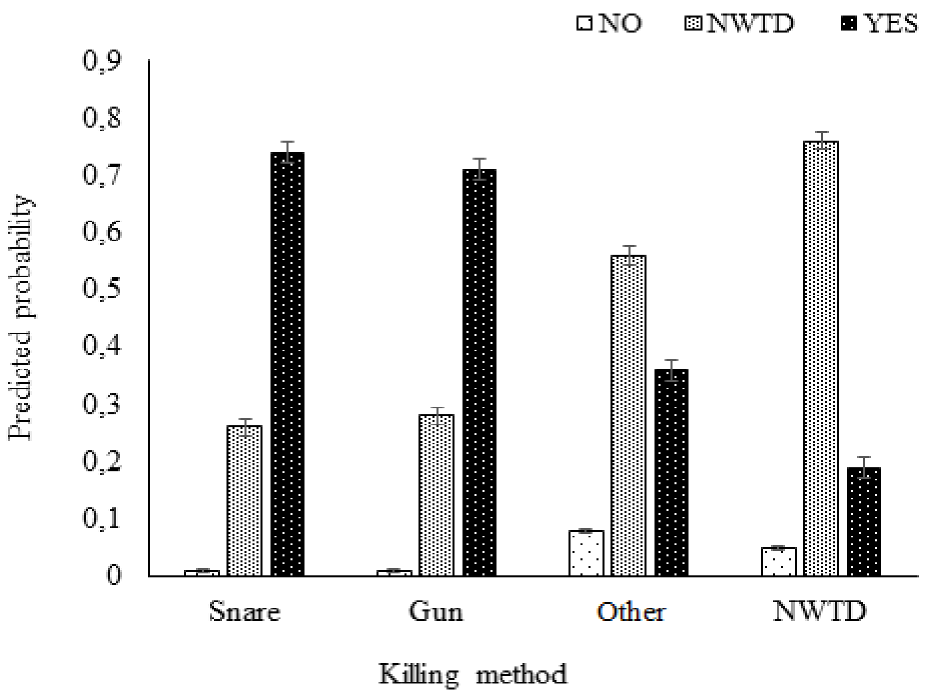
Predictor (level)	**B**	**S.E**	**t-value**	**P value**
Distance (Wildlife Zone)	-2.41	0.86	-2.82	0.00*
Distance (within ten km)	-2.17	0.82	-2.63	0.01*
Hunting zone (inside PA)	20.02	1.52	13.18	0.00*
Hunting zone (NWTD)	16.81	0.75	22.55	0.00*
Hunting zone (outside PA)	14.71	0.65	22.52	0.00*
Employment status (pensioner)	13.03	0.00	$1.18e^{+7}$	0.00*
Employment status (self-employed)	-3.97	1.43	-2.77	0.01*
Employment status (unemployed)	-2.79	1.39	-2.01	0.04*
Hunting season (dry season)	-3.90	2.07	-1.89	0.06
Hunting season (NWTD)	3.53	1.33	2.65	0.01*
Hunting season (Wet season)	-1.45	2.05	-0.71	0.48
Harvesting bad | Harvesting good	11.57	1.71	6.78	0.00*
Harvesting good | NWTD	12.81	1.68	7.61	0.00*

* Indicates values that are significant



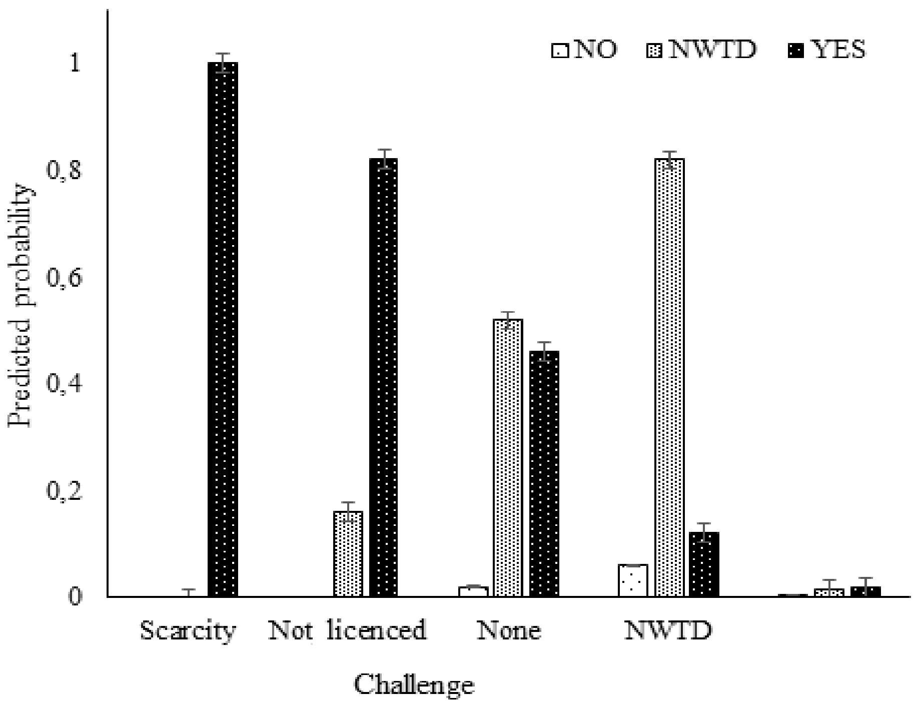
NO
NWTD
YES
Predicted probability
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
Poachers
Quota/PAC
NWTD
Bushmeat source

(a)



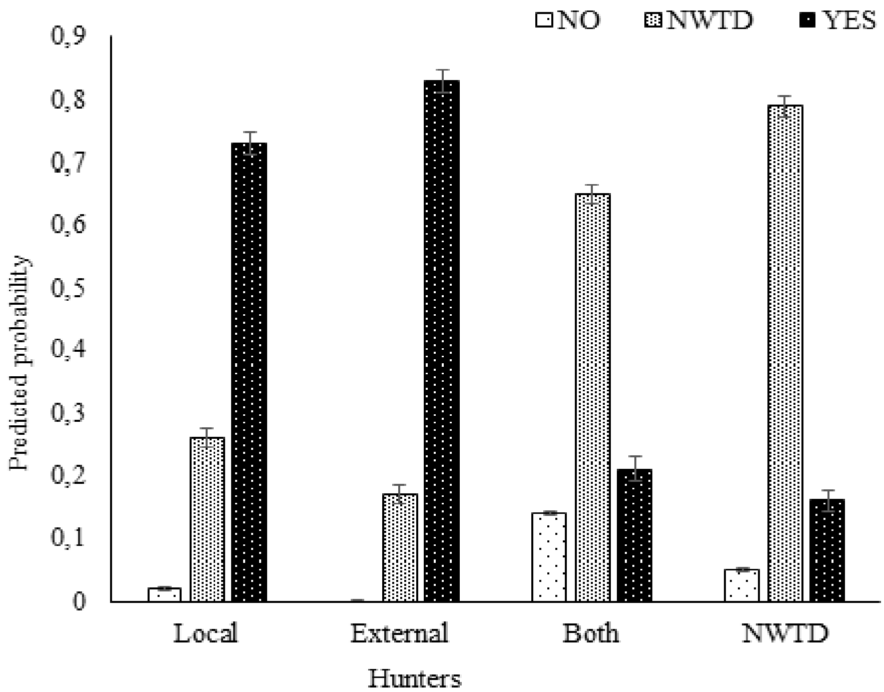
NO
NWTD
YES
Predicted probability
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
Snare
Gun
Other
NWTD
Killing method

(b)



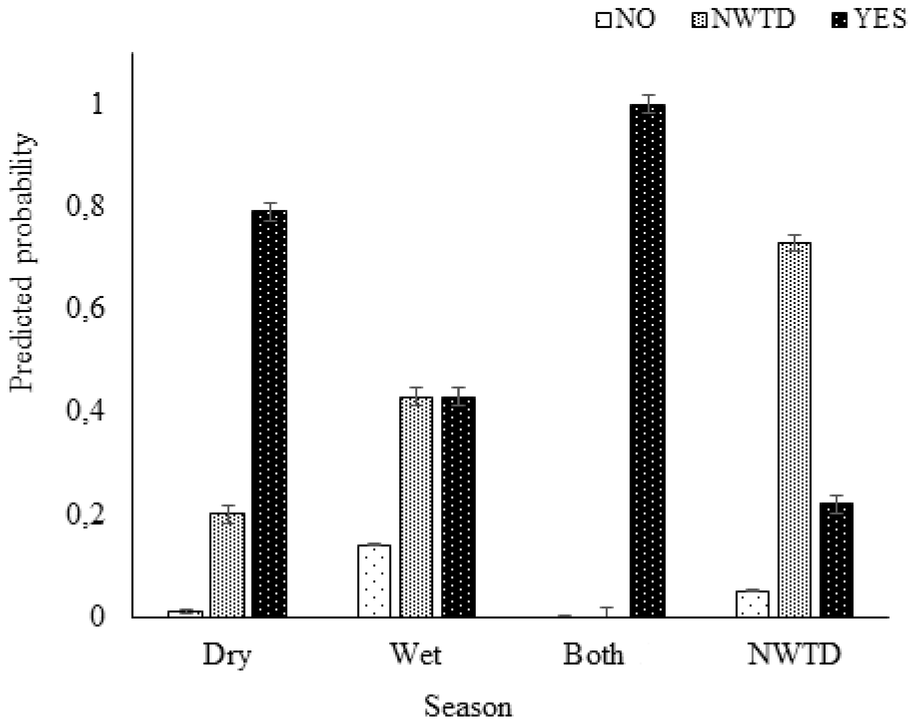
NO
NWTD
YES
1
0,8
0,6
0,4
0,2
0
Predicted probability
Scarcity
Not licenced
None
NWTD
Challenge

(c)



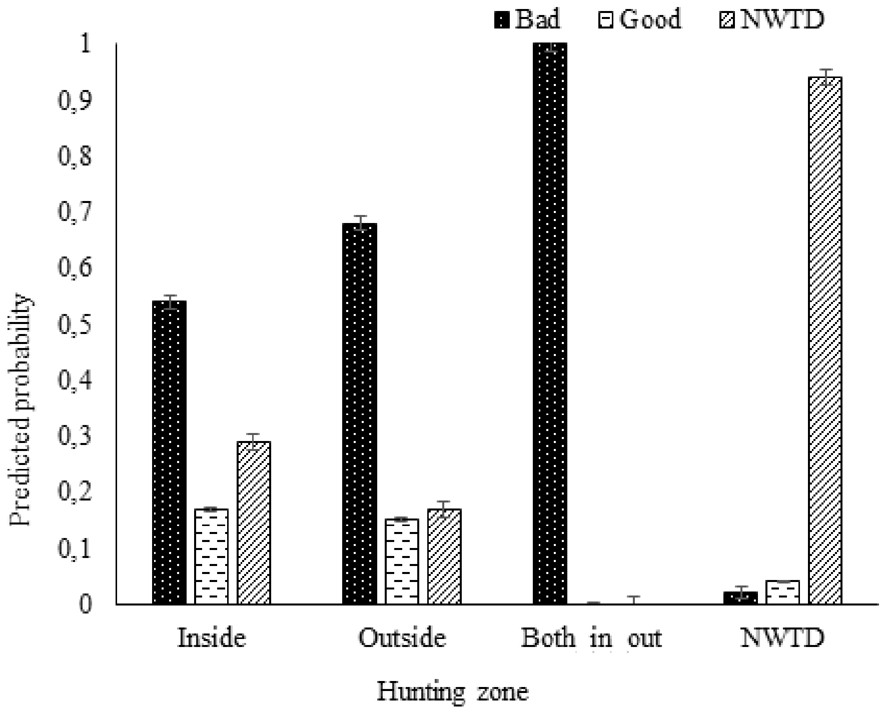
NO
NWTD
YES
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
Predicted probability
Local
External
Both
NWTD
Hunters

(d)



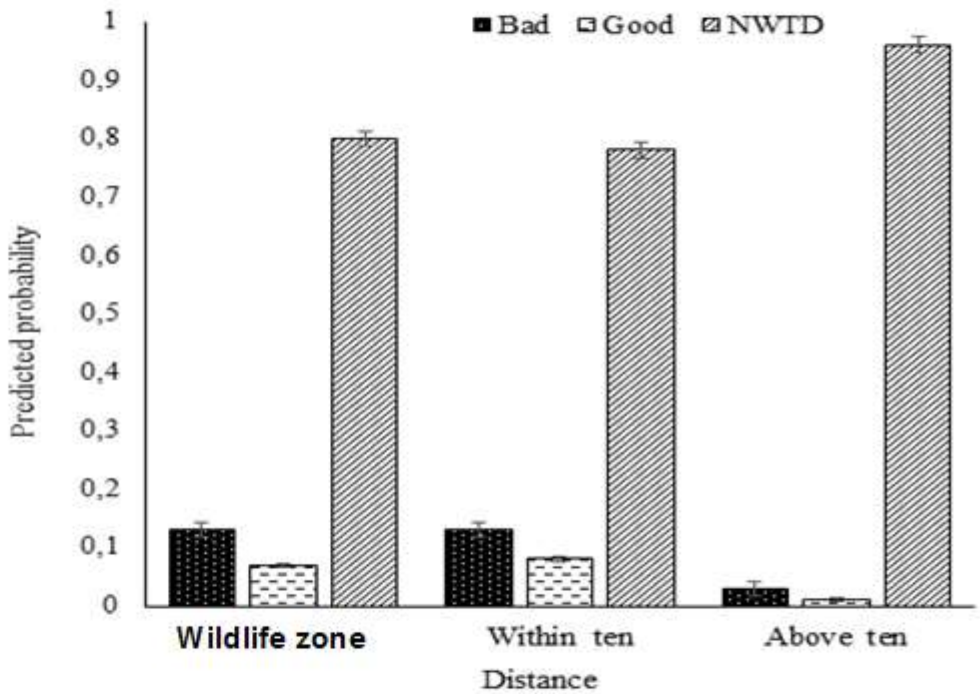
(e)

Fig. 6.2 Predicted probabilities of the five predictor variables in the top model that were influential on illegal bushmeat demand in Jambezi and Matetsi areas (The perception was based on whether they considered demand of bushmeat high or not. Expected responses were “Yes” if demand was high and “No” if they presumed it low or NWTD if they were not at liberty to reveal the information about demand. NWDT –‘not willing to disclose’; challenge- what hinders the respondent from accessing bushmeat frequently ; hunters; origins were perceptions on whether hunters were local or external people and killing method was the way the animals for bushmeat were usually killed by poachers (snare, gun, or combined methods including dogs and pitfalls).



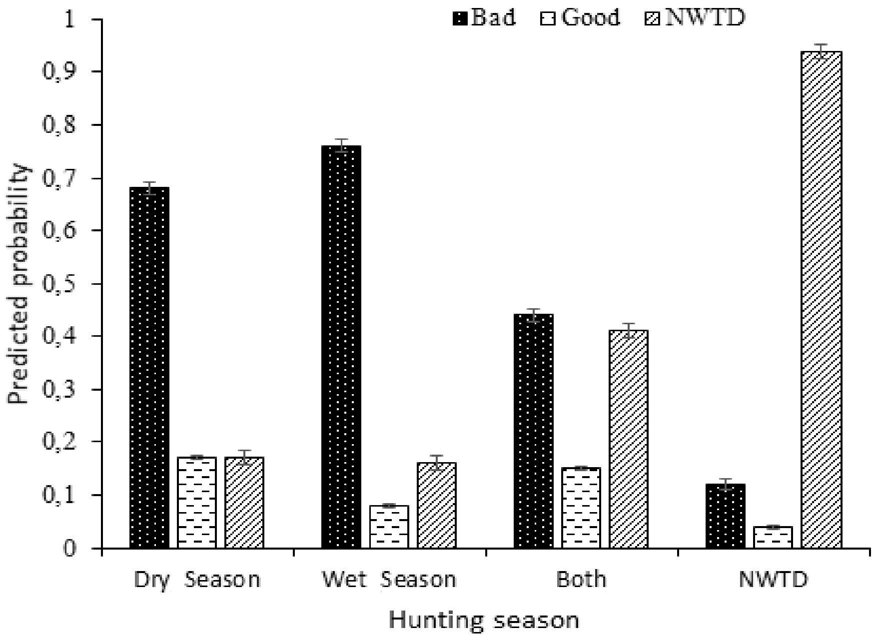
Bad
Good
NWTD
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
Predicted probability
Inside
Outside
Both in out
NWTD
Hunting zone

(a)



Bad
Good
NWTD
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
Predicted probability
Wildlife zone
Within ten
Above ten
Distance

(b)



(c)

(d)

Fig. 6.3 Predicted probabilities of the four predictor variables in the top model that were influential on perceptions about effects of illegal bushmeat trade on conservation efforts in Jambezi and Matetsi areas. (GOOD (positive) and BAD (negative) refer to perceptions on whether illegal bushmeat harvesting was good or bad for conservation in Jambezi and Matetsi areas).

6.4 Discussion

Our study confirmed that bushmeat demand is high in western Zimbabwe because it is an alternative source of protein. As such, bushmeat consumption was likely to affect conservation efforts in the study area. The availability of bushmeat from sport hunting quota made it easier for poachers to sell their meat concurrently. Thus, bushmeat supply was assumed to link strongly to hunting season as a cover up scheme for the poached product. When excluding those who were not willing to disclose (NWTD) information about bushmeat consumption, predicted probabilities clearly showed that respondents perceived bushmeat to be from poachers more than any other possible source in the area.

There was an effect of season on bushmeat supply which was increased during the dry season. As such, there was a high likelihood that most hunting activities occur in the dry season. The findings implied that the dry season had a likely negative impact on conservation efforts because of high bushmeat hunting (Martin et al. 2012). Unlike in Serengeti National Park where there are clear migratory patterns in ungulates, wildlife in Zimbabwe is generally confined to Protected Areas and does not migrate. The main determinant of animal local movement in most wildlife areas in western Zimbabwe is water availability. As such, during the wet season, wildlife in most Protected Areas will be scattered throughout the landscape due to availability of temporary water sources. However, during the dry season, animals are restricted to areas closer to water sources like artificial and perennial pans (Valeix et al. 2010), hence poachers target those waterholes where prey often congregate (León and Montiel 2008; Valeix et al. 2010; Lindsey et al. 2011b; Mzumara et al. 2015;).

The perception on methods used to hunt indicated that poachers were likely to use snares than other methods. The majority of respondents who claimed that bushmeat demand was high perceived snaring as the main technique effective for subsistence poachers in the area (Moreto and Lemieux 2015; Wadley 2010). Although other methods likely existed, the setup of the community Protected Areas makes it difficult to effectively employ other hunting methods like use of guns or hunting dogs except inside Protected Areas. Generally, commercial poachers use guns mainly targeting ivory while subsistence poachers use snares (Moreto and Lemieux 2015) as gun noise would expose them to rangers. In addition, the use of hunting dogs for poaching requires rearing several dogs, which, however, will stimulate suspicion of illegal bushmeat activities. Consequently, snares would be preferred because of lower detection by rangers in Protected Areas while it is also a cheaper and more silent method of killing wildlife (Gandiwa 2011; Williams et al. 2016).

Although bushmeat trade was taking place in the area, demand was very high for poachers to satisfy. As results, poachers are likely to continue their illegal activities because of the readily available market (Mbete et al. 2011) So long there is a market for bushmeat in the area with high unemployment, the illegal harvesting will be a more attractive source of income. Unfortunately, this will be detrimental to conservation efforts (Grey et al. 2010; Mbete et al 2011). As a result, to curb bushmeat activities in western Zimbabwe, the mitigation measures must not ignore the consumers of bushmeat supplied by poachers. Whatever mitigation measures, these must also fill the gap for protein and income obtained from bushmeat.

Of interest was that bushmeat harvesting was more likely to take place in the communal areas in as much as it would in the Protected Areas. The hunting zone had a significant effect on bushmeat demand. Findings indicated that most bushmeat was hunted inside Protected d Areas. Similar findings have been recorded elsewhere (Conteh et al. 2015; St John et al. 2010). Based on our knowledge of the study area, hunting outside Protected Areas using snares would be problematic because livestock will be killed in snares leading to a conflict with owners.

Illegal bushmeat activities were independent of distance from the Protected Area boundary. Communities in wildlife zones and those within 10 km from the Protected Areas boundary had positive perceptions about wildlife conservation. This was evidenced by their strong response against illegal bushmeat activities, which were regarded as affecting conservation. This finding was contrary to our prediction that communities close to Protected Areas are disturbed by edge effects through human-wildlife conflicts, and hence would likely favour bushmeat trade as a way of deterring offending animals. This was also in contrast to earlier research (Lindsey et al. 2013; Williams et al. 2016). If communities do not benefit from wildlife and continue to lose their livelihoods to wild animals that reside in Protected Areas, then no positive perception can be expected from them (Dickman et al. 2011; Mishra et al. 2003; Kansky and Knight 2014). High probability of bushmeat trade are inevitable and such behaviour among communities adjacent to Protected Areas is a risk factor against conservation efforts in Zimbabwe.

Our study emphasises that incentives from wildlife conservation could have influenced the positive anti-poaching perceptions in communities within and near Protected Areas in western Zimbabwe. In particular, ECAs follow the CBNRM programme effectively and could be influencing such a positive attitude about conservation. Once communities realise the benefits of conserving wildlife at household level, perceptions generally change and people become tolerant of and hence can coexist with wild animals (Dickman et al. 2011; Kansky and Knight 2014). In such instances, bushmeat activities and hence negative perception about conservation can be reduced.

Protected Areas with adjacent communities exhibiting high unemployment rates are likely to experience more illegal bushmeat activities and negative perceptions about conservation. We found that those who are employed or self-employed were likely to tolerate wildlife and hence not partake in illegal bushmeat activities. This was seen as one of the options to curb poaching and promote ongoing conservation efforts. These findings are similar to previous studies done in Zimbabwe and elsewhere (Duffy et al. 2015; Gandiwa 2011; Pangau-Adam et al. 2012; Pratt et al. 2004) where unemployment and hence poverty were major driving forces for illegal bushmeat harvesting.

A number of solutions have been proposed to reduce illegal bushmeat trade including alternative livelihoods, re-aligned land-use planning and creating buffer zones near CAs among other solutions (Lindsey et al. 2013). Unfortunately, continued threats to conservation though bushmeat harvesting are likely to increase because of the economic incentives brought by the trade in the meat (Kümpel et al. 2010; Zhang et al. 2008). However, these solutions should be area specific (Nyaki et al. 2014) but would mainly depend on the political and the socio-economic conditions in the area. In Jambezi, alternative livelihoods would be the priority option in solving the bushmeat crisis because the area is drought stricken while a wildlife-based rural development economy would also be of much significance in reducing illegal bushmeat activities (Mhlanga, pers. obs.). Investing in anti-poaching technology would be of much importance but would not be effective if livelihood needs are not solved., the mitigatory measures will not be effective if incentives from wildlife resources are not realised by the community. Moreover, increase in human-wildlife conflicts will always trigger anti-wildlife perceptions that lead to a number of problems, one of which is retaliatory illegal bushmeat trade.

Bushmeat harvesting in Zimbabwe and several other countries in Africa is generally conducted illegally if without a permit (Parks-and-Wildlife-Act 1975). Regrettably, not much research has been done in landscapes where bushmeat harvesting has been criminalised hence the existence of several unanswered questions. What then are the implications of our findings to wildlife management? Earlier studies have recorded demand for bushmeat in both rural and urban centres, highlighting that it fuelled increased harvesting (Pangau-Adam et al. 2012; Zhang et al. 2008) and hence probably reducing the number of available prey for the spotted hyenas and other large carnivores (Macdonald and Sillero-Zubiri 2002). Prey depletion by the communities residing outside and inside Protected Areas has a negative feedback on the same people's livestock and hence on conservation efforts. That is, large carnivores as African lions and spotted hyenas will expand their home ranges and consequently overlap into human settlement where they kill livestock as alternative prey.

As such, there is need to revise some wildlife policies and remodel some of the CBNRM programmes that exist in the country. Furthermore, research needs to be done on bushmeat harvesting countries in southern Africa. Of concern in this survey, as reported elsewhere in other studies (Mancini et al. 2011), were the number of respondents who were not willing to disclose (NWTD) information in fear of victimisation no matter how much assurance was offered on confidentiality of the study and their safety. The sensitive nature of information required to compile statistics makes it difficult for illegal hunters to disclose the extent of illegal bushmeat activities in their area (Nuno and St John 2015). As a result, gaps exist in formulating ways of gathering the scarce but urgently required information in order to protect our wildlife.

Hence, we conclude that communities in western Zimbabwe harvest bushmeat mainly for protein and income generation. A seasonal variation in bushmeat activity indicates that wildlife is mostly in danger of poaching during the dry season. Mitigation efforts must identify driving forces leading to increased activity during the dry season in addition to ease of following prey near water holes and poverty. Our study showed that bushmeat harvesting has a crucial role on human perceptions about conservation in Jambezi and Matetsi areas. We therefore conclude that incentives and livelihood alternatives can be used in solving the bushmeat crisis in addition to improved anti-poaching activities and aggressive conservation education.

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CHAPTER 7

Conclusions and Recommendations

7.1 Introduction

This chapter presents the summarised main findings of the research. The discussions of the findings are in relation to the research objectives. Overall management recommendations and directions for future research are presented.

Continued growth of the human population and anthropogenic land-use changes are a major threat to the survival of the spotted hyena *Crocuta crocuta*. The threat makes the species conservation dependent (Bohm & Horner, 2015). Although there are various threats, the spotted hyena forages in optimal habitats that are prey-rich even when such a decision involves risks like attack by humans.

7.2 Research findings and discussion

This study found that, in western Zimbabwe land-use and wild prey influence habitat use and detection probability by spotted hyenas (Chapter 2). The species preferred disturbed habitats that are associated with human presence, particularly the safari area, and ranch in the wet season and selected the national park during the dry season probably due to availability and concentration of prey. Thus, various factors including disturbances by humans through spatial and temporal use of various landscapes influence prey distribution hence habitat selection by the spotted hyena. Such a response by the spotted hyena ultimately shapes its population dynamics in a semi-arid ecosystem. Water, particularly during the dry season, plays a pivotal role in the hunting strategy of hyenas. The species targets ungulates in the national park, probably due to the ease at which the spotted hyena catches prey near water points as shown in similar studies (Crosmary *et al.*, 2012). Management priorities should thus focus on improving habitats for prey to enhance survival of the spotted hyena. Once the protected areas become prey-rich, there is subsequent reduction of livestock predation. That ultimately contributes to the reduction of the human-spotted hyena conflict (Boydston *et al.*, 2003, Pangle & Holekamp, 2010a).

The study further investigated the extent of co-occurrence of the spotted hyena with mesocarnivores (Chapter 3). Co-occurrence between the spotted hyena and mesocarnivores was a function of many factors. The optimal foraging theory postulates that animals use intelligence to select habitat and prey that will enhance chances of survival while reducing competition and waste of energy while searching within patches and hunting (Bartumeus & Catalan, 2009). The study found that small carnivores avoided the spotted hyena to prevent direct contact, but overall, the mesocarnivores were likely to coexist in the same habitat while temporally differing in habitat use. As such, spatial and temporal occupancy of the habitat by the spotted hyena was largely in response to prey occurrence and land-use type. During the dry season, the activity of the spotted hyena increased in the national park compared with other land-uses probably due to a high congregation of wild prey searching for water in artificial water pans. Consequently, the spotted hyena influenced the choice and use of the habitat by mesocarnivores. Temporal overlap with the spotted hyena varied between mesocarnivore (Chapter 3). The African civet *Civettictis civetta* remained strictly nocturnal in both seasons while other mesocarnivores showed variations and limited diurnal activity in addition to expected nocturnal behaviour (Chapter 3). As such, land-use management should minimise excessive habitat loss while increasing conservation education in ecosystems outsides protected areas. That will increase small and large carnivore habitats particularly during the dry season.

Furthermore, the study found that the feeding ecology of the spotted hyena differed between the safari area and the national park (Chapter 4). It was found that prey plays a pivotal role in the survival and population dynamics of the spotted hyena (Hofer & East, 1993c) . The study found confirmed earlier studies which also found that the spotted hyena prey on small to large-sized (Yirga & Bauer, 2010, Mbizah *et al.*, 2012). The type of the prey eaten by the spotted hyena was attributed to successful hunting (Holekamp, 2006), scavenging (Kolowski & Holekamp, 2008) or kleptoparasitism (Watts *et al.*, 2010). However, in the current study the spotted hyena preyed more on impala than other herbivores and that confirmed findings by Mbizah *et al.*, (2012). Habitat management in and outside protected areas in the region should maintain an adequate prey base to enhance spotted hyena prey choice thereby reducing interspecific competition from other large carnivores (Bluwstein, 2016).

The study also assessed human attitudes towards the spotted hyena (Chapter 5) as well as the extent of edge effects in the form of illegal bushmeat harvesting (Chapter 6) in a modified landscape. As habitats continue to deteriorate contact between man and carnivores is inevitable. (Boydston *et al.*, 2003). The contact further induces negative attitudes towards wildlife, particularly towards the hyena. As shown in Chapter 5, communities on the periphery of protected areas have developed negative attitudes towards the spotted hyena due to loss of livestock to the species. Depredation of livestock by the spotted hyena was catalysed mainly by home range expansion into human settlements due to numerous confounding factors inside protected areas. Foraging in habitats outside of protected areas was thought to be catalysed by poor husbandry practices exhibited by farmers in the study area. Lax herding of livestock, particularly during the dry season, exposed livestock to predators. Hence, immediate mitigatory measures should not only focus on eliminating predators but also develop advanced husbandry techniques especially during the dry season ction.

In Chapter 6, it was found that the negative effect of bushmeat harvesting on conservation was understood by communities residing in wildlife zones compared with those in communal areas. People living in areas demarcated as Environmental Conservation Areas (ECAs), understood the disadvantages of illegal bushmeat harvesting and thus showed a positive understanding towards conservation. The positive perception was however thought to be influenced by the incentivised model of natural resources that was implemented in the ECA, resulting is meaningful income from wildlife-based activities. However, bushmeat activity decreased as the distance from protected areas increased.

The study found that incentives matter in wildlife-community interactions (Chapter 5). Villagers resettled within (ECAs) had experienced tangible benefits from wildlife were tolerant towards the spotted hyena and were willing to coexist with wildlife unlike their counter parts in communal areas. Although the ECA model showed improvement in attitudes, applying the model in communal areas with high human density would be very difficult. There is need to consider remodelling the existing community based natural resources management scheme in Zimbabwe. Of particular interest is the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), which has been in existence for approximately three decades. Although such programmes are essentially noble, mismanagement of revenue leads to mistrust and development of negative attitudes hence making the programme less effective in meeting its objectives.

7.3 Future work

A number of questions have been answered in this study, yet it also few more questions that would benefit from further research:

This study found that spotted hyenas prefer clayey environments for denning purposes in all the three study areas. The study area represents a good location to test different management plans of the spotted hyena in the midst of land-use change. Further studies on various ecological aspects of the spotted hyena in disturbed areas should be done. Specific research questions are:

1. What is the average seasonal distance travelled by spotted hyena as they commute to forage? Compiling GPS location data for kills as well as denning sites can provide insight into possible feeding events which will clearly highlight the rate of hunting and prey biomass consumed.
2. What is the habitat occupancy of the hyenas in relation to different land management practices in larger landscape? Answering this will enable establishment of predator to prey ratios in the conservation areas.

Community members around protected areas in western Zimbabwe have negative attitudes towards spotted hyenas. As such, they find it difficult to co-exist with the species because of livestock depredation. Further research questions can explore the following areas:

1. What are the characteristics of 'grazing lands' and what technique can be employed to reinforce livestock herding practices? There is need to characterize subsistence farming that exists in the former commercial wildlife farms in terms of human density, crop and livestock diversity and densities, rangeland management, density and abundance of predators, income and livelihoods alternative.

2. There is need to establish and characterise the economic value of livestock losses caused by hyena versus household economic status and settlement type (communal or environmental conservation area (ECA)).

This information can be used to compare subsistence farmland in different regions and identify key factors that can enhance livelihood of local communities. Further, identifying whether there are habitual livestock killing individuals to ascertain who among clan members have home ranges overlapping into human settlements, hence device means of discouraging such individuals from wandering into livestock human settlements.

The spotted hyena is thought to be excess in protected and surrounding areas. There is need to establish current populations and assess the possible relationship between Zimbabwe's Land Reform Programme and outbursts of human-spotted hyena conflicts.

7.4 Conclusions

This dissertation provides explanations for the ecology of the spotted hyena in and outside protected areas in western Zimbabwe and the attitudes and perceptions of the people on the edges of conservation areas towards the species in relation to land-use change. The results are a reflection of the interaction of spotted hyenas with other species and humans in different level of habitat disturbance. The study highlights aspects of human livelihoods versus feeding ecology of the spotted hyena. The study bridges the information gap on the habitat use, co-occurrence and feeding ecology of the spotted hyena in varying land disturbances, which is key in conservation management of the species in relation to other carnivores and humans. The recommendations of the study add to the available scientific and socioeconomic knowledge pool required for current and future management of the spotted hyena throughout its range.

7.4 References

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