The ecology of spotted hyena, *Crocuta crocuta*, in Majete Wildlife Reserve, Malawi

by

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Declaration

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Abstract

The management of predators plays an important role in conservation management today because of the intensive management requirement of small fenced off protected areas. Apex predators such as spotted hyena, *Crocuta crocuta*, are situated at the top of food chains and have the ability to influence the composition and density of meso-predators and herbivores. Knowledge of apex predators through research can assist in effective management decisions which will ensure ecosystem functioning.

Majete Wildlife Reserve (MWR) in the south of Malawi, is a 700km^2 reserve, which had no information on the resident spotted hyena population until this study. The aims of this study were to gather and make available as much information as possible on the ecology of this apex predator in the reserve for management purposes.

A total of 47 camera traps were stationed throughout the reserve for 22 months from 2013 - 2015 and from these data population size, the number of clans (groups), home range size and activity patterns were determined. Faecal analysis was performed to identify the preferred species preyed upon.

The reserve has two small, low density resident spotted hyena populations, each with a large home range. These are distinct traits of hyenas residing in arid regions with a clumped resource distribution. The activity patterns of MWR hyenas were similar to East African hyenas in some aspects but peaks in activity differed between the two populations. A total of 17 prey species were identified, with some obvious preferred species.

Based on the results from this study, is it recommended that management should make decisions which would favour an increase in the hyena population. At this stage, further lion, *Panthera leo*, reintroductions should be avoided, as they are the number one competitor of spotted hyena. Both prey and hyena numbers should be monitored in the future to determine whether the hyena population might be in an Allee effect, in which case hyena reintroduction may be considered to restore the balance. It is also suggested that local communities should be educated about hyenas and their role in the environment. This would increase the protection of hyena clans outside the reserve boundaries. These populations are needed for genetic diversity in the MWR hyena population since contact between the populations has been found. Genetic diversity is important for the long term conservation of small populations such as the spotted hyena population in MWR.

Opsomming

Die bestuur van roofdiere speel ‘n belangrike rol in wildbewaring vandag a.g.v die intensiewe bestuur van klein omheinde bewaar-areas. Top roofdiere soos gevlekte hiëna wat bo aan voedselkettings sit, het die vermoë om die samestelling en digtheid van meso-roofdiere en herbivore te beïnvloed. Kennis van top roofdiere deur navorsing, kan bestuur help om effektiewe besluitnemingskeuses te maak wat ekosisteem funksionering sal verseker.

Majete Wildlife Reservaat (MWR) in die Suide van Malawi, is ‘n 700km^2 reservaat wat geen inligting gehad het tot en met hierdie studie, rondom die residensiële hiëna bevolking nie. Die studie het beoog om soveel as moontlik inligting rondom die residensiële hiëna bevolking te versamel en beskikbaar te stel vir bestuur doeleindes.

Kamera lokvalle was gestel regoor die reservaat vir 22 maande van 2013 - 2015 en van hierdie data was bevolkings grootte, die getal groepe, gebieds grootte en aktiwiteitspatrone bepaal. Fekale analises was gedoen om verkose prooi spesies te identifiseer.

Die reservaat het twee klein, lae digtheid residensiële hiëna bevolkings, elk met ‘n groot gebied. Hierdie is kenmerkende eienskappe van hiënas wat woon in dorpebiede met oneweredige hulpbron verspreiding. Die aktiwiteitspatrone van hiënas in MWR het ooreengestem met die van Oos Afrika hiënas in sommige aspekte, maar aktiwiteits pieke het verskil tussen die twee populasies. ‘n Totaal van 17 prooi spesies was ge-identifiseer, met duidelike verkose spesies.

Op grond van hierdie navorsingsresultate, word aanbeveel dat die bestuur besluite moet neem wat sal lei tot ‘n toename in die hiëna bevolking. Op hierdie stadium moet verdere leeu hervestiging vermy word, aangesien hul die grootste kompetisie vir gevlekte hiëna’s is. Beide prooi en hiëna getalle moet ook gemonitor word om vas te stel of die hiëna bevolking tans in ‘n Allee effek is. Indien wel, kan hiëna hervestiging oorweeg word om die balans te herstel. Dit word ook voorgestel dat plaaslike gemeenskappe opgevoed moet word rondom hiëna’s en hul rol in die omgewing. Dit sal die beskerming van hiëna populasies buite die reservaat grense verbeter. Hierdie populasies is noodsaaklik vir genetiese diversiteit in die MWR hiëna populasie aangesien daar kontak tussen beide populasies gevind was. Genetiese diversiteit is belangrik vir die langtermyn bewaring van klein populasies soos die hiëna bevolking in MWR.

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Chapter 1: Literature review

Introduction

Large predator conservation is often a difficult concept as it is not valued to the same extent by different parties involved. The reason is that conservation of large predators normally comes at a cost to local communities, where predators inflict socio-economic costs on local livelihoods through livestock predation and the loss of human life (Winterbach et al. 2013). Other parties involved highly support predator conservation because such costs are not experienced by them and only the intrinsic value that such species hold are enjoyed (Lee et al. 2012). These opposing views can create conflict amongst stakeholders of predator conservation as local livelihoods may feel that management decisions do not reflect their opinions (Lee et al. 2012). However, predator conservation has been successful where conservation attempts were coordinated on regional, local and international levels and addressed both the ecological and human aspects involved (Winterbach et al. 2013).

African large carnivore guilds are a crucial component of biodiversity (Winterbach et al. 2013), because of each predator's different prey spectrum and one species can therefore not act as a substitute for another (Hayward et al. 2007). Predators also control herbivore numbers which allows for vegetation communities to become more diverse which in turn favours species dependent on the vegetation community and so ensures a more biodiverse ecosystem (Lee et al. 2012). The loss of predators in an ecosystem can have serious imbalance complications because of their top-down control of other species in trophic cascades, which is the flow of energy over several food webs (Watts and Holekamp 2009, Brook, Johnson and Ritchie 2012, Lee et al. 2012). A lack of apex predators may result in the release of meso-predators and increased herbivore numbers, which can lead to serious detriment of the environment and can inflict economic costs (Watts and Holekamp 2009). The lack of apex predators has led to a dramatic caracal, *Caracal caracal*, and black-backed jackal, *Canis mesomelas*, population increases in South Africa, to the cost of local farmers who lose animals and wildlife to these predators (Winterbach et al. 2013).

Animal Ecology

Population

The term population refers to a group of animals of a single species living in a general area that rely on the same resources and have breeding potential (Campbell et al. 2008). Population ecology is important because it illustrates animal interactions with the environment, which determines survivorship and reproduction in a population (Richardson et al. 1994).

Populations are the result of historical events, which can be used to test ideas of relationships between groups of animals. The total population of species are divided into subpopulations, each with a unique gene pool (Richardson et al. 1994). A population can be best described through density, i.e.: the number of individuals per unit area, and dispersion, which is the pattern of spacing of individuals in a population. Density of a population is determined by birth- and death rates and where possible immigration and emigration (Campbell et al. 2008). Dispersion is an important aspect as it describes variation in population density because of social interaction and environmental association with the habitat most suitable for an organism. The most common form of dispersion is a clumped dispersion where individuals aggregate in patches (Campbell et al. 2008). Other forms of dispersion include a uniform arrangement, where animals are equally spaced out which is often the result of territoriality, and random dispersal, which is independent of the position of other individuals (Campbell et al. 2008).

Population regulation arises from the idea that animal populations are not able to increase indefinitely, and refers to the process of populations returning to equilibrium (Williams et al. 2002). Equilibrium points are not fixed population sizes but rather stationary distribution of population densities, which are set by limitation factors which include both density dependent and density independent factors. A population may have several equilibria and may move between these as environmental conditions change (Williams et al. 2002). Animal populations are regulated by individual responses to changes in the environment, especially by the neonatal age class in animal populations (Lochmiller 1996). Protein availability is one of the main drivers of demographic changes, however, population regulation factors can be described as either abiotic or biotic. Abiotic factors include water availability, soil type and normally influence population dynamics through multiple population processes. Biotic factors include intraspecific and interspecific species interactions such as predation and competition (Williams et al. 2002).

Home range

Most animals are not nomadic but live in a confined area known as a home range in which foraging, mating and caring of young takes place (Powell 2000). A home range can be defined as the spatial expression of behaviours performed to survive and reproduce, and is the result of individual characteristic interactions with the external environment (Borger et al. 2000). The reason why animals obtain home ranges is because of the advantages which knowledge of an area may provide to an animal, such as locating limited resources and avoiding predation (Powell 2000 and Harless et al. 2009). Home range ecology is important because of the restricted movement by having a home range, which influences population regulation, animal distribution and predator prey dynamics (Borger et al. 2008). It also illustrate animal needs which is especially important to be identified for threatened species (Bath et al. 2006). In carnivores, the distribution of available prey species and energy requirements are the main influences on predator home range size (Newsome et al. 2013).

Animal interactions with the external environment are normally expressed through home range size, but interspecific and intraspecific interactions are also able to influence animal space use (Borger et al. 2006) which in turn can influence areas of animal activity in a home range (Dixon and Chapman 1980). Not all areas in an animal’s home range is used with the same intensity, and the point in a home range with the greatest activity is referred to as the activity centre (Dixon and Chapman 1980). This is often the case of non-uniform distribution of resources (Harless et al. 2009). Animal distribution in a home range can be classified into several categories (Bath et al. 2006). Unbiased use is where all areas in a home range are used equally; core foragers return to a specific area such as a nest or a den after foraging; while some animals are territorial where large amounts of time are spent at the boundaries of a home range to defend the home range with resources from neighbours; and other animals have a skewed distribution, where animals largely focus their movement within a restricted area because of a specific habitat or environmental condition required (Bath et al. 2006).

Diet

Animal diet is influenced by habitat usage, behaviour, morphology and physiology (Hawlena and Perez-Melano 2009). Understanding predator diet is important because they are able to influence the diversity and abundance of prey species in an ecosystem by means of predation, but also by creating avoidance behaviour on prey species which can affect survivorship negatively (Brodin et al. 2006). Individual fitness is also influenced by foraging behaviour and it is likely that offspring of an individual would have a similar foraging behaviour (Pyke 1984). Therefore it is thought that animal foraging behaviour in a population has evolved which provides the greatest fitness for a species (Pyke 1984). Generally larger prey are consumed with a larger predator body size and can be seen where larger bodied predators prefer larger bodied prey species (Jackson et al. 2004). Overall predator diet choice is influenced by predator energy requirements, time availability and predation risk of prey (Jackson et al. 2004).

Optimal foraging theory tries to explain animal diet choice in terms of costs and benefits of certain diet choices (Yahnke 2006). The theory explains that when given equal handling time the food item with the greatest energy gain will be chosen. Also food items with a high density may be selected for because of the decrease in foraging time (Yahnke 2006). Predators are often in an environment with a non-uniform distribution of food resources and thus predators have to decide what patches to visit and whether to remain in a resources patch or to move on to another resource patch as the food intake rate decreases the more time is spent in a resource patch (Charnov 1976). Animals also have to make a decision whether or not to forage in a group which may assist in increased food intake by bringing down larger prey species, or animals must forage alone to avoid feeding competition (van Gils et al. 2015).

Activity Patterns

Animal activity patterns are a trade-off between interactions of an animal with its environment (Gervasi et al. 2006) and determines the pattern of interactions between predators and their prey (Orpwood et al. 2006). Activity patterns illustrate the time of optimal foraging for a species and how animals expend their daily energy budgets (Andrews et al. 2009 and Reimers, et al. 2013). Thus, activity patterns are used for characterizing a species' lifestyle (Post 1981).

Animal activity patterns are a result of animal circadian clocks, which are key internal regulatory systems, which coordinate physiological processes and act as a timing reference for animals (Bloch et al. 2013). However, circadian clocks are adaptable and animal behaviour is rather a combination of adaptation to environmental stimuli and circadian clocks (Bloch et al. 2013; Kolowski et al. 2007). Environmental stimuli include prey availability, predation risk and environmental temperature (Kolowski et al. 2007). Other biotic factors such as sex and reproductive state can also play a role in animal activity behaviour (Kolowski et al. 2007) as well as prey circadian rhythms (Andrews et al. 2006). Sub-populations of species have unique activity patterns which are the result of differences in resource availability in different environments (Post 1981), but also any disturbances can cause a change in activity patterns

(Ditchkoff et al. 2006). Changes in activity patterns due to disturbances can have a negative impact on animal fitness by influencing diet and reproduction (Ditchkoff et al. 2006). By studying activity patterns a researcher will gain an understanding of habitat use which is needed for effective management and conservation of a species (Monroy-Vilchis et al. 2009).

General spotted hyena ecology

Phylogeny

The family Hyaenidae is a heterogeneous feliform group and is one of the smallest mammalian carnivore families with only four living species (Koepfli et al. 2006, Frembgen 1999, Drea and Frank 2003). The family forms part of the Superfamily Feloidea, which also includes three additional families, Viverridae, Herpesidae and Felidae (Uemura, et al. 2009). The Hyaenidae family consisted of at least 24 species at the peak of hyaenid diversity, in the late Miocene some 12 to 6 million years ago [MYA] (Watts and Holekamp 2008, Koepfli et al. 2006). Though the family may currently be small, they make up for it in social and ecological diversity, with social organisation varying from monogamy to large groups and almost every possible habitat from Southern Africa to the Middle East is occupied by the family, the latter by the striped hyena (Frembgen 1999). It is estimated that Hyaenidae diverged from their sister feliform group, which consisted of a clade of two mongoose species (Herpestidae) and a Viverrid species, around 29.2 MYA, in the Middle Oligocene period (Koepfli, et al. 2006).

The smallest and oldest member of the Hyaenidae family is the aardwolf, *Proteles cristata*, which is a termite-feeding specialist (Koepfli et al. 2006) while the remaining three members of the family; striped hyena, *Hyaena hyaena*, brown hyena, *Parahyaena brunnea*, and spotted hyena, *Crocuta crocuta*, have a craniodental morphology and are adapted for cracking open bones of carcasses (Koepfli et al. 2006). The largest and most social member of the Hyaenidae family is the spotted hyena and the species is the second oldest of the Hyaenidae family after splitting off from a common ancestor around 8.6 MYA (Watts and Holekamp 2008).

Social structure

Spotted hyena have the most complex social structure of all large carnivores. Their social structure is actually more similar to primate social partitioning than feliformous (Holekamp, Smith, et al. 2012). It is thought that complex social systems and behavioural strategies, as in primates and spotted hyena, could be drivers of intelligence (Drea and Frank 2003). Like baboon and macaque species, spotted hyena groups consist of relatively unrelated individuals from different matrilineal lineages, called a clan, living cooperatively (Holekamp et al. 2012). Relatedness in a spotted hyena clan is relatively low due to male-mediated gene flow among clans (Van Horn et al. 2004), as most males leave their natal clans to become members of neighbouring clans at the onset of reproductive maturity between the ages of two and five years (Holekamp et al. 2012). However, in areas where dispersal opportunities are limited, males may spend their entire lives within their natal clan but when dispersal does take place it is done voluntarily and individuals are not driven out by conspecifics such as in many other species. Spotted hyena are also similar to primates with regard to group size, interaction frequency amongst kin and unrelated individuals and hierarchal structure (Holekamp et al. 2012).

Social living normally evolves due to reduced predation pressure and/or an increase in utilisation of resources. Spotted hyena are the largest hyaenid species and also the most social and it is therefore assumed that increased resource utilisation has selected group living in spotted hyena as opposed to reduced predation pressure (Watts and Holekamp 2008). However, 75% of successful hunts are conducted alone, which suggests that the cooperative defence of resources could have selected cooperative living, as large bodied ungulate species that spotted hyena prey on are readily replaced and allow for high predator densities (Watts and Holekamp 2008). Spotted hyena have therefore evolved to live in a fission-fusion society where members spend significant amounts of time alone while foraging but are also highly social at communal dens when not hunting (Drea and Frank 2003). Other hyena species largely focus on termites and scavenged carrion as a food source. These food sources are relatively scarce and hyena populations that focus on carrion are therefore limited to low densities (Watts and Holekamp 2008).

Intra-group aggression sometimes occurs within clans, and other than just inflicting injury it also creates additional adverse effects such as damage to social relations, which are important as group co-operation is needed for capturing large prey, defending a clan’s home range and acquiring coalitions for maintaining social rank (Wahaj et al. 2001). Non-aggressive approaches and initiated greetings are considered to be reconciliation attempts. Subordinate hyenas who initiate such attempts experience less aggression from their former opponents than those who do not. Recipients of aggression are also the ones to initiate reconciliation as it favours such individuals more to have coalitions with dominant individuals in a social hierarchy society (Wahaj et al. 2001). Male aggression towards spotted hyena females does occur, and especially when females are most likely to conceive a litter, suggesting that aggression of males towards females serves to inform females of their fitness (Szykman et al.

2003). On the other hand male-male aggression is rare because to be accepted as a mate a male has to build a relationship with a female, which is non-transferable after aggression (East et al. 2003).

The Pseudo-penis

Spotted hyena females are the only mammals on earth lacking an external vaginal opening but rather have a unique feature called a pseudo-penis (Glickman et al. 2006). It consists of an elongated hypertrophied clitoris that resembles the male genitalia both in form and size (East et al. 1993). Mating, urination and birth takes place through a urogenital canal which exists at the tip of the hypertrophied canal (Glickman et al. 2006). This is however a reproductive cost as it results in more than half of first births in captive hyenas being stillborn because the meatus has to tear to be able to give birth. This is a time consuming process and with the short umbilical cord of spotted hyena often cubs suffer severe anoxia. The labia majora has also fused to form a false scrotum making spotted hyena females the most masculinized mammal females on earth (Glickman et al. 2006).

For centuries it was believed that the spotted hyena was a hermaphroditic animal and capable of changing sex (Funk 2012). Masculinization of female spotted hyena genitalia was first described by Watson (1877), who published a series of anatomical studies of female spotted hyena genitalia. However, the Dutch amateur zoologist, Robert Jacob Gordon, made the same discovery a century before Watson but was unfortunate to not publish his findings (Funk 2012).

The development of a urogenital phenotype results from androgen secretion of foetal testes and anti-Mullerian hormones responsible for regression of the Mullerian duct system which develops the female urogenital system (Glickman et al. 2006). At first it was thought that hyena ovaries produce androgens because of abundant interstitial tissue and paucity of follicles, but it was found that rather the foetal testes than the foetal ovaries contained steroidogenic enzymes responsible for producing androgens at 30 days of gestation. The search for female androgens was then moved towards the placenta of spotted hyena females, which is rich in dehydrogenase activity that converts androstenedione into androgen which is then transferred to the foetus via the umbilical vein making the placenta an endocrine transducer (Glickman et al. 2006).

The pseudo-penis is used during initial greetings between clan members in spotted hyena society called ceremonies. The penis or pseudo-penis is erected in a nonsexual context, while the anogenital region is being sniffed and licked while standing parallel to one another (Eastet al. 1993).

Female domination

Spotted hyena is the only mammal species on earth where females are dominant over males (Dloniak et al. 2004). Females obtain a rank just under their mother at birth which is stable for long periods of time, though changes in clan rankings may occur where daughters dominate aging mothers or after major fights where social coalitions form between low ranking matrilines that over throw smaller higher ranked matrilines (Holekamp et al. 2012). Male hierarchy is determined by arrival in a clan and is confined to a strict queuing convention, where newly dispersed males submit to every hyena that they encounter and enter a new clan as the bottom ranked individual where even cubs are dominant over newly immigrant males (Holekamp et al. 2012). Hormones such as androgen also play a role in hyena behaviour and ranking, where immigrant males have a higher androgen concentration than natal males (Dloniak et al. 2004).

Females are on average 10% larger than males in body size (Szykman et al. 2003) however the species is regarded as being monomorphic even though females weigh more than males (Dloniak et al. 2004). During foetal development a female foetus is exposed to extreme levels of androgens making them both stronger and more aggressive than males. During adulthood males have higher levels of circulating androgens than females, however this is debatable as varied results have been found (Dloniak et al. 2004). It has been hypothesized that this rare phenomena of female dominance developed because of a female's need to secure enough food for her and her dependant young because social ranking determines feeding priority and spotted hyena communities have intense feeding competition (Dloniak et al. 2004). However, this phenomena of "female dominance" should then be apparent in other species with similar feeding habits such as wolves, *Canis lupus*, and African wild dogs, *Lycaon pictus*, but this is not so (Watts et al. 2009). In fact it is thought that female dominance in *Crocuta* developed because of a constrained development in jaw and skull muscularity which is needed for durophagy (feeding of bones) which is not the case for other carnivores such as wolf and African wild dog. The skull is not fully developed until 34 months of age which is well beyond the mean age for weaning (12 months) and sexual maturity (24 months). Young hyenas are therefore still dependent on their mothers after weaning because of this constrained developmental feature. It is thought that their dominance over males would assist in fending for post-weaned young, as young of lower ranked females have a higher mortality rate during the period of post-weaning until a fully developed skull is apparent at the age of 34 months (Watts et al. 2009).

Reproduction

A polygynous mating system reigns in spotted hyena society where males and females will mate with multiple partners when females are in oestrus, which is not seasonally bound (Drea and Frank 2003). Clans are resident in what is called a communal den site which consists either out of drain pipes, old warthog holes or holes which have been excavated by the hyenas themselves (Holekamp et al. 2012). The communal den consists of a network of underground tunnels which are accessible for both cubs and adults and are changed on average every month and a half (Holekamp et al. 2012).

During copulation, cooperation of both male and female is needed as males have to insert their penis' vertically into the extended clitoris, which forms the pseudo-penis, and leads to the genital tract (East et al. 2003). Spotted hyena mating takes place with males displaying extreme approach-avoidance conflict behaviour when courting a female because of larger and more aggressive females that can cause serious injury (Drea and Frank 2003). To accommodate copulation a female will retract her extended clitoris so that it is level with her abdominal region and further consent is needed from females for successful copulation (Drea and Frank 2003) as males have to physically hold on to females because of vertical penetration (East et al. 2003).

The Den

The young of hyena from all females are kept at a common area which normally consists of an old aardvark, *Orycteropus afer*, or warthog, *Phacochoerus africanus*, holes which is called a communal den (Watts and Holekamp 2009). When a female is ready to give birth she leaves the communal den to find a natal den where she will give birth, after a gestation period of 110 days (Drea and Frank 2003) to often only a single cub if it is her first litter. More experienced females normally have 2 cubs per litter (Holekamp and Smale 1998). New born cubs weigh approximately 1kg and unlike other carnivores are born with their eyes open and with canines (Holekamp and Smale 1998) as a result of their relatively long foetal development (Drea and Frank 2003). Cubs will be kept in the natal den for up to 4 weeks before being introduced to the communal den where up to 20 cubs are raised until they are 8 to 9 months old (Holekamp and Smale 1998).

Young development

The development of cubs can be assigned into 5 stages (Holekamp and Smale 1998). The first stage of a spotted hyena's behaviour development occurs within the natal clan where a rank relationship is established between littermates by using their sharp canines that they were born with. Play behaviour is seldom observed during this stage of their life as energy is needed and conserved for rapid growth. In latter behavioural stages playing will be more often observed by well-fed cubs of higher ranked females than in cubs of subordinate females. When interactions with conspecifics are initiated for the first time, hyena cubs will react in what is called head bobbing, which displays appeasement (Holekamp and Smale 1998). Stage two of hyena development starts when cubs are introduced to the communal den site after mothers have carried their cubs individually to the communal den site. During stage two cubs are introduced to all clan-members and rank-relationships are built and odours of clan members are exchanged. Rates of play are much higher at the communal den site which serves to establish relations and to develop physical strength and endurance (Holekamp and Smale 1998). Play in spotted hyena cubs emerges much earlier than in other carnivores which may suggest the importance of play as a socializing function and helps to integrate cubs into a clan (Drea and Frank 2003). In the third stage of development the hyena cub leaves the communal den for the first time with its mother which coincides with exploratory behaviour of the home range (Holekamp and Smale 1998). Hereafter cubs will start to accompany hunting forays at usually between 6 and 12 months of age (Drea and Frank 2003). At this stage the den is no longer being used for shelter and when threatened youngsters will flee above ground rather than seeking shelter within the den (Holekamp and Smale 1998). Nursing still takes place during this stage but feeding with other members at ungulate kills also occurs. In the fourth development stage cubs are weaned and have to start living off a solely meat diet. This involves a reversal of gut enzymes used to obtain nutrients from milk to enzymes associated with a carnivorous diet. This is a crucial stage of spotted hyena development because young hyenas do not yet have fully developed jaw muscles and canines, have limited hunting experience and are mostly of a subordinate rank which results in limited access to kills. This results in young hyenas often living off carrion. The fifth and final stage of development entails the animals becoming sexually mature and ends with death (Holekamp and Smale 1998).

This relatively long infant dependency is a life variable associated with intelligence and has the advantage for young to learn survival and social skills (Drea and Frank 2003). Nursing of spotted hyena young by mothers can take place either above ground or inside a den (Drea and

Frank 2003, White 2003). When nursing occurs inside a communal den access to young is determined by female social rank, where higher ranked females are able to displace a nursing subordinate female or prevent a subordinate female from entering a communal den (White 2003). The milk of spotted hyena has the highest protein count of all fissiped carnivores and requires high maternal output to produce such milk corresponded with extended infant dependency. Little cooperative nursing occurs in spotted hyena society unlike in striped and brown hyenas (Drea and Frank 2003).

Diet

Spotted hyenas are one of the indicator species on the African continent (Trinkel 2009), meaning that the species are able to reflect ecosystem health as hyena density is determined by prey density (Holekamp et al. 2012), thus reflecting the capability of an ecosystem to maintain a sufficient number of prey species. The species' adaptability in diet (Hayward 2006) has enabled them to fully utilise their surrounds and to survive in the harshest conditions where other predators are often not able to do so. Unlike other large predators such as leopard *Panthera pardus*, and lion, *Panthera leo*, spotted hyena do not have a general preferred species of prey but rather preys on the most accessible species within an area (Carnaby 2008). However, there is a preference for prey within a specific weight range (56-182kg), even though they are capable of bringing down prey four times their size such as Cape buffalo (Carnaby 2008). Spotted hyena are also able to change their diet within an area, for example in Ethiopia during a religious fasting period spotted hyena change their pre-dominant diet of anthropogenic waste to actively hunting donkeys because of limited available human waste during the fasting period (Yirga et al. 2012). Scavenging does form part of spotted hyena diet but to a far lesser extent than previously thought, where it was found that lion scavenged more from spotted hyena kills than the other way round (Kruuk 1972).

Social ranking determines feeding priority within a clan at feeding events (Watts et al. 2009). Often a carcass is too large for a dominant individual to finish or to take control of, this is when a feeding frenzy breaks out where subordinate individuals try and gorge themselves while feeding simultaneously with dominant individuals (Watts et al. 2009). Feeding is therefore an intense competitive occasion and the ability to feed rapidly is an important determinant as to the amount of food an individual can ingest. This results in a +/- 120kg animal being consumed within 13 minutes (Watts et al. 2009).

Human Relationships

Hyaenid-Human interactions can be traced back to early human development where it is thought that the evolutionary path of hominid hunting lies within the scavenging of carcasses from creatures such as hyenas by early human beings (Pokines et al. 2007). However, the opposite was also true where carcasses were often scavenged from early human beings by spotted hyena and often hominids fell prey to hyenas. Present day fatalities and attacks on human beings by spotted hyena are still an occurrence within Africa, where the young and weak make easy prey (Pokines et al. 2007, Moyo 2014). In Malawi from 1955-1962, a clan of spotted hyena were responsible for killing between five and eight people annually around the town of Mulanje, and were thought by local people to be stronger and bigger than normal spotted hyena (Clarke 2012). Far more common is attacks on livestock by spotted hyena which defies the relationship between man and hyena with recognized conflicts around Serengeti National park, Tanzania (Holmern, et al. 2007); the Caprivi strip in Namibia (Dwane 2013) and in Northern Ethiopia (Yirga et al. 2012). In the Serengeti alone it was reported that spotted hyena caused an annual loss of over $12000, which equalled more than two-thirds the average annual income of a household (Holmern et al. 2007).

This conflict has led to a situation where the intrinsic and ecological value of these creatures are overseen, and instead they are often regarded as vermin and a liability to local communities (Carnaby 2008).

Value

Although they are responsible for economic losses by occasionally preying on livestock, spotted hyena are responsible for several ecological maintenance functions to ensure healthy and sustainable ecosystems (Carnaby 2008). By preying on the weak and the sick, the spread of disease is prevented and healthy herbivore communities are maintained. Their strong jaws and strong digestive system enables them to utilize almost every part of their prey's body except hair, and so valuable nutrients are recycled back into ecosystems (Carnaby 2008). Spotted hyena also provide ecosystem services to humans by regulating herbivore numbers (Snyder et al. 2006) which in turn prevents environmental degradation such as soil erosion and overgrazing. Spotted hyena are apex predators that benefit ecosystems by displaying top-down control of both herbivores and mesopredators. The latter are; smaller predators whose fitness is controlled by larger predators through exploitation and harassment (Brook et al. 2012, Watts and Holekamp 2009). In the absence of apex predators, such as spotted hyena, an increase is found in mesopredator numbers. This is called mesopredator release, and can result in a decline in bird-, reptile-, rodent- and ungulate species (Watts and Holekamp 2009).

Furthermore, spotted hyena are valuable game viewing animals in wildlife reserves and prized trophies in hunting concessions where great sums of money are paid to hunt these animals in their natural environments and so contributing directly towards economic prosperity in a country (Spotted hyena hunts 2010).

Threats and conservation

Historically spotted hyena occurred across the whole of Southern Africa including areas such as the Cape of Good Hope (Stuart and Stuart 2007) at least until the late eighteenth century (Ulrich 2009). Habitat loss and poaching/over-hunting of their prey species has led to increased human-hyena conflict and retaliatory killing of the species, a direct threat to their existence [Appendix 2, Figure 20] (Holekamp 2007). Hunting of spotted hyena can be used as a management tool for conservation because of the money raised through such practices, however, it can also disrupt social organization and population dynamics where undetected morality of cubs offset planned sustainable off-take (Ordiz et al. 2013).

Being endemic to Africa the species has the third highest conservation priority of large African predators, after the endangered Ethiopian wolf, *Canis simensis*, and African wild dog (Winterbach et al. 2013). The species is however only listed under the category, "least concern", by the IUCN (Bohm and Honer 2015) because of an adult population that well exceeds 10 000 in number (Bohm and Honer 2015). Hyena are often found in neglected wildlife reserves because of their great adaptability to changing environments and their ability to survive where other predators are unable to do so (Trinkel 2009). In contrast to this, their numbers outside of protected areas are continually declining although, for the time being at least, it is not sufficient enough to impede the species' survival (Bohm and Honer 2015). Being in the apex position of trophic systems, changes in hyena populations will result in reconfigurations of biodiversity and ecological communities (Ordiz et al. 2013). The decline of carnivores due to human persecution has created loss and reconfiguration of biodiversity in many ecosystems (Ordiz et al 2013).

However, even though apex predators are drivers of ecosystem functioning, the conservation of large predators is challenging because of the large areas needed for their conservation. Historically a decline was associated with large predators in areas with high human densities

(Linnell et al. 2001), but in modern conservation efforts have proven that through effective management strategies conservation of large predators in areas with high human densities is possible (Linnell et al. 2001). Apex predator communities therefore need to be managed effectively, which can be assisted through research.

False legends passed on through generations in African communities of spotted hyena has portrayed the species in a negative light in local communities across Africa. In the western world the species are also portrayed negatively, where spotted hyena often play villain roles in movies (Holekamp 2007). However, through research it is possible to assist in conservation of the species. For example, through research it was possible to declare the long thought myth that spotted hyena were mainly scavengers, false (Kruuk 1972). Research and education can help break stigmas and rather replace them with admiration that will assist in the conservation of the species, although compromises would still be necessary because of political and economic constraints (Ordiz et al. 2013).

Myths

The spotted hyena is an animal which provoked fear in the hearts of people for centuries which resulted in many myths about their physiology and behaviour from as early as the Roman Empire (Holekamp 2007). Myths ranged from being hermaphroditic, exclusive scavengers and with various spirits living in hyenas (Holekamp 2007). These myths may actually have assisted with spotted hyena safekeeping where people were too afraid to hunt the animals.

In African folklore the spotted hyena is depicted as an ambivalent creature considered as fearsome, stupid and dangerous (Frembgen 1999). In West African Tales spotted hyena are sometimes depicted as a Muslim that challenges local animism. In central Africa it is described as a solar animal responsible for the sun’s rays on earth and throughout Africa it is believed that hyenas are ridden by witches. Spotted hyena are also used in African rituals where West African masked dancers transform into these creatures that play a role of dirty habits and are used to create fear, which urges initiates to avoid such behaviour in life. Kujamaat hunters believe when killing a hyena the carcass has to be treated as if a human body as precautionary measurements against the wicked spirit of the hyena. Other folklore include a half man half hyena creature and countless other myths and folklores, that are mostly depicted in a negative light (Frembgen 1999).

Spotted hyena research

One of the first and probably the most famous spotted hyena research studies was conducted by Hans Kruuk in 1972 in Serengeti and Ngorogoro National Park, Tanzania. This study was a pioneer study on spotted hyena with the first proof that the species are actually formidable hunters thereby discontinuing the myth that the species were exclusive scavengers (Kruuk 1972). In later years the hyaena specialist group was founded as part of the IUCN species survival commission and aimed to promote hyena conservation through research and to change people's attitude towards hyena through education (Holekamp 2007).

To date, research on wild spotted hyena has been conducted throughout Africa. A total of 34 published articles on wild spotted hyena research were found (search words:"spotted hyena", search engines; www.google.com/scholar and www.sun.ac.za/library) of which 18 were from the Talek clan in the Masai Mara National Park, Kenya. Of the 34 peer reviewed articles 25 were conducted in East Africa (Kenya and Tanzania), indicating a need for spotted hyena research in different geographical areas of the species' home range. Spotted hyena research was also conducted in Ethiopia, South Africa, Botswana, Senegal, Zimbabwe and Cameroon.

Certain areas of spotted hyena ecology have been well documented such as the animal's diet. However, spotted hyena show great variation in diet (Holekamp et al. 1997) making it difficult to apply findings of research conducted in different geographical regions. Other areas of ecology such as activity patterns, is not well documented and more research is needed on these fields to better understand and protect the species.

Camera trap use in modern research

Camera types

The first animal-triggered camera was developed in 1890, by George Shiras, who made use of a magnesium flash-system and trip wires to trigger his cameras to take pictures (Kucera and Barrett 2011). The trip wire was placed across game trails and baited to induce interference with scavenging creatures that would trigger the camera. Shiras captured 18 species on camera in a North American forest. Modern-day camera traps make use of microwave motion- and infrared heat sensors as photographic triggers. Camera traps, however, were not used to census animal populations until 1984 following technological developments, and were soon considered as the most effective, non-intrusive way of monitoring conspicuous species such as spotted hyena (Kucera and Barrett 2011).

Modern camera traps can be classified into two major categories, triggered- and non-triggered systems (Swann et al. 2011). Non-triggered cameras are programmed to take pictures at set time intervals where triggered cameras are only programmed to take a picture after it has been triggered. Cameras are typically triggered by animal movement, which breaks an infrared light source to initiate the taking of a picture (Swann et al. 2011). Non-triggered cameras are generally used when a study event occurs frequently or if a continuous record of events is needed. While triggered cameras are used for infrequent events or to study the presence of an animal in an area. Generally non-triggered cameras need more power making them less effective at remote locations (Swann, et al. 2011). The cameras used for this study were of a triggered nature because of nocturnal spotted hyena activity, making events of activity infrequent.

Invasive techniques

Many spotted hyena research studies conducted to date have made use of radio-collars, actively following study animals or playing sound recordings to lure the animals in (Sillero-Zubiri and Gottelli 1992, Hayward and Hayward 2006, Kalowski et al. 2007). All of these methods are invasive and can alter normal wild behaviour and afflict stress or injury to the animals (McCallum 2013). Other adverse effects of such techniques on study animals have been reported which includes effects on reproduction, weight, behaviour and survivorship (Moorhouse and Macdonald 2005).

Much animal ecological data can be retrieved from camera traps including occupancy, home range use, habitat selection and patterns of activity (McCallum 2013). Therefore, it was decided that when possible camera traps would be used to study certain aspects of spotted hyena ecology in Majete Wildlife Reserve (MWR), because of the difficult environment, the time consuming task of locating and habituating spotted hyena and the undesired adverse effects on the study animals from other techniques.

Advantages and disadvantages of camera traps

The use of camera traps is considered to be a non-invasive technique with minimal interference on animal behaviour (Swann et al. 2011, Boyer-Ontl and Pruetz 2014). Other advantages of the camera trapping technique is that the data can be reviewed by other researchers, unlike other techniques which make use of observed data; it has a low-labour cost; is robust in environmental variation and is very effective in studying cryptic nocturnal species in difficult terrain (Pettorelli et al. 2010).

However, there are some limitations to using camera trap data. Probably the main issue with camera trap use is equipment failure, where data are lost due to memory card or camera damage (Swann et al. 2011). Often cameras are placed in remote locations and are checked upon at irregular time intervals because of the logistical difficulty of getting to such locations. This can then result in the loss of significant amounts of data (Swann et al. 2011). Another limitation to camera trap use is the time consuming task of analysing photographic data (McCallum 2013).

Study Area

The Importance of Protected Areas to conservation

More than 12% of the World's land cover is under formal protection today (Loucks, et al. 2008) and deemed as important for biodiversity conservation as these areas are often the last stronghold for large mammals in Africa (Brenneman et al. 2009, Burton et al. 2010). Most protected areas in Africa were created by colonial powers in an era of so called protectionist approaches, which aimed at the exclusion of people from wildlife (Attwell and Cotterill 2000). This led to the alienation of local people from wildlife and protected areas were viewed as the "playground" for expatriate tourists. Most protected areas were created in areas infested by tsetse flies (*Glossina morsitans*) and which were climatically unsuitable for agricultural activities, but opposition to traditional protectionist approaches see it in a political light (Attwell and Cotterill 2000). Lack of resources has seen the degradation of many of these protected areas, and the decline of many species even within protected areas (Burton et al. 2010, Prins,et al. 1994, Fynn and Bonyongo 2010, Twinomugisha and Chapman 2006). Modern conservation approaches attempt to create sustainable approaches to conservation which includes local livelihoods in management plans for their benefit (Attwell and Cotterill 2000).

However, there have been developments in African conservation with the creation of transfrontier conservation areas (TCA's). The Greater Limpopo Transfrontier Park which was established in 2002, was the first of its kind where the border fence was removed to increase the size of the uninterrupted protected area (Noe 2010). Since then there has been the creation and proposed creation of several trans-border conservation areas in Africa. For example, areas such as the Kgalagadi Transfrontier Park between Botswana and South Africa, the proposed Okavango Delta-Makgadikgadi-Savuti-Chobe-Hwange complex which stretches from Namibia's Caprivi strip through Botswana to Zimbabwe and the Selous-Niassa complex between Niassa National Reserve in Northern Mozambique and Selous Game Reserve in Tanzania, which are connected by an 8000km^2 wildlife corridor (Noe 2010). Transfrontier conservation areas are aimed at protecting sufficient areas that would support wildlife, in particular ungulates in natural migration processes, because it has been found that the lack of natural migration leads to the rapid decline of ungulate species even within protected areas (Noe 2010). This was found in the Kruger National Park where the western and eastern boundary fences constructed in 1961 prevented ungulates from migrating towards areas of higher annual rainfall along the western escarpment and the south east in Mozambique. This led to an 85% decline in ungulates such as blue wildebeest in the decade following the erection of the boundary fence (Noe 2010). Conservation management on such a large scale impacts spotted hyena because their density is determined by prey density (Holekamp et al. 2012).

Spotted hyena still occur outside protected areas but it is within these protected areas that the species flourishes, primarily due to retaliation attacks outside protected areas which limits their numbers (Mills and Hoffmann 2008).

Majete wildlife reserve

Majete Wildlife Reserve (MWR) is situated in the southern tip of the Great Rift Valley on the banks of the Shire River, Malawi, (Appendix 1, Figure 1) and forms part of the Middle Shire Valley (Morris 2006). The reserve is close to the border with Mozambique and the country's economic capital, Blantyre (Appendix 1, Figure 2) (Kasuka 2013). Initially, a non-hunting area was declared in 1951 around the Majete hill in the centre of the reserve today, to try and conserve the remnant elephant, *Loxodonta Africana*, populations in the valley. In 1955 an area of 500 km^2 was declared as a game reserve for conservation purposes and it was extended to 690 km^2 in 1969 to include the Mkulumadzi and Shire Rivers. This was done in order to allow animals' access to water in the dry season (Morris 2006). The area was also home to lion, leopard, wild dog and buffalo and was the last refuge for eland, *Taurotragus oryx*, and waterbuck, *Kobus ellipsiprymnus*, in the Shire Valley. However, due to a lack of law enforcement by the Department of National Parks and Wildlife (DNPW), almost all large game were decimated in MWR by the early 1990's. In 1989, Brian Sherry who conducted a pioneering study on elephant ecology within the Middle Shire Valley, estimated an elephant population of around 300. Within a mere five years poachers with high-powered rifles decimated the then recent, thriving elephant population. Game scouts and law enforcement officials were described as being "completely ineffective in controlling illegal hunting in the reserve" (Morris 2006).

The state of the park dramatically changed in 2003 when a 25 year partnership was signed between the Malawian Government and African Parks Ltd. to ecologically restore MWR by relocating wildlife back into the park (Liou 2012). In just ten years, over 2554 animals were relocated to Majete (Liou 2012), giving this project the name; "the Noah's Ark operation". Today Majete Wildlife Reserve is the only refuge for Africa's Big 5 in Malawi and has become a prime destination on the tourist route. This project made Majete Wildlife Reserve the first of African Park's now nine parks where parks are being rehabilitated and restored to former glory in a sustainable manner within Africa, through signing long-term Public Private Partnerships with governmental bodies and private funders (Our Approach 2011).

Terrain and climate

The reserve consists of hilly terrain with the Shire River (Appendix 1, Figure 5) close to the eastern boundary with the actual boundary fence about 1km from the river on the east bank of the Shire. The only other perennial river in the reserve includes the Mkulumadzi in the north which has its confluence with the Shire River within the park. Other perennial sources of water include nine artificial waterholes situated throughout the reserve (Appendix 1, Figure 3) and natural springs (Appendix 1, Figure 4).

Other sources of open water include several non-perennial rivers (Appendix 1, Figure 7) and seasonal pans, known as dambos (Appendix 1, Figure 6) during the wet season (Chidant-Malunga 2011).

Seasons

Hall-Martin (1983) recognised three seasons for neighbouring Lengwe National Park based upon rainfall and temperature which are assumed to be the same in MWR because of the close proximity (approximately 5km).

- Hot Wet Season – November to March
- Cool Dry Season – April to August
- Hot Dry Season – September to November

Rainfall varies from 750mm in the south-east to 1000mm in the north-west of the reserve with a mean annual rainfall of 810mm (Sherry 1989). The month of January receives the most rain when the Inter-Tropical Convergence Zone lies over southern Malawi, as it migrates over the tropics in a response to changes in location of maximum solar heating (Gasse 2000). Occasional light rain may occur during the months of April to October because of moist tropical hot air blown from the Mozambique coastline by south-easterly winds towards the Chiperone mountain range in the north-west of Mozambique bordering Malawi (Sherry 1989). As the hot air rises it is being pushed up by the highlands and the moist air cools off, condensates, creates clouds and forms rain in the Middle Shire Valley (Sherry 1989).

Altitude varies from 150m along the Shire River to over 800m at isolated peaks in the West of the reserve (Staub et al. 2013). The soils are lithosols and has been described as being shallow and stony, making it not suitable for cultivation (Sherry 1989).

Vegetation

The earliest record describing the vegetation of the middle Shire valley dates back to 1960 and describes it as a "Tropical Dry Woodland" (Sherry 1989). Later it was classified as a deciduous, miombo savanna woodland by Wild and Barbosa (1967). Several authors there after chose to use the term "pratt" instead of "savannah" to describe the area's vegetation, meaning that it consists of woodland-, scrubland-, thicket- and wooded grassland communities (Staub et al. 2013).

Later the vegetation in the reserve was classified into two major woodlands. The woodland towards the higher lying western regions of the reserve was described as being dominated by *Brachystegia boehmii* and *Julbernardia* species with medium to tall trees and a medium to closed canopy. The vegetation in the lower lying east was described as an *Acacia*-dominated woodland with *Combretum, Terminalia sericea* and *Sclerocarya caffra* species being dominant with an open canopy (Appendix 1, Figure 8) (Staub et al. 2013).

Miombo woodland is a seasonal dry tropical forest (Appendix 1, Figure 9) that is confined to nutrient poor-soils and consists of the 21 *Brachystegia* tree species in combination with the three *Julbernadia* and *Isoberlina* species respectively (Kanschik and Becker 2001). The features include trees that can reach heights of up to 10-20m and consists of a single storey, with a discontinuous understorey of shrubs and a continuous herbaceous layer (Kanschik and Becker 2001). Miombo woodland extends throughout southern- and eastern Africa from the southern regions of the Democratic Republic of Congo, Tanzania, Angola, Zambia, Malawi, Mozambique and Zimbabwe and is divided into dry- and wet woodland. Dry miombo is deciduous while wet miombo is evergreen (Kanschik and Becker 2001) and an annual rainfall of 1000mm serves as an isohyet for separating the two (Vinya et al. 2013).

Research Objective

For conservation to become a societal priority it needs to move away from set experimental design and needs to engage more in the “real world” through reaching scientific conclusions when knowledge is incomplete (Robinson 2006). This incomplete knowledge has been described as the lack of knowledge of how the loss of species would affect human livelihoods, and thus often fails to engage people in conservation biology. Secondly, conservation biology needs to incorporate conservation values into research. These values can be described as preventing the loss of functionally natural ecosystems. These values need to be incorporated into research through the assessment of conservation value and recommendations of remedial action. Thirdly, insights from social sciences need to be incorporated in conservation biology principles, because it is thought that biology alone is not sufficient for conservation (Robinson 2006). When seeing conservation as being about people, it is easier to incorporate social principles into conservation. By doing so, conservation becomes more relevant to society, especially when socioeconomic considerations are incorporated. Fourthly, conservation biology needs to address conservation in a human-dominated landscape (Robinson 2006).

Modern conservation has successfully addressed this, with the development of community based conservation, where human needs are included in the design of protected areas and not excluded as in the traditional preservation approaches to protect ecosystems from human influence (Attwell and Cotterill 2000). Lastly conservation biology needs to evaluate the contribution which it makes to human livelihoods (Attwell and Cotterill 2000).

Aims of study

The aims of this study were to gain as much information as possible on the ecology of the spotted hyena at MWR. Therefore each chapter of this thesis is dedicated to one aspect of their ecology which includes; population, distribution, diet and activity patterns. Based on the findings of the research chapters, the thesis is then concluded with a management recommendation chapter for the spotted hyena at MWR. These recommendations have the potential to safeguard the species and making local livelihoods value their natural heritage in the spotted hyena species.

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Chapter 2: The spotted hyena, *Crocuta crocuta*, clans of Majete Wildlife Reserve, Malawi

Abstract

Currently, there are no data on spotted hyena,*Crocuta crocuta*, population size and clan numbers at Majete Wildlife Reserve (MWR). A total of 47 camera traps were stationed throughout the reserve at waterholes, game trails and roads. These photographs were used to identify individual hyenas from unique spot patterns and other identifying features such as missing limbs. Population size was estimated from individual capture histories, using capture recapture models from the software programme CAPTURE. The model M_o, which assumes an equal capture probability for all individuals, was concluded to be the most accurate for spotted hyena at MWR. The model estimated a total population size of 16 adult individuals during the dry season of 2014, assuming no births, deaths, immigration or emigration during this period. These individuals were divided into two resident clans, the Pende clan in the east and the Pwadzi clan in the west which comprised of eight and five individuals respectively in early 2015. It seemed that contact existed between reserve hyena clans and free roaming clans outside of the reserve as new individuals (all male) were consistently identified The hyena density was 0.039 per km^2, which is comparable to hyenas living in arid regions with a clumped resource distribution. It is thought that severe poaching over previous decades, resulting in local prey species extinctions, is responsible for the low hyena density at MWR. The reintroduction programme of prey species in 2003 is yet to affect the spotted hyena population at MWR and any further reintroductions of lion, *Panthera leo*, should rather be considered when spotted hyena density at MWR is comparable to the hyena density in other savannah areas.

Introduction

Population ecology

Population biology is integral to wildlife conservation as a population's size influences all other aspects of conservation (Williams et al. 2001). Populations are defined as a group of interbreeding organisms of the same species in a particular time and space and can be described in context of their relevant population dynamics (Williams et al. 2001). Most commonly, populations are described in context of their population dynamics, such as their sex ratio or different life strategies. All populations are limited in their growth potential and once equilibrium has been reached populations do not deviate much. Equilibrium points are set by so called limitations, and can be either density dependent or density independent (Williams et al. 2001). For instance, prey density is a classic example of a density dependent limitation on predator populations. Each population has a maximum rate of increase (r_{max}) with optimal space, resources, lack of competition and predators (Wilson 2000).

Biological populations are seldom determined by census because of large area occupancy, open populations and incomplete knowledge of conspicuous animals, making population knowledge potentially uncertain (Corral 2012). Therefore, surveys are conducted using one of two categories which include i) counts that include all animals in the sampling unit (total counts) and ii) counts that are incomplete on the sampling unit due to the overlooking of certain individuals by researchers because the population or area are too large, necessitating subsampling (Williams et al. 2001). It is assumed that population estimates are based on count statistics which represent a fraction of the total number of individuals in the total population (Williams et al. 2001). This fraction of sampling which has been conducted needs to be extrapolated in order to have meaningful data which can be used in management of a species.

Spotted hyena population dynamics

Wildlife reserves in Africa are increasingly becoming closed off systems with limited movement between animal populations because of fenced off sanctuaries and encroachment from increasing human populations. Therefore it is necessary to monitor populations to ensure ecological integrity. The spotted hyena, *Crocuta crocuta*, are the most abundant of all large carnivores in sub-Saharan Africa (Watts and Holekamp 2009) and are able to adapt and survive in areas where lion, *Panthera leo,* and even leopard, *Panthera pardus*, are unable to do so (Trinkel 2009). Spotted hyena are indicator species because their density is influenced by prey availability and may be an indicator of ecosystem health, making them suitable for monitoring ecosystem function. They are resilient to environmental change and are able to survive in habitats in which other large predators are unable to such as lion, wild dog, *Lycaon pictus*, and cheetah, *Acinonyx jubatus*. Therefore if spotted hyena vanish from an ecosystem it can be regarded as degraded (Trinkel 2009).

Large carnivore populations may be influenced by either bottom-up- or top-down forces or both (Watts and Holekamp 2009). Bottom-up population control forces such as prey availability may result in starvation, an increased susceptibility to disease or a lack of energy for reproduction. Top-down forces would include direct anthropogenic influences such as eradication of spotted hyena or indirect anthropogenic forces where predator behaviour is altered thereby reducing their foraging efficiency (Watts and Holekamp 2009). For example, in the Masai Mara National Park, Tanzania, spotted hyena have altered their activity patterns, social behaviour and use of space in a response to increased livestock grazing within the park (Holmern et al. 2007). Disease is also considered a top-down force (Watts and Holekamp

2009), where outbreaks such as canine distemper virus, rabies and bacterial outbreaks of, *Streptococcus equi*, has had a decreasing effect on spotted hyena populations (Honer, et al. 2006).

Spotted hyena have the most complex social structure of all large carnivores and live in social groupings called clans (Holekamp et al. 2012). A clan consists of several matrilineal kins where all females in a clan are breeding and usually give birth to a litter of two cubs every 24 months (Holekamp et al. 2012). Young hyenas are vulnerable to den flooding, infanticide, siblicide, lions, disease and starvation when a mother has died (Watts and Holekamp 2009). Cubs of higher ranked females have higher survival rates than those of subordinate females, because higher rank confers priority of access to food, which cubs are heavily dependent on even after they have been weaned. The skull, which is needed for durophagy (bone diet), is not yet fully developed until after sexual maturity has been reached which limits its ability to hunt and a mother is needed to supplement its diet (Watts et al. 2009). Wild spotted hyenas can live for 25 years (Joubert 1996) and mortality rates are highest in the first two years, before the onset of sexual maturity (Watts and Holekamp 2009). After two years, the mortality threat stabilises, with lion and humans being the main threat to an adult hyena (Watts and Holekamp 2009). Mean spotted hyena density is 0.45 hyena/km but varies from 0.009 in the Kgalagadi Transfrontier Park to 1.65 hyena/km in the Serengeti (Holekamp et al. 2012). Areas with high hyena density support large clan sizes, with a consequent increase in reproductive output, which is related to large numbers providing greater protection of young and assisting in capture of larger prey species (Watts and Holekamp 2009). However, there may be a limit to effective clan size, as large clans are more vulnerable to disease outbreaks and decreases in per capita prey availability (Watts and Holekamp 2009).

Females tend to remain with their natal clans, although rarely, females may form a "fission event" where several females leave a clan to form a new clan in a separate territory, which usually occurs during peaks of both juvenile and overall clan size (Watts and Holekamp 2009). This could be a natural mechanism for preventing a decrease in reproduction as mentioned above in a large clan. Spotted hyena clan size varies from three to as many as 90 members. Most males, especially sons of high ranking females, emigrate to form part of neighbouring clans (Carnaby 2008). Rainfall can also affect clan recruitment rate, where recruitment is negatively correlated with rainfall (Watts and Holekamp 2009). This could be linked to the threat of den flooding to young hyenas, however this is a rare occurrence. Another possible effect of rainfall is an increase in infectious disease during periods of high rainfall, but disease does not seem to be a major controlling factor in hyena populations (Watts and Holekamp 2009). Rainfall may indirectly bring hyenas into conflict with humans during periods of high rainfall, as rainfall promotes plant growth causing their natural prey to disperse and making livestock an easier alternative (Watts and Holekamp 2009).

Camera traps in wildlife monitoring

In wildlife reserves throughout Africa, apex predators like the spotted hyena play an important role but are threatened by human encroachment (Winterbach et al. 2013). Thus, monitoring of apex predator populations is needed. Ideally, long term monitoring should involve a non-intrusive technique, which does not alter animal behaviour.

Previous studies have used feeding stations to be able to assist observation of hyenas, which involved carcasses being placed at a feeding station and study animals called in by the playing of sound recordings of hyenas at a kill and of inter-clan fights (Sillero-Zubiri and Gotelli 1992). This technique is however intrusive on spotted hyena foraging behaviour, as animals are lured away from areas where they would be naturally foraging. Calling-station surveys have been used to determine densities of these social predators over large areas such as the Kruger National Park, Okavango Delta and Masai Mara Reserve (Cozzi, et al. 2013). However, calling stations are biased towards adults as cubs remain at den sites and are thus not included in population estimates. The use of camera traps is an easy and cost-effective, non-intrusive technique for monitoring species. There have been notable, recent advances in the use of camera traps for population and density studies of conspicuous species (Kucera and Barrett 2011). Over large areas camera trap studies are less cost effective and they become time consuming and costly. However, in small and medium sized protected areas and reserves, the use of camera traps is more cost effective. Majete Wildlife Reserve is a relatively small reserve ($700km^2$) in the south of Malawi, and was suitable for camera trap studies.

Dense vegetation combined with the spotted hyena nocturnal behaviour makes regular observation of hyena at MWR difficult, thereby constructing effective studies of their population dynamics difficult. This lack of observations has led to a lack of knowledge on population dynamics. Camera trap studies at MWR require opportune camera placement to allow for spatial differences in hyena activity. Previously, camera traps have been used to identify individuals of spotted hyena clans by fixing cameras near communal dens (Dwane

2013). Waterholes are, for example, a good location for camera traps, because hyenas have no sweat glands and are forced to find water to help them thermoregulate, particularly so after a successful hunt when their body temperatures are elevated (Carnaby 2008). Roads and prominent game trails are also effective locations for camera traps because they are often used by hyena and prey species for easy movement through areas of thick undergrowth (Carnaby 2008).

The aims of this study were:

- Determine the total size of the MWR hyena population including the sex ratio of adults
- Determine the number of clans resident in MWR

Materials and Methods

Camera placement

In this study, Cuddeback Attack (model 1149) and Cuddeback Ambush (model 1170) cameras (manufactured by Cuddeback Ltd. in De Pere, United States) were used, which are both white flash cameras that take quality nocturnal images. These images made for easy identification of hyena individuals by their spots (Dwane 2013) and highlighted unique body characteristics, such as scars and missing limbs.

Capture recapture models require as many recaptures as possible making camera placement in areas of high spotted hyena activity crucial. Nevertheless, efforts cannot be so focused that areas potentially occupied by hyena are not surveyed (Soisalo and Cavalcanti 2006). A total of 47 single cameras were placed at seven artificial waterholes on MWR and monitored for a period of 22 months from July 2013 to April 2015. Cameras were checked at least once a month depending on the accessibility of the waterhole. Cameras were also placed on trees at communal dens found (Appendix 2, Figure 17). During camera checks, battery life was monitored and SD cards were changed. Cameras were set on a de-activation mode where cameras de-activated for one minute after an initial photograph was taken. This saved battery life when large herds congregated and lingered at waterholes for an extended period of time.

In addition to the methods described above, during both the dry-, (April-October) and the wet- (November-March) seasons (Sherry 1989) of 2014 and 2015, eight cameras were placed in four altitudinal regions ranging from 75m to over 450m above sea level. The cameras were placed in a north-south grid approximately 4-5km apart and were left at each altitudinal gradient for a period of 30 days, starting at the highest altitude. Of the four vegetation groups defined in the reserve, the high altitude vegetation group were areas 300m above sea level and was dominated by miombo woodland. Next was the second vegetation group which was defined as the medium altitude group between 200m and 300m above sea level, which was a transition zone between mixed- and miombo woodland. The low altitudinal vegetation group were areas between 100m and 200m above sea level consisting of mixed woodland dominated by an *Acacia*-woodland with *Combretum* spp, *Terminalia sericea* and *Sclerocarya caffra* with an open canopy (Staub, et al. 2013). The final group was defined as the riverine group and cameras were placed along the Shire River representing the parks lowest point under 100m above sea level. This area is dominated by large *Ficus lutea*, *Andansonia* spp, *Vachelia tortillis* and trees of the Sterculaceae family.

Opposite facing cameras were placed at nine of the total 47 camera stations which were situated along roads, trails, communal den sites, which are visited by both males and females (Holekamp et al. 2012), and at carcasses that were found in the field, which gave left and right flank photos of individuals.

Spotted hyena population size

Capture recapture models used in this study assumed a closed population with no birth, immigration, death or emigration (Silver et al. 2004). A sample period of not more than three months was assigned to ensure these assumptions were realistic (Silver, et al. 2004). The model also assumes that no animal has a zero probability of being captured on camera and that individuals are distinguishable from one another (Silver et al. 2004). Capture-recapture models are also based on the assumption that the proportion of captures to the population remains the same at each occasion. Capture recapture data can be simply explained with the formula:

$$\frac{x}{y} = \frac{X}{r}$$

Where x is the number of individuals recaptured, y the second sample size, X the first sample size and r the population size. The programme CAPTURE, developed by White et al. (1994), is a free online software package specifically designed to estimate population size and density in a closed population with capture-recapture model principles (White et al. 1978). The program functions on commands known as “tasks” given by the user after entering the capture history of all identifiable individuals.

Identikits of each spotted hyena were constructed in Adobe® based on unique spots and body characteristics as previously mentioned. Capture histories of all spotted hyena identified during a three month time period from 02 July 2014 – 29 September 2014 were entered into CAPTURE. This specific time period was used because two of the three dens were found during this time frame, cameras used in the altitudinal study were placed in both clan territories during this time frame and more images were obtained in the dry season than in the wet (see chapter five).

Capture histories were entered into what is known as an “x matrix” where an animal’s capture occasions are explained with a set of binary figures. The three month capture period was divided into 10 day segments which represented a capture occasion. In each capture occasion, an individual was allocated a “1” or a “0” based on it being captured or not captured respectively.

Different capture-recapture models exist based on different capture probabilities of the study animal. Models explain variation in capture probability through time (M_t); individual heterogeneity (M_h), where the model assumes a heterogeneity in capture probability between individuals which is not obvious such as individual dominance where dominant individuals may displace subordinate individuals (White et al. 1982); animal behaviour (M_b) and equal capture probability (M_o) (Lee and Chao 1994). CAPTURE is able to select the model most suitable for the capture histories presented by performing a goodness of fit test (see table 1, Appendix 1).

Spotted hyena density

To be able to compare the spotted hyena population of MWR to other areas, a density was calculated. This was done by dividing the population estimate obtained from CAPTURE by the size of the survey area. The survey area size was calculated by connecting all the outer camera stations to create a maximum convex polygon (MCP). However, first a buffer value had to be assigned around the survey area (Maffei et al. 2004). This was done to estimate the entire area sampled for spotted hyena because some areas outside the MCP were sampled because of areas near camera stations in which animals may be within (Efford 2015). A buffer width (W) is calculated by using half the mean maximum distance moved (di) by an individual, divided by the number of individuals captured more than once (m) (Martins 2010).

$$d = \frac{di}{m}$$

By using half the Mean Maximum Distance Moved (MMDM), which is more accurate than using the full MMDM (Dilion and Kelly 2008), a buffer width distance was calculated to portray around the sampled area polygon.

$$w = \frac{d}{2}$$

The coordinates of all camera stations were used to create a layer in Quantum GIS (QGis), a free software downloadable from http://www.qgis.co.za/en/site/forusers/download.html (accessed 28/06/2015). The camera station vector layer was laid over a vector layer of the reserve's boundaries. A polygon was then created by connecting all the outermost lying camera stations which functioned as the MCP of the trapping grid. Finally, the buffer width was added encompassing the MCP. All areas of polygons were calculated in QGis with the field calculator function.

Identifying clans

The number of clans were identified based on the association of different individuals at different locations, especially at waterholes and the communal dens where a large number of spotted hyena images were taken. The first communal dens were found by dividing the reserve into square kilometre blocks. Each block was then searched starting with areas of high spotted hyena activity such as waterholes. Other dens were found by game scouts during anti-poaching patrols. The focus was rather on adult spotted hyenas and not cubs as hyena cubs have a high mortality rate in spotted hyena society and therefore a high chance that cubs may not form part of the population as adults (Watts and Holekamp 2009).

Recruitment rate

Cameras were in the field for an extended length of time, thereby allowing the use of the Jolly-Seber test, an open population capture-recapture model which assumes death, birth, immigration and emigration in the population. This was used to calculate an average recruitment rate. The calculations were done online in the software program JOLLY available at http://www.mbr-pwrc.usgs.gov/software/jolly.html (accessed 19/06/2015) which operates on similar principles to CAPTURE. The capture histories of all individuals captured during the period that cameras were stationed in a territory were entered into the program.

Like in CAPTURE, capture history data was binary where a trapping "occasion" was represented by a month. For example, if an individual was captured in October 2013 the value "1" was entered and "0" if not. JOLLY differed from CAPTURE in that it required the number of individuals with a specific capture history to be entered at the end of each capture history. Jolly calculations were done separately for each clan because cameras were not placed in each territory for equal amounts of time.

Table 1. Capture history entered into JOLLY of all individuals captured in the Pende clan during July 2013 – March 2015.

```
x=TITLE=HYENA - MONTHS 1-20
PERIODS=20
FORMAT=(20I1)
00000000000000000011   2
00000000000000000101   1
10000000000000000000   2
11000000000000000000   1
00000000000011000100   2
00000000000011100000   1
11000000011111100100   1
00000000000111010000   1
11111000110100100000   1
11001000011101110000   1
11000000011111110111   1
11111110011111110111   1
11110010011111110110   1
10010000010111000110   1
```

This model includes parameters φ_i, the probability that an animal identified in sampling period i survives until time period i + 1, and X_i, which is the probability that an animal which survives and is part of the study population is not detected during any sampling period. The following equation displays the probability of detection.

$$X_{i=(1-\varphi_i)+\varphi_1(1-p_{i+1})X_{i+1}}$$

Table 2. Capture history entered into JOLLY of all individuals captured in the Pwadzi clan during February 2014 – March 2015.

```
x=TITLE=MAJETE HYENA PWADZI CLAN - MONTHS 1-13
PERIODS=13
FORMAT=(13I1)
0010000000000  2
0000011100010  1
0000011100000  1
1100011000001  1
0100011000000  1
1100011110010  1
0100001110011  1
0000001000000  1
```

Results

Population

The model, M_o which assumes a constant probability of detection was selected by CAPTURE to be most suitable to estimate the spotted hyena population size in MWR. The model, M_h which takes individual heterogeneity capture probability into consideration was considered the second most appropriate model by CAPTURE (Table 3).

Table 3. Estimates of the spotted hyena population size with standard error and 95% confidence interval for the capture-recapture models M_o and M_h during the time frame 02 July 2014 – 28 September 2014 as calculated by CAPTURE.

	Model M_o	Model M_h
Population estimate	16	17
Standard error	0.2153	1.3229
95% confidence	16-16	17-23

Throughout the 22 month period of data collection, several individuals were identified of which many came and went (all male). Two adult males were last captured on camera during the dry season of 2013, and it was assumed that they possibly emigrated from the reserve while two other individuals were only captured and identified in June 2014 and November 2014 respectively, much later than all other individuals, and it was assumed that the two males immigrated into the reserve. According to local people and tracks that were found outside the reserve, spotted hyena still do occur naturally outside MWR's boundaries, and these males may have emigrated to and immigrated from these clans resident outside the reserve. Dispersal of males from these clans into the park and dispersal of young males from the reserve into villages cause the spotted hyena population to fluctuate in MWR. These inter-reserve movements justify its treatment as an open population.

Two males from the Pende clan were never captured at the communal den and seemed to be nomads inside the Pende territory with no association with females, although they were captured with other males that did visit the communal den.

Density

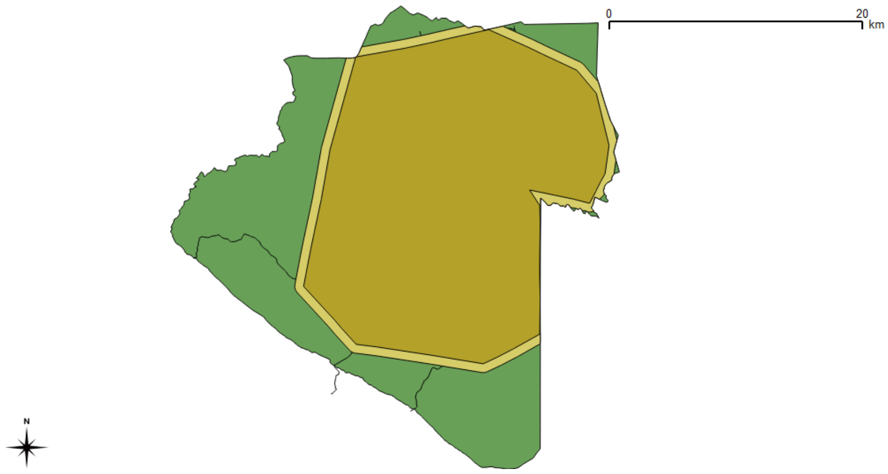

Figure 1 Maximum convex polygon (MCP) of the trapping grid with buffer width surrounding the trapping grid.

The MCP area of the trapping grid was 407.1km^2, the maximum distance moved by an individual between camera trap stations was 25.8km and the buffer width (W) was only 700 metres (Table 4).

Table 4. Maximum distance moved is the furthest distance between two camera stations that a hyena individual was recorded to move. The mean maximum distance moved (MMDM) is the maximum distance moved divided by the number of hyena individuals that were captured more than once. Trap polygon area is the area of MCP of the trapping grid. Trap polygon area is the area of the trapping grid MCP with the added buffer width (W) around it. The spotted hyena density was calculated by dividing the most conservative population estimate (n=16) by the trapping MCP area with buffer width.

Maximum distance moved	(km)	25.8
Full MMDM	(km)	1.4
Trap polygon area without buffer	(km^2)	366.4
Trap polygon area with buffer	(km^2)	407.1
Hyena Density	(per km^2)	0.039

Cubs

Three communal dens were found and five cubs were identified. Approximate cub ages were three of three months and two of five months old (Appendix 2, Figures 12, 13, 14 & 15). Another den housing a sub-adult was found but it was unclear whether the den was a communal den or a nursing den (Appendix 2, Figure 16), the latter being probable as the sub-adult and mother were only captured once. Two other sub-adults of unknown sex were also caught away from the dens and were only caught once in June 2013 and April 2014 respectively.

Clans

Two clans were identified to be resident in MWR (Table 5). One in the lower lying south-eastern part of the reserve (Pende clan) and one in the more hilly north-western region of the reserve (Pwadzi clan). As mentioned, size fluctuations were evident in both clans but at the end of the research period (April 2015), the clans were constructed as follow:

Table 5. Clans resident in MWR and their sexual make-up at the end of the study period.

Clan	Female	Male
Pende	4	4
Pwadzi	4	1

Recruitment rate

The results from JOLLY estimated a survival probability of 0.98 (0.0188 SE) and an average recruitment rate of 0.11 (0.05 SE) for the Pende clan. The Pwadzi clan had a lower survival probability of 0.89 (0.0748 SE) and the recruitment rate was found to be negative -0.02 (0.86 SE). Two males emigrated from Pwadzi to Pende during the research period which may have influenced these statistics.

Discussion

Density

The spotted hyena density in MWR is similar to, but slightly lower, than that of Etosha National Park, Namibia (Table 6) (Gasaway et al. 1989). The low density in Etosha was ascribed to non-uniformly distributed resources. Patchy resource distribution may require spotted hyena to search over a wider area for resources, which increases home range size and results in a low density population (Gasaway et al. 1989). Equally, where resources are evenly distributed, hyena occur in higher densities (Gasaway et al. 1989). Waterholes which are scattered widely contribute to patchy resource distributions (Tilson and Henschel 1989). This is probably true of MWR where prey species concentrate around the Shire River and at artificial waterholes in the south-eastern section of the reserve. Spotted hyena populations, especially those of low density such as at MWR, are regulated by resource availability, competition and aggregation of clan members (Tilson and Henschel 1986).

Table 6. Spotted hyena density in different localities across Africa.

Location	Density per km^2	Reference
Serengeti National Park, Tanzania	0.17	(Kruuk 1973)
Ngorogoro Conservation area, Tanzania	1.7	(Kruuk 1973)
Hwange National Park, Zimbabwe	0.07	(Holekamp and Dloniak 2006)
Etosha National Park, Namibia	0.05	(Gasaway et al. 1989)
Namib Dessert, Namibia	0.004-0.0085	(Holekamp and Dloniak 2006)
Aberdare National Park, Kenya	1.34	(Sillero-Zubiri and Gotelli 1992)
Masai Mara National Park, Kenya	0.94	(Holekamp and Dloniak 2006)
Mkuzi Game Reserve, South Africa	0.13	(Skinner et al. 1992)
Umfolozi Game Reserve, South Africa	0.36	(Skinner et al. 1992)
Kruger National Park, South Africa	0.07-0.13	(Holekamp and Dloniak 2006)
Timbavati Game Reserve, South Africa	0.48	(Holekamp and Dloniak 2006)
Kgalagadi Transfrontier Park, South Africa	0.009	(Mill 1990)

MWR, based on published studies, has the lowest density of spotted hyena recorded for a savannah habitat. Such low densities are usually associated with arid regions (see table 6). Decades of high level poaching at MWR may have contributed to the low hyena density because of consequent low prey densities which determines hyena densities (Holekamp et al. 2012).

Population

Communal dens are changed on average every six weeks (Holekamp et al. 2012) and it is assumed that several communal dens were not found during the 15 month period when searching for communal dens. Furthermore, swollen teats of females identified on camera trap photographs, suggests that several cubs may have not been counted, and indicates that successful breeding does occur within MWR. The fact that so few sub-adults were photographed may indicate that the mortality during the sub-adult life stage is high in MWR. This life stage is the most vulnerable life stage of a spotted hyena because although sub-adults are weaned, the skull is not yet fully developed which makes hunting difficult (Watts et al. 2009). This fact, combined with a clumped resource distribution, may result in a low survival rate to adulthood in MWR.

A reintroduction programme of more than 2500 head of potential prey species between 2004 and 2010 seems to have had little effect on the hyena population size in MWR. This illustrates the effect that anthropogenic factors, such as poaching and placement of waterholes, has on prey dispersal (Valeix et al. 2009) and consequently spotted hyena numbers. One reason for the limited effect of the reintroduction might be that it was largely comprised of large ungulate species such as waterbuck, *Kobus ellipsiprymnus*, buffalo, *Syncerus caffer*, sable, *Hippotragus niger*, and eland, *Taurotragus oryx*. Such large prey species are difficult for spotted hyena to bring down alone without suffering injury. Assuming an even smaller hyena population during 2003, which may have meant that rather small species would have been focused on as prey, and because small antelope species were never reintroduced they still would have focused on prey species with a low density. The greater protection of small antelopes after 2003 would have slowly increased small prey species' density which in turn would have slowly increased spotted hyena density. Therefore any beneficial effect of greater protection may be delayed.

The small spotted hyena population in MWR may also be attributable to the Allee effect. The Allee effect is defined as the positive relationship between fitness and density (Stephens et al. 1999), where animals experience a decrease in rate per capita increase because of low density (Courchamp et al.1999). This is due to a decrease of survival and reproduction in intraspecific cooperative species such as spotted hyena. But although they are highly social animals, spotted hyena, unlike other hyenid species, do little or no cooperative rearing of young (De Waal and Tyack 2003). Therefore a low hyena density would not seem to effect cub survival in the way it would other large social predators such as wild dog (Courchamp et al. 2000). Large hyena clans do, however, favour survival of hyena cubs because they provide greater protection for the young at the communal den and the group's ability to bring down larger prey increases food availability (Watts and Holekamp 2009).

Another reason for the small hyena population at MWR may be the potential predation of hyena cubs by warthogs which may be a threat to cub survival in MWR. In Kenya a male warthog, *Phacochoerus africanus*, was recorded killing the young of a Thomson's gazelle, *Gazella thomsonii*, (Roberts 2012) and in MWR during the study period, cannibalism by warthog males on warthog young was documented twice. Hyenas and warthogs are found in close proximity, as they use the same cavities for dens and refuges (Kingdon 1989) and warthogs were captured on camera, on several occasions, at the hyena communal den entrances in MWR (Appendix 2, Figures 1 & 2). Although predation on hyena young by warthogs was never documented in MWR, is it plausible because of the high warthog density in MWR (see chapter four).

Management recommendations

The proposed reintroduction of another pride of lions into the Pende region in the south of the reserve should be carefully considered. Lions and humans are the two main threats to hyena (Holekamp et al. 2012) and reintroducing lions into spotted hyena territory may further decrease hyena density. If such a reintroduction were to take place it should happen when spotted hyena density in MWR is comparable to densities of other areas with a similar habitat structure, the latter being a major influence on hyena density (Holekamp and Dloniak 2006, Tilson and Henschel 1986) and therefore spotted hyena density in MWR should be monitored. If the spotted hyena population in MWR seems to either decrease or stagnate while prey species density increases, it should be assumed that the lack of population increase might be due to the Allee effect. Reintroducing spotted hyena to resident clans could then be considered.

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Chapter 3: Spotted hyena, *Crocuta crocuta*, home ranges of Majete Wildlife Reserve, Malawi

Abstract

Spotted hyena, *Crocuta crocuta*, home range size in the Majete Wildlife Reserve (MWR), Malawi, was determined using data collected from camera traps. Cameras were placed throughout the reserve at artificial waterholes and along game trails and roads. Maximum convex polygons were calculated for each sex in each clan using capture history and latrine locations, which are visited by both sexes. Lion, *Panthera leo*, home range utilisation was determined based on kernel density estimates. Spotted hyenas used areas less frequented by lions. The average home range size for spotted hyena clans in MWR was 290.5km^2 which was generally comparable with home ranges of spotted hyena living in arid regions with clumped resource distributions. These relatively large vertebrate home ranges for a savannah habitat may reflect the clumped resource distribution at MWR, a legacy of severe poaching. Artificial waterholes and lion presence also seemed to have had an influence on hyena home range usage. Proposed future reintroductions of more lions and the creation of more artificial waterholes needs to consider the influence it may have on spotted hyena distribution.

Introduction

Animal home range

Determining an animal's home range use is important in ecological studies as it reflects basic ecological processes such as its distribution, diet, abundance, habitat selection, reproductive output and predator-prey relationships (Borger et al. 2008, McKenzie et al. 2009). Home range describes non-random, non-migratory movements within a landscape (McKenzie et al. 2009). For example, spotted hyena movement is thought to be non-random because of their need to nurture young at fixed den sites (McKenzie et al. 2009).

Home range is often confused with the term "territory", which includes defensive behaviour of exclusive resources, relating to the principle of competitive exclusion which suggests that competitors may only co-exist with some form of resource differentiation (Ronconi and Burger 2011). A territory may be only part of an animal's home range (Powell 2000). Animals might become territorial over a limited resource such as food, which tends to influence territory size (Borger et al. 2006). The term home range specifically refers to: "the spatial expression of behaviours animals perform to survive and reproduce", and are based on an individual's behaviour when interacting with a surrounding productive or stable environment (Borger et al.

2006, Roshier et al. 2008). A home range is estimated using sequential location points recorded over time (Powell 2000). Therefore a home range needs to be defined according to certain time scales (Powell 2000, Borger et al. 2006). The longer the time scale is, the more data points there are available to quantify home range size, but the more likely it is that the home range has changed. The interaction between time and data points may create patterns of space use and are illustrated through home range size (Borger et al. 2006).

For an animal to have a set home range, the daily costs, C_D, and the costs of monitoring, maintaining, defending, developing and remembering critical resources, C_R, needs to be less than the benefits, B, gained from having a set home range (Powell 2000).

$$C_D + C_R < B$$

These costs must ultimately be calculated in terms of animal fitness. If costs exceed benefits an animal needs to move on and adapt to a nomadic lifestyle, as opposed to showing site fidelity (Powell 2000).

Site Fidelity

Habitat selection is a relatively poorly understood aspect of animal ecology as it is difficult to understand why an animal would not occupy a suitable habitat when it is physically able to do so (Campbell et al. 2008). Often biotic factors may influence an animal's ability to stay in a suitable habitat, where negative interactions such as predation and competition may limit an animal's distribution (Campbell et al. 2008). Alternatively, an animal's distribution might be limited by the absence of other species on which it depends (Campbell et al. 2008).

Site fidelity is the tendency of individuals to stay in an area or return to one previously occupied (Janmaat et al. 2009, Giuggioli and Bartumeus 2012). Various factors may cause an animal to return to previously utilized areas. Often areas are acquired and used for the rearing of young, social interactions or they simply form part of an animal's daily activities based on benefits gained from establishing a home range (Giuggioli and Bartumeus 2012). Site fidelity is associated with home range establishing behaviour and can therefore be used to determine whether or not an animal has established a home range (Powell 2000, Giuggioli and Bartumeus 2012). The benefits of site fidelity or having a home range, include the advantages it confers on both foraging and safety through knowledge of the occupied area (Janmaat et al. 2009). Site fidelity may also simply reflect areas in a heterogeneous landscape with stability in limited resources. However, mammals can show site fidelity even with a change in the location of valuable resources (Janmaat et al. 2009). The conservation significance of quantifying site fidelity is to understand the level of exploitation of profitable habitat by certain species. Profitability can be directly related to the intensity of space use, which can be incorporated into effective management plans of protected areas and also to see how competing species diverge in their spatial use (Giuggioli and Bartumeus 2012).

Movement

Animal movement data can be used to explain both intra and inter-species interactions and animal interactions with their environment (McKenzie et al. 2009). Determinants of animal movement have been described by optimal foraging- and habitat selection theories (Roshier et al. 2008). However, increasing evidence suggests that animal's movements are not limited to resource distribution, but rather are a complex relationship involving breeding status, competition, predation risk and past experiences (Roshier et al. 2008). Hence, individuals of the same species can move differently in similar environments with similar resources. Other factors such as possible food gains, amount of foraging time and the travel time spent to reach a new resource patch may all influence movement (Stephens 2008). Resource rich habitats should have short travel times among resource patches which will incentivise an animal to move in case they lose out on an opportunity by staying in the same resource patch for too long (Stephens 2008). Occasionally, animals will make exploratory forays outside of their home range (Powell 2000). Areas not utilised after initial exploration are not considered part of their home range, as these areas are not being used for survival and reproduction.

Spotted hyena territorial behaviour

Spotted hyena, *Crocuta crocuta*, are highly social animals which live in groups called clans, that vary in size from three to 90 members (Watts and Holekamp 2009) and they defend their territories fiercely against possible invasion from other clans (Boydston, et al. 2001). Members advertise their group's presence in a territory by both scent marking and depositing faeces at so called latrine sites, which are areas of communal defecating (Apps 2000). Scent marking is done via an anal sac situated between the tail and rectum of an animal (Theis et al. 2013). These social odours are produced by bacteria that ferment or metabolize nutrient-rich substrates in the anaerobic environments within scent glands. Bacterial communities also vary amongst different social groups in clans such as by sex, group membership and individual (Theis et al.

2013). Spotted hyena scent mark approximately every 2.5km to 7.5km during nocturnal patrols in significant areas, such as territory boundaries and at large kill sites (Apps 2000). Scent marking is achieved by an animal walking over clumps of grass or over a single grass sward, where a muscular lining of the anal sac forces the apparatus outwards. The sac is then dabbed against the grass leaving a white smear 2.0cm – 5.0cm in length. Scent marking is also performed by scratching and pounding the ground surface which releases secretions from glands between the toes (Apps 2000).

Clan members of both sexes will defend a clan's territory fiercely against any encroachment by neighbouring clans, although females invest more time in territorial activities than males (Boydston et al. 2001). A possible reason for a female's increased investment in territorial defence is because their reproductive success depends on priority access to food, and territorial defence is normally associated with competition over food as foraging is undertaken within a clan's territory. Same sex encounters also appear fiercer than opposite sex encounters between members of different clans. Thus, it seems that defensive behaviour is dependent on an individual's need to protect resources within its territory against intruders (Boydston et al. 2001).

The mean spotted hyena clan home range size from 18 published studies is 175km^2, but home range size varies from 13 - 1065km^2 depending on factors such as hyena density, prey availability and habitat type (Holekamp and Dloniak 2006). As hyena density increases, home range size decreases although this is a non-linear relationship (Hayward et al. 2009). A home range is not used equally, certain areas are used more intensely than others (Hayward et al. 2009). Ultimately, the home range of a predator, including that of spotted hyena, is related to the metabolic energy requirements needed to sustain themselves (Hayward et al. 2009). Other factors also influence an individual's home range use, for example, spotted hyena females with den-dwelling cubs forage closer to the communal den than females without them (Boydston et al. 2003). Individual distribution also plays an important role in home range size and intensity of use (Borger et al. 2006). Spotted hyena home ranges can be very dynamic, possibly to ensure that benefits outweigh the costs of having a home range (Honer et al. 2005). Home range may vary seasonally according to changes in the areas of highest profitability, perhaps through an influx of migratory prey, even if it means crossing into neighbouring territories to take advantage of it (Honer et al. 2005). These forays into neighbouring territories are usually done by lower ranked individuals that forage further afield than higher ranked individuals to avoid conflict with them over food (Borger et al. 2006). Generally, hyena home ranges are said to be more stable in areas where there are no migratory prey species (Trinkel et al. 2004). Anthropogenic influences also affect spotted hyena home ranges, they may alter their habitat use because of conflict with humans (Boydston et al. 2003).

The role of water

Water plays a fundamental role in wildlife ecology because all species, to a certain extent, are dependent on it. Thus, it is common for game reserves and national parks to create artificial waterholes, often solely for tourist reasons, as these attract great numbers of animals. Much research has been conducted on the effects of waterholes on game numbers but mostly involving herbivore communities (Smit et al. 2007, Redfern et al. 2003, Valeix et al. 2009). Little is known about how they affect predator guilds. It is commonly known, however, that predators do make use of waterholes to easily stalk and attack drinking prey caught off guard (Valeix et al 2009). Water is commonly used by spotted hyena, not just for drinking and hunting, but also to cool off after a successful hunt, as digesting food increases body temperature (Carnaby 2008). Hyenas cannot perspire, making panting their main means of thermoregulation which is assisted by emersion in water. Hence, spotted hyena are often found cooling off at artificial waterholes (Carnaby 2008).

Artificial waterholes are thus prime territory for spotted hyena, providing both hunting grounds and a means of thermoregulation. Dominant spotted hyena forage over smaller distances than their subordinate counterparts, dominance allowing them use of a home range's prime territory (Holekamp et al. 2012). Therefore female spotted hyena, being dominant over males, should spend more time at waterholes than the males, males having to forage elsewhere to avoid conflict. Additionally, a young hyena's post-weaning survival depends on its mother's ability to assist with foraging (Watts and Holekamp 2009). As waterholes make prime hunting territory, dominant mothers focus time and efforts in such areas. However this does not mean that males avoid waterholes and females entirely, because a male's reproductive success is dependent on interacting with breeding females within a clan (Boydston et al. 2001).

Aims

Usually, home range studies involve radio-collaring animals and home range size is determined from GPS fixes retrieved from the collar. This, however, is expensive and highly intrusive as study animals need to be captured, darted and possibly habituated during the process. Collar data also assumes that the animal collared is representative of an entire group of animals

(Moorhouse and Macdonald 2005). This is especially biased for social animals, such as spotted hyena, where an individual's home range size may differ according to its social rank (Holekamp et al. 2012). Camera traps offer a cheaper and non-intrusive technique to study spotted hyena movements.

The aim of this study was to:

1) Identify the total size, boundaries and intensively used areas of home ranges of the two resident hyena clans in MWR by making use of non-intrusive camera traps.
2) Determine if there were sex related differences in home range usage.

Materials & methods

Camera placement and hyena identification

A total of 47 stations of cuddeback cameras (model 1149 and 1170, manufactured by Cuddeback Ltd. in De Pere, United States) were placed across the reserve of which seven were permanently stationed at artificial waterholes and one permanent spring within the reserve. The cameras produced a white flash when triggered by movement that allows for colour images at any time of day or night. A Bushnell infra-red flash camera (model 119736C), was placed at a waterhole situated at a lodge because it does not produce a white flash and would not disturb guests. Infra-red images are, however, of a lower quality making it difficult to identify hyena individuals and thus were not included in the analyses. Cameras were stationed, constantly for 17 months at waterholes (July 2013 – December 2014) and were checked at regular intervals of 2 – 4 weeks depending on the remoteness of the waterhole. White flash cameras were also placed along roads which are often used by animals because of ease of access (Carnaby 2008) and hyena images from vegetation grid sampling were also used for home range analyses (see chapter two).

Hyena individuals were identified from camera trap images based on unique spot patterns and other features such as scars and missing limbs. These features were used to create identikits for each individual using Adobe®. Individuals were sexed based on phallus structure which is pointed in males and rounded in females [Appendix 2, Figures 8 & 9] (Holekamp 2007). Other features such as swollen teats of lactating females were also used to determine sex.

Home range boundaries and area

The simplest model for determining a home range is the maximum convex polygon (MCP) method, a polygon surrounding all the known locations of an animal (Row and Blouin-Demers 2006). Through this method the extremities of areas used are connected (Glessner and Britt 2004). Camera stations in combination with latrine location were used to construct the MCP (Mann 2014) for each sex in each clan. Areas of overlap between members of the two resident clans were assumed to be home range boundaries between the two clan's respective home ranges. MCP has the advantage of not being dependent upon the underlying statistical distribution, although it does not specify selection within the home range.

The MCP method can over estimate home range area when placing cameras in grids where cameras are spread approximately equidistant from each other (Maffei et al. 2004). In this study, cameras were placed in ecologically significant areas, such as waterholes and game trails, which provided the optimal chance of capturing hyena images and resulted in an irregular pattern of camera placement with varying distances between stations (Royle et al. 2009). In such cases, the MCP is deemed sufficient for describing home range size of a species (Maffei et al. 2004).

A buffer width can be placed around each camera trap station which represents the area each station surveys (Dillon and Kelly 2008). A buffer width distance is retrieved by determining the mean maximum distance moved (MMDM) from the longest distance an animal moved between camera stations, and then dividing the MMDM by the number of individuals caught more than once on camera (Martins 2010). The standard buffer is ½ MMDM which is more accurate than the full MMDM (Dillon and Kelly 2008). Buffer width (W) was calculated for each sex in each clan and was used to create each group's respective MCP in Quantum GIS (QGis), a free software package used for analysing geographical information, [http://www.qgis.co.za/en/site/forusers/download.html (accessed 16/06/2015)]. The area of each MCP was calculated in QGis by using the field calculator function.

Home range usage

Camera trap rate was used to determine habitat usage (Kelly and Holub 2008) of spotted hyena in MWR. The methods of Bowkett et al. (2007) were followed by calculating the camera-trap rate per camera station for spotted hyena to determine areas that had high spotted hyena use. This was done by dividing the number of spotted hyena images with the number of trap nights per site (Bowkett et al. 2007).

Lion home range usage was compared with that of spotted hyena. At the time of this study, MWR had five lions (two males, one female and two sub-adults one of each sex). African Parks collared one adult female and one adult male with GPS collars for general monitoring of the animals and not specifically for the study. These collars sent a fix once every 24hrs for management purposes. These data were used to compare lion home range usage with that of spotted hyena in MWR. Only fixes obtained during the research period (July 2013 – May 2015) were used although lions were allready collared in 2012. However, fixes were only obtained from 01 July 2013 – 09 December 2013 and 01 July 2014 -30 April 2015 due to collar battery failure inbetween. A total of 1277 fixes were recorded.

A fixed kernel density estimater in QGis was used to identify areas with high lion use based on these fixes. In kernel density estimate analysis a smoothing factor (*h*) has to be assigned, which is the size of the radius around each fix in the analysis (Sheather and Jones 1991). The more radii from fixes overlap, the greater the assumed habitat preference. A smoothing factor *(h*) of 3000 metres was used for lions, which is the average distance moved by lions per day (Mosser, et al. 2009). A spotted hyena kernel density estimate analysis was also performed using the capture rate from camera stations, specifically to visually illustrate spotted hyena home range usage compared to that of lions. The average number of spotted hyena captures per 100 trapping nights were used as fixes. To be sure that each fix would be recognized, the location of each fix from a station was modified slightly (at the fourth decimal) from the camera station GPS location (Mann 2014). The band width (W) as calculated by the MMDM, was used as the smoothing factor (*h*) for each spotted hyena clan kernel density estimate (Holekamp and Kalowski 2009)

Finally, spotted hyena home range usage between sexes of the Pende clan (see chapter two) was tested by comparing capture rate for each sex in different areas of their territory. This was not done for the Pwadzi clan because limited cameras were placed in the Pwadzi territory. To assess differences in home ranges between sexes, the Pende territory was divided into a north and south region where different sexes seemed to focus their hunting efforts. The north region was higher in altitude, above 300m in places, and was dominated by tree species such as *Brachystegia boehmii* and *Julbernardia* (Staub et al. 2013). The north region extended eastwards to the Shire River and also included four artificial waterholes. The Shire and the artificial waterholes were inside a 14,000 ha area known as the old sanctuary, and was originally fenced off whilst animals were still being reintroduced to the reserve. The south region consisted of mixed woodland vegetation typical of low altitude areas in the reserve which was dominated by trees such as *Combretum* sp, *Terminalia sericea* and *Sclerocarya caffra* with an open canopy (Staub et al. 2013). The null-hypothesis was that male and female hyena home range usage did not differ in the Pende territory. Home range usage between sexes was then compared based on capture rate from camera stations assuming that image frequency represented home range utilisation (Kelly and Holub 2008, Bowkett et al. 2007). Capture rate from each camera stations in each section per sex was compared using a Mann-Whitney U test from an online programme called, socscistatistics.com, (http://www.socscistatistics.com/tests/mannwhitney/). Data was sorted into contingency tables, and a significance level of $p \leq 0.05$ was selected.

Results

The average estimated home range size of spotted hyena in MWR is 290.5km^2 and male home ranges were larger than female home ranges (Table 1; Figures 2, 3, 8 & 9).

Table 1. Home range size calculated with buffer width (W) around the MCP for each sex in each clan.

Home Range	MMDM(km)	Buffer Width (km)	Area km^2
Pende Female	21.2	1.9	318.8
Pende Male	19.3	2.6	346.4
Pwadzi Female	15.6	2.6	175.2
Pwadzi Male	22.6	3.8	321.4
Average			**290.5**

Territory boundaries

There were six camera trap stations across the reserve visited by members from both clans. The camera stations were connected with a straight line to form the territorial boundary between each clan. When connecting these stations with a straight line, was the last camera station 6.33km away from the reserve's boundary. The territorial boundary was extended from the last camera station to the reserve's boundary by continuing the territorial boundary line at a similar angle towards the reserve's boundary (Figure 1).

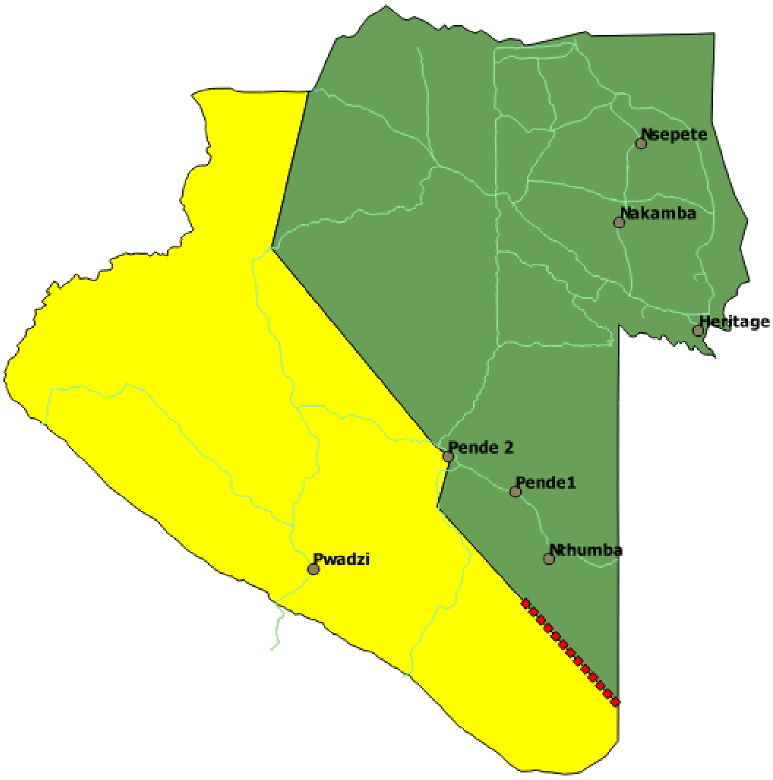

Figure 1. Pende (green) and Pwadzi (yellow) territories with respective waterholes in each territory. The black central line connects camera stations where members from both clans were found and are potential patrol areas. The dashed line is an extension of the patrol line because of the inaccessibility of the area to install cameras. The light green lines represent Majete's road network.

Pende home range

The Pende home range was approximately 332.6km^2 and the core of the territory was along the south eastern boundary fence where two communal dens were found including an old abandoned den. The north of the home range (Figure 2) was used more by males than females ($z=1.963$; $p<0.05$) but the south of the home range was used equally between sexes ($z=-1.0596$, $p=0.14$). The average distance of camera stations in the north, where only males were captured, was 17.3km from the centre of the clan's territory.

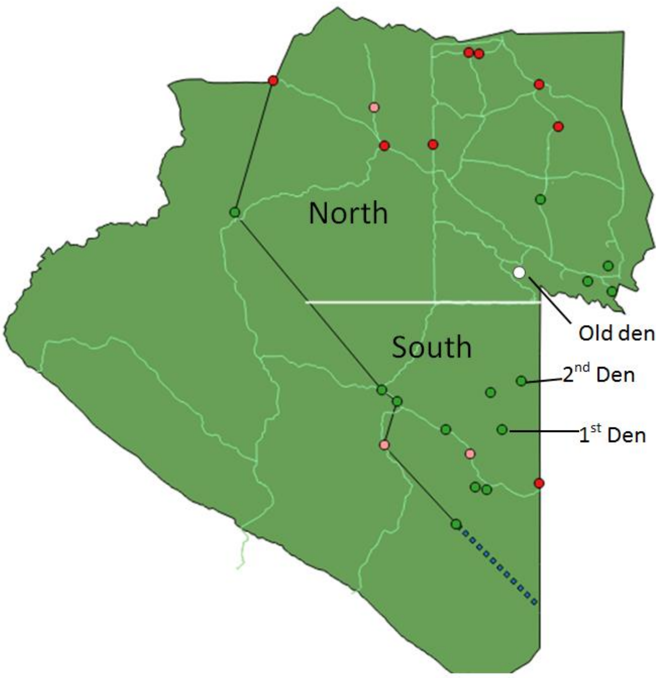

Figure 2. The Pende territory divided into a north and south region to compare home range usage between sexes. The fixes represent camera stations in the territory. Green fixes represent stations where both sexes were captured, red represents stations where only males were captured and pink represents fixes where only females were captured. The location of the two dens found and another den, which was recently abandoned at the time of discovery, are also marked.

Females used the southern part of the home range more than the northern part ($z=-2.752$; $p<0.05$), whereas male usage did not differ between north and south ($z=-0.4562$, $p=0.11$). The null hypothesis was thus rejected and it was accepted that males and females utilise the Pende territory differently with females focusing their hunting efforts in the south and males having no specific area of focus.

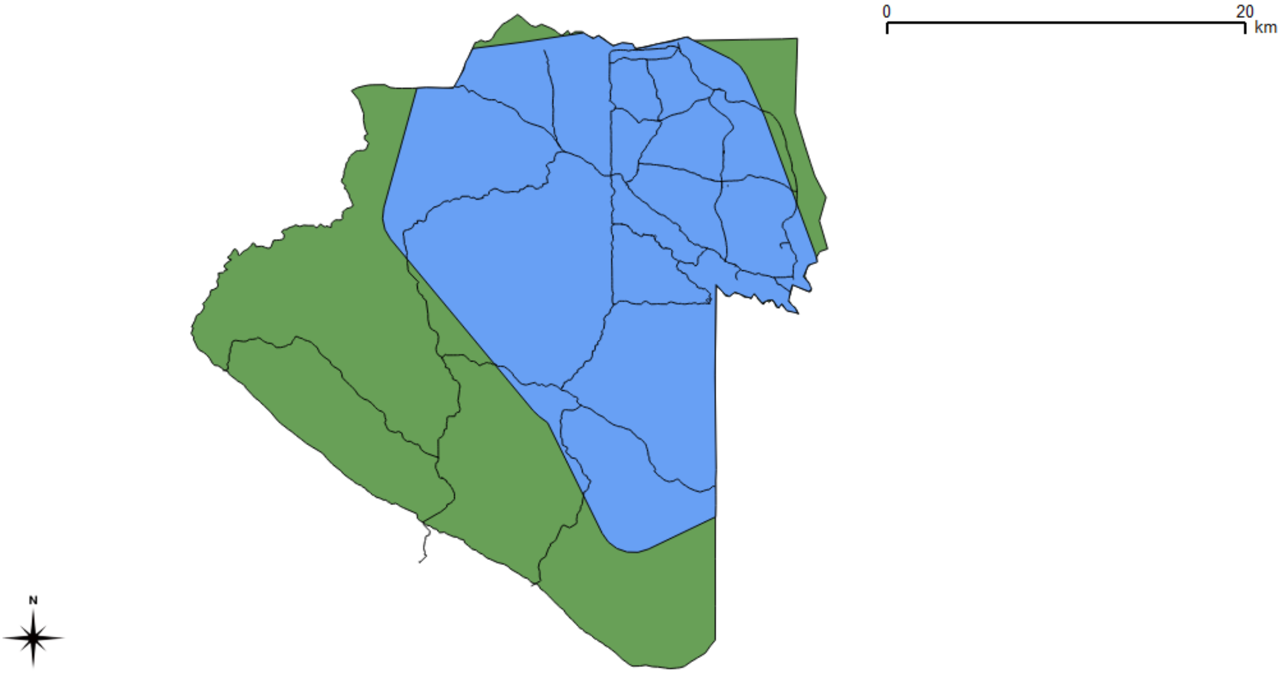

Figure 3 Pende male home range with buffer width.

Pende males had a larger home range than Pende females (Table 1), it extended to the northern boundary of the reserve (Figure 3) while the Pende female home range did not extend to the northern boundary of the reserve and was more westerly orientated than the Pende male home range was (Figure 3 & 4).

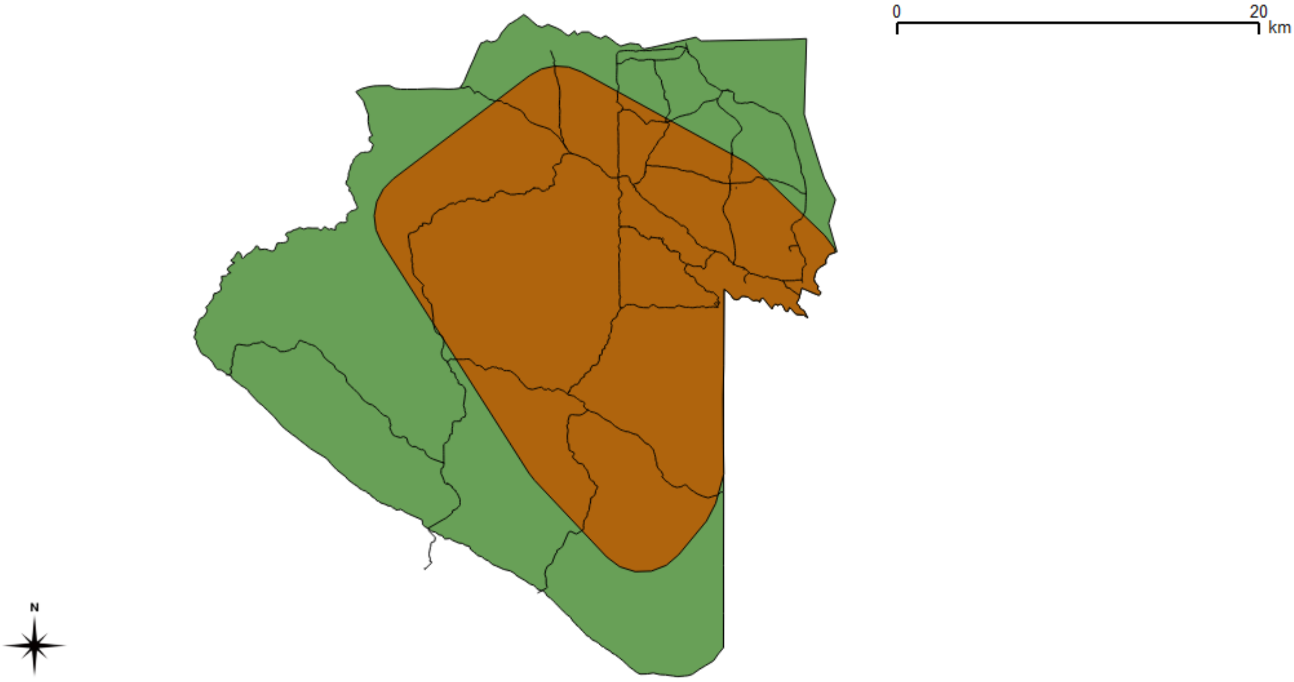

Figure 4 Pende female home range with buffer width.

The communal dens had the highest capture rate within the Pende home range but these areas were only utilised for a limited period of time, before the communal den was moved (Holekamp et al. 2012). The first den of the Pende clan (34˚.68651 E; 15˚.97677 S, Appendix 2, Figure 3) had one entrance in a low lying flood plain known as a dambo. The second den of the same clan (34˚.69565 E, 15˚.95314 S, Appendix 2, Figure 4) was situated on the banks of the non-perennial Manase River, and had three entrances. This was also the only one of the three dens found where adults were documented going inside the den (Appendix 2, Figure 5).

Table 2. Artificial waterholes in the Pende territory. Trap nights are the number of nights that a camera was stationed at a respective waterhole. Captures represent the cumulative count of hyenas captured at respective waterholes and is expressed as the average number of hyenas captured per 100 nights. The "individuals" column represents the total number of different hyena identified at each waterhole based on unique spot patterns and other features.

Waterhole	Trap Nights	Captures	per 100 nights	Distance from clan centre (km)	Individuals
Pende 1	296	100	34	3.4	7
Heritage	464	66	14	10.7	10
Pende 2	226	30	13	5.6	6
Nthumba	323	42	13	5.1	7
Nakamba	419	17	4	12.3	3
Nsepete	523	10	2	15.2	3

Waterhole use by hyenas generally decreased as distances increased away from the communal den. This was evidenced by more frequent visits to the waterholes closest to the two communal dens within the Pende clan's home range, Heritage waterhole excepted, than to waterholes further away (Table 2, Figure 2). Waterholes in the north (Figure 1) had a lower capture rate and were mostly visited by males, especially the Nakamba and Nsepete waterholes (Table 2). The Pende hyenas focused their activities around the Pende 1 and Nthumba waterholes with the Heritage waterhole area also being used regularly, although less so than the Pende 1 waterhole area (Table 2, Figure 5). The waterholes in the south are the only sources of permanent open water and are just over 14km on a direct line from the Shire River.

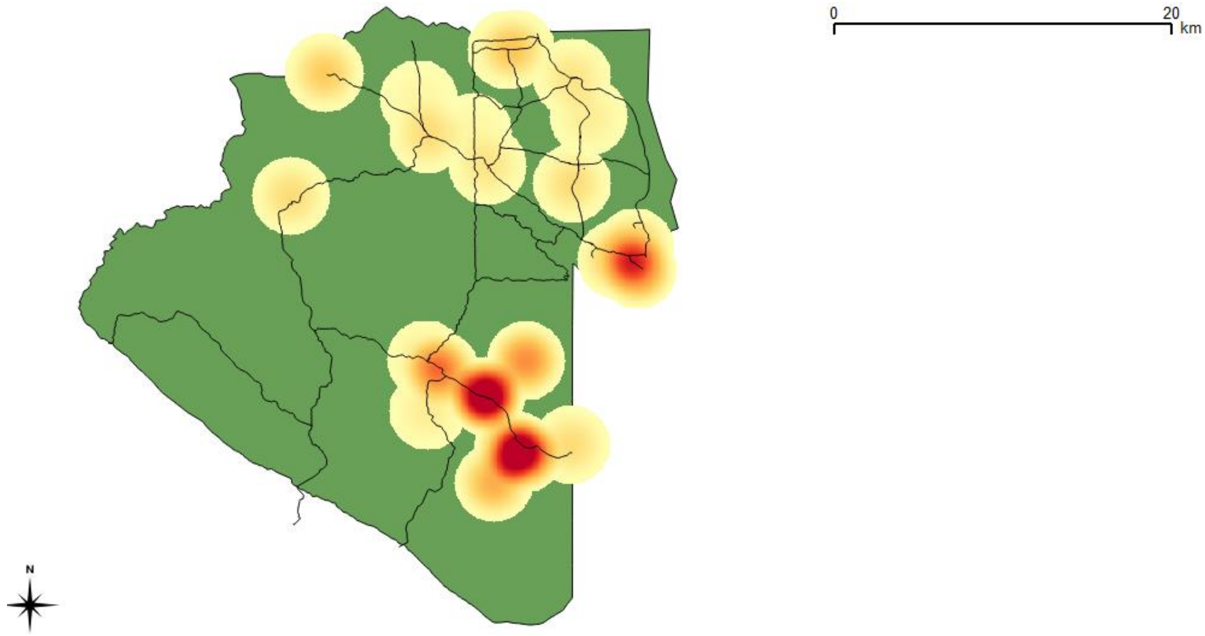

Figure 5 Pende spotted hyena activity based on capture rate from camera stations. Red represents camera stations of high activity, orange stations with medium activity and yellow stations with low activity.

It also seems that some individuals utilised areas outside of the reserve's boundary fence based on images of hyena patrolling the fence line (Appendix 2, Figure 6) and was confirmed by the presence of livestock hair in some scat samples (n=2, see chapter four). However, only males were found to patrol the fence and were probably responsible for any possible livestock loss.

Pwadzi home range

The Pwadzi clan (see chapter two) was found in the higher lying miombo woodland in the west of the reserve. The Pwadzi clan's estimated home range was approximately 248 km^2 (Table 1).

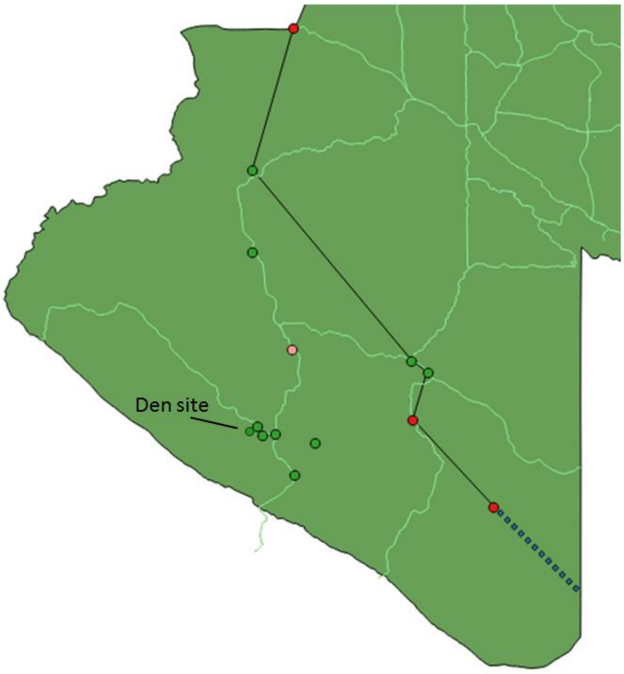

Figure 6. Pwadzi spotted hyena territory with fixes representing camera stations. Green fixes represent stations where both sexes were captured, red where only males were captured and pink where only females were captured.

There was no discernible divergence in home range utilisation between sexes within the Pwadzi territory. Only one communal den site was found in the Pwadzi territory (Figure 6) by an anti-poaching patrol unit. The den was situated next to a small non-perennial river in a termite mound and had two entrances (15.9908 S 34.5590 E, Appendix 2, Figure 7).

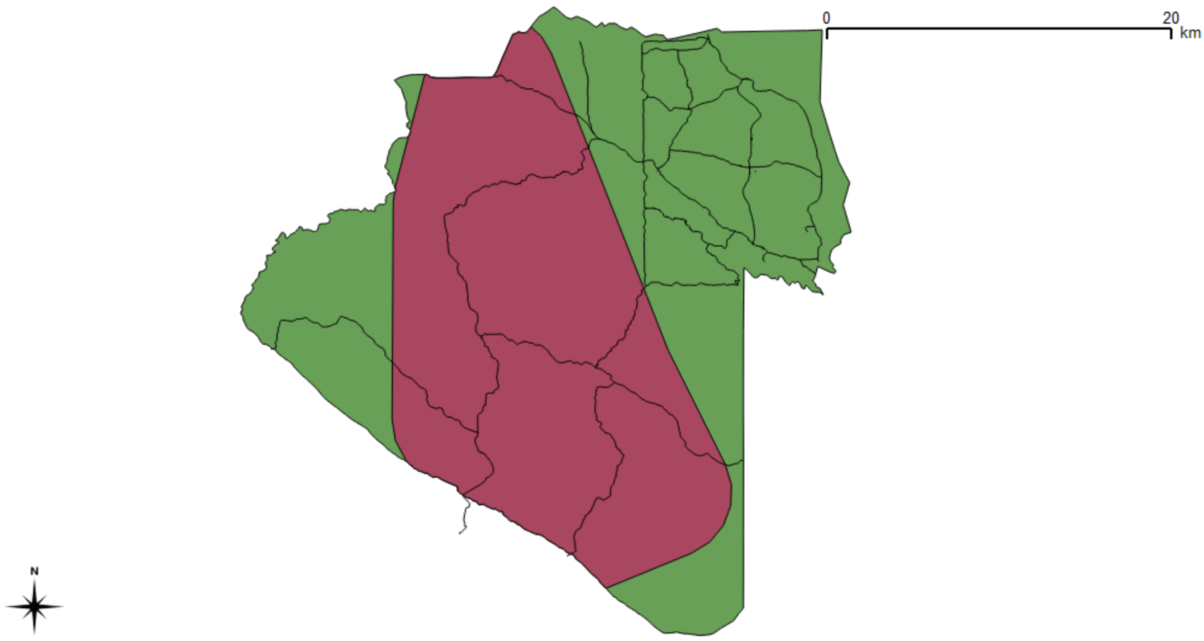

Figure 7. Pwadzi male home range with buffer width.

As in the Pende clan, males had larger home ranges than females in the Pwadzi clan (Table 1, Figures 7 & 8). Pwadzi male home range extended further north and further east than the Pwadzi females' home range (Figure 7 & 8).

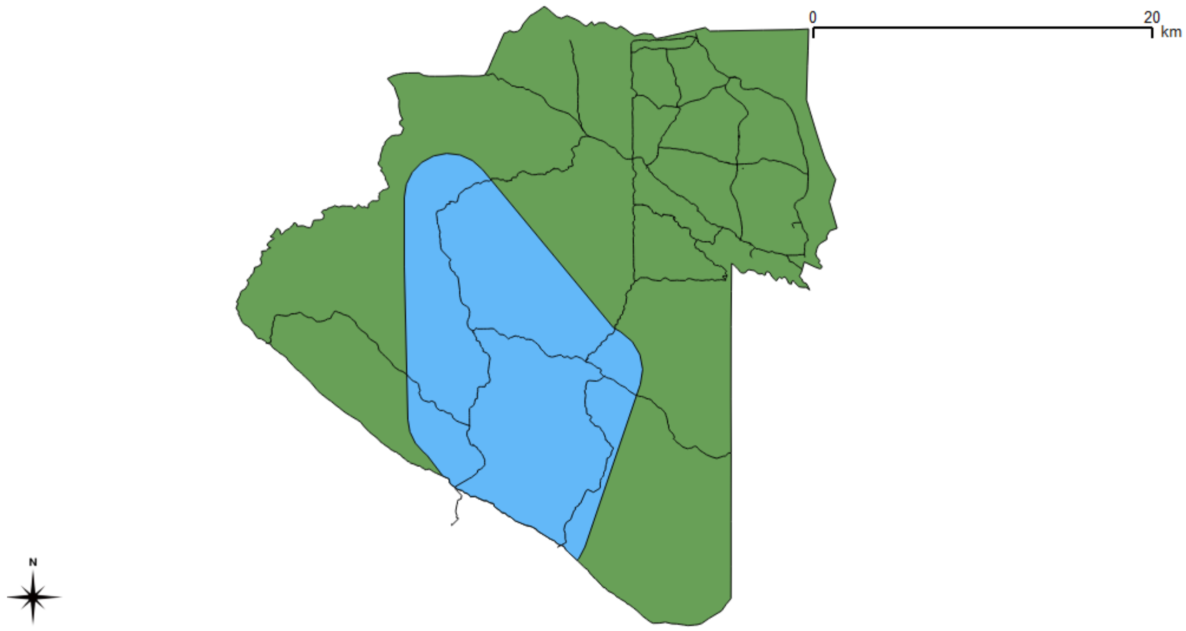

Figure 8. Pwadzi female home range with buffer width.

The southern region of the Pwadzi territory seemed to be preferred (Figure 9), it contained the only known sources of permanent water in the territory, the Pwadzi waterhole and spring (Figure 1). The only other known source of permanent water was the Pende 2 waterhole (Figure 1) which formed the boundary between the two clans. It appears this waterhole was largely dominated by the Pende clan as 86% of all hyena images taken were from the Pende clan, compared with only 14% from the Pwadzi clan.

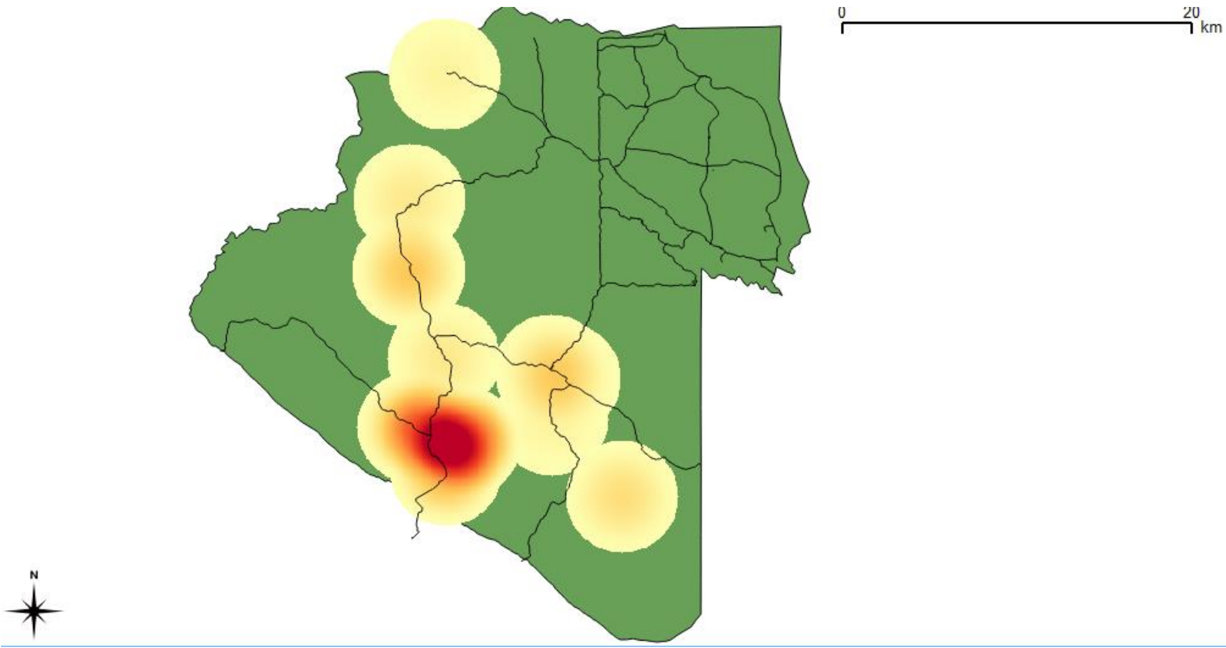

Figure 9. Pwadzi territory of areas with high spotted hyena activity (red) based on capture rate from camera stations.

Lion home range

Lions mostly used the north of the Pende hyena territory in the old sanctuary with occasional visits to the south, as far as the Pwadzi hyena territory (Figure10).

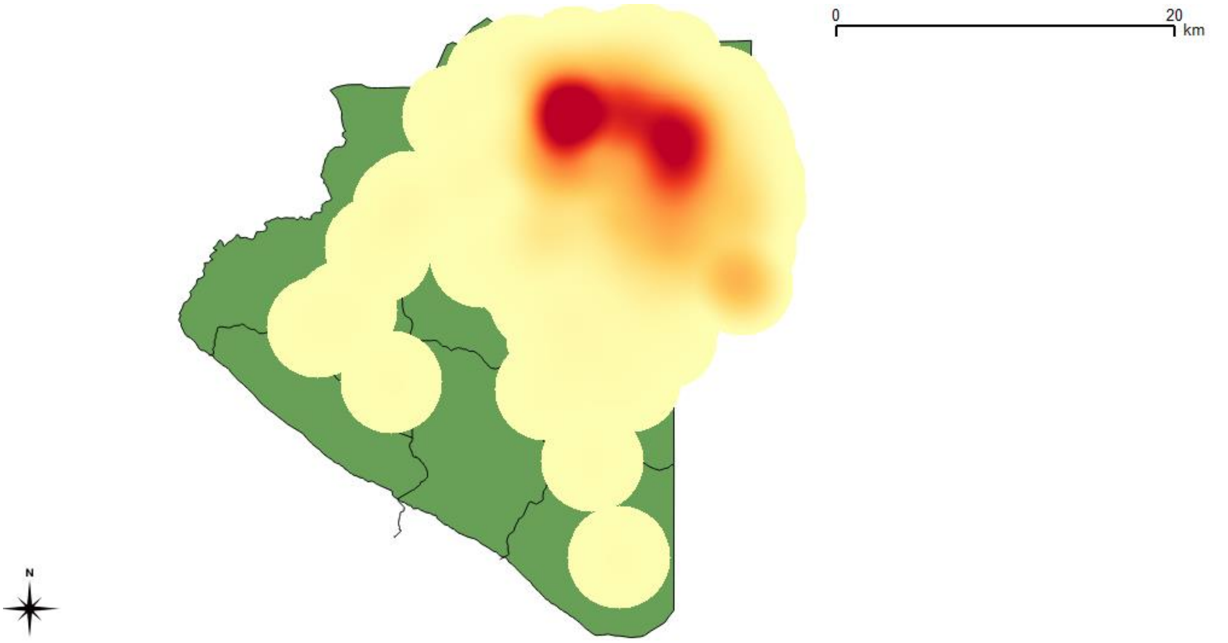

Figure 10. Lion activity based on fixes from collar data. Red representing areas of high lion use, orange areas with some lion use and yellow areas with little lion use.

Spotted hyena home range size estimates vary among protected areas but are generally smaller in savannah habitat in east and south-east Africa than in the three arid regions (Namib, Kagalagadi and Etosha) (Table 3).

Table 3. Average spotted hyena estimated home range size in different protected areas across Africa

Location	Home range (km^2)	Reference
Namib desert, Namibia	570	(Tilson and Henschel 1986)
Aberdare NP, Kenya	32	(Sillero-Zubiri and Gotelli1992)
Masai Mara NP, Kenya	60	(Cooper et al. 1999)
Etosha NP, Namibia	360	(Gasaway et al. 1989)
Hluhluwe GR, South Africa	13	(Holekamp and Dloniak 2006)
Ngorogoro Crater CA, Tanzania	23.8	(Honer et al. 2005)
Kgalagadi Transfrontier Park, South Africa	1095	(Mills 1990)
Kruger NP, South Africa	130	(Holekamp and Dloniak 2006)
Timbavati GR, South Africa	25	(Holekamp and Dloniak 2006)
Chobe NP, Botswana	101	(Holekamp and Dloniak 2006)

Discussion

MWR hyena home ranges

The home range size of spotted hyena in MWR is comparable with that of spotted hyena in the arid Etosha National Park, Namibia (Gasaway et al. 1989). Spotted hyena home ranges are reported to be larger in areas with a clumped resource distribution, such as in arid areas (Tilson and Henschel 1986). The large home ranges of spotted hyena in MWR combined with a low density of hyena (see chapter two) is typical of animals inhabiting an area with clumped resource distribution (Tilson and Henschel 1986).

The home range of an animal is associated with the spatial distribution of limiting resources, needed for basic survival, the prime factor determining home range use (Mitchell and Powell 2004). Clumped resource distribution also affects competition, as the number of competitors increase as resources become increasingly clumped (Jacobson et al 2015). Over decades, high levels of poaching has has been responsible for declines in ungulate prey species across Africa (Breuer 2005, Lwanga 2006), making them a clumped resource (Lwanga 2006). Consequently, this could have created high levels of competition for these resources between spotted hyena clans, forcing low ranked individuals, such as males, to forage over long distances to avoid feeding competition with females thereby increasing male home ranges. As males in a clan are all ranked below females (Holekamp et al. 2012). This would explain the larger male home ranges in MWR.

Difference in home range usage between sexes

A possible reason why females rarely visit the north of the Pende territory is because of the females tendency to limit the distance they move from the communal den site (Boydston et al. 2001). The mean one way distance to camera stations in the north of the Pende territory, which was not visited by females, is 17.3km which is too far for a female with dependant, den dwelling cubs to travel. Their foraging round trips are generally limited to 20km per night, the maximum hyena foraging distance (Carnaby 2008). Males do not care for cubs and do not have to return to the communal den every night, this allows them to range three to four times further from a clan's territory centre than females can (Boydston et al. 2001) while benefitting from reduced resource competition with females. The reason why the area around the Heritage waterhole seems to be the only area in the old sanctuary used by females is possibly a combination of its distance from the territory centre and its close proximity to the reserve's boundary which might be patrolled on a regular basis assuming that the reserve and clan have the same boundary. Females conduct border patrols more regularly than males (Holekamp et al. 1997) and the Heritage waterhole might provide a hunting opportunity for females whilst on patrol. The low capture rate of females at other waterholes in the old sancuary, such as Nakamba and Nsepete, is possibly because there is an increased chance of lion encounters. These waterholes are far from the clan's territory centre and are not close to the territory border and thus do not need to be patrolled.

Denning locations

The north of the Pende territory is abundant in prey and water, especially in the old sancuary area, making it a suitable area for denning, although denning was not known to occur there. The only limiting factor in the north of the Pende territory was the presence of lions. Lions, pose the greatest threat to spotted hyena in protected areas (Holekamp et al. 2012), and are the reason why denning seems to be limited towards the south of the reserve. Avoidance behaviour between spotted hyena and lions has been documented in Addo Elephant National Park, South Africa, where both predators are found in low density (Hayward and Hayward 2006) as in

MWR. Future plans to reintroduce another pride of lions into the south of the Pende hyena territory may affect their choice of denning location and home range use and needs to be carefully considered given their possible effect on spotted hyena distribution.

Based on the communal dens found, the Pende clan located the centre of their territory close to the boundary of the reserve rather than in the centre of the territory, which may be understandable given spotted hyena behaviour (Boydston et al. 2001). The selection of their territory centre may be a combination of lion avoidance behaviour, the hunting opportunities provided by the southern waterholes and existence of suitable denning locations. All the dens found were either along river beds or in low lying flood plains. Creating communal dens, created by both warthogs, *Phacochoerus africanus*, and aardvark, *Orycteropus afer*, and then taken over by hyena (Kingdon 1989), from the moist soil of low lying areas should be easier to do than in the dry, compact soils of higher lying areas. Hence, the current Pende clan territory appears to be the optimal area for avoiding lions, for access to hunting grounds and for suitable denning areas.

Pende home range vs Pwadzi home range

Spotted hyena home range size has a linear relationship with clan population size and is the probable reason why the Pwadzi clan home range was smaller than the Pende clan home range (Honer et al. 2005) (see chapter two). Limited presence of lions suggests lion avoidance is not a factor governing home range use of the Pwadzi clan, otherwise their home range use appears similar to that described for the Pende clan. The general trend in both clans that female spotted hyena have smaller home ranges than males makes it seem that males forage at greater distances in MWR, possibly to avoid feeding competition with females, which has been recognized in other spotted hyena populations (Holekamp et al. 2012).

Effect of waterholes

Spotted hyena has been reported to be a water independent species (Hayward and Hayward 2012) but in MWR both clans focused their movement within areas of permanent sources of water away from the Shire River. The possible clumped distribution of prey may put more importance on waterholes which attracts prey species during dry seasons (Valeix et al. 2009) and seems to have had influences on denning locations and the centre of hyena territories. Future management decisions about waterhole distribution will need to consider the effect that it has on prey distribution and ultimately spotted hyena home range use.

Conclusion

Management at MWR should carefully consider the influence which future waterholes may have on the spotted hyena distribution and ultimately prey species. The large spotted hyena home ranges may be indicative of an area with a very low prey density. Further reintroductions of lions may have a negative impact on the spotted hyena population due to an increased inter-specific competition in an already intra-specific competitive environment.

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Chapter 4: Diet of Spotted hyena, *Crocuta crocuta,* in Majete Wildlife Reserve, Malawi

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Abstract

This research represents the first attempt to determine the diet of spotted hyena, *Crocuta crocuta,* in the Majete Wildlife Reserve (MWR), Malawi. Diet was determined from analysing scats collected over 13 months between 2014 and 2015. Jacobs Indices were used to establish hyena dietary preference by using prey abundance data from distance sampling and corrected frequency of occurrence (CFO) from scat analyses. Based on biomass consumed, the largest contributors to the spotted hyena diet were Boehm's zebra, *Equuz boehmi* (191.4kg, 24.2%), waterbuck, *Kobus ellipsiprymnus* (157.9kg, 20%), kudu, *Tragelaphus strepsiceros* (78.5kg, 9.9%) and sable antelope, *Hippotragus niger* (73.2kg, 9.3%). The preferred prey items were common duiker, *Sylvicapra grimmia* (0.82); bushbuck, *Tragelaphus Sciptus* (0.74), Boehm's zebra (0.72) and reedbuck, *Redunca arundinum* (0.73). Despite impala, *Aepyceros melampus*, and warthog, *Phacochoerus africanus,* being the two most common species, comprising 24% of potential prey biomass, neither was selected for as prey (<-0.5). High population densities and low predation rates of these species may be contributing to the structure of Majete's vegetation composition.

Introduction

Importance of carnivore diet

Understanding the diet of a species is an important aspect of ecology, it provides insight into its ecological niche, thereby assisting in ecosystem management and conservation (Shehzad et al. 2012; Sih and Christensen 2001). Carnivores are recognised as playing an important part in the shaping of trophic levels. Considered a "top-down" view (Hairston et al. 1960), apex predators feeding on secondary consumers, thus in turn impacts primary consumers (Watts & Holekamp 2009). Behavioural responses of prey towards predators have been documented to effect entire ecosystems as with the wolf, *Canis lupus,* re-introductions in Yellowstone National Park (Ripple & Beschta 2004). As such, habitat and species composition may be significantly impacted by loss or gain of predators, and the dietary preferences of those predators (Terborgh and Estes 2010).

Therefore the loss of predators through extirpation can significantly impact ecosystem functioning (O'Connor and Bruno 2009) through the shortening of food chains which alters the intensity of herbivory and, consequently, the vegetation composition of an ecosystem, a process called trophic downgrading (Estes et al. 2011). The impacts of trophic downgrading act synergistically with anthropogenic influences, such as pollution and habitat destruction, to alter ecosystem function. Trophic downgrading incorporates the idea that all organisms are part of an interactive web and hence one species can influence numerous others (Estes et al. 2011).

An understanding of predator diet is an important component of competition and niche utilisation studies (Hayward and Kerley 2008), and can be used to quantify both an area’s predator and prey carrying capacity (Hayward et al. 2007). Recent reintroductions of leopard, *Panthera pardus*, and lion, *Panthera leo*, have led to increased competition among large predator populations in MWR. This study hopes to enable informed management decisions concerning them and their future monitoring in MWR. However, it is difficult to determine diet of nocturnal predators in areas with dense vegetation, such as MWR, other than through non-invasive means such as DNA, macro and microscopic faecal analysis. Here, prey species were identified through remains such as bone fragments and undigested hair.

Factors influencing prey selection

Predator diet can be explained by the “modal mass concept” (Shehzad et al. 2012) and “optimal foraging theory” (Sih and Christensen 2001). According to the modal mass concept, predators hunt the largest prey item possible based on them receiving the biggest net energy gain relative to the energy expended immobilizing the prey, provided that the prey can be safely killed (Shehzad et al. 2012). The optimal foraging theory suggests the value of predator’s prey is represented by the energy yield per unit handling time relative to the abundance of valuable prey species. A quantitative threshold occurs at which predators decide whether to include or exclude certain species for an optimal diet (Sih and Christensen 2001). Variation in prey reproductive cycles, behaviour and seasonality alter predator hunting success and prey selection (Owen-Smith 2008). For example, during fawning season, juveniles constitute easy prey, while certain adult male ungulates may be at greater risk to predation during the rut or mating season, when constantly distracted in contests with other males. Females run a greater risk of being preyed on during the terminal stages of their gestation period, when weighed down by an almost fully developed foetus and again immediately after giving birth (Owen-Smith 2008). Kills made in the late dry season can be indicative of nutritional shortcomings in ungulate species which make them easy prey items (Owen-Smith 2008). Prey availability and distribution are also known to influence prey selection (Breuer 2005).

Spotted hyena diet

The spotted hyena, *Crocuta crocuta*, is the only large African carnivore truly adaptable in both foraging and diet. Unlike lion and leopard which are primarily hunters, spotted hyena are able to hunt and scavenge (Apps 1992). Furthermore spotted hyena, like leopards, have a varied diet (Schubert et al. 2010; Hayward et al. 2006) which may relate to prey availability and ranges from termites to elephants, *Loxodonta Africana*, and may even include garbage and dung (Yirga et al. 2012). Hyenas tend to hunt medium to large ungulates (Holekamp et al. 1997), their preferred prey weight ranges from 56-182kg (Carnaby 2008). Spotted hyena hunting strategies are organised and hunting party size may be prey species specific (Holekamp et al. 1997).

Depredation of livestock by hyena results in human-wildlife conflict and often leads to retaliatory killings by farmers (Holmern et al. 2007). A study of livestock depredation in villages surrounding Serengeti National Park, Tanzania, showed that spotted hyena was responsible for 98% of livestock kills (Holmern et al. 2007) hence their opportunistic behaviour resulting in conflict with humans. Humans are the second biggest threat, after lions in protected areas, to an adult hyena (Watts and Holekamp 2009). The human threat can be ascribed to habitat loss, because hyenas need large home ranges, which may bring them into contact with farmland resulting in human-hyena conflict (Graham et al. 2004).

Spotted hyena are the dominant large predator of MWR, and therefore their impact on prey populations would expected to be greater than that of other large predators present. The aims of this study were to:

1. Determine the diet and prey preferences of hyena;
2. Quantify relative species biomass for prey consumed by hyena.

Materials and methods

Scat collection

85 Hyena scats were collected both opportunistically and whilst conducting vehicle and walking transects in Majete Wildlife Reserve (MWR), Malawi, between April 2014 - May 2015 (see chapter one for study area). Approximately 2700km were driven using a closed

vehicle and 335km were walked. Driving transects were conducted on designated roads within the reserve totalling approximately 97km, which were driven every four weeks. Walking transects consisted of eight routes between 10- and 12km long which were demarcated using a hand-held GPS and walked on a rotational basis with each of the eight routes being walked over an eight week period. Collected scats were placed in brown paper envelopes then marked with the date and GPS-location and then air dried and stored in a cool dry place until analysed.

Most scats were collected at latrine sites. As such, not all samples at a latrine site were collected in order for a latrine site to fulfil its territorial purpose as latrine sites are used by hyena as territorial markers (Apps 1992). Hyena faeces could be distinguished from those of lion and leopard as they differed in shape and colour. Hyena faeces were ball- or clump-shaped and yellow-green in colour when fresh and always white when dry due to the high calcium concentration, while leopard and lion scats are sausage shaped and do not necessarily turn white when old (Carnaby 2008). Scats collected in latrine sites were chosen that were similar in colour to ensure they were of similar age, to be able to see whether individuals may have fed on the same prey item.

Faecal analysis

Scats were first macerated and soaked in methylene spirits for 24hrs to kill any parasites. Separated faecal material were placed in a wire sieve and hand washed until only undigested hair and bone matter remained which was then dried. Where macroscopic identification, using hair colour or antelope hooves was not possible, hairs were examined under a microscope to identify prey to species level (Trites and Joy 2005). Cross-sections of hairs were prepared by sucking hair with warm wax into a plastic pipette (Trites and Joy 2005). After the wax cooled and set, was the pipette cut into cross-sections. Cross-sections from individual scat samples were placed on separate microscope slides with wax. Identification was based on the hair cross-section which is unique to every species (Keogh 1983). Hairs were microscopically compared to a reference hair sample (Breuer 2005) collected from Buck ‘n Bass taxidermy, Cape Town. Prey species were identified based on the cortex, medulla colour, thickness and shape of the undigested hair (Keogh 1983).

Distance sampling

Distance sampling of potential prey species was conducted during the dry season of 2013 and 2014 (June – December) when visibility was reported to be the best (Giadet-Drapier et al.

2006). Distance sampling and scat collection was carried out simultaneously on the same transects both on foot and by vehicle. Observations during distance sampling recorded species identification and herd composition (number, age/size class and sex) of all mammals. These data were used to calculate the relative abundance of each prey species by calculating the total number of animals observed for each species and dividing this by the total number of animals observed.

Data analysis

Frequency of occurrence (FO), where prey species identified are compared as a percentage of the total number of scat that contained a certain prey species were used (Trites and Joy 2005). Large prey were most likely hunted by hyena groups (Holekamp et al. 1997) and therefore an over estimate of FO was possible if more than one scat contained undigested remains from the same kill. To prevent this, scats that were collected no more than three days apart, from the same or neighbouring latrines which contained the same prey species were counted as a single scat sample.

Jacobs' indices were used to determine hyena prey preference by combining hair frequency data with prey abundance data (Mann 2014). To obtain an absolute preference value for each hyena prey species, Jacobs preference index were used by combining hair frequency data with prey abundance data (Jacobs 1974) calculated as:

$$D = (r - p)/\{(r + p) - (2rp)\}$$

D ranges between +1 for maximum preference and -1 for maximum avoidance and *r* is the rate of utilisation of a species by spotted hyena and *p* equals the proportion of abundance of a species. Rather than using FO as *r,* the corrected frequency of occurrence (CFO) was used (Mann 2014). This prevented over estimation of small prey species that may have occurred with other species in the scat sample (Mann 2014). A weighting was given for each prey species per scat sample depending on the number of species identified in a single scat. Prey species that were found alone in samples were given a weight of 1, otherwise weighting was given by dividing one with the number of species found in a scat sample. For example: scats containing two and three species would carry weightings of 0.5 and 0.33 for each species respectively. Six records of spotted hyena hunts were recorded during the study period from July 2013 - May 2015. This included camera trap photos and actual observations of hyena kills. These records were added to the data with species recorded given a CFO weighting of 1. The proportion of a species' CFO required to calculate a Jacobs index value which was obtained by dividing the total of scats and hunting records (n=91) by the specie's CFO score (Mann 2014). Finally Mann-Whitney U tests were used to test whether some prey species were significant more abundant than others in an online program called socscistatistics (http://www.socscistatistics.com/tests/mannwhitney/).

Consumed biomass

The biomass of each species consumed was calculated to more accurately determine the dietary preference of spotted hyena. Ackerman (1984) developed a linear model for biomass consumed by cougars, *Puma concolor* (Ackerman et al. 1984), that has been applied to other species including snow leopards, *Uncia uncia* (Lyngdoh et al. 2014), leopards (Mann 2014) and tigers, *Panthera tigris* (Manoj et al. 2015). Using this relationship, the average biomass of each prey species consumed per unit scat was calculated from the linear function:

$$y = 1.98 + 0.035x$$

Where y equals the biomass consumed of a prey species per scat and x is the average weight of a prey species (Ackerman, et al. 1984). Total prey biomass consumed per prey item was then calculated by multiplying the number of scats containing a prey item with the average biomass consumed of each prey species per scat (Lyngdoh et al. 2014). For large prey species the average adult weight was multiplied by 0.7 when preying on sub-adults and 0.3 for juveniles (Mann 2014), however, large prey were rarely taken. It was assumed, based on the literature, that spotted hyena would most likely prey on juvenile Cape buffalo, *Syncherus caffer* and both juvenile and sub-adult Boehm's zebra, *Equus boehmi* and eland *Taurotragus oryx* (Skinner and Chimimba 2005). With other large prey species such as adult kudu, a recorded prey species of spotted hyena in MWR, the average adult weight was used in each case for calculating the Ackerman et al. (1984) linear equation.

A volumetric estimate of scat content was not calculated because spotted hyena are able to regurgitate large amounts of skin and other parts of ingested prey and would therefore have little value (Di Silvestre et al. 2000). The results therefore only show a frequency of occurrence of prey species within a scat with the relative amount of biomass consumed by spotted hyena per species with their respective preference or avoidance indices. Hyena diet statistics published in the literature were used as a comparison to my study (Table 4).

Results

A total of 17 prey species were identified in scats or from documented kills, of which Boehm's zebra (20.6%), waterbuck, *Kobus ellipsiprymnus* (14.3%) and common duiker, *Sylvicapra grimmia* (7.9%), were the most prevalent (Table 1). The total prey biomass consumed over the survey period was 790.7kg. The most important prey species based on biomass derived from scats were Boehm's zebra (191.4kg, 24.2%), waterbuck (157.9kg, 20%), kudu, *Tragelaphus strepsiceros* (78.5kg, 9.9% and sable antelope, *Hippotragus niger* (73.2kg, 9.3%).

Table 4. Prey items found in spotted hyena scat (n=85) and documented kills (n=6) by spotted hyena. The weight given for each species was the average adult weight, except for zebra, buffalo, eland and python which was proportional to the assumed age class hunted. Occurrence in scat was the number of times a species was found to be in hyena scat. The number of documented kills were confirmed kills by spotted hyena on prey species based on camera traps and sightings. The number of individuals killed based on scat collection, is the number of individuals killed per species based on the date and location of scat collected, where several scats might have originated from the same kill. Frequency of occurrence (FO) was the percentage of the number of times a species occurred in scat proportional to the total number of prey items found. The corrected frequency of occurrence was the percentage of occurrence for a species in scat after a corrected weight was given that took into account the number of species occurring in a scat. Corrected prey biomass was the percentage that was consumed of a species after calculating the amount with the equation developed by Ackerman et al. (1984).

Species	Weight (Kg)	Occurrence in scat	Number of documented kills by hyena	Number of individuals killed based on scat collection	FO (%)	CFO (%)	Consumed prey biomass (%)
Boehm's Zebra	153.8	26	0	18	20.6	19.3	24.2
Waterbuck	208.8	17	1	15	14.3	12.6	20
C-Duiker	16.1	9	1	8	7.9	7.4	3.2
Bushbuck	49.5	9	0	8	7.1	5.8	4.2
Cape buffalo	165.5	8	0	8	6.3	7.1	7.9
Sable	205	8	0	7	6.3	7.4	9.3
Kudu	192.6	8	1	8	7.1	8.9	9.9
Nyala	61.8	7	2	9	7.1	9.9	4.7
Impala	47.7	6	0	4	4.8	3.8	2.8
Warthog	68.1	5	1	4	4.8	4.0	3.3

Reedbuck	45	4	1	4	4	6.1	2.2
Bushpig	70.1	4	0	4	3.2	2.5	2.2
Aardvark	45	3	0	3	2.4	3.7	1.3
African rock python	34.7	3	0	2	2.4	1.5	1.2
Goat	40	2	0	2	1.6	1.5	0.9
Eland	238.8	1	0	1	0.9	0.7	1.3
Porcupine	12.2	1	0	1	0.8	0.5	0.3
Hartebeest	171.7	1	0	1	0.8	0.4	1

The preferred prey species according to the Jacobs' Index was common duiker (0.83) [Appendix 2, Figure 19], bushbuck (0.75), reedbuck (0.73) and Boehm's zebra (0.72) which were all strongly preferred (>0.5) (Figure 1). Species such as Cape buffalo, kudu, nyala, sable, eland and hartebeest were preyed upon in similar proportion to their relative abundance (Table 3). The three most abundant species of prey, namely impala, waterbuck and warthog were all consumed less than in proportion to their relative abundance, especially impala (-0.88) and warthog (-0.69) which were strongly avoided (<-0.5) (Figure 1).

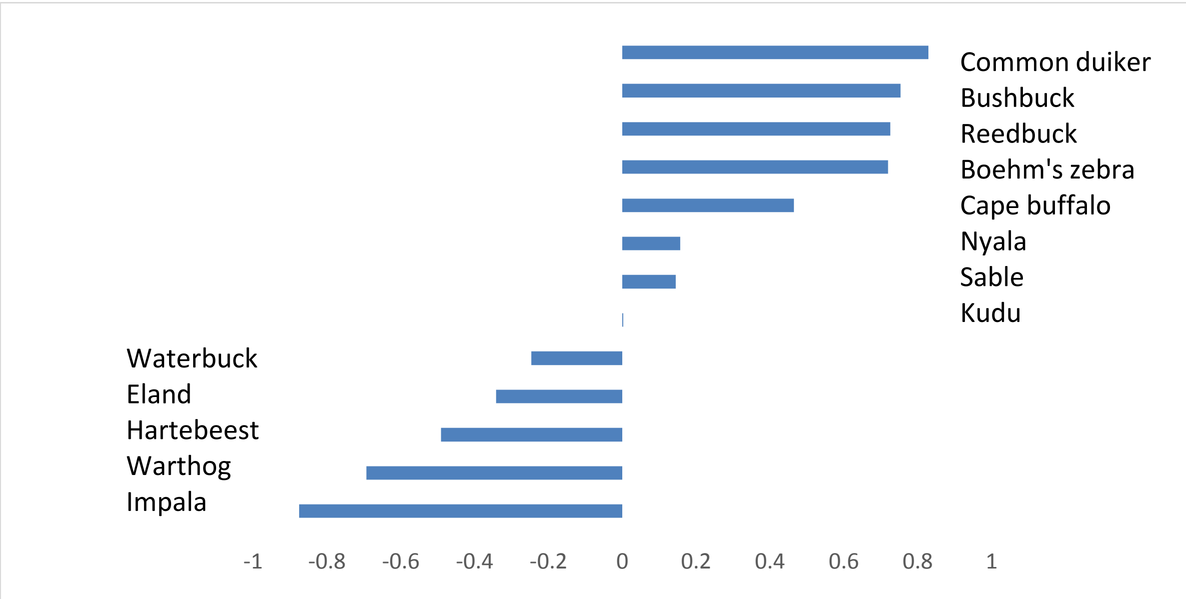

Figure 1. Jacobs index scores for prey species on the CFO and each species' relative abundance. Warthog and impala scored less than –0.5, indicating that spotted hyena avoided feeding on them.

Most scat was collected during the dry season (81%) compared to the wet season (19%) (Table 2).

Table 5. Number of scat samples collected per month during April 2014-May 2015.

Month	Number of Samples
April	8
May	6
June	1
July	13
August	27
September	8
October	6
November	9
December	7
Total	**85**

The species accumulation was identified from scat samples collected. The accumulation curve started to reach an asymptote at approximately 20 scats collected (Figure 2). Observed kills were not included in the species accumulation curve because some observations occurred prior to the onset of scat collection.

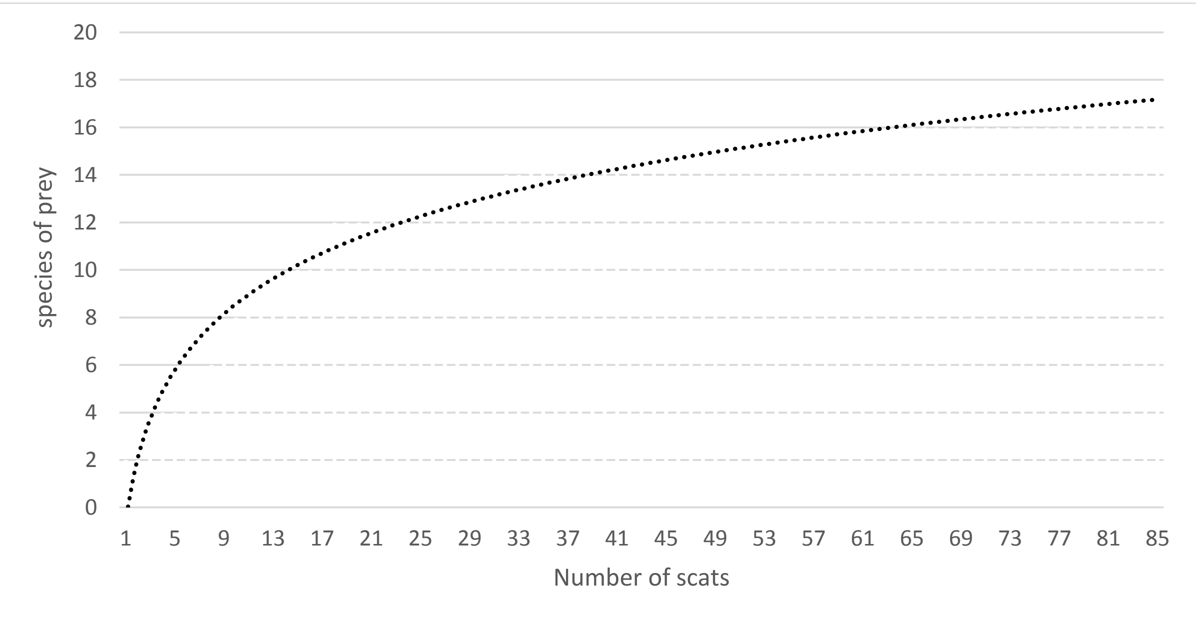

Figure 2. Species accumulation curve for the number of species identified to the number of scats collected.

Impala was the most common species of prey in MWR. They were significantly more common than waterbuck ($p=0.0164$, second most common) and warthog ($p=0.0005$, third most common). The difference in abundance between waterbuck and warthog was not significant ($p=0.267$) and therefore it was assumed that spotted hyena had an equal chance of locating the two prey species. Similarly, the abundance of nyala and sable antelope did not differ ($p=0.28$) (Table 3).

Table 6. Relative abundance (RA) of species expressed as a percentage of total number of animals counted during distance sampling. Relative biomass of prey species was calculated by multiplying the average weight of species by the RA. Jacob's Indexes which were calculated based on the CFO which was comparable to Jacob's Index values obtained by Hayward et al. (2007) who created values based on 15 different spotted hyena diet studies.

Species	Weight	RA(%)	Biomass (Kg)	Jacob's Index MWR	Hayward et al. (2007) Jacob's Index
Impala	50	36.6	1830	-0.89	-0.09
Waterbuck	210	18.6	3897	-0.25	-0.02
Warthog	70	18.1	1264	-0.69	-0.20
Nyala	60	7.2	432	0.16	-0.33
Sable	205	5.4	1106	0.14	-1
Bohm's Zebra	310	3.6	1122	0.72	-0.44
Kudu	190	2.8	526	0.002	0.11
Cape buffalo	550	2.6	1412	0.46	-0.39
Eland	480	1.5	699	-0.34	-0.34
Hartebeest	170	1.3	213	-0.49	-0.36
Reedbuck	45	1	45	0.73	-0.52
Bushbuck	50	0.8	42	0.75	0.10
Common duiker	16	0.7	11	0.83	-0.45

The published literature confirms that across Africa, the prey species of spotted hyenas varies (Table 4), with their diet in some areas being similar to that in MWR, but very different in others.

Table 7. The most commonly preyed on species by spotted hyena in various localities across Africa. All studies used FO to analyse data.

Location	Species	Reference
Niokolo Koba National Park, Senegal	buffalo, hartebeest, warthog	(Di Silvestre et al. 2000)
Faro National Park, Cameroon	kob	(Breuer 2005)
Ngorogoro Crater, Tanzania	blue wildebeest, Plains zebra	(Kruuk 1972)
Moremi Game Reserve, Botswana	zebra, warthog, impala	(Cooper 1990)
Harrar city, Ethiopia	garbage, donkeys	(Yirga et al. 2011)
Kgalgadi Transfrontier Park, South Africa	gemsbok	(Mills 1990)
Mkuzi Game Reserve, South Africa	impala, nyala	(Skinner et al. 1992)
Umfolozi, South Africa	impala, nyala	(Skinner et al. 1992)
Namib Naukluft National Park, Namibia	gemsbok	(Skinner et al. 1992)
Kruger National Park, South Africa	impala, warthog, kudu	(Henschel and Skinner 1990)
Masia Mara National Park, Kenya	wildebeest, zebra, topi	(Cooper et al. 1999)
Aberdare National Park, Kenya	bushbuck, suni, buffalo	(Sillero-Zubiri and Gottelli 1992)

Discussion

MWR spotted hyena diet compared to other areas

Jacobs Index values for spotted hyena prey species at MWR, derived from scat analyses and recorded hunts, were comparable to those recorded by Hayward et al. (2007) for some species. In both studies, index values were similar for eland, hartebeest, kudu and waterbuck. Yet, species such as buffalo, reedbuck, common duiker, nyala, *Tragelaphus angasii*, sable and Boehm's zebra were selected for in this study, more so than they were in the study by Hayward et al. (2007). Sable in the study by Hayward et al. (2007) had a Jacob's index value of -1, which indicates total avoidance. It was not possible to distinguish between hunted and scavenged prey of spotted hyena in MWR. Sable may have been selected for in this study because of scavenged sable carcasses by spotted hyena from sable kills by lions.

Waterbuck are common throughout MWR, and are within the preferred weight range of spotted hyena, making it an ideal prey species for them. Conversely, zebra, as with giraffe, *Giraffa* *camelopardus*, and buffalo, are known to be species that are avoided by spotted hyena (Hayward 2006). Zebra, however, have been found to be an important prey species for spotted hyena in other areas (Di Silvestre, et al. 2000). Zebra were also one of the most commonly preyed on species in the Serengeti National Park, Tanzania (Grange, et al. 2004) and in Moremi Game Reserve in Botswana, where zebra foals made up 80% of spotted hyena diet during the wet season (Cooper 1990). Another area where hyenas appear to have a similar diet to that in MWR are in Aberdare National Park, Kenya (Sillero-Zubiri and Gottelli 1992)

Possible reasons for choice of prey in MWR

Spotted hyena normally feed on the most commonly available prey species within their preferred weight range of 56 – 182kg (Hayward 2006) although they do prey on species outside this range (Carnaby 2008). When preying on ungulates, spotted hyena's diet choice is related to prey availability, size and abundance and common species are usually preferred over rare species (Breuer 2005). However, prey species vulnerability is not normally considered when assessing large predator diet, like that of spotted hyena. In Niokolo-Koba National Park, Senegal, it was found that rather than preying on common species as is reported (Breuer 2005) they preyed on hartebeest, a less common species. Perhaps because the intensive poaching of this species provided dead and wounded animals making them vulnerable to scavenging and predation (Di Silvestre et al. 2000).

Although zebra historically occurred in MWR (Morris 2006) its vegetation is much denser than areas like the Serengeti, where large herds of zebra roam. When under attack zebras congregate as a herd with mares and foals in the front and the stallions at the rear (Apps 1992). A potential advantage of a zebra's stripes is that individuals can easily locate each other and this facilitates congregating, especially at night when attacks are most probable (Apps 1992). The dense foliage of MWR may not favour the "herd strategy" where individuals are easily separated as vegetation constantly needs to be avoided during the confusion of a predator attack. Once separated, a single zebra may make an easy target as the stripes provide little camouflage for an individual and as the potential advantage of having stripes may now work against it. There have been similar findings in the Kruger National Park, South Africa, where zebra numbers are far lower compared to the more open Serengeti (Skinner and Chimimba 2005). Zebra are also highly dependent on water and are rarely found more than 8km away from it (Apps 1992) which may also make them vulnerable to predators. The spotted hyenas of MWR focus their hunting efforts around the three man-made waterholes in the south of the reserve (see chapter three) which are approximately 3.2km away from one another and are the only sources of permanent water in the area. Thus, zebra are likely to be within or near this small area in which the hunting effort is focused. The dense foliage and zebra's dependency on water, could be important factors as to why hyenas select them as prey in MWR.

Three of the four strongly preferred prey species at MWR fall outside the preferred weight range of spotted hyena (Hayward 2006). Interestingly, all three species-, namely the common duiker, bushbuck and reedbuck, were not part of the reintroduction programme as they occurred naturally in the area, albeit in low numbers, initially. A reason why these species are so strongly preferred at MWR could date back a decade when these three species were probably the most dominant ungulate species in the reserve, as kudu still occurred at the time but at very low numbers. Hyenas may have developed a taste for, and the skill to, hunt these small antelope and continue to do so. Predation on the common duiker may be elevated because it remains active until late at night (Apps 1992) when spotted hyena are most active (Kolowski et al. 2007). Duiker may appear less common than suggested by distance sampling because sampling took place in the morning, when duiker were less active (Apps 1992) and therefore less detectable. Hence, although it appears that hyena are preying on a species of low abundance, this may be a function of the sampling method and the species may be less selected for than suggested by Jacob's Index.

Hyena scat samples contained little impala hairs despite impala being the most common potential prey species at MWR (Table 3), indicating that this species is strongly avoided by hyena. This is contrary to several other reserves where impala are a main prey species of hyena (Cooper 1990, Skinner et al. 1992). Hyenas' avoidance of impala at MWR may be related to impalas' predator avoidance strategies. They can jump great distances when threatened (Apps 1992) making it difficult for spotted hyena to follow them during a hunt in thick undergrowth. Warthog, the second most common prey species with waterbuck, were also, surprisingly, consumed less than expected. Other studies have found warthogs to be a preferred prey species (Cooper 1990, Di Silvestre et al. 2000). Warthogs defend themselves ferociously using their canines, longer than a lion's, to inflict serious stab and thrashing wounds on their assailant (Apps 1992). This threat may be too great for a hyena when other less dangerous and larger bodied prey species are available. Primates, such as the yellow baboon, *Papio cynocephalus*, which are common in the reserve, were also avoided, which is similar to the findings of Hayward et al. (2007). The reason for avoidance of baboons as prey may be because baboons are inaccessible, they roost in trees at night when hyenas are most active.

Only two domestic goat hair samples were found in 85 hyena scat samples indicating that livestock do not form a major component of spotted hyena diet in MWR during the dry season. This, however, may differ in the wet season when human predator conflict is higher (Watts and Holekamp 2009). Wet season scat samples were difficult to find due to the density of the summer vegetation and the heavy rains that washed samples away. Other studies have also encountered this problem (Di Silvestre et al. 2000). Livestock also featured little in the spotted hyena diet in Umfolozi, South Africa, a fenced game reserve adjacent to farmland (Skinner et al. 1992). MWR is also fenced, possibly suggesting that spotted hyena are not as likely to prey on livestock in fenced reserves.

Management effects

The top down control of herbivores by hyena and the consequent effect on vegetation composition is important for effective management of MWR. Of the strongly preferred prey species, zebra are the only grazer (Skinner and Chimimba 2005). The biomass of reedbuck, bushbuck and common duiker (if not significantly affected by distance sampling) is so low (<1%) that predation on these species, has little effect on vegetation. Of the preyed upon species waterbuck will influence the vegetation component the most as they contribute 30.9% towards the total biomass. Although waterbuck had the second highest FO in hyena scat, spotted hyena preyed less upon the species than in proportion to their relative abundance (Figure 1). The species are largely grazers and feed on *Cynodon dactylon*, *Digitaria* spp, *Heteropogon contortis*, *Themeda triandra* and *Chloris* species of grass (Skinner and Chimimba 2005).

Boehm's zebra feed on any available species of grass, but favour young sprouts in burned areas and compete with waterbuck for food. The high predation rate on Boehm's zebra will therefore favour waterbuck. Waterholes are able to influence herbivore distribution and zebras have a strong association with waterholes while waterbuck has no clear association with waterholes but rather with rivers (Smit et al. 2007). Burning areas close to waterholes could possibly favour zebra, because of their strong association with waterholes, which would increase palatable species availability and create a more open habitat suitable for zebra (Skinner and Chimimba 2005). This may allow zebra to be more competitive towards waterbuck and may force hyena to prey more on other species such as waterbuck, because of an open environment around waterholes which would make it more difficult to hunt zebra, which may ultimately reduce waterbuck reproduction in the reserve.

Conclusion

Theory suggests that size-selective predation, as shown by spotted hyena (Hayward et al. 2007), would result in a decrease in competition for remaining resources in prey species which should stimulate higher reproductive outputs of potential prey (Persson et al. 2007). Even though spotted hyena shows high ecological resilience (Winterbach et al. 2012), one would assume that a decrease in preferred prey species would result in a population decrease because hyena density is correlated to prey density (Holekamp et al. 2012). However, hyena at MWR have high diet variability, with 17 different species consumed. This corroborates with other studies where hyenas were also recorded having high diet variability (Di Silvestre et al. 2000, Yirga et al. 2011).

It is hoped that this study would be used for future monitoring of predator populations in MWR, as spotted hyena in MWR may be competing with both lion and leopard for certain preferred prey species, namely common duiker and bushbuck, which are also preferred prey species for leopard and Boehm's zebra (Hansen 1975) which is a preferred prey species of lion (Hayward et al. 2007).

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Chapter 5: Activity patterns of spotted hyena in Majete Wildlife Reserve

Abstract

Although not always considered, animal activity patterns are an important component of animal ecology as they reflect an animal's resource utilisation. Spotted hyena, *Crocuta crocuta*, activity patterns in Majete Wildlife Reserve (MWR) were analysed using camera trap photographs (n=935). Activity patterns were compared between sexes, between time spent at, and foraging away from communal dens using hourly capture frequencies, and for waterhole usage between sexes within each season. Males and females had similar patterns of activity (r_s = 0.747540; p<0.05), whilst hyenas visited communal dens mostly during early evenings (20:00-20:59), and the peak foraging time was early morning (02:00-02:59). Hourly frequencies differed between communal den visits and foraging as the correlation was not found to be significant (r_s =0.23; p=0.36). It is thought waterholes offer less hunting opportunities during the wet season because of natural pools and ephemeral rivers which provide alternative water sources for prey species. Female spotted hyena activity at MWR was somewhat similar to spotted hyena activity in East Africa, but onset of activity of males at MWR differed from that of males in East Africa. It is thought that hyena activity in MWR is a reflection of it being an area with a clumped resource distribution.

Introduction

Importance of activity patterns

The study of animal activity patterns is a subset of the broader study of animal behaviour (Bridges and Noss 2011). Activity patterns illustrate a species' temporal and spatial resource utilisation, where animal activity is defined as: movement of body parts or movement of the animal itself. In other words, being physically active during the process of reproduction and survival (Bridges and Noss 2011). Activity mechanisms of an animal are a fine trade-off between physiological properties and environmental interactions (Gervasi et al. 2006). Photoperiod, temperature and other abiotic factors may determine activity patterns including optimal foraging times. Biotic factors such as anthropogenic influences, predator avoidance, foraging, competition and social behaviour also influence an animal's activity patterns (Lucerini et al. 2009).

Activity patterns can be used to determine niche overlap between similar foraging species, where an animal's niche is the temporal and spatial interactions that occur between it and its environment as a consequence of it surviving and reproducing. Activity patterns can also evidence a change in behaviour related to avoidance of inter-specific competition and are important for management and conservation purposes as they reflect time of potential anthropogenic interactions which can create conflict (Gervasi et al. 2006). This activity pattern data can then be used for developing effective conservation plans based on an understanding of an animal's ecology (Lucerini et al. 2009).

The optimal activity time for a terrestrial predator is determined by a combination of daily temperature variation, prey availability and predation risk (Kolowski et al. 2007). Other factors such as sex, reproductive state and social ranking might also influence a predator's daily activity pattern. Spotted hyena, *Crocuta crocuta*, are pre-dominantly nocturnal animals with approximately only 10% of their activity occurring during daylight hours, most of which occurs in the two hours after sunrise. Their behaviour, however, is highly adaptable, and their activity shows significant spatial variability (Kolowski et al. 2007) although research on spotted hyena activity patterns is limited (Hayward and Hayward 2006, Kolowski et al. 2007).

Spotted hyena activity

Spotted hyena society has a complex social structure where all members have a ranking, and dominant individuals get prior access to a kill (Watts et al. 2009). Dominance of females over males in a clan, may potentially result in intersexual differences in behaviour, including activity patterns.

The most detailed, published study of spotted hyena activity in a savannah environment was done by Kolowski et al. (2007) in the Masai Mara National Park, Kenya. This study recorded spotted hyena males spending more time foraging than females did, with peaks in male activity between 22:00 – 23:00 and 06:00 – 07:00. Females showed no clear activity peaks. Dominance allows females to spend less time foraging than males, which enables females to focus time on nursing and fending for their cubs, who depend on their mother for food even after they are weaned because of delayed skull development. It only becomes fully developed after sexual maturity (Watts et al. 2009). Kolowski et al. (2007) also showed that socializing (usually done at communal dens) takes place in the early evening with some limited social activity in the early morning.

Effect of water on activity patterns

No research has focused on the effect of waterholes on spotted hyena behaviour and few studies address their effect on predators in general. Waterholes are usually optimal hunting grounds because they draw in great numbers of prey species (Hayward and Hayward 2012). Spotted hyena in MWR spend most of their time around artificial waterholes (see chapter three) and quantifying to what extent and when they do this may provide useful information for reserve information management.

Activity patterns study methods

Studies of animal activity patterns can be difficult because of logistics and the limits posed by restrictive environments. Previous studies on animal activities have made use of radio-telemetry, where motion-sensitive collars produce a certain signal type by animal movement which is then altered by a change in movement, such as resting, however, subjective interpretation of collar signal is needed (Gervasi et al. 2006). Another problem with radio-collars is that there is a time delay between each animal movement and changes in signal (Gervasi et al. 2006). This method is also very costly and biased towards collared individuals when studying social animals such as spotted hyena. Study animals also need to be sedated twice to fit and remove radio collars which is highly intrusive. Although animals can be actively followed for extended periods, this technique is only possible in open areas (Gervasi et al. 2006), such as the East African plains and the Kalahari Desert. Human presence when tracking may also alter an animal's natural behaviour.

Making use of camera traps to study activity patterns of a cryptic species in a challenging environment such as MWR, can be an effective non-intrusive technique (Kucera and Barrett 2011).

The aims of this study were to:

1) Determine the time of day when spotted hyena are most active and whether male and female activity patterns differ.

2) Determine to what extent waterholes were used between seasons and sexes, by making use of a cost effective non-intrusive technique.

Materials & Methods

Cameras

A total of 47 stations of Cuddeback cameras (model 1149 and 1170, manufactured by Cuddeback Ltd. in De Pere, United States) were used to monitor spotted hyena activity, where the time of capture of the images was used to study daily activity patterns, and records of hourly image captures were regarded as an index of activity (Oliveira-Santos et al. 2008). Cameras were placed in areas of high animal activity such as waterholes and roads. Both camera models were strobe flash cameras with a trigger speed of 0.25 seconds and a photo quality of 5 mega-pixels.

Hyena identification

Cameras were stationed at seven artificial waterholes and were monitored every 7 to 28 days. During camera monitoring batteries were checked and replaced if needed, time & date settings were checked and camera cards were replaced. Following collection of camera cards, images were scrutinised and all hyenas identified and sexed. Identikits of each hyena captured were created in Adobe® based on unique spot patterns (Dwane 2013) and other features such as scars and missing limbs. Sex was determined based on erect phallus morphology, where females have a rounded phallus compared to males' pointed shaped phallus (Appendix 2, Figures 8 & 9) (Holekamp et al. 2012). However, clear images of an erect phallus was not possible for all individuals. In such cases the curve of the abdominal region was used, where males have an upward curve before the back legs and females a flat abdominal region (Holekamp et al. 2012).

Left and right flank images of hyena individuals were obtained by placing opposite facing cameras along roads which were often preferentially used by hyena, to avoid travelling through thick undergrowth. Opposite flank images were also obtained by placing cameras at communal dens which are visited by both males and females (Holekamp et al. 2012). The first communal den was found by dividing the area around the Pende 1 waterhole into square kilometre blocks The Pende 1 waterhole had a high capture rate of spotted hyena,. Each block was then actively searched for a communal den by a search team that spread out and walked in a straight line. The first communal den was found in the third square kilometre block and cameras were placed around the communal den on nearby trees. Other dens were found by anti-poaching units while on patrol.

Male vs Female activity

For the analysis of activity patterns only images of adult spotted hyena were used as juveniles behave differently to adults. Images from both the Pende clan and Pwadzi clan were combined to create a cumulative count of captures (n=935) as too few images were obtained from the Pwadzi clan to make inter-clan comparisons of activity patterns possible. Individual capture history was documented based on time, date and location of capture. Capture histories of all individuals were used to compare male and female spotted hyena activity. The time of capture of all capture history data from communal dens, waterholes and the field were placed into contingency tables for both sexes based on the hourly frequency of capture between specifics. Differences in activity were tested using a Mann-Whitney U test in an online program called socscistatistics (http://www.socscistatistics.com/tests/mannwhitney/). (Hayward and Hayward 2006). The null hypothesis was set that there was no differences in activity between sexes.

Foraging activity vs communal den activity

Activity patterns at the communal den were compared to foraging patterns that took place away from the communal den. This was done by comparing capture history of all adult individuals captured at communal dens with capture histories of all adult individuals away from communal dens which included captures at waterholes and the field. Data were sorted into hourly frequency of capture and was compared with a Spearman rho test http://www.socscistatistics.com/tests/spearman/). The null hypothesis was set that patterns of activity between visiting the communal den and foraging differed.

Waterhole use activity

Seasonal use of waterholes was also compared based on capture histories of individuals between the dry and wet season. The wet season in MWR was from November-March and the dry from April-October (Staub et al. 2013). However, because of the late onset of summer rains in 2014 images of spotted hyena at waterholes in November 2014 were classified as being in the dry season. Therefore captures were classified as a dry season capture when caught between 01 July 2013 – 31 October 2013 and 01 April 2014 – 30 November 2014 and a wet season capture when caught between 01 November 2013 – 31 March 2014 and 01 December 2014 - 31 March 2015. Only captures at waterholes from the Pende clan were used due to a lack of waterholes and a consequent lack of waterhole captures in the Pwadzi territory.

Following classification by season, the number of nights that each individual spotted hyena did or did not visit waterholes were counted within each season. The individual counts were added to create a cumulative count for both males (n=4) and females (n=5). Only individuals with capture histories that spanned the length of the study (February 2014 – April 2015), were used to ensure that individuals were present and could have visited waterholes in both seasons. A chi-square test http://www.socscistatistics.com/tests/chi-square/) was used to compare the use of waterholes between sexes and seasons with the null hypothesis being that there was no seasonal difference in waterhole use and that conspecifics used waterholes equally.

Results

Overall hyena activity

Spotted hyena activity in MWR had a bimodal pattern. Activity gradually increased in the late afternoon from 16:00 (Figure 1), where most activity occurred around the communal den (Figure 3). The first peak in activity was reached between 21:00 to 21:59 (Figure 1) mainly because of activity occurring at the communal den (Figure 2). Thereafter there was a decrease in activity with a trough between the hours of 00:00 to 01:59 (Figure 1). During these hours several images were captured of spotted hyena resting at the communal den and only playing cubs activated cameras (Appendix 2, Figure 10). Between 02:00 to 05:59 activity restarted (Figure 1) with the second peak in hyena activity reached between 03:00 to 05:59, which was mainly due to a combination of male foraging activity (Figure 2) and further activity at communal dens (Figure 3). Subsequently, hyena activity gradually decreased until 09:00 - 09:59 after which no activity was recorded (Figure 1). All captures of spotted hyena occurred between 16:00 and 09:59 but 86.5% of all images were captured in the dark between 18:00 and 05:59, indicating that spotted hyena in MWR are nocturnal. Daylight captures of spotted hyena occurred mostly in the early morning hours after 06:00 with 71.3% of all daylight captures occurring in morning hours (Figure 1).

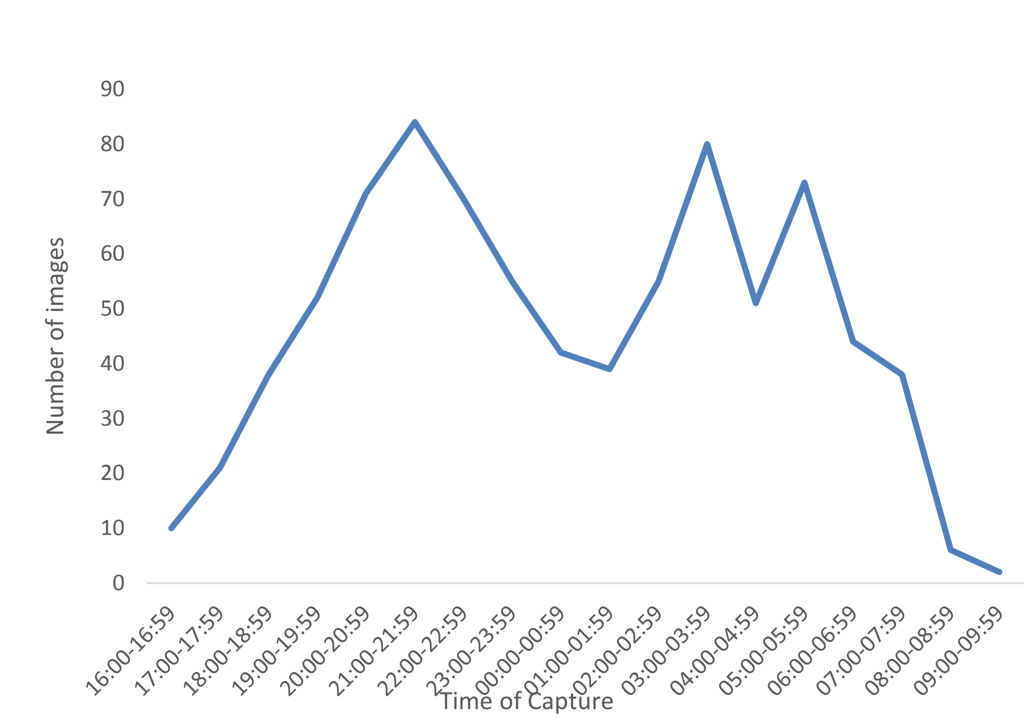

Figure 1. Time of capture of spotted hyena males (n=6) and females (n=6) at communal dens, waterholes and in the field.

Male vs Female activity

Male and female overall activity was strongly correlated (r_s = 0.75; p<0.05) and the null hypothesis, that activity patterns differed among sexes, was rejected. However, females were more active than males for longer periods of time, with the earliest and latest times of capture of foraging hyena being female, one hour earlier and later respectively than captures of foraging males. Females were captured significantly more than males (U=248; U1=58). Foraging activity between males and females was significantly correlated (r=0.73; p<0.05) and thus the null hypothesis, that foraging patterns differed among sexes, was rejected. Males did, however, showed a clear peak in foraging activity between the hours of 02:00 - 02:59 (Figure 2), while females showed no clear peaks although the highest number of female captures was also between 02:00 – 02:59 (Figure 2).

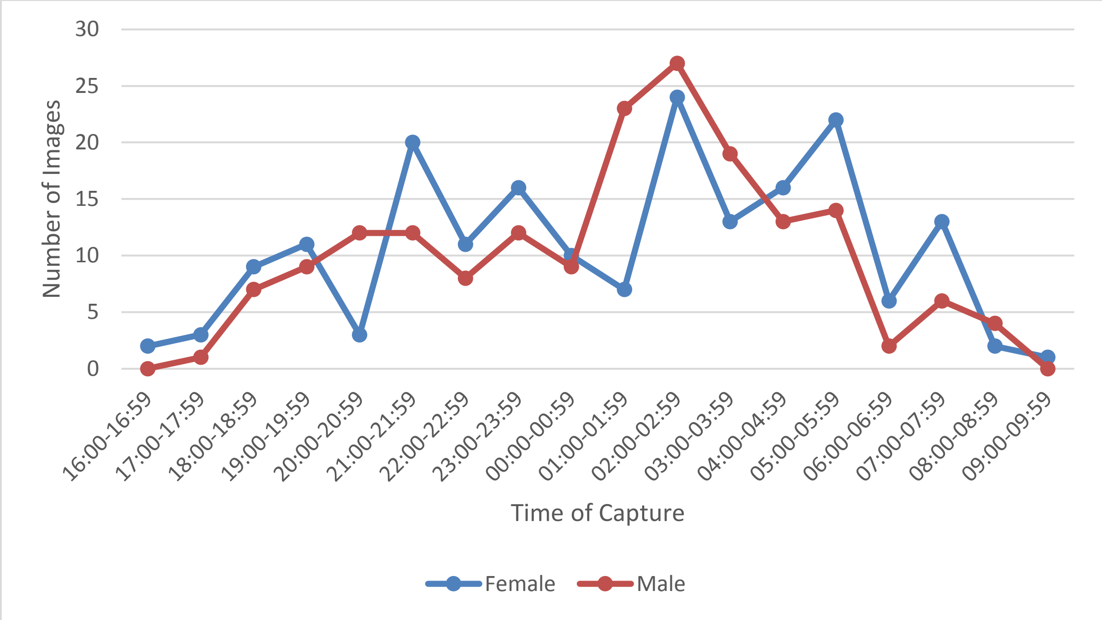

Figure 2. Time of capture for spotted hyena females (n=6) and males (n=7) whilst foraging at waterholes and in the field.

Forage activity vs communal den activity

Cameras were only placed at communal den sites for 2.5 months due to the difficulty of locating dens, but significantly more hyena images were taken at dens when compared to hyena captures at waterholes or in the field (U=84; U1=204). Spotted hyena activity patterns at communal dens differed from foraging activity patterns as the correlation was not found to be significant (r_s =0.23; p=0.36) (Figure 3) and the null hypothesis, that activity patterns differed between foraging activity and visiting the communal dens, was accepted.

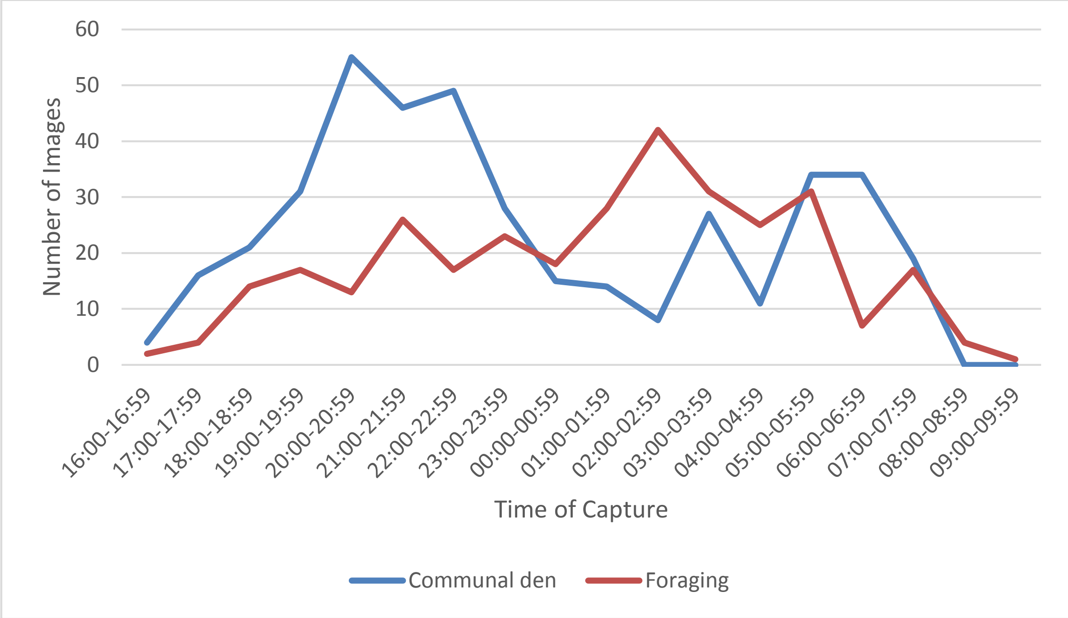

Figure 3. Time of image capture at the communal den sites and foraging whilst at waterholes and in the field.

Spotted hyena activity at communal dens was proportionally highest during early evenings, reaching its peak between 20:00-20:59 (Figure 3). Thereafter, activity at the communal den gradually decreased with another slight increase in activity after 04:59 leading to a small peak between 05:00-06:59 (Figure 3).

Spotted hyena activity away from the communal den was assumed to be foraging activity because most social activity occurs at the communal den (Holekamp et al. 2012). Foraging activity increased gradually after 17:59 and then increased rapidly reaching its peak between 02:00-02:59 (Figure 3). Thereafter foraging activity decreased gradually until 05:59 when there was a marked reduction leading to no foraging activity being recorded by 09:59.

Waterhole activity

Waterholes were used more frequently during the dry season than the wet by both males ($X^2 = 24.34$; p<0.05) and females (X^2= 49.33; p<0.05) and the null hypothesis, that season did not affect waterhole use, was rejected. Females used waterholes more during the dry season than males (X^2= 5.28; p=0.02) but during the wet season use between sexes did not differ (X^2= 0.045; p=0.5) (Table 1). The null hypothesis, that sexes use waterholes to the same extent, was also rejected.

Table 1. Number of nights that waterholes were visited, and not visited, by male (n=3) and female (n=4) spotted hyena.

	Dry season nights WH visited	Dry season nights WH not visited	Wet season nights WH visited	Wet season nights WH not visited
Female	90	1378	8	1080
Male	45	1056	4	812

Discussion

Male vs Female

Hyena behaviour at MWR was strongly nocturnal, similar to hyena activity recorded by Kolowski et al. (2007) at the Masai Mara National Park, Kenya. Foraging behaviour did not differ between the sexes at MWR, suggesting that males had not changed their foraging behaviour to avoid feeding competition from females, females being known to be dominant over males (Holekamp et al. 2012). However, the peak in male foraging activity between 01:00 – 02:59 might reflect different male hunting strategies. Being subordinate to females forces males to forage alone to avoid feeding competition (Holekamp et al. 2012) and females are more likely to associate with other females (Smithet al. 2007). Solitary hunting in hyenas is less effective than hunting in a group, where the hunting success rates can increase by up to 75% (Holekamp et al. 2012). The male hunting peak of 02:00 to 02:59, not mirrored in females, may suggest this is an opportune time for the lone male to hunt, perhaps because they are physiologically prepared. Whereas females are more likely to form a hunting group with other females (Smith et al. 2007) and may not need to take advantage of a "window of opportunity" as males do, reflected by the lack of hunting peaks in female temporal activity.

The peak in male foraging activity at MWR differed from that reported by Kolowski et al. (2007) where male activity peaked between 22:00 – 23:00 and 06:00 – 07:00. Kolowski et al. (2007) also found males were active for longer than females, the opposite to this study. A reason why females were captured earlier and later than males might be because females were captured significantly more often than males which potentially recorded activity better than male activity and differences may be an artefact of sampling. The decrease in hyena activity between 00:00 – 00:59 is comparable to the period by Kolowski et al. (2007) and that of other studies (Mills 1990, Kruuk 1972). Spotted hyena can cover great distances searching for prey

(Holekamp et al. 2012) and foraging and hunting can require a great amount of energy expenditure to be successful. The trough in hyena activity at MWR (Figure 1) may illustrate a transitional resting period between social and foraging behaviour, the rest being necessary before strenuous foraging activity.

Forage activity vs communal den activity

As they did in Kolowski et al. (2007) hyenas at MWR were social in early evenings and early mornings, when most of the captures of hyena at communal dens occurred. The significant difference between hourly captures of foraging activity and social activity at communal dens suggest they obey a set activity pattern at MWR where individuals tend to be social in the early evenings, with a slight decrease in overall activity around midnight, and a marginal increase in the proportion of individuals being social around sunrise.

For hyena to show similar patterns of socialising in two different habitats (Masai Mara & MWR) indicates “set” hyena behaviour that it is advantageous to hyena survival and therefore the development of such behaviour is favoured. Cub care is a priority for females, thus visits to communal dens are done before foraging. Males would follow this behaviour because males need to form strong social bonds with females to procure a mate (East, et al. 2003). The early morning activity at the communal den may be ascribed to females inspecting young before going to rest during the day. Early mornings were also when females brought prey leftovers to communal dens from previous night hunts (Appendix 2, Figure 11), which is not common spotted hyena behaviour, but has been documented before (Holekamp and Smale 1990). This was documented three times in the two and a half months in which den activity was monitored

Waterhole activity

The reason why both males and females visited waterholes less frequently during the wet season may be due to other available water sources such as ephemeral natural pools and rivers which are filled and available during the wet season (Chamaille´-Jammes et al. 2013). These alternative water sources would allow potential prey species to spread out more evenly across a landscape and therefore waterholes will provide less reliable hunting ground than they are in the dry season.

The reason why females visited waterholes more often than males during the dry season is probably because waterholes are productive hunting areas and females are able to exclude males from hunting there because of their dominance. The lack of prey frequenting waterholes during the wet season may be the reason why their use between sexes was similar.

Conclusion

Spotted hyena activity patterns at MWR shared some similarities with those of East Africa. The main difference between the two populations was the onset of activity between sexes and the peaks in male activity. The reason for temporal differences in male activity peaks might relate to the different environment in East Africa compared to MWR. The hyenas at MWR operate in an area with clumped resource distribution which may force hyena to have large home ranges (see chapter three) whereas in the Masai Mara, Kenya, spotted hyena have small home ranges of a maximum of $76km^2$ (Holekamp and Dloniak 2006). Small home ranges in spotted hyena may be associated with areas where resources are evenly distributed (Tilson and Henschell 1986) and they probably have different environmental conditions to MWR. Thus, it is possible that spotted hyena activity patterns are adapted to meet the demands of an individual's specific environment.

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Chapter 6: Management recommendations for spotted hyena at Majete Wildlife Reserve, Malawi

Abstract

The low hyena density at MWR should be increased to a density comparable with reserves with similar habitat and environmental conditions. The increase of hyena density should be considered as the main conservation objective for spotted hyena at MWR and should be prioritized to any reintroduction plans of more lions which may have a negative impact on hyena density. The protection of hyena outside MWR should also be considered because of the genetic contribution they make to the hyena at MWR. Educating local communities should be regarded as the first step to conserving these hyenas and a strong leadership that understands the conservation objectives is essential.

Conservation planning for predators

The less uncertainty there is on the ecology of a species, the more effective conservation objectives can be modelled for a species (Arthur et al. 2004, Constable 2001). The priority management objective for predators such as spotted hyena at MWR should be to maintain ecological relationships between spotted hyena and relevant species needed for survival (Constable 2001). These include relationships with prey species (see chapter four) and hyena communities outside MWR boundaries, which are hoped, would ultimately lead to an increase in hyena density in MWR.

The current hyena density of 0.04 hyenas/km^2 (see chapter two) is the lowest recorded in a non-arid region and should be increased to a density comparable with other Savannah habitats. Hwange National Park in Zimbabwe also comprises out of a miombo woodland habitat as in MWR (Dudley 1999) and can be used as a reference to compare MWR hyena density with. Hwange National Park has a hyena density of 0.07 hyenas/km^2 (Holekamp and Dloniak 2006) and the first objective should be to almost double the hyena density in MWR to about the same density as in Hwange. Understanding spotted hyena reproduction may assist in reaching such objectives. The most critical life stage in spotted hyena is between the age of one year and the onset of sexual maturity (Frank and Holekamp 1995). The lack of sub-adult hyenas photographed during the study period (see chapter two) may indicate that few hyena at MWR survive during this life stage. It is thought that the main reason for this increase in mortality is due to sub-adult hyena's undeveloped skull which limits successful hunting. Hence, mothers still need to fend for their sub-adult offspring. Dominant females have priority of access to kills which allow them to fend better for their offspring than subordinate females. The greater success in rearing young by dominant females contributes significantly more to clan reproduction than subordinate females (Frank and Holekamp 1995).

The low hyena density (see chapter two) and large hyena home ranges (see chapter three) indicate that MWR has a clumped prey distribution. A natural increase in prey species should lead to an increase in hyena density, as mothers would be able to find prey for dependent sub-adults more easily. However, the addressing of stochastic processes alone is not sufficient to prevent local extinctions of large predators. Rather reserve size has to be increased or carnivore persecution has to be mitigated in border and buffer areas surrounding a reserve, as humans are normally the single most important factor in adult mortality (Woodroffe and Ginsberg 1998).

Neighbouring clans

Current conservation efforts should think beyond the boundaries of a protected area because any wildlife conflict has the ability to influence people's attitudes towards conservation. This can have a negative effect on community based conservation efforts, which is practised at MWR, where local community skill, enthusiasm and interest are needed (Hackel 1999).

Another issue with the hyena population at MWR is potential inbreeding because of the small population size. Although not an immediate issue, because of male dispersal from neighbouring clans outside MWR which still occurs (see chapter two). If these clans were to turn locally extinct inbreeding may become a problem, because male dispersal significantly contributes towards the prevention of a genetic bottleneck (Watts, et al. 2011). These clans are most likely under threat because of reported livestock losses and there was one documented killing of a hyena by local farmers outside MWR during the study period (Appendix 2, Figure 20). However, the economic challenges and rapid population growth facing many African livelihoods surrounding reserves such as MWR, has the potential to offset any impacts that community based conservation may have on hyena conservation (Hackel 1999). Many African livelihoods in rural communities are faced with serious economic and environmental challenges and often farm with crops and livestock which forms their main source of income. Any wildlife which has the ability to harm their livelihoods is normally not wanted, especially spotted hyena which can create great loss in livestock (Mills and Hofer 1998). Education should be used as a tool in conservation and can contribute significantly towards spotted hyena conservation if local communities are educated (McKinney 2002). Education can also be seen as a first step in effective management of a species such as spotted hyena, where species first need to be viewed in a positive light before further management plans can be implemented (Mills and Hofer 1998).

Local communities should be educated on farming techniques found to be effective in other areas where livestock farming takes place in the presence of spotted hyena. These techniques include keeping livestock fenced in a kraal at night, when hyena are most likely to attack livestock, with a herdsman sleeping at the kraal (Mills and Hofer 1998). Any commotion from a hyena attack should wake the herdsman who is then able to take quick action. A combination of using kraals and dogs is most effective in preventing depredation of livestock from hyena (Mills and Hofer 1998). Strong leadership from both parties also plays a large role in community based conservation. Educating leaders in local communities can contribute to protection of species outside of protected areas by setting an example of a non-retaliatory attitude (Shankar, n.d.). Even though human density may increase in an area, it has been found that effective enforcement of legislation which favours the survival of a species contributes significantly towards large predator conservation (Linnell et al. 2001). Combining education with effective enforcement of a legislation, agreed upon by both parties, may contribute towards protecting hyena outside of MWR.

Lion reintroduction

Another reintroduction of lions at MWR should not take place until the conservation objective to increase hyena density at MWR has been reached. Lions are the main threat to spotted hyena in protected areas (Holekamp et al. 2012). Interspecific competition between predators can also have an influence on lower trophic cascades by influencing subordinate species (such as spotted hyena) population and behavior dynamics (Watts, et al. 2010). Spotted hyena females avoided areas that were used by lions at MWR (see chapter three), although variation in spotted hyena behavior towards lions does occur. Lions can be a potential source of food for hyena when scavenging and certain hyena individuals might seek lions (Watts et al. 2010). However, the current hyena population is so low at MWR that it would be difficult for them to overpower lions. Additionally, lions were absent form MWR from 1976-2011 and in that time the hyena had to adapt to an almost exclusive hunting lifestyle, and thus lions may benefit hyena very little at MWR.

If more lions were to be reintroduced to MWR, the Pende region, where the Pende hyena clan currently reside (see chapter three), would most likely be colonized by the newly reintroduced lions because of the suitable hunting grounds provided by the waterholes in the area and that the current lion population use the area very little (see chapter three). This would increase hunting competition for the Pende hyena clan, in an area with an already clumped prey resources distribution (see chapter two and three), and would be a direct threat to hyenas. Lions also easily become overabundant after reintroductions (Hayward, et al. 2007) and interspecific competition can be a strong limiting factor on carnivore populations (Creel 2001) making it highly possible to outcompete hyena resulting in a population crash. The objective to almost double the hyena density to 0.07hyenas/km^2 at MWR should enable hyena to compete effectively with lions.Another lion reintroduction should only be considered once that objective has been reached.

Hyena Reintroduction

Another option would be to coincide another lion reintroduction with a spotted hyena reintroduction. Reintroducing female hyenas would contribute the most towards the reproduction rate of hyena at MWR because females raise cubs and would be able to assist in keeping cubs safe, and because females are larger they should assist more in bringing down larger prey species than males would. There is also the risk that reintroduced males may emigrate to neighbouring clans outside MWR. The complex social structure in hyena communities means that if female hyenas are reintroduced at MWR, that it would be needed to keep animals in bomas for longer than if a whole clan were to be reintroduced to be sure a social bond exists between resident hyena and reintroduced hyena (Hayward, et al. 2007). However, reintroduction of both spotted hyena and lion is not recommended because of the intensive human effort needed and stress it creates on animals, both reintroduced and resident. Also prey density at MWR may not be at a level to support both more lions and hyenas.

A reintroduction of only spotted hyena may be justified when found that the MWR may be in an Allee effect (see chapter two). It is recommended that prey species and hyena should be monitored and when prey species were to increase, with a stagnant or decreasing hyena density, can reintroduction of hyena then be considered.

Conclusion

For effective conservation planning research needs to form a primary role by providing baseline information needed for success (Weber and Rabinowitz 1996). Cultural, economic and political factors which may play a role needs to be identified and included in conservation planning for long-term success, especially so for transboundary conservation efforts (Weber and Rabinowitz 1996). This way, different interests and concerns may be acknowledged which may go a long way in reducing possible conflicts. Also experimental sustainable-development activities are applicable in already converted land such as unprotected areas outside of MWR, and any activities which may assist in community based conservation should be considered. The final step in effective conservation planning is monitoring and giving feedback to applicable parties involved (Weber and Rabinowitz 1996).

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Appendix 1

Table 8 X matrix of spotted hyena capture histories from 02/07/2014-29/09/2014 used in CAPTURE available online at http://www.mbr-pwrc.usgs.gov/software/capture.html (accessed on 17/09/2015). The matrix consist out of 9 occasions where 1=capture and 0=no capture.

```
title='population estimate of spotted hyena, Majete'
task read captures occasions=9 x matrix
format='(T1,A3,1X,11F1.0)'
read input data
h01 000010111
h02 111100000
h03 111110110
h04 101100111
h05 000000011
h06 100110000
h07 100100111
h08 101110110
h09 000000010
h10 000110100
h11 111111001
h12 011000010
h13 011111000
h14 110111000
h15 100001010
h16 100111001
task closure test
task model selection
task population estimate ALL
task population estimate NULL JACKKNIFE REMOVAL ZIPPEN MT-CH MH-CH MTH-CH
task population estimate APPROPRIATE
```

Figure 1. The location of MWR, Malawi, in East-Central Africa.

Figure 2. Aerial photo of MWR. The reserve's boundaries are clear because of deforestation in the surrounding area.

Figure 3. An example of an artificial waterhole in the reserve.

Figure 4. The Pwadzi spring: an example of a natural spring in the reserve.

Figure 5. The Shire River, the largest river in the reserve close the reserve's Eastern boundary.

Figure 6. An example of a dambo, a natural pool, which fills up during the wet season.

Figure 7. A non-perennial river, which has dried up in the dry season.

Figure 8. Mixed woodland in the lower lying East of the reserve with an open canopy.

Figure 9. Dry miombo in the higher lying West of the reserve.

Appendix 2

Figures 1 & 2. Warthog males captured at hyena dens.

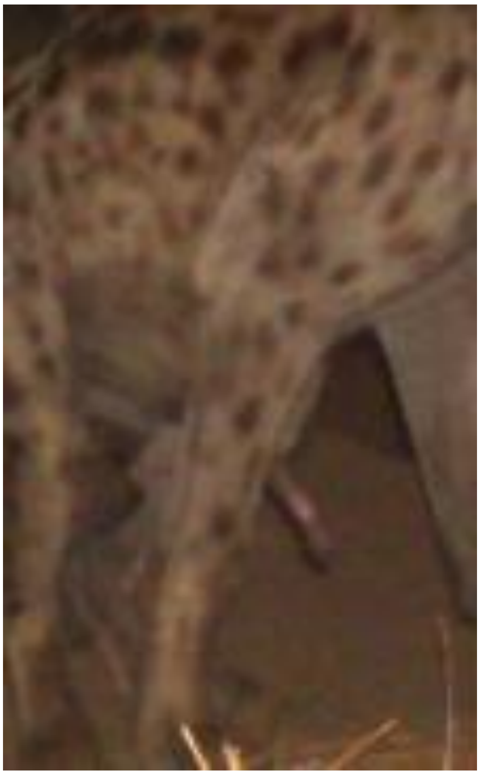
Figure 3. First den found in the Pende territory.

Figure 2. The second den found in the Pende territory.

Figure 3. Female hyena exiting through the den entrance at the second den found in the Pende territory.

Figure 4. Hyena male from the Pende clan patrolling the fence line. Possibly wanting to exit the reserve in places such as the then recently fixed fence in the picture.

Figure 5. A hyena walking towards an entrance of the den found in the Pwadzi territory.



Figures 6 & 9. Difference between female (left) and male (right) phallus regions.

Figure 10. A hyena mother resting at midnight.

Figure 11. A Pende female bringing food back to the communal den for pups.

Figure 12. Two pups of approximately three months of age with two adult females at the first den found in the Pende territory.

Figure 13. A pup of approximately three months of age at the second communal den found in the Pende territory.

Figure 14. A pup captured at the Pwadzi den of approximately five months of age.

Figure 15. A pup of approximately five months of age captured close to the first communal den found in the Pende territory.

Figure 16. A female hyena standing at the entrance of a den found in the Pwadzi territory. It is unclear whether this den was a communal den or nursing den because of limited photos captured at the den.

Figure 17. An example of how cameras were tied to trees close to communal dens.

Figure 18. Spotted hyena scat at a latrine.

Figure 19. A common duiker killed by spotted hyena in the Pwadzi clan.

Figure 20. An unidentified hyena which was killed outside the reserve after caught killing chickens.