Is the grass greener on the other side? : testing the ecological trap hypothesis for African wild dogs (Lycaon pictus) in and around Hwange National Park

Ester van Der Meer

To cite this version:

Ester van Der Meer. Is the grass greener on the other side? : testing the ecological trap hypothesis for African wild dogs (Lycaon pictus) in and around Hwange National Park. Agricultural sciences. Université Claude Bernard - Lyon I, 2011. English. NNT : 2011LYO10095 . tel-00839251

HAL Id: tel-00839251
https://theses.hal.science/tel-00839251

Submitted on 27 Jun 2013

A thesis submitted to the University of Lyon (Université Claude Bernard Lyon I)
for the degree
Doctor of Philosophy

Is the grass greener on the other side?

Testing the ecological trap hypothesis for African wild dogs (*Lycaon pictus*) in and around Hwange National Park

Presented on the 27th of May 2011 by
Ester van der Meer

Jury:

Prof. Dominique Pontier	(*Examiner, President of the jury*)
Dr. Hervé Fritz	(*Director of the thesis*)
Prof. Carmen Bessa-Gomes	(*Reviewer*)
Prof. Claudio Sillero-Zubiri	(*Reviewer*)
Prof. Rob Slotow	(*Reviewer*)
Prof. Daniel Fortin	(*Examiner*)

I kindly acknowledge the following people, organizations and associations for supporting me and providing me with the opportunity to carry out this research:

The Zimbabwe Parks and Wildlife Management Authority

Forestry Commission

The Research Council of Zimbabwe

Immigration Control Zimbabwe

The farmers of the Gwaai Intensive Conservation Area

Chief Nelukoba Dingani

Wilderness safaris

The Hide

Hwange Safari Lodge

Sikumi tree lodge

Prince Bernhard Fund for Nature

Fonds Dr. Christine Buisman

The Harber Foundation

Stichting Painted Dog Conservation

Painted Dog Conservation

CNRS HERD project

Bever Zwerfsport

Technolyt

Mammut Nederland

Opmeer drukkerij b.v.

Vis Landrover Supplies

Abstract

Testing the ecological
trap hypothesis
for
African wild dogs
in and around
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Abstract

Over the past century, like in other African countries, the African wild dog (*Lycaon pictus*) population in Zimbabwe has declined. In particular in Hwange National Park, an area that used to harbour a viable population, a sharp decline in the population has been documented. One of the main reasons for this decline is that over the years African wild dog packs either moved closer to or into the buffer zone along the northern boundary of the National Park. Within the buffer zone African wild dogs get increasingly exposed to human activity resulting in mortality, this is also known as an ‘edge effect’. The mortality rate is so high that it exceeds natality and ultimately there is no recruitment and packs fall apart in groups far below their optimal pack size necessary for successful reproduction.

When animals show a preferential choice for sink habitat they are said to have been caught in an ecological trap. Habitat choice behaviour is beneficial in classic source-sink systems, as animals living in high quality habitat (natality>mortality) only choose to migrate into low quality habitat (natality<mortality) when there is not enough high quality habitat available. Within an ecological trap habitat choice is detrimental and can lead to rapid extirpation of a species, as animals living in high quality habitat choose to migrate into low quality habitat even when there is enough high quality habitat available. Ecological traps occur when sudden natural or human induced changes cause formerly reliable settlement cues to be no longer associated with an adaptive outcome, causing animals to make a maladaptive habitat choice. To be able to distinguish a sink from an ecological trap additional knowledge of the relationship between habitat preference and habitat quality is required. Within the Hwange system African wild dogs seem to base their habitat choice on the right fitness enhancing ecological cues. They experience a higher hunting efficiency in the buffer zone outside Hwange National Park, less competition with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) and a better access to suitable den sites. As a result African wild dogs outside the National Park give birth to larger litters of pups. However, due to an ‘edge effect’, human induced mortality in the buffer zone is so high it exceeds natality. African wild dogs nevertheless make a maladaptive habitat choice and move into the mortality sink outside the safety of the protected area as they are unable to judge habitat quality accurately by taking this human induced mortality risk into account. In other words, African wild dogs in the Hwange system are caught in an ecological trap in the buffer zone outside Hwange National Park.

Within an ecological trap, habitat choice is detrimental and likely to result in a rapid collapse of the system and extirpation of the species involved. The fast decline in the African wild dog population in and around Hwange National Park supports the finding that the Hwange system serves as an ecological trap. In order to ensure a fast recovery of the population it is recommended to expand conservation efforts beyond the borders of the protected area and focus on countering the human induced mortality in the buffer zone surrounding Hwange National Park.

Résumé

Au cours du siècle dernier, de même que dans les autres pays africains, la population de lycaon (*Lycaon pictus*) du Zimbabwe a diminué. En particulier dans le parc national de Hwange, une zone qui autrefois abritait une population viable, une nette diminution de la population a été documentée. Une des principales raison de ce déclin, est qu'à mesure du temps, les lycaons soit se sont rapprochés, ou bien ont pénétré dans la zone tampon située le long de la lisière nord du parc national. Dans la zone tampon, les lycaons sont de plus en plus exposés aux activités humaines, aboutissant à de la mortalité, ceci étant aussi connu sous le nom d'effet-lisère. Le taux de mortalité est si élevé qu'il excède le taux de natalité. Au final il n'y a pas de recrutement biologique, et la taille du groupe d'individus décroît bien en deçà de la taille optimale de groupe, nécessaire au succès reproducteur.

Lorsque des animaux montrent un choix préférentiel pour un habitat à effet puits, on dit alors qu'ils sont capturés par un piège écologique. La sélection de l'habitat est bénéfique dans les systèmes classiques de type source-puits, puisque les animaux vivant dans des habitats de haute qualité (natalité>mortalité), choisissent de migrer vers des habitats de faible qualité (natalité<mortalité), uniquement lorsqu'il n'y a pas suffisamment d'habitat de haute qualité disponible. A l'intérieur d'un habitat de type piège écologique le choix est dangereux, et peut conduire à l'extirpation rapide d'une espèce, puisque les animaux vivant dans des habitats de haute qualité choisissent de migrer vers des habitats de faible qualité, même lorsqu'il y a suffisamment d'habitat de haute qualité disponible. Les pièges écologiques ont lieu lorsque des changements naturels ou induits par l'homme se produisent rapidement et que des déterminants de la sélection de l'habitat qui étaient alors sélectionnés deviennent trompeurs, entraînant des choix d'habitats inadaptés de la part des animaux. Pour distinguer un habitat de type puits d'un piège écologique, des connaissances complémentaires sont nécessaires, sur la relation entre les préférences d'habitat et la qualité de l'habitat. Dans l'écosystème de Hwange, les lycaons semblent baser le choix d'habitat sur les déterminants écologiques améliorant la fitness. Ils ont une meilleure efficacité de chasse dans la zone tampon à l'extérieur du parc national de Hwange, une compétition moindre avec les lions (*Panthera leo*) et avec les hyènes (*Crocuta crocuta*), ainsi qu'un meilleur accès à des sites de terrier. En conséquence, à l'extérieur du parc national, les lycaons donnent naissance à des portées de chiots plus grandes. Cependant, la mortalité induite par l'homme, en raison de l'effet lisière, est si grande qu'elle excède la natalité. Néanmoins, du fait qu'ils sont incapables de juger avec justesse de la qualité de l'habitat, en intégrant la mortalité induite par l'homme, les lycaons font un choix d'habitat inadapté, et ils se déplacent vers le puits de mortalité, à l'extérieur de la sécurité de l'aire protégée. En d'autres mots, les lycaons de l'écosystème de Hwange sont capturés par le piège écologique, que constitue la zone tampon située à l'extérieur du parc national de Hwange.

A l'intérieur d'un piège écologique, la sélection d'habitat est désavantageuse, et résulterait probablement en un rapide effondrement du système et à l'extirpation de l'espèce impliquée. Le rapide déclin de la population de lycaons, dans et aux alentours du parc national de Hwange, soutient l'idée que le système de Hwange agit comme un piège écologique. Afin d'assurer un rapide rétablissement de la population, il est recommandé d'étendre les efforts de conservation au delà de la lisière de l'aire protégée, en visant à réduire la mortalité induite par l'homme, dans la zone tampon entourant le parc national de Hwange.

Introduction

Testing the ecological trap hypothesis for African wild dogs in and around Hwange National Park

Introduction

An increase in the human population worldwide has resulted in fragmentation of habitat available to wildlife, thus forcing animals to live in close proximity to humans (Woodroffe 2000, Inskip and Zimmermann 2009). Protected areas are often not big enough to maintain large populations and particularly wide ranging carnivores regularly range beyond reserve borders (Woodroffe et al. 1997, Woodroffe and Ginsberg 1998). By crossing reserve borders into unprotected areas animals inevitably get exposed to anthropogenic mortality, as outside the reserves animals are accidentally (e.g. collisions with cars) or deliberately (e.g. animals being shot or caught in snares) killed by humans (Woodroffe and Ginsberg 1998, Loveridge et al. 2007, Balme et al. 2009, Inskip and Zimmermann 2009). This so called 'edge effect' may turn border areas of reserves into population sinks where anthropogenic mortality exceeds natality (Woodroffe and Ginsberg 1998). These human created 'edge effect' sinks largely contribute to the extinction of wide ranging carnivores (Woodroffe and Ginsberg 1998).

One of the wide ranging carnivores for which an 'edge effect' around reserves has contributed to a rapid population decline is the African wild dog (*Lycaon pictus*) (Woodroffe et al. 1997, Woodroffe and Ginsberg 1998). The territories of African wild dogs on average range between 423 and 1318 km^2 (Woodroffe et al. 1997), and are much larger than would be expected based on their body size (Gittleman and Harvey 1982). Due to these large territories African wild dog packs inhabiting protected areas may travel extensively outside reserve borders where they encounter human activity and its related threats (Woodroffe et al. 1997). One of the main reasons for the decline in African wild dog numbers are human prosecution and habitat loss due to human encroachment (Woodroffe et al. 1997, 2004). Approximately 61% of the adult mortality is directly caused by humans (Woodroffe et al. 1997). African wild dogs are snared, shot, poisoned or killed on the road. Natural factors like competition with other predators and diseases also contribute to the decrease in African wild dog numbers. The remaining 39% of adult mortality is caused by diseases like rabies and canine distemper virus, and predation by lions (*Panthera leo*) (Woodroffe et al. 1997). The main reasons for pup mortality are natural (96%) with lions and other African wild dogs being the main cause of death (Woodroffe et al. 1997).

The decrease of the African wild dog population is accelerated by the fact that, due to their sociality resulting in a positive relationship between aspects of fitness and pack size, African wild dogs are susceptible to the Allee effect (Courchamp et al. 2000). African wild dogs are obligate co-operators that live in packs of up to twenty adults and their dependent offspring (Creel and Creel 1995, Woodroffe et al. 1997). Packs are formed when small same-sex subgroups leave their natal group and join with other subgroups of the opposite sex (McNutt 1996). African wild dogs in a pack hunt cooperatively (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Rasmussen 2009). Within a pack generally only the alpha pair breeds, the other pack members assist in caring for the pups by regurgitating food and defending the pups against natural enemies (Fuller et al. 1992, Woodroffe et al. 1997). The need for helpers is likely to result in inverse density dependence at the pack level which can create an Allee effect (Courchamp et al. 2000); a reduction of individual fitness (e.g. reproduction or survival) at small pack sizes

(Rasmussen 2009). For African wild dogs pack size has indeed been found to be positively related to the production and survival of pups (Malcolm and Marten 1982, Vucetich and Creel 1999, Courchamp and Macdonald 2001, Rasmussen 2009). A minimum pack size of approximately six individuals seems to be necessary for successful reproduction, when packs become smaller than this critical size their capacity to maintain themselves is jeopardized (Courchamp and Macdonald 2001, Courchamp et al. 2002, Rasmussen et al. 2008, Rasmussen 2009). As a result of Allee effects, social species, particularly obligate co-operators like the African wild dog, will be especially vulnerable to extinction (Courchamp et al. 1999, Stephens and Sutherland 1999, Brassil 2001, Burec et al. 2006).

African wild dogs were formerly distributed throughout the biggest part of sub-Saharan Africa. These days they have disappeared from most of their former home range and there are fewer than 8000 African wild dogs left in the wild (Hunter et al. 2010) (Figure 2). With an acceleration in their decline over the last thirty years, African wild dogs have become one of Africa’s rarest carnivores and consequently are red listed by the International Union for the Conservation of Nature (IUCN) as endangered (McNutt et al. 2008). African wild dogs represent a unique lineage within the wolf like canids (Girman et al. 1993) (Figure 1) and, as a result of this phylogenetic distinctiveness, they have a high conservation value (Woodroffe et al. 1997).

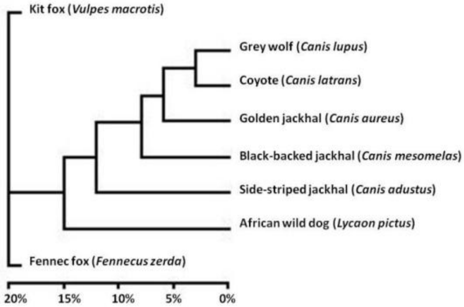

Figure 1. Taxonomy of African wild dogs and related canid species (Girman et al. 1993).

Zimbabwe is among the few countries that hold African wild dog populations larger than 100 individuals (Fanshawe et al. 1991, Woodroffe et al. 1997, 2004) (Figure 2). Over the past century, like in other African countries, the African wild dog population in Zimbabwe has declined (Rasmussen 1997, Zimbabwe Parks and Wildlife Management Authority 2009). In 1997 it was estimated that there were approximately 700 African wild dogs in Zimbabwe (Rasmussen 1997) at present the population is believed to number around 520 individuals (Zimbabwe Parks and Wildlife Management Authority 2009). In particular in and around Hwange National Park, an area of 20 000 km^2 that used to harbour a viable population (a population size which guarantees local population persistence and the avoidance of inbreeding (Lehmkuhl 1984, Hanski et al. 1996)), a sharp decline in the population has been documented. In 1997 it was estimated that African wild dog numbers in and around Hwange National Park ranged between 150 and 225 individuals (Rasmussen 1997, Woodroffe et al. 1997). These days the population is believed to exist of approximately 50 to 70 individuals (Zimbabwe Parks and Wildlife Management Authority 2009, Blinston 2010). With a minimum viable pack size of six individuals (Courchamp and

Macdonald 2001, Courchamp et al. 2002, Rasmussen et al. 2008, Rasmussen 2009) this potentially leaves Hwange National Park with eight to twelve breeding units only.

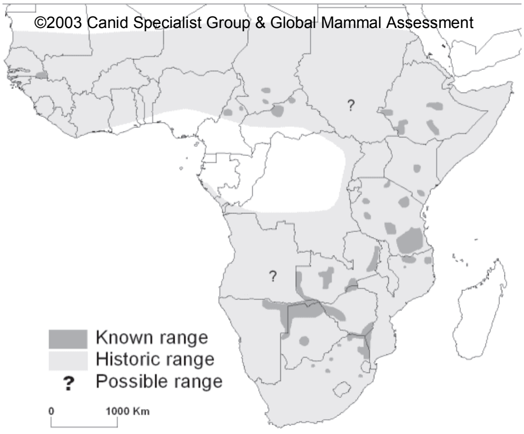

Figure 2. Historic range and current distribution of African wild dogs (*Lycaon pictus*) (Woodroffe et al. 2004).

Hwange National Park is situated in the northwest of Zimbabwe (19°00'S, 26°30'E). The Hwange region is classified as semi-arid. Over the last century mean annual rainfall has been 606 mm, with a wet season from October to April. During the dry season surface water is primarily restricted to artificial waterholes. Vegetation consists of scattered woodland scrub mixed with grassland. Prey species present include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), the natural competitors of African wild dogs (Mills and Gorman 1997, Creel 2001), occur in Hwange National Park and the areas surrounding the park. African wild dogs exist in a wide range of habitats (Fanshawe and Fitzgibbon 1993, Mills and Gorman 1997, Creel and Creel 2002) and, in theory, could be distributed throughout the biggest part of Hwange National Park. However, the distribution of permanent surface water in the National Park is likely to impose a constraint. When Hwange National Park was founded there were no permanent sources of surface water in the park, it was therefore decided to create artificial waterholes by pumping underground water to create a year round water supply (Davidson 1967). Most of these waterholes (90%) can be found along the northern boundary of the National Park (Valeix 2006). In arid and semi-arid savannah systems large herbivores are generally more abundant in the vicinity of waterholes (du Toit et al. 2003, Redfern et al. 2003, Valeix et al. 2009[a]). An aggregated distribution of prey around waterholes will inevitably affect the movement of predators. Lions in Hwange National Park have indeed been found to reduce their search effort by selecting areas within 2 km from waterholes (Valeix et al 2009[b]). With an aggregated distribution of prey around waterholes it is likely that African wild dogs, like lions, will try to maximise their search efficiency by spending most of their time in the vicinity of waterholes. With the majority of the permanent waterholes being situated along the northern boundary, it is likely that the largest part of the African wild dog population can be found along this northern National Parks boundary.

Along the northern boundary of Hwange National Park African wild dogs regularly range beyond the National Park border into the buffer zone (Rasmussen 1997). Land use in this buffer zone can be divided into trophy hunting and photographic safaris (44%) (Forestry commission and FC safari area), trophy hunting and cattle (23%) (commercial farms), trophy hunting only (10%) (commercial farms), communal area (4%) (stateland) and pure cattle ranging (20%) (commercial farms). The main tar road from Bulawayo to Victoria Falls runs along the northern boundary of the Park (Figure 3).

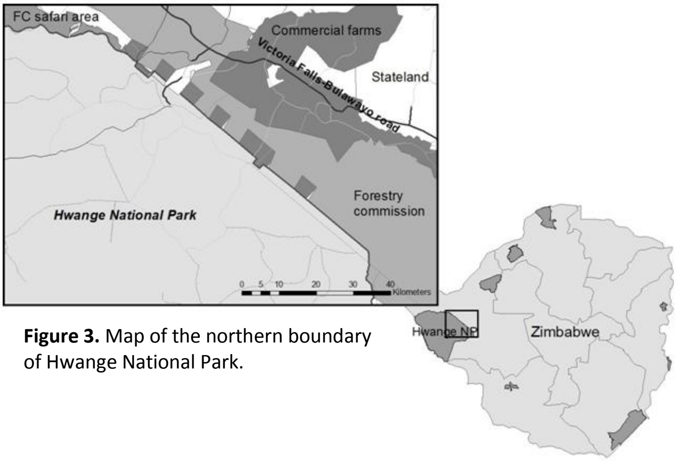

Figure 3. Map of the northern boundary of Hwange National Park.

African wild dogs in the Hwange system seem to suffer from an 'edge effect' around the Hwange National Park border. Particularly in the buffer zone along the northern edge of the park snares and road traffic seem to be a main cause of mortality (Rasmussen 1997, Woodroffe et al. 1997). Due to the strong positive relationship between pack size, survival and reproduction (Creel and Creel 2002, McNutt and Silk 2008), the loss of a single individual can be detrimental for an entire pack of African wild dogs (Courchamp and Macdonald 2001, Rasmussen 2009). A pack in which membership drops below a size of six individuals may be caught in a positive feedback loop: poor reproduction and low survival further reduce pack size, culminating in failure of the whole pack (Courchamp and Macdonald 2001, Courchamp et al. 2002, Rasmussen et al. 2008, Rasmussen 2009).

For predators the optimal choice for habitat depends on the density of prey and the search efficiency in each habitat (Fryxell 1997, Morris 2003). Predators have been shown to select habitat according to prey densities (Litvaitis et al. 1986, Murray et al. 1994, Spong 2002, McCarthy et al. 2005). Higher densities of prey are generally believed to result in a higher search efficiency due to higher encounter rates (Norberg 1977, Draulans 1987). For a predator, searching for prey is not the only component of foraging though; chase and capture of prey are an essential part as well. If a predator is able to approach its prey at closer distances this generally reduces chase distances and increases the likelihood of a kill (Reich 1981, Fitzgibbon 1988, Hilton et al. 1999). Several studies have shown that, regardless of prey densities, predators prefer habitat in which, due to specific biotic and abiotic landscape attributes, prey is easier to catch (van Dyk and Slotow 2003, Rhodes and Rhodes 2004, Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007). Another factor likely to play a role in habitat selection is predator interactions. Predator-prey studies are often based on a three trophic level system where predators forage free from predation risk while in fact predator-prey interactions regularly take place at a four trophic level system in which intermediate predators face a trade off between obtaining food and being safe (Mukherjee et al. 2009). Interactions between intermediate and top predators can have direct effects in the form of kleptoparasitism or intraguild predation or indirect effects in the form of resource competition and active avoidance (Caro and Stoner 2003). Interactions with top predators are therefore likely to affect habitat choice of intermediate predators (Mills and Gorman 1997, Fedriani et al. 1999, Creel 2001, van Dyk and Slotow 2003).

Animals rely on environmental cues to assess habitat quality from the true quality of the environment in order to choose a suitable habitat (Schlaepfer et al. 2002, Kristan 2003). Sudden environmental changes might cause these formerly reliable cues to be no longer associated with adaptive outcomes, causing animals to make a maladaptive habitat selection (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Kristan 2003, Gilroy and Sutherland 2007, Pärt et al. 2007). When an animal shows a preferential choice for a habitat in which its reproductive success or adult survival is less than in other available habitat it is said to have been caught in an ecological trap (Kokko and Sutherland 2001, Kolbe and Janzen 2002, Schlaepfer et al. 2002, Kristan 2003, Schlaepfer 2003, Battin 2004, Robertson and Hutto 2006, Gilroy and Sutherland 2007, Pärt et al. 2007). Ecological traps have been observed in both natural and human altered settings, and are an inevitable result of the rapid changes that occur in natural landscapes worldwide (Schlaepfer et al. 2002, Robertson and Hutto 2006, Gilroy and Sutherland 2007). Human activity can result in an ecological trap when it reshapes appearance and biological functioning. For example hunting can change a habitat into a trap by increasing adult mortality (Delibes et al. 2001), or human modifications of a nesting habitat can lead to maladaptive nest site selection resulting in a reduced reproductive rate (Kolbe and Janzen 2002).

Until recently, ecological traps were considered a kind of source-sink system where an ecological trap was defined as an attractive sink. Source-sink theory cannot fully describe ecological traps or predict their consequences for a population though, as it does not model maladaptive habitat choice (Kristan 2003). Habitat choice behaviour is beneficial in source-sink systems, but detrimental in ecological traps. In general sinks are less catastrophic to populations than ecological traps as, unless poor habitat is extremely abundant relative to good habitat, the presence of poor habitat is neutral or beneficial (Kristan 2003, Battin 2004). A favourite habitat can act not just as a mortality sink but as an ecological trap when animals originally occupying source habitats migrate to replace conspecifics that have died (Kristan 2003, Battin 2004). In this case sink populations can be temporarily sustained by the source before resulting in a rapid collapse of the whole system. Landscapes that, viewed in a source-sink framework, would be expected to support a stable population may instead lead to extirpation of a population if sinks are actually traps (Delibes et al. 2001, Kokko and Sutherland 2001, Gilroy and Sutherland 2007). Although sinks and ecological traps have very different consequences at a population level they differ only in the ability of organisms to judge habitat quality accurately. Sources have been distinguished from sinks based on whether populations are net exporters or importers of recruits (Pulliam 1988, Morris 1991, Donovan et al. 1995, Dias 1996, Holt 1997). This would also differentiate sources from ecological traps. To be able to distinguish a sink from an ecological trap additional knowledge of the relationship between preference and habitat quality is required (Kristan 2003). Within a classic source-sink system animals will show a preferential choice for the high quality source habitat and will only move into the sink when the source has reached its maximum density (Kristan 2003). Within an ecological trap animals will show a preferential choice for low quality sink habitat based on sound ecological cues that are no longer associated with an adaptive outcome, and will move into the sink regardless of the density in the source (Kokko and Sutherland 2001).

In this study we tried to determine whether African wild dogs prefer to establish territories in the northern buffer zone outside Hwange National Park. We investigated what effect territory placement had on natality, mortality and recruitment and whether territory placement in the buffer zone resulted in exposure to an ‘edge effect’. Based on these findings we tried to determine whether the buffer zone outside Hwange National Park is more likely to serve as a mortality sink or as an ecological trap and what ecological cues are likely to be used in habitat selection by African wild dogs in the Hwange system.

The impact of diseases on African wild dog populations is believed to have been underestimated and might be particularly severe in small populations (Woodroffe et al. 2004). There are several pathogens that are known to affect free ranging populations of African wild dogs (Woodroffe et al. 1997). Both rabies and canine distemper virus are diseases known to cause high mortality in African wild dogs and there are several examples where rabies has led to rapid extirpation of the population (Kat et al. 1995, Woodroffe et al. 1997, 2004). Although some African wild dog populations in Zimbabwe have been severely affected by rabies (R.Groom, Lowveld Wild Dog Project; pers. comm.) the decline in the African wild dog population in and around Hwange National Park is unlikely be explained by diseases like rabies and canine distemper virus. Over the past two decades only one case of rabies has been reported in a free ranging African wild dog and no cases of canine distemper virus have been observed in the area (P.Blinston, Painted Dog Conservation project; pers. comm.). Within this study we have therefore not taken these diseases into account.

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Structure thesis

Testing the ecological
trap hypothesis
for
African wild dogs
in and around
Hwange National Park

Structure of the thesis

Territorial drift

In chapter 1, I present a study on territory placement of African wild dogs in and around Hwange National Park and its effect on reproduction and survival. I use historical position data of African wild dog packs to determine whether there is an active preference to establish territories in the buffer zone surrounding the northern edge of the park. Data on reproduction and survival are combined with data on territory placement to see what effect territory placement has on recruitment, whether territory placement in the buffer zone outside the park results in exposure to an 'edge effect' and whether the Hwange system is likely to serve as an ecological trap.

Ecological cues

In chapter 2, 3, 4 and 5 I look at the relationship between habitat quality and preference. I try to determine whether there are differences in the main ecological cues likely to be used by African wild dogs in their habitat selection that could explain the observed habitat preference.

Prey

In chapter 2, I look at foraging efficiency of African wild dogs inside and outside Hwange National Park. Within this study I use historical data on hunt follows of African wild dogs and look at the main aspects of hunting in order to see whether differences in prey availability and prey catchability could explain African wild dog habitat preference. Within this study I take vegetation density inside and outside Hwange National Park into account.

In chapter 3, I present a study on anti predator behaviour of kudus and impalas, the main prey species of African wild dogs, when mimicking predation risk by African wild dogs. This study allowed me to determine whether differences in anti predator behaviour of prey could potentially affect foraging efficiency of African wild dogs inside and outside Hwange National Park.

Predator competition

In chapter 4, I look into predator competition with lions and spotted hyenas by using historical empirical data on hunt follows of African wild dogs and experimental data of additional call ups with the sounds of African wild dogs. I try to determine whether interspecific competition with these predators is directly related to their densities and whether differences in the risk and costs of kleptoparasitism could affect African wild dog habitat choice.

In chapter 5, I investigated whether interspecific competition with lions and spotted hyenas plays a role in den site selection by African wild dogs and whether den site availability could play a role in habitat selection. I studied vegetation characteristics around former den sites inside Hwange National Park, where large predator densities are relatively high, and outside the National Park, where large predator densities are lower. I compared den sites with random sites to see what characterises an African wild dog den and looked at the spatial distribution of features that could potentially play a role in den site selection like distance to roads and waterholes.

Ecological trap

In chapter 6, I use an energy cost benefit approach in order to try and explain habitat selection. I look at territory sizes to investigate whether there might be differences in the availability and distribution of resources and translate the different components of the hunt and interspecific competition into energetic costs in order to be able to compare costs and benefits inside and outside Hwange National Park. Based on these calculations I determine whether the ecological cues used to select habitat lead to a maladaptive habitat choice leaving the African wild dogs in the Hwange system ecologically trapped.

Chapter 1

Territorial drift into an attractive sink and its consequences for the reproduction and survival of African wild dogs

Chapter 1

Territorial drift into an attractive sink and its consequences for reproduction and survival of African wild dogs

Ester van der Meer, Hervé Fritz, Peter Blinston, Gregory S.A. Rasmussen

Abstract

Protected areas are often not vast enough to maintain large populations of wide ranging carnivores. Hence, these carnivores regularly move outside protected areas where they get exposed to human activity resulting in mortality. Such an ‘edge effect’ around protected areas seems to have resulted in a rapid population decline of the endangered African wild dog. Data from 15 radio collared African wild dog packs were used to examine whether African wild dogs in Hwange National Park, Zimbabwe, also experienced an ‘edge effect’ and whether the buffer zone outside the National Park could act as an attractive sink, also known as an ecological trap. Over the years African wild dog packs moved their territories closer to or over the Hwange National Park border. An increase in distance from the border outside the National Park increased reproductive success but also increased mortality within packs. Between 1989 and 2009, 327 African wild dogs were reported dead. Most of these deaths (71.6%) occurred in the buffer zone outside the park and human activity was the main cause of death (Inside Hwange National Park; road traffic 5.4%, Outside Hwange National Park; snares 25.6%, road traffic 12%, shot 18.8%). As in the buffer zone outside the park mortality exceeded natality there was no recruitment and African wild dog packs fell apart below the critical size necessary for successful reproduction. Larger litter sizes outside the park indicate that the buffer zone is likely to serve as an ecological trap with fitness enhancing factors attracting African wild dogs to the sink area where they are incapable to perceive the higher mortality risk caused by an ‘edge effect’. The speed at which the African wild dog population in and around Hwange National Park has declined (1997; 150-225 individuals, 2009; ± 50-70 individuals) supports this theory. As ecological traps can cause rapid extinction of a species this finding has important implications for African wild dog conservation and shows the need for conservation efforts to range beyond the borders of protected areas.

Key words: *African wild dog, ecological trap, habitat selection, edge effect, attractive sink, protected area, reserve border, wide ranging carnivore*

Status: submitted (*Animal Conservation*)

Introduction

An increase in the human population worldwide has resulted in fragmentation of habitat available to wildlife, thus forcing animals to live in close proximity to humans. Protected areas are often not big enough to maintain large populations and particularly wide ranging carnivores regularly range beyond reserve borders. By crossing reserve borders into unprotected areas animals inevitably get increasingly exposed to human activity. In many cases this exposure results in mortality, as requirements of carnivores often conflict with those of humans. This 'edge effect' may turn border areas of reserves into population sinks. Previous research has shown that these human created 'edge effect' sinks largely contribute to the extinction of wide ranging carnivores (Woodroffe and Ginsberg 1998).

Within a classic source-sink system surplus animals from the high quality source habitat immigrate into low quality sink habitat where mortality exceeds natality (Pulliam 1988). Animals rely on environmental cues to assess habitat quality in order to choose a suitable habitat. Sudden natural or human induced changes might cause formerly reliable cues to be no longer associated with adaptive outcomes, causing animals to make a maladaptive habitat choice (Kolbe and Janzen 2002, Kristan 2003). When animals shows a preferential choice for a habitat in which their reproductive success or adult survival is less than in other available habitat they are said to have been caught in an ecological trap (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006, Pärt et al. 2007). Ecological traps are different from classic source-sink systems. In a source-sink system habitat choice is advantageous as animals prefer to be in high quality source habitat (natality>mortality) and only move into low quality sink habitat (natality<mortality) when there is not enough high quality habitat available. In an ecological trap habitat choice is disadvantageous as animals living in high quality source habitat actively choose to be in low quality sink habitat and migrate to replace dead conspecifics (Kristan 2003, Battin 2004). In this case sink populations can be temporarily sustained by the source before resulting in a rapid collapse of the whole system (Kristan 2003).

One of the wide ranging carnivores for which a human created 'edge effect' sink around reserves has resulted in a rapid population decline is the African wild dog (*Lycaon pictus*). African wild dogs were formerly distributed throughout the biggest part of sub-Saharan Africa. These days African wild dogs have disappeared from most of their former home range and there are fewer than 8000 African wild dogs left in the wild (Hunter et al. 2010). With an acceleration in its decline over the last thirty years, the African wild dog has become one of Africa's rarest carnivores and consequently is red listed by the International Union for the Conservation of Nature (IUCN) as an endangered species. One of the main reasons for the decline in African wild dog numbers are human prosecution and habitat loss due to human encroachment (Woodroffe et al. 1997, 2004). The decrease of the African wild dog population is accelerated by the fact that, due to their sociality resulting in a positive relationship between aspects of fitness and pack size, African wild dogs are susceptible for the Allee effect (Courchamp et al. 2000). If an Allee effect is strong, population growth will be negative when individuals become rare. As a result of Allee effects, social species, particularly obligate co-operators like the African wild dog, will be especially vulnerable to extinction (Courchamp et al. 1999, Stephens and Sutherland 1999, Brassil 2001, Burec et al. 2006).

Zimbabwe is one of the few countries that hold an African wild dog population greater than 100 individuals (Fanshawe et al. 1991, Woodroffe et al. 1997). Over the past century, like in other African countries, the African wild dog population in Zimbabwe has declined (Childes 1988, Rasmussen 1997, Zimbabwe Parks and Wildlife Management Authority 2009). In 1997 it was estimated that there were between 150 and 225 African wild dogs in and around Hwange National Park, one of the few areas in Zimbabwe harbouring a viable population of African wild dogs (Rasmussen 1997, Woodroffe et al. 2004). Nowadays the population in this area is believed to exist of approximately 50 to 70 individuals (Zimbabwe Parks and Wildlife Management Authority 2009, Blinston 2010). In this study we tried to determine the main reasons for this decline, we examined whether African wild dogs in Hwange National Park experienced an 'edge effect', what effect territory placement had on recruitment and whether the buffer zone outside the park served as an attractive sink, also known as ecological trap. Only a few empirical studies have been able to show the existence of an ecological trap (Robertson and Hutto, 2006) and most of these studies were conducted on birds. To our knowledge this is one of the first carnivore studies in which we empirically try to identify an ecological trap.

Method

Study area

Hwange National Park covers approximately 15 000 km^2 in the northwest of Zimbabwe (19°00'S, 26°30'E). The Hwange region is classified as semi-arid. Over the last century mean annual rainfall has been 606 mm, with a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Prey species present include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), the natural competitors of African wild dogs (Mills and Gorman 1997, Creel 2001), occur in the study area. Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the park is designated for trophy hunting and to a lesser extent for photographic safaris. Most of this land is privately owned or state owned and managed by Forestry Commission. The main tar road from Bulawayo to Victoria Falls runs through part of the study area (Figure 1).

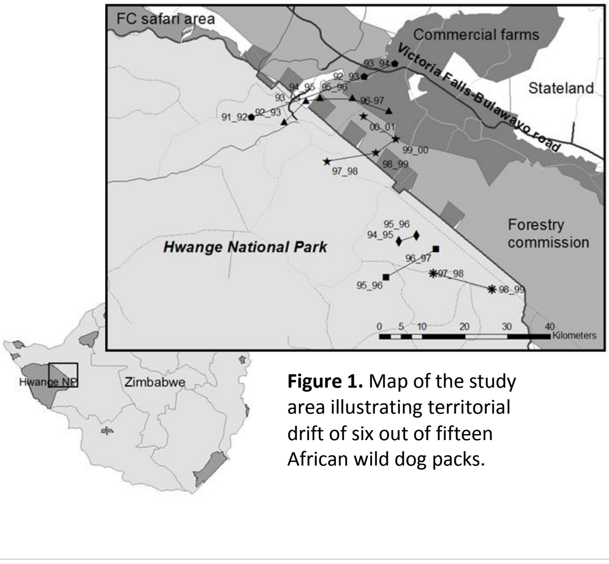

Figure 1. Map of the study area illustrating territorial drift of six out of fifteen African wild dog packs.

Data collection

Data were collected by G.S.A. Rasmussen, with the use of radio tracking and opportunistic independent observations. Individual African wild dogs were identified using their unique coat markings. In this study data from 15 radio collared African wild dog packs were used. These data were collected between 1991 and 2002, with an average study duration of 29.5 ± 20.1 months (mean ± SD) per pack. As soon as a pack had been located it was monitored continuously from a distance of ≥ 50m for as long as practically feasible (max 28 days). Activity was monitored visually or from motion sensors incorporated in the radio collars. Activity patterns were recorded at 5 min scan intervals. Whenever a change in activity mode or direction occurred location fixes were taken by using triangulation or visual observations and a GPS unit.

Packs were followed for successive years and pack sizes, litter sizes, immigration, dispersals and deaths were recorded. African wild dogs in and around Hwange National Park reproduce during the coldest period of the year, with pups being born around May/June. To analyse the data, yearly periods were defined starting with the denning season in May/June and ending just before the denning season of the following year. Age of individual African wild dogs was classified as follows; adult ≥ 2 years old, yearling ≥ 1 year and < 2 years old, pups < 1 year old. For an overview of African wild dog mortality over the years, the data from the known individual packs as well as data based on sightings and reports between 1989 and 2010 were used.

Statistical analysis

For each pack all position data for a given year were plotted with the use of ArcGis® version 9.3. If there were several points for a given day, the centroid of these points was taken to avoid pseudo replication. The activity centres were determined per pack per year by using the centroid of 95% minimum convex polygons and, based on the method used by Tolon et al. (2009), by using the average of the X and Y coordinates of the position data for that given year. For each sequential year the distance from the activity centres to the National Park border was determined. As the two methods used did not differ in the distance of the activity centres to the National Park border ($F_{(1,91)}=0.07$, $p=0.797$), and it is generally believed that the use of minimum convex polygons should be avoided in ecological studies as they create unpredictable bias (Burgman and Fox 2003, Borger et al. 2006), the activity centres and distances to the border based on the average of the X and Y coordinates were used for analyses.

Distances to the border were linked to pack size, reproductive success and mortality rates based on years. Distances inside Hwange National Park were marked as positive values, distances outside Hwange National Park were marked as negative values (Tolon et al. 2009). This way a gradient was created with a decrease in distance the further a pack would move outside the National Park. Because for different packs data were collected over several different years a new variable was created by, for each pack, numbering sequential years.

A linear mixed model was used to analyse whether over succeeding years the distance to the border became increasingly smaller. To control for possible pseudo replication due to the fact that some packs were followed over more sequential years than others, we added individual pack identity as a random effect in the analysis. Pack size in relation to distance to border was analysed with the use of a linear regression model with pack size as the dependent variable and distance to the border as an explanatory variable. In order to analyse reproductive success in relation to distance to the border, a linear regression model with pups born as the dependent variable and pack size and relative distance to the border as explanatory variables was used. A logistic regression model was used to analyse overall mortality rate in relation to distance to the border. Mortality causes were analysed by displaying the frequencies in a contingency table and using a Pearson's Chi-square test to see whether there was a significant relationship between inside or outside Hwange National Park, and human or natural caused mortality.

All statistical analyses were performed using SPSS software for MS Windows release 16.0 (SPSS Inc, Chicago, USA).

Results

Over the years African wild dogs inside the National Park moved their territories closer to or over the Hwange National Park border (B=-3.49, SE=1.24, t=-2.81, p=0.007). African wild dogs staying in Hwange National Park eventually ended up with a territory in the buffer zone outside the National Park (Figure 1, 2). Pack size was not significantly affected by distance to the border (B=0.06, SE=0.05, t=1.28, p=0.209) but the amount of offspring produced became higher with an increase in pack size (B=0.46, SE=0.20, t=2.30, p=0.026) and decreased with an increasing distance inside the National Park (B=-0.20, SE=0.06, t=-3.37, p=0.002) (Figure 3). African wild dogs with a territory outside Hwange National Park thus produced more pups but the likelihood of mortality also became significantly higher with an increase in distance from the National Parks border (SE=0.10, z=-6.14, p<0.001) (Figure 4).

From 1989 up to 2010, 327 African wild dogs were reported dead. To put this into perspective and give an indication of the significance of this loss; the population at the start of this period was estimated to be between 100 and 150 individuals only (Childes 1988). The majority of the deaths, 71.6%, occurred in the buffer zone outside Hwange National Park at a ratio of 1 dead individual inside Hwange National Park against 2.5 dead individuals outside the National Park. Humans directly caused the death of 61.8% of the reported dead African wild dogs, and caused the death of 73.3% of the reported dead African wild dogs if the indirect effects were accounted for: pups and yearlings that died of starvation due to the fact that adults were killed by humans (Table 1).

Table 1. Reported dead African wild dogs from 1989 up to 2010 in and outside Hwange National Park (HNP).

		Snare	**Road traffic**	**Shot**	**Lions & Hyenas**	**Starvation**	**Natural**	**Un-known**	**Total**
Inside HNP	%	0.0%	5.4%	0.0%	17.2%	12.9%	20.4%	44.1%	28.4%
	nr	0	5	0	16	12	19	41	93
Outside HNP	%	25.6%	12.0%	18.8%	3.9%	11.5%	9.8%	18.4%	71.6%
	nr	60	28	44	9	27	23	43	234

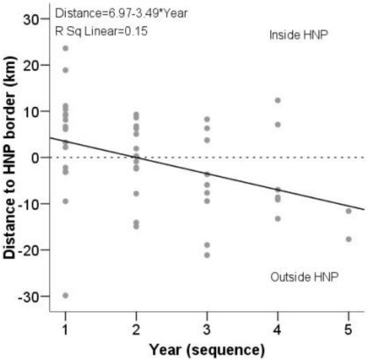

Figure 2. Yearly change in distance of African wild dog territories from the Hwange National Park (HNP) border.

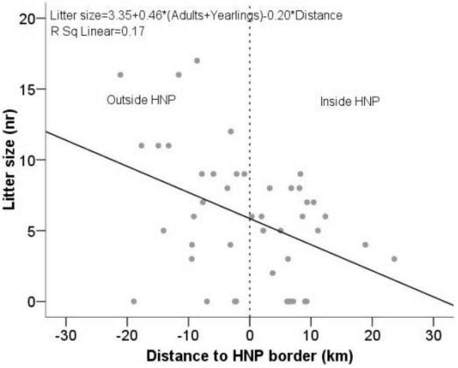

Figure 3. Number of pups born in a litter for a pack of six dogs in relation to distance of the territory to the Hwange National Park (HNP) border.

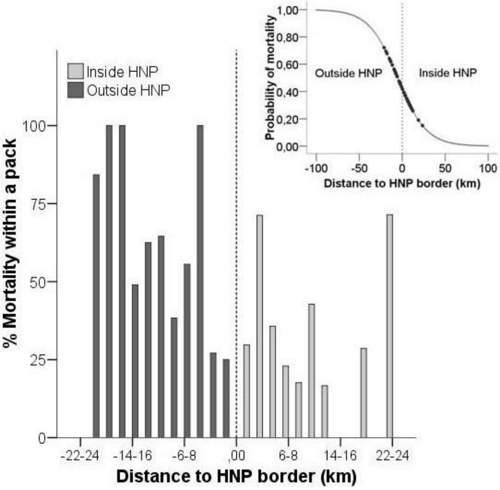

Figure 4. Mean percentage of mortality within an African wild dog pack in relation to the distance of the territory to the Hwange National Park (HNP) border, insert represents the logistic regression model of the probability of mortality in relation to distance to the HNP border.

There was a significant association between inside or outside the National Park and whether or not mortality was caused by human or natural circumstances ($\chi^2=100.99$, $p<0.001$). Based on the odds ratio, the odds of mortality caused by humans were 46.71 times higher outside the National Park indicating an 'edge effect' in the area outside Hwange National Park. Even though the number of pups born outside Hwange National Park was higher, the overall mortality of African wild dogs was so high that there was effectively no recruitment and packs fell apart in groups far below the minimal pack size of six individuals, necessary for successful reproduction (Courchamp and Macdonald 2001, Courchamp et al. 2002, Rasmussen et al. 2008) (Table 2). Both results could well explain the absence of recruitment within the Hwange system (Table 2).

Table 2. Average recruitment for a reproductive year in relation to placement of territory in, at the border or outside Hwange National Park (HNP).

Location territory		Pack size start*	Pups born	Mortality pups	Mortality ad/yy	Immigration	Dispersal	Pack size end*	Recruitment
Inside HNP	Mean	**4.94**	**4.11**	**2.06**	**0.50**	**0.00**	**0.50**	**6.00**	**1.06**
(n=18)	SE	0.57	0.74	0.49	0.17	0.00	0.29	0.84	0.49
Border	Mean	**4.97**	**4.88**	**2.55**	**1.48**	**0.39**	**1.21**	**5.00**	**0.03**
(n=33)	SE	0.42	0.71	0.44	0.37	0.24	0.32	0.51	0.56
Outside HNP	Mean	**5.23**	**7.23**	**4.54**	**2.54**	**0.23**	**2.00**	**3.62**	**-1.62**
(n=13)	SE	1.09	1.73	1.25	0.87	0.12	1.12	0.82	1.34
Total	Mean	**5.02**	**5.14**	**2.81**	**1.42**	**0.25**	**1.17**	**5.00**	**-0.02**
(n=64)	SE	0.34	0.56	0.38	0.27	0.13	0.29	0.40	0.43

*) Mean pack size at the start of the reproductive year and the end of the reproductive year

Between 1989 and 2002 the full life history of twenty African wild dog packs in the study area was documented, fifteen of these packs extirpated of which eleven known to be due to human caused mortality. Although detailed information about pack sizes and territorial movement were mainly collected between 1989 and 2002, individual observations show that up to date the problem of maladaptive habitat choice still exists. Just over the year 2009, 3429 snares were collected in the buffer zone around Hwange National Park (Blinston 2009). In August 2009 a pack of seven African wild dogs was released inside Hwange National Park. The pack moved out of Hwange National Park and within less than three months was extirpated, two African wild dogs were killed on the main road, two were killed by snares, one dispersed, one individual was never seen again and presumed dead, one African wild dog was recaptured. A similar scenario occurred in October 2006 when a pack of eleven African wild dogs was released from the Painted Dog Conservation facilities. The pack established a territory outside Hwange National Park, within three months the first individuals were killed by snares. Of the eleven African wild dogs released, five died in snares, one individual was seriously injured by a snare and had to be recaptured to recover, two individuals were killed by lions, two of the three remaining African wild dogs died for unknown reasons, one individual was recaptured.

Discussion

With the persistent loss of African wild dogs in the buffer zone outside Hwange National Park and the population size as low as it is now, it is critical to be able to determine whether the area outside Hwange National Park serves as a classic sink or as an ecological trap as landscapes that, viewed in a source-sink framework, would be expected to support a stable population may instead lead to extirpation of a population if sinks are actually traps (Delibes et al. 2001, Kokko and Sutherland 2001, Gilroy and Sutherland 2007).

In order to be able to identify an ecological trap Robertson and Hutto (2006) suggested to use three criteria: 1) Individuals have to show a preference for one habitat over the other or an equal preference, 2) There has to be a measure that allows the identification of differences in fitness among habitats, 3) The fitness outcome for individuals settling in the preferred habitat must be lower than in the other available habitat. Following these criteria, the results of this study suggest that African wild dogs in Hwange National Park have been caught in an ecological trap: 1) Over the years they moved closer to or over the Hwange National Park border indicating a preference to establish territories outside the protected area, 2) In the buffer zone outside the National Park African wild dog packs seemed to experience a higher fitness as they gave birth to larger litters, 3) Due to human activity resulting in an 'edge effect', mortality outside the park exceeded natality resulting in no recruitment and ultimately a population decline.

It seems that Hwange National Park serves as an ecological trap with fitness enhancing factors attracting African wild dogs to the sink area outside the park where they are incapable of perceiving the higher mortality risk caused by an 'edge effect'. The rapid population decline supports this theory; in just five years time (2004-2009) the African wild dog population in and around Hwange National Park has been reduced with more than 75% (Woodroffe et al. 2004, Zimbabwe Parks and Wildlife Management Authority 2009). This fast reduction is likely to be the result of a collapse of the system due to a maladaptive habitat choice for trap habitat, accelerated by the so called Allee effect, where population growth becomes negative when individuals become rare (Courchamp et al. 2000).

Robertson and Hutto (2006) described several circumstances under which an ecological trap may occur: 1) The attractiveness of a habitat increases while the quality remains the same, 2) The quality of a habitat decreases without a loss in attractiveness, 3) The attractiveness of a habitat increases while at the same time the quality decreases. The Hwange system is most likely to follow scenario three, where the attractiveness of the habitat outside the National Park has increased, in our case resulting in a higher reproductive success, while the quality decreased, resulting in no recruitment due to a higher mortality rate because of human induced changes like poaching and shooting. The increased attractiveness of the habitat outside the National Park could either be a direct increase or a relative indirect increase due to a (natural) decrease in attractiveness of the habitat inside the National Park.

As ecological traps can cause extirpation of a population, they have obvious management implications. The rate at which extirpation takes place is first of all determined by the initial population size and second of all by the ability of animals to adapt to a changing environment. Time plays a vital role; the less time animals have to adapt to changes in the environment the more likely they are to make maladaptive habitat choices (Schlaepfer et al. 2002, Battin 2004, Gilroy and Sutherland 2007). In order to conserve a species, the attractiveness of a trap can be decreased by removing the cues on which the maladaptive habitat choice is based or by increasing the quality of the trap habitat in such a way that there will be a positive population growth rate (Donovan and Thompson 2001, Battin 2004). Another possibility is to focus on alternative habitat by introducing appropriate cues used for habitat selection into suitable but unoccupied areas (undervalued resources) (Gilroy and Sutherland 2007). In order to adequately conserve a population there is a need to ensure that cues for habitat choice correctly correlate with quality (Kokko and Sutherland 2001), because as long as there is a mismatch between habitat preference and habitat quality simply conserving high quality habitat is not enough to prevent species from extirpation.

In order to develop an adequate conservation strategy to protect ecologically trapped species from extirpation additional knowledge of the relationship between preference and habitat quality is required. Two factors likely to affect the habitat choice of African wild dogs are hunting success and interspecific competition with lions and spotted hyenas. Although the relationship between prey densities, hunting success and African wild dog densities does not seem to be clear (Creel and Creel 1998), it has been shown that survival and reproductive success of African wild dogs depend on their ability to secure prey (Rasmussen et al. 2008, Rasmussen 2009). Chasing prey has been found to be extremely costly (Rasmussen et al. 2008) and even though the actual outcome of a hunt might not differ, the costs could differ substantially if chase distances are taken into account. It is likely that distribution of prey and factors associated to chase distances play a major role in the habitat selection of African wild dogs. Another important factor is interspecific competition. Several studies have shown that habitat choice of African wild dogs is affected by competition with lions and/or spotted hyenas (Mills and Gorman 1997, Creel and Creel 1998, Creel 2001, van Dyk and Slotow 2003). Lions and/or spotted hyenas are known to exclude African wild dogs from preferred habitat (Mills and Gorman 1997, Creel 2001), kill pups and adult African wild dogs (Ginsberg et al. 1995, Woodroffe et al. 1997) and steal their prey (Fanshawe and Fitzgibbon 1993, Carbone et al. 1997, Gorman et al. 1998). Additional studies will be necessary to determine which are the main cues African wild dogs used to establish territories outside Hwange National Park.

An ‘edge effect’ has been described for several wide ranging carnivores (Woodroffe and Ginsberg 1998). There are few empirical studies that have shown the existence of an ecological trap though (Robertson and Hutto 2006). Although an ‘edge effect’ has been described to turn reserve borders into mortality sinks (Woodroffe and Ginsberg 1998), this is one of the first studies that empirically identified the existence of an ecological trap for a carnivorous mammalian and shows that an ‘edge effect’ can turn reserve borders into ecological traps. As mortality sinks and ecological traps have different conservation implications there is a need for conservationists to be able to distinguish between the two. Although additional information about the settlement cues used for habitat selection are necessary to set up an adequate conservation strategy, this study does show the need to approach nature conservation with a broad view and not focus all conservation and research efforts on protected areas, as when mortality sinks are in fact ecological traps the buffer zone surrounding the protected area might be more crucial to the survival of the species than the protected area itself.

Acknowledgement

The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. In addition we would like to thank the Hwange National Parks and Wildlife Management Authority, the Natural History Museum of Zimbabwe, Forestry Commission, Touch the Wild, The Hide, Hwange Safari Lodge, Lions den enterprises, and the various farmers within the Gwaai Intensive Conservation Area for allowing us access onto their premises and supporting our fieldwork. We further thank Jealous Mpofu for assisting with the field work. We wish to thank Simon Chamaillé-Jammes and Marion Valeix for their fruitful comments on previous drafts. We thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation and the Painted Dog Conservation project.

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Chapter 2

Differences in foraging efficiency lead African wild dogs to make a maladaptive habitat choice

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Differences in foraging efficiency lead African wild dogs to make a maladaptive habitat choice

Ester van der Meer, Gregory S.A. Rasmussen, Justice Muvengwi, Hervé Fritz

Abstract

Previous research has shown that over the years the African wild dogs in Hwange National Park actively move their territories into the buffer zone outside the protected area. Although their reproductive success is higher outside the park, adult mortality due to human activity is so high it exceeds natality. Because of the high energetic output while hunting, foraging costs for African wild dogs directly affect their survival and reproductive success. It is therefore likely that the more successful reproduction in the areas outside Hwange National Park is related to a higher foraging efficiency in the buffer zone. In this study we used the data of hunt follows of 22 VHF collared African wild dog packs in order to see whether differences in foraging efficiency could explain African wild dog preference for the buffer zone outside the park. Diet composition, the number of hunts per day and foraging distance did not differ indicating that prey availability is similar inside and outside the National Park. Foraging efficiency nevertheless differed substantially due to more successful chases and shorter chase distances in the buffer zone outside the park. Several different predators have been found to actively select habitat with landscape attributes that makes prey easier to catch and it has been shown that for African wild dogs chase distances are reduced in low visibility habitat. Inside Hwange National Park kudu and impala kills tended to be made in high visibility habitat. The observed differences in hunting efficiency between the National Park and the buffer zone outside the park are thus likely to be attributed to differences in vegetation characteristics and it seems that African wild dogs preferentially select habitat in the buffer zone to increase their hunting efficiency.

Key words: *African wild dog, foraging efficiency, vegetation characteristics, habitat selection, prey availability, kill site, chase distance, hunting success*

Status: unpublished manuscript

Introduction

It is generally assumed that animals tend to optimize foraging behaviour because natural selection ultimately favours individuals that choose food that conveys the maximum net benefit. The foraging activities of carnivores can roughly be divided into two stages; the search for prey and the pursuit, capture and consumption of prey (Carbone et al. 2007). Due to the difficulty of capturing and subduing large prey the foraging costs for large carnivores are usually higher than for small carnivores making them more vulnerable to historic and future extinction (Carbone et al. 2007). Various parameters, like the energy obtained from the prey item and the time spend handling and searching for prey, affect foraging costs (Pyke 1984, Carbone et al. 2007).

Carnivores adopt both behavioural and ecological strategies to minimise foraging costs. Some carnivores show a preferential choice for sick or weak prey that is incapable of fleeing large distances (Reich 1981, Fitzgibbon and Fanshawe 1989, Pole et al. 2004). Some choose to attack prey that is non vigilant and therefore slower in their response and thus more likely to be killed upon attack (Fitzgibbon 1988). Others have been shown to actively select landscape attributes that increase their chances to capture prey (Hebblewhite et al. 2005, Hopcraft et al. 2005). For example, leopards (*Panthera pardus*) selected intermediate cover levels that allowed them to approach prey within charging distance herewith increasing the likelihood of a kill (Balme et al. 2007) and African wild dogs (*Lycaon pictus*) used barriers like game fences, rivers and dams to increase their hunting success and the possibility to hunt for large prey (van Dyk and Slotow 2003, Rhodes and Rhodes 2004).

African wild dogs are widely foraging carnivores that generally face extremely high hunting costs (Huey and Pianka 1981, Gorman et al. 1998, Rasmussen et al. 2008). The survival and reproductive success of African wild dogs depends both on their ability to secure prey and on minimising foraging costs (Rasmussen et al. 2008, Rasmussen 2009). One of the ways to reduce foraging costs is to hunt cooperatively. An increase in African wild dog pack size has been found to result in a decrease in chase distance and an increase in hunting success, prey mass and the likelihood of multiple kills (Creel and Creel 1995, Rasmussen et al. 2008). Once a chase has been initiated there seems to be no relationship between pack size and the likelihood of making a successful kill (Rasmussen et al. 2008). There exists a trade off between pack size and foraging time though, as with an increase in pack size foraging time increases as well. When pack size exceeds ten individuals the initial benefits of communal hunting have been found not to outweigh the extra foraging costs involved (Rasmussen et al. 2008).

Prey density in itself does not seem to affect African wild dog numbers or hunting success; African wild dogs are not more abundant in ecosystems with high prey densities and a comparison of data from different ecosystems showed that hunting success is similar in high and low prey density systems (Creel and Creel 1998). Like for other carnivores, habitat structure does seem to affect hunting efficiency. Although Fanshawe and Fitzgibbon (1993) found that in relatively open habitat the height of surrounding vegetation did not affect the probability of African wild dogs making a successful kill, cover does seem to affect hunting efficiency. Pursuing prey in thick habitat seemed to increase the likelihood of making a kill (Creel and Creel 2002), and African wild dogs were able to approach their prey at shorter distances in areas with low visibility compared to areas with high visibility resulting in smaller chase distances in the low visibility habitat (Reich 1981).

Previous research has shown that over the years the African wild dogs in Hwange National Park actively moved their territories closer to or into the buffer zone outside the

National Park (van der Meer et al. submitted (chapter1)). Although reproductive success in the buffer zone is higher there is effectively no recruitment due to the high rate of mortality caused by an increased exposure to human activity (van der Meer et al. submitted (chapter 1)). As survival and reproductive success of African wild dogs have been found to be directly related to foraging efficiency (Rasmussen et al. 2008), it is likely that differences in foraging costs play a role in the establishment of territories outside Hwange National Park. In this study we compare hunting success, chase distance, foraging distance, diet choice and quality of the kill inside and outside Hwange National Park in order to see whether differences in foraging efficiency could explain why African wild dogs prefer to establish territories outside the National Park. As habitat structure has been found to affect hunting efficiency (Reich 1981, Creel and Creel 2002), we take visibility around kill sites inside and outside the National Park into account in order to try to explain possible differences in hunting efficiency.

Method

Study area

Hwange National Park covers approximately 15 000 km^2 in the northwest of Zimbabwe (19°00’S, 26^{o}30’E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the park is designated for trophy hunting and to a lesser extent photographic safaris. Most of this land is privately owned or state owned and managed by Forestry Commission. Prey species present include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), the natural competitors of African wild dogs (Mills and Gorman 1997, Creel 2001), occur in the study area.

Hunt follows

Data from 22 radio collared African wild dog packs were collected by G.S.A Rasmussen between 1991 and 2002, with a study duration of 29.5 ± 20.1 months (mean ± SD) per pack. As soon as a pack had been located it was monitored continuously from a distance of ≥ 50m for as long as practically feasible (max 28 days). Activity was monitored visually or from motion sensors incorporated in the radio collars. Activity patterns were recorded at 5 min scan intervals. Whenever a change in activity mode or direction occurred location fixes were taken by using triangulation or visual observations and a GPS unit. A hunt period was defined as the period from rest to rest within which a pack was actively searching for prey. A chase was defined as the high speed pursuit of prey, chase distance was defined as the sum of all inter-fix distances during a chase, and a chase was considered successful when resulting in a kill. Only verified kills were included in the analysis. Hunt follows were classified as hunts inside or outside the National Park. Data were collected during two periods of a reproductive year; the denning season (when pups are too small to follow the pack on hunts and the pack needs to return to the den) and the nomadic season (when pups follow the pack on hunts). Previous analyses of cross sections and scale patterns of hairs extracted from faeces have confirmed that visual observations provided a reliable indicator of the consumption of smaller prey species (Rasmussen et al. 2008).

Vegetation characteristics

In order to determine in which way vegetation affected chase distances in the Hwange system we measured visibility around the most recent kill sites (1997 till 2002). Nevertheless there is a gap of a minimum of five years between the actual kill being made and this vegetation study. The main factors likely to cause a quick alteration of the vegetation structure in the Hwange system are elephants and bush fires. The distance between the kill sites measured inside Hwange National Park and the National Parks border was a maximum of 18.33 km. The maximum distance from the kill sites measured in the buffer zone outside the park and the border of the National Park was 22.98 km. As Hwange National Park is unfenced it is likely that, at these maximum distances, the magnitude of the impact of elephant and bush fires is similar inside and outside Hwange National Park. Of the 76 kill sites and 152 random sites only 4 were recently affected by fire and excluded from the analysis. Because of the time difference, the results should be interpreted with care. However, due to the robustness of the method used they do give an indication of possible differences in visibility between kill sites inside and outside Hwange National Park.

In total 41 impala kill sites were monitored; 26 inside the park and 15 in the buffer zone outside the park. For kudus, visibility was measured around 35 kill sites; 17 inside and 18 outside Hwange National Park. At each kill site visibility at the actual site was measured in the north, east, south and west direction by having one person sitting on the ground and letting another person walk away from this person using the GPS to measure the distance at which this person went out of sight. This was repeated at points at a random distance between 10 and 1000 meters from the kill site, in the north, east, south and west direction. The visibility figure around each kill site therefore consists of the mean of 20 measurements, 4 measurements at 5 different points, in order to give us a reliable indication of the visibility in the area in which the prey was chased and killed. Visibility around the kill site was classified into three categories, 0 to 25 m, >25 m to 50 m and >50 m. As the visibility around none of the kill sites fell into the 0 to 25 m category we simply ended up with two visibility categories; medium visibility (>25 m to 50 m) and high visibility (>50 m). General differences in visibility inside and outside Hwange National Park were determined by measuring the visibility at 148 random sites following the same method as described above. Random sites were selected by adding a random distance between 0 and 30 km to the X and Y coordinates of the kill sites, this was repeated twice per kill site.

Statistical analysis

Number of hunts per day and pack sizes

A Mann-Whitney U test was used in order to check whether the hunt follows inside and outside Hwange National Park were biased in terms of the number of hunts per day and the number of adults and yearlings in a pack, pups were not taken into account as they do not actively participate in the hunt. These analyses were performed for all prey species together and for the main prey species separately.

Diet

Diet composition was analysed by looking at the frequencies of the different prey species killed. We used a Pearson's Chi square test to test whether there were differences in the number of impalas, kudus and duikers in the diet inside and outside Hwange National Park. Pearson's Chi-square tests were also used to see whether, per species, there was a preferential selection for males or females and adults or juveniles. A binary logistic regression model was used to explore which variables determined the number of kudus versus impalas in the diet. A backwards step-wise selection procedure was used to remove variables for which $P > 0.05$. Variables added to the model were the number of adults and yearlings in the pack, whether the African wild dogs were denning or nomadic, whether the hunt took place inside or outside Hwange National Park, and whether the hunt took place in the morning, afternoon or at night. The interactions between pack size and whether the hunt took place inside or outside the National Park and time of hunt and inside or outside the National Park were taken into account as well.

As an indicator of the quality of the kill, it was determined whether the stomach capacity of the individuals in a pack was met or not. The estimated stomach capacity of African wild dogs is 9 kg (Creel and Creel 1995, Pribyl and Crissey 1999). To assess whether the stomach capacity of a pack was met or not met the number of individuals in a pack was multiplied by their stomach capacity taking seasonal differences into account. In the denning season the maximum capacity was calculated by multiplication of the number of adults and yearlings in a pack times 9 kg. In the nomadic season we added the number of pups times 9 kg divided by two to be conservative (following Creel and Creel 1995). Prey masses were obtained from Rasmussen et al. (2008). The maximum stomach capacity of a pack was subtracted from the prey mass. If this resulted in a negative number the pack was said not to have met its stomach capacity. If this resulted in a positive number the pack was said to have met its stomach capacity. We used a Pearson's Chi-square test to see whether there was a relationship between inside or outside the National Park and whether or not the stomach capacity was met.

Hunting success and distances

Which variables determined whether the outcome of a chase was successful or not was analysed with the use of a binary logistic regression model. A step-wise backwards procedure was used to remove variables that were not significant. Variables entered in the model were; the number of adults and yearlings in a pack, whether the hunt took place inside or outside Hwange National Park, whether the African wild dogs were denning or nomadic, and whether the hunt took place in the morning, afternoon or at night. The interaction between pack size and whether the hunt took place inside or outside the National Park was taken into account as well. The interactions between the time the hunt took place and whether the African wild dogs were hunting inside or outside Hwange National Park was added to the model to test for possible differences in activity pattern due to differences in land use. This analysis was performed for all prey species together, for the main prey species only and for kudus and impalas separately. Sample sizes for duikers were too small to perform a separate analysis. Sample sizes for pack sizes of twelve adults and yearlings and seventeen adults and yearlings were small ($n \leq 3$) and only included failed chases, as these observations created an artificial pack size effect they were left out of the analysis.

Chase distances were analysed with the use of linear mixed effects models using the same variables as in the model for the outcome of the chase. Pack identity was added as a random factor as the hunt follows include repeated observation of the same packs. A backwards selection procedure was used to successively remove variables for which $P > 0.05$. This analysis was performed for all chases and for successful and failed chases separately, for all prey species together, for the main prey species only and for kudus and impalas separately. Sample sizes for duikers were too small to perform a separate analysis. Whenever a significant interaction was found analyses were performed for inside and outside Hwange National Park separately with the variables; pack size, denning or nomadic and the time of day a hunt took place.

A linear mixed effects model with a backwards step-wise selection procedure was used to analyse foraging distance. A square root transformation was necessary to meet the normality assumption. The same variables were used in the model as those used in the model for the outcome of the chase and the chase distances, with pack identity as a random factor.

Vegetation

Vegetation characteristics were analysed by displaying the frequencies in a contingency table and using a Pearson's Chi-square test to see whether there was a significant relationship between placement of the kill site, e.g. inside or outside Hwange National Park, and the prey being encountered in medium or high visibility vegetation. Similar analyses were used to determine whether there were differences in availability of low, medium and high visibility habitat inside and outside Hwange National Park.

All statistical analyses were performed with the use of SPSS software for MS Windows release 16.0 (SPSS Inc, Chicago, USA).

Results

Number of hunts per day and pack sizes

There was no significant difference in the number of hunt periods per day inside (n=95) and outside (n=158) Hwange National Park (Mean_{In}=1.58, Mean_{Out}=1.68, U=6820.00, z=-1.38, p=0.169). Overall there was no significant difference in the pack size of African wild dog hunt follows inside (n=658) or outside (n=1086) Hwange National Park (Mean_{In}=5.81, Mean_{Out}=5.51, U=340015.00, z=-1.723, p=0.085). If analysed per main prey species no difference was found for pack size of hunt follows during which impalas (Mean_{In}=5.99, Mean_{Out}=5.83, U=5940.50, z=-0.534, p=0.593) or kudus (Mean_{In}=6.81, Mean_{Out}=6.66, U=3707.50, z=-0.134, p=0.894) were killed. Duikers were killed by relatively larger packs outside Hwange National Park (Mean_{In}=4.44, Mean_{Out}=5.35, U=610.00, z=-2.308, p=0.021).

Diet

Both inside and outside Hwange National Park, impalas, kudus and duikers were the main prey species in the diet of African wild dogs (Figure 1). There was no difference in diet composition inside (n=253) and outside (n=320) the National Park (χ^2=4.71, p=0.095), neither were there significant differences in age and sex classes of the impalas (χ^2=7.30, p=0.121) or kudus (χ^2=2.45, p=0.653) killed (Table 1) inside or outside Hwange National Park. Overall the highest percentage of the impala kills were adult females (51%), for kudus the highest percentage of kills consisted of adult or sub adult females (51.5%) and juveniles (27.7%). For duikers there were not enough cases where both age and sex were determined to perform a statistical analysis. When the number of impalas and kudus in the diet was compared it was found that during the nomadic season the diet consisted of more kudus than impalas compared to the denning season (B=-0.60, SE=0.22, p=0.006, Wald=7.61), an increase in pack size resulted in more kudus relative to impalas in the diet (B=0.09, SE=0.04, p=0.010, Wald=6.70). The stomach capacity of the African wild dogs was as often met inside the National Park (35.2%of the hunts) as outside the National Park (38.9% of the hunts) (χ^2=0.73, p=0.392).

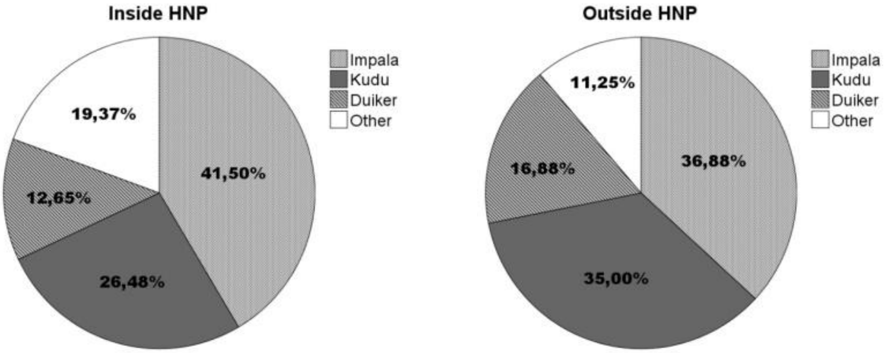

Figure 1. African wild dog diet composition inside (n=253) and outside (n=320) Hwange National Park (HNP).

Table 1. Sex and age ratio of impalas and kudus killed inside and outside Hwange National Park (HNP).

		Impala			**Kudu**		
		Inside HNP	Outside HNP	Total	Inside HNP	Outside HNP	Total
Adult Male	%	**18.3**	**28.3**	**23.8**	**10.9**	**5.5**	**7.5**
	nr	17	32	49	7	6	13
Adult Female	%	**51.6**	**50.4**	**51.0**	**25.0**	**27.5**	**26.6**
	nr	48	57	105	16	30	46
Sub adult Male	%	**7.5**	**10.6**	**9.2**	**15.6**	**11.9**	**13.3**
	nr	7	12	19	10	13	23
Sub adult Female	%	**8.6**	**4.4**	**6.3**	**23.4**	**25.7**	**24.9**
	nr	8	5	13	15	28	43
Juvenile	%	**14.0**	**6.2**	**9.7**	**25.0**	**29.4**	**27.7**
	nr	13	7	20	16	32	48

Hunting success and distances

The analysis of the outcome of the chase for all prey species combined showed that there was a non significant tendency for less successful chases inside compared to outside Hwange National Park (B=-0.46, SE=0.25, p=0.064, Wald=3.43) (Table 2). Pack size, time of hunt and whether the pack was denning or nomadic did not significantly affect the outcome of the chase (all p>0.126). When calculating the odds ratio for failed or successful chases inside or outside the park it was found that the chance of a failed chase was 1.57 times higher inside the National Park.

Similar results were found if this analysis was performed for the main prey species, impala, kudu and duiker combined (Table 2). There were significantly less successful chases inside Hwange National Park (B=-0.79, SE=0.36, p=0.027, Wald=4.91) and based on the odds ratio the likelihood of a failed chase was 2.21 times higher inside the National Park. Pack size, time of hunt and whether the pack was denning or nomadic did not affect the outcome of the chase (all p>0.229).

When analysed per species it was found that the difference in outcome of chases inside and outside Hwange National Park was mainly due to a difference in outcome of kudu chases. Kudu chases were less often successful inside the National Park (B=-1.61, SE=0.63, p=0.011, Wald=6.50) (Table 2). None of the other variables significantly affected the outcome of kudu chases (all p>0.113). The outcome of impala chases was not affected by whether the chase took place inside or outside the National Park (B=-0.59, SE=0.50, p=0.246, Wald=1.35) (Table 2), nor by pack size, time of hunt or whether the pack was denning or nomadic (all p>0.221).

Table 2. Percentage of successful and failed chases inside and outside Hwange National Park (HNP) for all prey species, main prey species (impala, kudu, duiker), impalas, kudus.

		Inside HNP		**Outside HNP**	
		Success	Failure	Success	Failure
Overall	%	**50.81**	**49.19**	**63.03**	**36.97**
	nr	63	61	104	61
Main prey	%	**59.46**	**40.54**	**78.89**	**21.11**
	nr	44	30	71	19
Impala	%	**65.00**	**35.00**	**86.92**	**23.08**
	nr	26	14	30	9
Kudu	%	**44.83**	**55.17**	**84.38**	**15.63**
	nr	13	16	27	5

The chase distance of successful and failed chases of all prey species together was neither affected by whether the chase took place inside or outside Hwange National Park ($F_{(1,226)}$=2.21, p=0.138), nor by time of hunt or whether or not the pack was denning or nomadic (all p>0.082). There was a non significant tendency for a decrease in chase distance with an increase in pack size ($F_{(1,227)}$=3.22, p=0.074). If these analysis were performed for chase distances of successful and failed chases of the main prey species, impala, kudu and duiker, combined, chase distances were longer inside Hwange National Park ($F_{(1,120)}$=6.94, p=0.010) (Table 3) and an increase in pack size resulted in a decrease in chase distance ($F_{(1,120)}$=7.78, p=0.006). The latter was largely due to a significant interaction between pack size and whether or not prey was chased inside or outside the park ($F_{(1,120)}$=4.38, p=0.039); inside the park chase distance decreased with pack size ($F_{(1,39)}$=5.34, p=0.026) while outside the park pack size did not affect chase distance ($F_{(1,77)}$=0.75, p=0.391). Time of hunt or whether the pack was denning or nomadic did not significantly affect chase distances (all p>0.117). The length of an impala chase was not affected by whether the chase took place inside or outside the park ($F_{(1,40)}$=0.33, p=0.568), an increase in pack size resulted in a decrease in chase distance ($F_{(1,41)}$=6.95, p=0.012). None of the other variables significantly affected the length of impala chases (all p>0.487). Kudu chases were longer inside compared to outside the park ($F_{(1,34)}$=5.31, p=0.027). Pack size did not affect the length of a kudu chase ($F_{(1,34)}$=2.21, p=0.155) but there was a significant interaction between whether a chase took place inside or outside the park and pack size ($F_{(1,34)}$=4.24, p=0.047). When a separate analysis was performed there was no effect of pack size on the length of kudu chases inside ($F_{(1,4)}$=0.02, p=0.890) or outside the park ($F_{(1,20)}$=0.04, p=0.839), neither of any of the other variables (all p>0.155).

Failed chases never lasted longer than two kilometres therefore a separate analysis was performed for successful and failed chases to see whether a similar pattern would be found as for all chases combined. Whether a successful chase took place inside or outside the National Park did not affect the distance ($F_{(1,100)}$=1.31, p=0.255), neither did pack size, time of hunt, whether the pack was denning or nomadic or any of the interaction added to the model (all p>0.108). For the main prey species, impala, kudu and duiker combined, successful chases were longer inside the park compared to outside the park ($F_{(1,65)}$=6.20, p=0.015). Pack size did not significantly affect the length of successful chases ($F_{(1,65)}$=2.21, p=0.088) but the interaction between inside and outside the park and pack size was significant ($F_{(1,65)}$=3.90, p=0.053). The time a hunt took place or whether the pack was denning or nomadic did not affect the length of a successful chase (all p>0.634). When a separate analysis was performed for successful chases inside and outside the park, none of the variables significantly affected the length of the chase (all p>0.132).

For impalas the chase distance of successful chases decreased with an increase in pack size ($F_{(1,26)}$=5.24, p=0.030), none of the other variables significantly affected chase distance of successful chases (all p>0.446). Successful kudu chases were longer inside the park ($F_{(1,23)}$=9.11, p=0.006). Although pack size did not significantly affect the length of a successful kudu chase ($F_{(1,23)}$=0.00, p=0.964) the interaction between pack size and inside and outside the park was found to be significant ($F_{(1,23)}$=7.78, p=0.010). None of the other variables affected the length of a successful kudu chase (all p>0.237). When a separate analysis was performed there was no effect of pack size on the length of successful kudu chases inside ($F_{(1,4)}$=0.02, p=0.890) or outside the park ($F_{(1,20)}$=0.04, p=0.839), neither of any of the other variables (all p>0.155).

Table 3. Average chase distances of successful and failed chases inside and outside Hwange National Park (HNP) for all prey, main prey species (impala, kudu, duiker), and per main prey species.

		Successful chase (km)		**Failed chase (km)**	
		Inside HNP	Outside HNP	Inside HNP	Outside HNP
Overall	**Mean**	**1.09**	**0.87**	**0.68**	**0.40**
	Min	0.05	0.02	0.05	0.05
	Max	4.04	4.63	1.40	1.60
	SE	0.18	0.13	0.20	0.09
	n	35	68	7	22
Main prey	**Mean**	**1.40**	**0.91**	**0.75**	**0.45**
	Min	0.10	0.02	0.10	0.10
	Max	4.04	4.63	1.40	1.60
	SE	0.22	0.17	0.65	0.19
	n	24	45	2	9
Impala	**Mean**	**1.28**	**1.05**	**0.75**	**0.60**
	Min	0.50	0.10	0.10	0.10
	Max	2.85	3.70	1.40	1.60
	SE	0.23	0.21	0.65	0.50
	n	11	17	2	3
Kudu	**Mean**	**1.79**	**1.14**	**.**	**0.75**
	Min	0.20	0.10	.	0.28
	Max	4.04	4.63	.	1.21
	SE	0.44	0.37	.	0.48
	n	10	17	0	2
Duiker	**Mean**	**0.55**	**0.33**	**.**	**0.18**
	Min	0.10	0.20	.	0.10
	Max	0.91	6.00	.	0.32
	SE	0.24	0.08	.	0.05
	n	3	11	0	4

As sample sizes were too small to perform an analysis per prey species, failed chases were analysed for all prey species together. Inside the park failed chases lasted longer than outside the park ($F_{(1,24)}$=7.16, p=0.013). The length of failed chases was not affected by pack size, time of hunt, whether the pack was denning or nomadic or the interactions added to the model (all p>0.121).

There was no difference in foraging distance between hunts inside or outside Hwange National Park ($F_{(1,179)}$=1.23, p=0.269). Foraging distance increased with an increase in pack size ($F_{(1,230)}$=9.66, p=0.002). The time a hunt took place, whether the pack was denning or nomadic or the interactions between inside and outside the park and time of hunt or pack size did not affect foraging distance (all p>0.192).

Vegetation

For impalas, there was a significant association between whether they were killed inside or outside the National Park and whether or not this was in medium or high visibility vegetation (χ^2=11.13, p=0.001) (Figure 2). Based on the odds ratio, the odds of an impala being killed in high visibility habitat was 11.00 times higher inside the National Park. For kudus, there was also a significant association between whether they were killed inside or outside the National Park and whether or not this happened in medium or high visibility vegetation (χ^2=6.56, p=0.010) (Figure 2). Based on the odds ratio, the odds of a kudu being killed in high visibility habitat was 6.50 times higher inside the National Park.

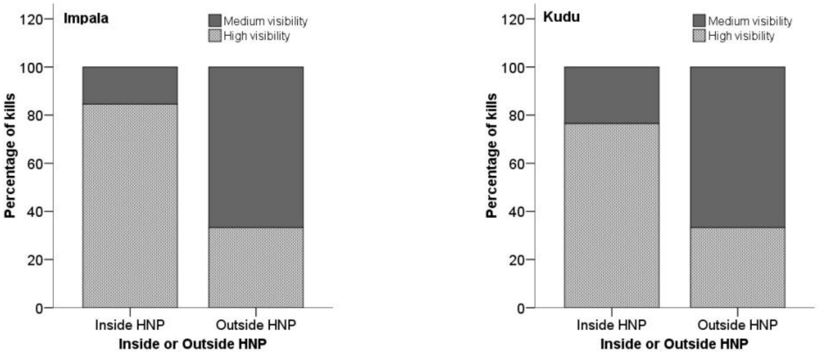

Figure 2. Percentage of African wild dog impala and kudu kills in medium or high visibility vegetation inside and outside Hwange National Park (HNP).

The visibility of the plots measured inside and outside Hwange National Park differed significantly (χ^2=9.74, p=0.008). Overall more low visibility habitat was found outside Hwange National Park. Medium visibility habitat was found at the same proportion inside and outside the Park. High visibility habitat was mostly found inside Hwange National Park (Figure 3).

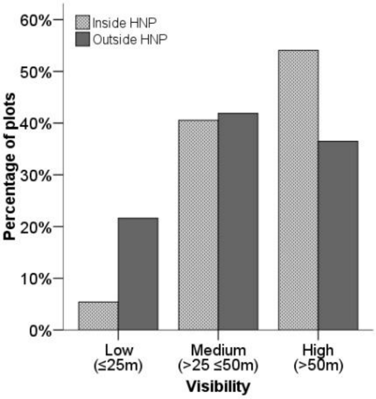

Figure 3. Visibility of the available habitat inside and outside Hwange National Park (HNP).

Discussion

African wild dog pack size has generally been found to affect chase distance, hunting success, prey mass and the likelihood of multiple kills (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Rasmussen et al. 2008). For the interpretation of the results of this study it is therefore important to note that, except for duiker, there was no difference in average pack size of hunt follows inside Hwange National Park and hunt follows in the buffer zone outside the park. The number of hunt periods per day and the likelihood that the stomach capacity of the individual African wild dogs in the hunting group was met was also similar inside and outside the park.

African wild dogs are efficient hunters that hunt for small to large antelopes (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Mills and Gorman 1997). Like in other parts of Zimbabwe (Pole et al. 2004), both inside and outside Hwange National Park, African wild dogs predominantly hunted for impalas, kudus, and duikers. Apart from species, sex and age of the prey seem to be taken into account as selection criteria as well. Some studies have shown that African wild dogs preferentially select adult male impalas (Pole et al. 2004) while others have found that predation on female impalas was more pronounced (Reich 1981). For kudus a strong selection for adult females was found (Reich 1981). Although African wild dogs do attack adult impalas and kudus, for both species they seem to preferentially target juveniles (Pole et al. 2004). Overall, in this study, the number of kills in the different age and sex classes suggests a preference for female adult impalas, female adult and sub adult kudus, and juvenile kudus. There was no difference in the age and sex classes of prey killed inside and outside Hwange National Park. The number of kudus in the diet relative to the number of impalas was found to increase with an increase in pack size. This result can partly be explained by the fact that it is easier for bigger packs to bring down bigger prey (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995), and partly by the fact that bigger packs have higher energetic needs and therefore simply need to catch bigger prey (Rasmussen et al. 2008). The latter is also likely to explain the found increase in the number of kudu kills relative to the number of impala kills during the denning season.

Both survival and reproductive success of African wild dogs seem to largely depend on the ability to secure prey and the foraging costs made to secure this prey (Rasmussen et al.

2008, Rasmussen 2009). African wild dog packs inside Hwange National Park experienced a lower hunting success compared to packs in the buffer zone outside the National Park as chases inside the park less often resulted in a kill. This difference in hunting success was largely due to a higher number of successful kudu chases in the buffer zone outside the park. Several studies have shown a positive relationship between pack size and hunting success (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995). In this study no relation between pack size and the likelihood of a successful chase was found. Which might indicate that with the excessive costs of chasing, packs use an "all or nothing" strategy as soon as a chase has been initiated and energetic expenditure commences (Rasmussen et al. 2008).

On top of the lower hunting success, African wild dog packs inside Hwange National Park chased their prey over longer distances before they were able to make the kill. Although the differences in chase distance per prey species were too small to show significant results, chase distances for impalas, kudus and duikers were longer inside Hwange National Park compared to the buffer zone outside the park. African wild dogs have been found to burn 1500 kJ per 100 meter run (Rasmussen et al. 2008). With these high energetic costs and the positive relationship between survival and reproduction and foraging costs (Rasmussen et al. 2008), even non significant differences of 230 meter run for impalas and 650 meter run for kudus (Table 3) are likely to have a serious impact on African wild dog life history.

Although some studies show a decrease in chase distance with an increase in pack size (Creel and Creel 1995) others have found no effect of pack size on chase distance (Fanshawe and Fitzgibbon 1993). In this study we found a negative relationship between pack size and chase distance; an increase in pack size resulted in a decrease in chase distance. Apart from pack size other factors like the body condition and flight distance of prey (Reich 1981, Fitzgibbon 1988, Pole et al. 2004), and vegetation and landscape characteristics (van Dyk and Slotow 2003, Rhodes and Rhodes 2004, Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007) are also likely to affect chase distance and hunting success. Although in relatively open habitat the height of surrounding vegetation did not affect African wild dogs hunting success (Fanshawe and Fitzgibbon 1993), pursuing prey in thick habitat seemed to increase the likelihood of making a kill (Creel and Creel 2002).

Apart from hunting success vegetation density also seems to affect chase distance. Reich (1981) found that, due to the fact that African wild dogs were able to approach their prey at shorter distances, the average chase distance in low visibility habitat was smaller compared to high visibility habitat. The likelihood that an impala or kudu kill was made in high visibility habitat was found to be higher inside Hwange National Park, differences in vegetation characteristics could therefore have contributed to longer chase distances inside the park. Differences in vegetation characteristics might also explain why inside the park, for the main prey species combined, chase distance decreased with an increase in pack size while outside the park no such effect was found. The lower visibility habitat in which prey was killed outside the park is not only likely to enable African wild dogs to approach their prey at a closer distance (Reich 1981), it is also likely to favour the African wild dogs as they are usually more agile than the prey chased and prey seems to hesitate when encountering obstacles (Creel and Creel 2002). It is therefore possible that the effect of pack size is more pronounced inside the park compared to outside the park because inside the park African wild dogs do not have the added benefits of low visibility habitat.

Overall there is more high visibility habitat available inside Hwange National Park whereas medium visibility habitat was equally available inside the park and in the buffer zone outside the park. A higher availability of high visibility habitat is likely to result in a higher encounter rate of prey in this type of habitat, a preferred selection of open habitat by prey will further increase the likelihood of encountering prey in high visibility habitat. Prey seems to select micro-habitats that allow escape from predators (Wirsing et al. 2007). Previous research has shown that browsing and grazing herbivores in Hwange National Park tend to use more open habitats to avoid short-term predation risk (Valeix et al. 2009). This is in accordance with studies in other areas that have shown that buffalo and giraffe favour open habitat where flight is easier and anti-predator vigilance is more effective (Jarman 1974, Fritz and Loison 2006).

Although currently the lion densities in the study area in and around Hwange National Park are almost similar (inside the park; 2.6 lions/100km^2, outside the park; 2.2 lions/100km^2) (Elliot 2007), at the time of the hunt follows densities were likely to be lower outside the National Park due to the high pressure of sport-hunting (Davidson 2009). Therefore the overall perceived predation risk for prey, especially for kudus as they make up a main part of the lion diet (10-24%) (Loveridge et al. 2007), might have been higher inside Hwange National Park compared to outside the park. A higher predation risk could possibly reduce flight distance (Diego-Rasilla 2003, Ciuti 2008) and contribute to an increased preference for high visibility habitat over medium visibility habitat of prey. The preference of prey for high visibility habitat in combination with the fact that there is more high visibility habitat available could have resulted in a higher encounter rate of prey in high visibility habitat inside Hwange National Park herewith reducing the hunting efficiency of the African wild dogs.

Theoretical models generally view optimal habitat choice of predators as a function of prey density and its related search efficiency (Fryxell 1997, Morris 2003). Although a number of studies show that predators select habitat according to prey density (Litvaitis et al. 1986, Murray et al. 1994, Spong 2002) African wild dogs do not seem to be more abundant in ecosystems with a high prey density (Creel and Creel 1998). Foraging distance was similar inside and outside Hwange National Park, indicating that prey availability does not differ to the extent that it affects search efficiency. Nevertheless, due to differences in hunting success and chase distances, foraging costs differed substantially which makes it likely that for African wild dogs in the Hwange system prey catchability plays a bigger role in habitat selection than prey availability in itself. Several other studies have shown similar results; leopards were shown to prefer to hunt in habitats where prey was easier to catch rather than where prey was more abundant (Balme et al. 2007) and lions in the Serengeti preferred to hunt in areas with good cover rather than high prey density (Hopcraft et al. 2005).

For African wild dogs the chase is the most energetic costly part of the hunt (Rasmussen et al. 2008). Therefore higher prey catchability resulting in a reduction in chase distance and a higher percentage of successful chases is likely to be a main factor determining habitat choice, especially while securing prey and energetic expenditure are directly linked to life history traits like survival and reproductive success (Rasmussen et al. 2008). In a previous study by van der Meer et al. (submitted) (chapter 1) it was found that over the years African wild dogs moved their territories closer to or into the buffer zone outside the park where they experiences a higher reproductive success. This is likely to be largely the result of a higher hunting efficiency in the buffer zone outside the National Park. Although based on foraging efficiency establishing a territory in the buffer zone outside the National Park should increase African wild dog fitness, the opposite is true. Due to the high human induced mortality in this area mortality exceeds natality, resulting in a decline in the African wild dog population.

This study shows that it is important to take habitat characteristics that are likely to affect prey catchability into account in the conservation strategy of the African wild dogs as these characteristics, and not just prey availability in itself, might determine whether a habitat is suitable for African wild dogs or not.

Acknowledgement

The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. In addition we would like to thank the Hwange National Parks and Wildlife Management Authority, Forestry Commission, The Hide, Hwange Safari Lodge, Lions den enterprises, Touch the Wild and the various farmers within the Gwaai Intensive Conservation Area for allowing us access onto their premises and supporting our fieldwork. We thank Jealous Mpofu and Peter Blinston for their participation in the hunt follows. We also thank all people that participated in the complementary field work, especially Birton Sibanda, the members of the Painted Dog Conservation Anti Poaching Unit, Simeon Mudimba and the other rangers from National Parks who kindly assisted us. We wish to thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation, the Painted Dog Conservation project, the CNRS HERD project and the PCP Research Platform.

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Chapter 3

The effect of simulated African wild dog presence on anti predator behaviour of kudu and impala

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The effect of simulated African wild dog presence on anti-predator behaviour of kudu and impala

Ester van der Meer, Olivier Pays, Hervé Fritz

Abstract

We examined the behavioural, temporal and spatial effects of simulated African wild dog presence on its two main prey species, kudus and impalas. To determine costs related to anti predator behaviour we distinguished between high quality, but high costs, vigilance and total vigilance (high quality and low quality vigilance combined). We predicted that high quality vigilance of kudus and impalas increases when African wild dog presence is mimicked, with a more pronounced increase during the early morning and late afternoon when predation risk is likely to be perceived as high. Behavioural observations were made around waterholes inside Hwange National Park and the buffer zone outside the park. African wild dog presence was mimicked by spreading faeces around the waterhole and playing sounds of African wild dogs either upon arrival of the herd or early in the morning, depending on the experimental day. Individual kudus spent a higher proportion of time high quality vigilant when African wild dog presence was mimicked upon arrival of the herd, especially during the early morning. Although not significant, impalas inside the park showed a similar response. Both kudus and impalas only increased high quality vigilance when immediate predation risk was likely to be present. The experimental treatment did not affect the behaviour of the herds but it did seem to have temporal effects. Kudu and impala herds did not avoid the waterholes but seemed to adjust their behaviour according to the times of the day when predation risk is likely to be high. When immediate predation risk was mimicked less impala herds than expected came to drink during the early morning and late afternoon, kudus showed a non significant similar pattern. Kudu herds spent less time drinking at the waterhole in the late afternoon during the days when African wild dog presence was mimicked.

Key words: *African wild dog, prey vigilance, predation risk, kudu, impala, anti-predator behaviour, temporal adjustment*

Status: submitted (*Animal Behaviour*)

Introduction

Several behavioural mechanisms allow prey to reduce the risk of predation. The two most studied mechanisms are group formation and vigilance behaviour. Although foraging in groups increases intraspecific competition (Valone 1993, Molvar and Bowyer 1994), groups of individuals potentially benefit either by a collective ability to detect predators sooner than solitary individuals (Roberts 1996, Ruxton 1996) or by a reduction of the individual risk of being attacked by a predator due to a dilution effect (Wrona and Jamieson Dixon 1991, Roberts 1996). An increased level of vigilance behaviour is generally believed to allow an early detection of an approaching predator (Underwood 1982, Hunter and Skinner 1998). Many different factors affect the relationship between predation risk and vigilance behaviour e.g. herd size (Burger et al. 2000), distance to refuge (Whittington and Chamove 1995, Frid 1997) and quality and limitation of resources (Lima et al. 1999, Randler 2005). Even in the absence of imminent attack prey should maintain a baseline level of apprehension due to a constant risk of predation (Ripple et al. 2001, Childress and Lung 2003). Predation risk can vary over space and time, e.g. risky versus safe habitats or time of day (Brown 1999, Laundré et al. 2001, Schmitz 2005), the mechanisms underlying behavioural adjustments to variations in predation risk are not well understood in free ranging prey species.

Vigilance behaviour varies with predation pressure, when predation risk increases prey usually spends more time vigilant (Lima 1987, Jones et al. 2007). For example female elk and bison have been found to increase vigilance in areas where the risk of encountering wolves was high (Laundré et al. 2001, Lung and Childress 2007). Wildebeest and impalas spent more time vigilant in areas where large felids were reintroduced (Hunter and Skinner 1998), and kudus have been found to increase vigilance when lions were in the vicinity (Périquet et al. 2010). Although, even when predation risk is high, prey animals tend to reduce time spend vigilant when associated with conspecifics (Scheel 1993, Burger et al. 2000, Lung and Childress 2007, Périquet et al. 2010), it seems that individual predation risk is nevertheless also related to the individual vigilance level: cheetahs prefer to attack non vigilant Thomson's gazelles (Fitzgibbon 1988), and blue acara cichlid (*Aequidens pulcher*), a natural predator of the guppy, preferred to attack foraging guppies over non-foraging ones and nose-down foraging guppies over horizontally foraging individuals (Krause and Godin 1996). Non vigilant animals generally tend to react slower upon attack by a predator than vigilant individuals hence will not be able to create as much distance between themselves and the attacking predator and might therefore be more likely to be killed upon attack (Fitzgibbon 1988, Krause and Godin 1996, Hilton et al. 1999).

Within this study we examined the effect of simulated African wild dog (*Lycaon pictus*) presence on anti-predator behaviour of their main prey species, kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*), at both an individual and herd level and tried to assess the costs involved. We tested for vigilance while drinking and the temporal use of waterholes as water does not vary in type or quantity and predators are likely to search for prey in the vicinity of waterholes (Valeix et al. 2010). Predation risk has indeed not only been found to directly affect prey vigilance behaviour but has also been found to affect spatial distribution and induce temporal and spatial changes in activity patterns (Valeix et al. 2009^{a,b}). Previous studies have already shown that both kudus and impalas adjust their vigilance behaviour according to predation risk with more time spent vigilant when predation risk is high (Hunter and Skinner 1998, Matson et al. 2005, Périquet et al. 2010). Here, we studied with more scrutiny the short term response to (mimicked) predation risk by distinguishing between types of vigilance behaviour. Lima and Bednekoff (1999) suggested that vigilance sequences may actually involve alternating periods of high-quality, high-cost vigilance (overt scans) and lower-quality, low-cost, head-down vigilance (which does not detract from feeding). Blanchard and Fritz (2007) proposed to discriminate between two different types of head up vigilance; routine vigilance, used by an animal to monitor its surroundings during spare time, and induced vigilance, when responding to a stimulus. Unlike routine vigilance where animals can match with precision the particular ingestion process and scanning behaviour, induced vigilance may disrupt the ingestion process since it requires animals to react to unpredictable stimuli whatever the phase of feeding and therefore comes with considerable costs (Blanchard and Fritz 2007). In order to be able to determine differences in the costs involved in the presence of different types of predation risk we discriminated high quality vigilance, which detracts from all other activities, from low quality vigilance which is used to monitor the surrounding during spare time and therefore likely to be less costly.

We predict that mimicking African wild dog presence is likely to be perceived as an immediate predation risk, therefore increasing high quality vigilance of individual kudus and impalas and the proportion of vigilant individuals within a herd. Variations in predation risk and its likely lethality were introduced by using two different experimental treatments controlling for factors like herd size and visibility around the waterholes. African wild dogs are crepuscular, with hunts being most common at dusk and dawn or when sufficient moonlight is available (Reich 1981, Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Rasmussen 2009). We therefore expect the increase in high quality vigilance to be more pronounced during the periods of the day when predation risk is likely to be perceived as high; the early morning and late afternoon. In order to be able to determine whether kudus and impalas used temporal or spatial behavioural adjustments to avoid predation risk we recorded the number of herds and the time of day herds came to drink at the waterhole plus the amount of time individual herds spent drinking at the waterhole.

Method

Study area

Hwange National Park covers approximately 15 000 km^2 in the northwest of Zimbabwe (19°00'S, 26°30'E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the park is designated for trophy hunting and to a lesser extent for photographic safaris. Most of this land is either privately owned or state owned and managed by Forestry Commission. Prey species present in the study area include impala, kudu and duiker (*Sylvicapra grimmia*).

Historically a large proportion of impala (89.7%) and kudu kills (64.3%) made by African wild dogs are made within a range of one to two kilometres from a waterhole (van der Meer et al. unpublished manuscript (chapter 5)). We therefore selected six pumped waterholes that were situated within areas frequently visited by African wild dogs, three waterholes inside

Hwange National Park and three waterholes in the buffer zone outside the park. Other predators visiting these waterholes include lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), with lion densities being 2.6 lions/100km^2 in the area inside the National Park and 2.2 lions/100km^2 in the area outside the National Park, spotted hyena densities of 11.3 hyenas/100km^2 in the area inside the National Park and 5.5 hyenas/100km^2 in the buffer zone outside the National Park (Elliot 2007). Spoor densities indicate that leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatis*) are less abundant in the area inside Hwange National Park than the area outside the park (Elliot 2007). All six waterholes are within commonly used photographic safari areas and are therefore regularly visited by game drive vehicles. The minimum distance between waterholes was 10 km, the maximum distance 30 km. The waterholes were all situated in open areas with average visibility ranging between 115 and 192 meters. Two out of the three waterholes inside Hwange National Park, and two out of the three waterholes in the buffer zone outside Hwange the park were situated in areas with grassland.

Species

African wild dogs are communal hunters that use a widely foraging strategy. They are crepuscular with hunts being most common at dusk and dawn or when sufficient moonlight is available (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Rasmussen 2009). In Zimbabwe, African wild dogs predominantly predate on impalas and kudus (Pole et al. 2004, Rasmussen 2009).

The impala is a medium sized (female body mass c. 45 kg, male body mass c. 60 kg), selective mixed feeding antelope (Estes 1997). Impalas are gregarious and forage in groups, either in bachelor herds or female harems (Mooring and Hart 1995, Fritz and de Garine-Wichatitsky 1996). Impalas are vigilant and quick to take flight when discovering an approaching predator, using an alarm snort to signal the presence of danger (Estes 1997).

The greater kudu is a large (female body mass c. 170 kg, male body mass c. 257 kg), browsing antelope (Estes 1997). Females, calves and sub-adults occur in stable social units throughout the year. Adult males, except during the rut, associate in unstable bachelor groups (Owen-Smith 1990, 1993, du Toit 1995). Kudus standing in the thicket will rely on crypsis when encountering predators and will only flee when approached within their, relatively short, flight distance (Estes 1997).

Behavioural observations

Behavioural observations were made during the dry season in August and September when neither of the species are in rut. Waterhole attendance is high in these months as natural waterholes have dried up and animals are depending on artificial waterholes for water. All observations were made from the car, parked at a distance from the waterhole as not to disturb the animals, from 6:00h till 18:00h. We studied the two main prey species of the African wild dog, kudu and impala. As soon as a herd would come into view at a distance ≤ 150 m, the behaviour of all individuals in the herd would be monitored every 30 seconds by the means of a visual scan till all the individuals in the herd had been drinking and moved away from the waterhole at a distance ≥ 150 m. The number of animals drinking, feeding, salt licking, vigilant, moving or engaged in other behaviours was noted. As soon as 50% of the herd started drinking a video was taken from which the different behaviours, sex, age, body condition (classified as low, medium or good) and position of the individuals in the herd were determined. In cases where, for practical reasons, it was not feasible to take both scans and video focals, priority was given to the focals. When analysing the video the behaviour of the individuals within the herd was monitored during the same time span for the first two minutes or, in cases where this was not feasible, one minute.

Behaviours recorded were:

- **High quality vigilance**; the animal detracts from all other activities and is standing in a highly alert posture with its head up above shoulder level and ears pointed forward,
- **Total vigilance**; high quality and low quality (where animals monitor their surrounding during spare time) vigilance behaviour combined,
- **Moving**; the animal is walking at a normal pace,
- **Fleeing**; the animal is running away,
- **Drinking**; the animal has its head down and is drinking water,
- **Other head down activities**; for example grazing or salt licking,
- **Other behaviour**; for example grooming, territorial behaviour and any other activities that do not fall into the categories as mentioned above,

Each waterhole was visited three days in a row. The first day was used as a control day (C). During the second day immediate predation risk by African wild dogs was mimicked by spreading African wild dog faeces around the waterhole early in the morning and playing the sounds of African wild dogs commencing their hunt each time a herd of kudus or impalas came down to drink at the waterhole (FS). On the third day predation risk of African wild dogs was mimicked by spreading faeces around the waterhole and playing the sounds of African wild dogs commencing a hunt early in the morning with first light, the time African wild dogs normally commence their hunt, before any of the studied prey species had come down to the waterhole to drink (F). At each waterhole this experiment was repeated a month later.

The time a herd spend drinking was measured as the difference between the time when the last individual of the herd stopped drinking and the time the first individual of the herd had started drinking. The herd size and structure, as well as environmental factors that could have affected the observed behaviour, like the presence of predators or other herbivores, were noted. For each herd time at which the herd visited the waterhole was noted. Times were divided into four categories, early morning (06:00h-09:00h), late morning (09:00h-12:00h), early afternoon (12:00h-15:00h) and late afternoon (15:00h-18:00h). After the behavioural observations had been made, the waterholes were revisited and the visibility in the north, northeast, east, southeast, south, southwest, west and northwest direction was measured by having one person standing at the edge of the waterhole and letting another person walk away with a GPS to measure the distance at which this person went out of sight. An average of these distances was used as a visibility measure for the waterhole.

In total, scans were taken from 20 impala herds and 35 herds on the control day (C), 18 impala herds and 45 kudu herds on the second experimental day (FS) and 19 impala herds and

40 kudu herds on the third experimental day (F). Focals were taken from 34 impala herds and 40 kudu herds on the control day (C), 31 impala herds and 44 kudu herds on the second experimental day (FS) and 24 impala herds and 31 kudu herds on the third experimental day (F). Time spent drinking was measured for 32 impala herds and 36 kudu herds on the control day (C), 23 impala herds and 38 kudu herds on the second experimental day (FS) and 20 impala herds and 26 kudu herds on the third experimental day (F).

Statistical analysis

Kudus and impalas were analysed separately. To avoid pseudo replication, for the analysis of the individual anti predator behaviour the average of the proportion of time spent high quality vigilant and the average of the proportion of time spent total vigilance was taken from all individuals within a given herd. As all animals observed were in good body condition this variable was left out of the further analysis.

For the analysis of individual anti predator behaviour a linear mixed effects model was built to test for differences in the proportion of time spent on vigilance behaviour with experimental day, time of the day, and whether there were other herbivores present as factors. As there might be different predation pressures inside and outside Hwange National Park, whether the waterhole was located inside or outside the National Park was added as a factor as well. Herd size and average visibility around the waterhole were used as covariates. The interactions between experimental day and whether the waterhole was situated inside or outside the National Park, and time of day and inside or outside the National Park, were also taken into account. As the experiment was repeated at each waterhole one month after the first treatment, month was added to the model as a random factor. A backwards step-wise selection procedure based on the likelihood ratio was used to successively remove variables for which $P > 0.05$ allowing to find a minimal model in which only significant variables were included. The same analysis was performed for the proportion of time spent in high quality vigilant behaviour.

The visual scans taken from the herds every 30 seconds during their stay at the waterhole were used to determine the average proportion of the herd vigilant and engaged in head down activities for the entire scan duration. To meet the normality assumption all proportions were arcsine square root transformed. For the analysis a linear mixed effects model was used with the variables; experimental day, average visibility around the waterhole, herd size, whether the waterhole was located inside or outside the National Park, time of day at which the animals were present and whether there were other herbivores present at the waterhole. The interactions between experimental day and whether the waterhole was situated inside or outside the National Park, and time of day and inside or outside the National Park, were also taken into account. Month was added to the model as a random factor. We used likelihood-ratio tests (L-tests) to compare two linear mixed effects models and F-tests to compare two linear fixed effects models in a backward step-wise procedure (Faraway 2006). A backwards step-wise procedure was used to remove non significant variables. Time spent drinking was analysed using the same procedure as described above. For an overview of the independent variables used in the models, see Table 1.

Table 1. Overview of the independent variables used in the analysis.

Variable	Type	Classes
Experimental day	Categorical	Control day (C) Faeces and sound upon arrival (FS) Faeces and sound early morning (F)
In or outside Hwange National Park	Categorical	Inside HNP Outside HNP
Herd size of observed herd	Continuous	
Average visibility around waterhole	Continuous	
Time of the day	Categorical	Early morning; 6-9h Late morning; 9-12h Early afternoon; 12-15h Late afternoon; 15-18h
Herbivore presence around waterhole	Categorical	Present Not present
Month	Categorical	August September

As herd size could be an explanatory factor for some of the results found, we used Mann-Whitney U tests to test for differences in herd sizes. Chi-square tests were used to analyse whether there was any significant variation in the number of herds of kudus and impalas that came to drink at the waterholes, or the time periods at which the herds visited the waterholes, during the different experimental days.

All statistical analyses were performed with R software (R Development Core Team) or SPSS software version 16.0 (SPSS Inc, Chicago, USA).

Results

Impala

Individual anti-predator behaviour

Total vigilance

The proportion of time spent vigilant was significantly affected by whether the waterhole was located inside or outside Hwange National Park ($LR\chi^2=5.13$, $p=0.024$). Impalas spent a greater proportion of time vigilant at the waterholes outside compared to inside the park (average difference in proportion±SE=0.08±0.03). The proportion of time spent vigilant was not affected by the experimental treatment ($LR\chi^2=0.57$, $p=0.753$). Herd size, visibility, time of the day or the presence of other herbivores at the waterhole also did not affect the proportion of time spent vigilant (all $p\geq0.100$).

High quality vigilance

A similar effect of location of the waterholes was found for the proportion of time individuals spent high quality vigilant ($LR\chi^2=5.03$, $p=0.025$), with a greater proportion of time spent high quality vigilant outside compared to inside the National Park (average difference in proportion±SE=0.08±0.04), the experimental treatment had no effect on proportion of time spent high quality vigilant ($LR\chi^2=0.54$, $p=0.765$) (Figure 1, 2), nor did herd size, visibility, time of the day or the presence of other herbivores (all $p\geq0.118$). For the interpretation of the results it has to be kept in mind that impala herds of which focals were taken were larger inside than outside HNP ($Mean_{in}$±SE=17.81±3.87, $Mean_{out}$±SE=9.43±1.03, U=425.50, z=-2.80, p=0.005).

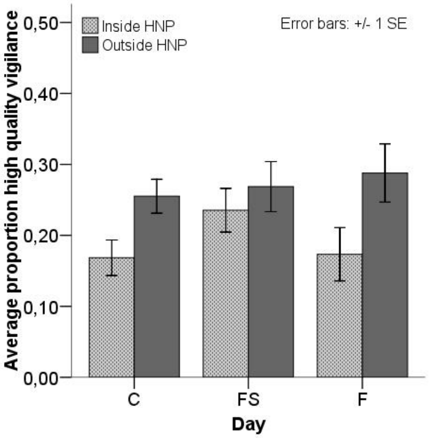

Figure 1. Average time individual impala spent high quality vigilant at waterholes inside and outside Hwange National Park (HNP) during the control day (C), the faeces and sound upon arrival day (FS) and the faeces and sound early in the morning day (F).

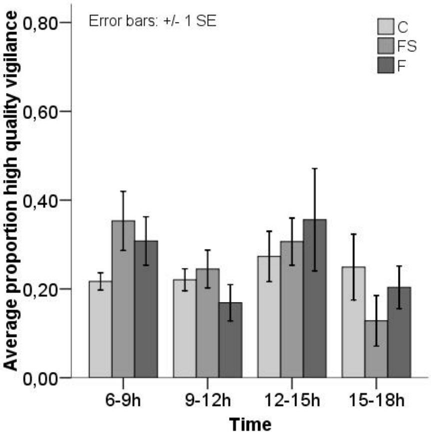

Figure 2. Average proportion of time individual impala spent high quality vigilant over the different periods of the day during the control day (C), the faeces and sound upon arrival day (FS) and the faeces and sound early in the morning day (F).

Herd anti-predator behaviour

Vigilance behaviour

The experimental treatment did not affect the proportion of the herd engaged in vigilant behaviour ($F_{(2,57)}$=0.34, p=0.714), neither did herd size, visibility around the waterhole, time of the day, location of the waterhole or the presence of other herbivores (all p≥0.119). The proportion of individuals with their head down was significantly affected by the location of the waterhole ($F_{(1,57)}$=4.62, p=0.036) and herd size ($F_{(1,57)}$=5.63, p=0.021). The proportion of the herd engaged in head down (i.e. risky) behaviour was lower inside Hwange National Park compared to outside the park (coef±SE=-6.00±2.79), an increase in herd size resulted in an increase in the proportion of the herd with its head down (coef±SE=0.47±0.20). The proportion of the herd engaged in head down behaviour was not affected by the experimental treatment ($F_{(2,57)}$=1.06, p=0.352). Visibility around the waterhole, time of the day or the presence of other herbivores did not affect the proportion of the herd engaged in head down behaviour (all p≥0.346). Average herd sizes of which scans were taken did not differ inside or outside Hwange National Park ($Mean_{in}$±SE=10.81±1.16, $Mean_{out}$±SE=9.24±1.08, U=246.00, z=-1.46, p=0.144).

Time spent drinking

The time impala herds spent drinking at the waterhole was significantly affected by visibility ($F_{(1,75)}$=11.00, p=0.001), and herd size ($F_{(1,74)}$=23.81, p<0.001). Time spent drinking increased with increased visibility (coef±SE=0.05±0.01). An increase in herd size also resulted in an increase in time spent drinking (coef±SE=0.11±0.02). The time spent drinking was not affected by the experimental treatment ($F_{2\text{-}74}$=0.19, p=0.828). Time of the day, location of the waterhole or the presence of other herbivores also did not affect time spent drinking (all p≥0.198). Average herd sizes for which time spent drinking was measured were larger inside compared to outside Hwange National Park ($Mean_{in}$±SE=20.00±5.50, $Mean_{out}$±SE=8.39±1.11, U=252.50, z=-2.85, p=0.004).

Spatial and temporal behavioural adjustments

There was no difference in the number of impala herds that came to drink at the waterhole during the different experimental days (χ^2=3.12, p=0.210). The number of herds that came to drink during the different times of the day did no differ on the control day (C) (χ^2=4.75, p=0.191), and on the third experimental day (F) (χ^2=3.60, p=0.308). On the second experimental day (FS) fewer herds than expected came to drink in the early morning and late afternoon compared to the late morning and early afternoon (χ^2=10.57, p=0.014).

Kudu

Individual anti-predator behaviour

Total vigilance

The proportion of time kudus spent vigilant was significantly affected by the experimental treatment ($LR\chi^2$=5.91, p=0.052), time of the day ($LR\chi^2$=7.98, p=0.046), herd size ($LR\chi^2$=4.48, p=0.034), presence of other herbivores ($LR\chi^2$=4.07, p=0.044) and visibility ($LR\chi^2$=4.82, p=0.028). Table 2 presents the minimal selected model including the sign of coefficients derived for each significant factor. On the second experimental day (FS) individuals spent a higher proportion of time vigilant compared to the control day (C). There was no difference in proportion of time spent vigilant between the third day (F) and the control day (C). Overall, a smaller proportion of time was spent vigilant in the late morning, early afternoon and late afternoon compared to the early morning. The proportion of time individuals spent vigilant decreased with an increase in herd size and when other herbivores were present and increased with an increase in visibility. There was no difference in the proportion of time spent vigilant inside or outside Hwange National Park ($LR\chi^2$=0.11, p=0.741).

Table 2. Minimal model for the proportion of time individual kudus spent vigilant.

	Coef	SE	df	t-value	p-value
Intercept	0.322	0.092	105	3.494	0.0007
Day (C used as a reference)					
FS	0.063	0.032	105	1.950	0.054
F	-0.007	0.035	105	-0.192	0.848
Visibility	0.001	0.0004	105	2.219	0.036
Time (6:00h-9:00h used as a reference)					
9:00h-12:00h	-0.112	0.050	105	-2.246	0.027
12:00h-15:00h	-0.105	0.050	105	-2.111	0.037
15:00h-18:00h	-0.150	0.055	105	-2.731	0.007
Herd size	-0.007	0.003	105	-2.053	0.043
Other herbivores (Not present used as a reference)					
Present	-0.061	0.031	105	1.953	0.053

High quality vigilance

When only looked at the proportion of time spent high quality vigilant, a significant effect was found of the experimental treatment ($LR\chi^2$=7.28, p=0.026), time of day ($LR\chi^2$=9.84, p=0.020) and visibility ($LR\chi^2$=7.31, p=0.007). Table 3 presents the minimal selected model including the sign of coefficients derived for each significant factor. A higher proportion of time was spent high quality vigilant on the second experimental day (FS) (Figure 3). There was no difference in proportion of time spend vigilant between the third day (F) and the control day (C) (Figure 3). A smaller proportion of time was spent high quality vigilant in the late morning, early afternoon and late afternoon compared to the early morning. This difference in vigilance level in relation to time of day is mainly due to an increase in the proportion of time spent vigilant during the early morning on the second experimental day (FS) (Figure 4). An increase in visibility resulted in an increase in proportion of time spent high quality vigilant. There was no difference in time spent high quality vigilant inside or outside the National Park ($LR\chi^2$=0.33, p=0.564). Herd size ($LR\chi^2$=3.29, p=0.070) or the presence of other herbivores ($LR\chi^2$=3.45, p=0.063) showed a non significant tendency to affect the proportion of time individuals spent high quality vigilant. There was no difference in average sizes of herds of which focals were taken inside or outside Hwange National Park (Mean_{in}±SE=5.85±0.52, Mean_{out}±SE=4.42±0.42, U=1209.00, z=-1.29, p=0.196).

Table 3. Minimal model for the proportion of time individual kudu spent high quality vigilant.

	Coef	SE	df	t-value	p-value
Intercept	0.213	0.088	107	2.414	0.017
Day (C used as a reference)					
FS	0.081	0.032	107	2.420	0.017
F	0.008	0.035	107	0.215	0.830
Visibility	0.001	0.0004	107	2.721	0.008
Time (6:00h-9:00h used as a reference)					
9:00h-12:00h	-0.144	0.050	107	-2.784	0.006
12:00h-15:00h	-0.129	0.050	107	-2.476	0.015
15:00h-18:00h	-0.170	0.055	107	-2.960	0.004

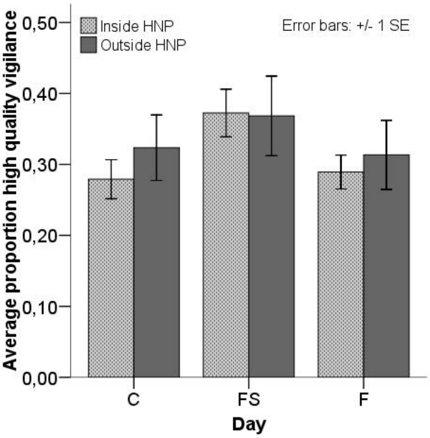

Figure 3. Average time individual kudu spent high quality vigilant at waterholes inside and outside Hwange National Park (HNP) during the control day (C), the faeces and sound upon arrival day (FS) and the faeces and sound early in the morning day (F).

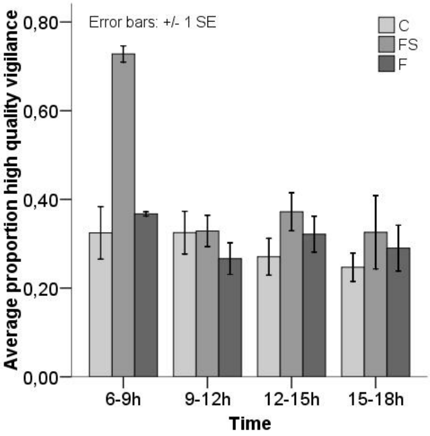

Figure 4. Average proportion of time individual kudu spent high quality vigilant over the different periods of the day during the control day (C), the faeces and sound upon arrival day (FS) and the faeces and sound early in the morning day (F).

Herd anti-predator behaviour

Vigilance behaviour

The proportion of the herd vigilant was affected by visibility ($F_{(1,120)}$=8.98, p=0.003) and the presence of other herbivores ($F_{(1,120)}$=4.28, p=0.041). The proportion of the herd being vigilant increased with an increase in visibility (coef±SE=0.07±0.03) and when there were no other herbivores present at the waterhole (coef±SE=6.83±2.28). The experimental treatment did not affect the proportion of the herd being vigilant ($F_{(2,120)}$=0.186, p=0.831), nor did herd size, the time of day or location of the waterhole (all p≥0.071). The proportion of the herd engaged in head down behaviour was also not affected by the experimental treatment ($F_{(2,120)}$=0.556, p=0.575). Herd size, visibility, time of the day, location of the waterhole or the presence of other herbivores did not affect the proportion of the herd engaged in head down behaviour (all p≥0.124). On average herds of which scans were taken were larger inside compared to outside Hwange National Park ($Mean_{in}$±SE=7.85±0.58, $Mean_{out}$±SE=4.81±0.44, U=965.00, z=-2.65, p=0.008).

Time spent drinking

The amount of time spent drinking increased with an increase in herd size ($F_{(1,98)}$=20.45, p<0.001) and visibility ($F_{1\text{-}100}$=10.87, p=0.001), and was longer at waterholes inside the park ($F_{(1,98)}$=7.36, p=0.008). In the late afternoon kudu herds spent less time drinking ($F_{(3,99)}$=3.54, p=0.017), which was largely due to a decrease in late afternoon drinking time during the second (FS) and third (F) experimental day (Figure 5). Overall time spent drinking was not affected by the experimental treatment ($F_{(2,98)}$=0.55, p=0.578) or the presence of other herbivores ($F_{(1,100)}$=0.09, p=0.760). Table 4 presents the minimal selected model including the sign of coefficients derived for each significant factor. On average herd sizes for which time spent drinking was measured did not differ inside or outside Hwange National Park ($Mean_{in}$±SE=5.54±0.55, $Mean_{out}$±SE=4.46±0.54, U=900.50, z=-0.49, p=0.627).

Table 4. Minimal model for the time kudu herds spent drinking.

	Coef	SE	df	t-value	p-value
Intercept	-5.848	2.119	97	-2.760	0.007
Inside or outside HNP (outside HNP used as a reference)					
Inside HNP	2.221	0.819	98	2.712	0.008
Visibility	0.036	0.011	100	3.297	0.001
Time (15:00h-18:00h used as a reference)					
6:00h-9:00h	3.846	1.226	99	3.138	0.002
9:00h-12:00h	2.204	1.011	98	2.180	0.032
12:00h-15:00h	2.110	0.992	99	2.126	0.036
Herd size	0.388	0.086	98	4.522	0.000

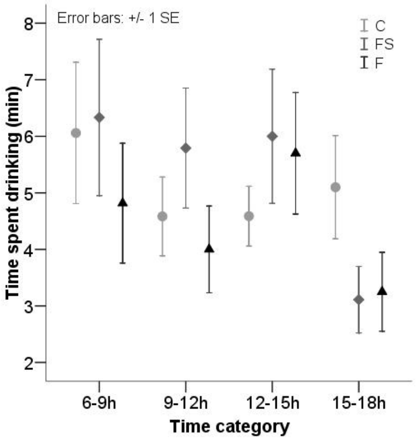

Figure 5. Average time kudu herds spent drinking at different times of the day during the control day (C) ●, the faeces and sound upon arrival day (FS) ♦ and the faeces and sound early in the morning day (F) ▲.

Spatial and temporal behavioural adjustments

There was no difference in the number of kudu herds that came to drink at the waterhole during the different experimental days (χ^2=2.48, p=0.289). The number of herds that came to drink in the early morning, late morning, early afternoon and late afternoon did no differ on the control day (C) (χ^2=4.22, p=0.238), and third experimental day (F) (χ^2=2.92, p=0.404). On the second experimental day (FS) there was a non significant tendency for less herds than expected to come and drink in the early morning and late afternoon compared to the late morning and early afternoon (χ^2=7.26, p=0.064).

Discussion

Individual kudus spent a higher proportion of time vigilant when African wild dog presence was mimicked upon arrival of the herd (FS). The proportion of time spent vigilant went back to the same level as on the control days (C) when African wild dog presence was mimicked in the early morning only (F). Although the effect of the experimental treatment was not significant, impalas inside Hwange National Park showed a similar pattern in their response as kudus (Figure 1, 3). Regardless of the experimental treatment the vigilance level of impalas in the buffer zone outside the National Park was as high as the vigilance level on the second experimental day (FS) inside the National Park thereby possibly masking the overall effect of the experimental treatment (Figure 1).

Several studies have shown that the risk of encountering predators influences herbivore behaviour (Scheel 1993, Hunter and Skinner 1998, Matson et al. 2005, Périquet et al. 2010). As all waterholes studied are frequently visited by predators it is possible that the baseline vigilance as found on the control day (C) reflects a vigilance level related to a relative high predation risk. Therefore the predation risk perceived on the third experimental day (F), when only mimicking African wild dog presence early in the morning when no prey species were present yet, is likely not to increase and differ substantially from the predation risk prey species experience on a day to day basis. Mimicking African wild dog presence upon arrival of a herd (FS) on the other hand is likely to be perceived as an immediate predation risk with a high likelihood of lethality, especially during the time frames when predators are normally active, hence increasing vigilance levels.

For kudus the time effect for the difference in the proportion of time individuals spent vigilant was mainly due to an increase in time spend vigilant in the early morning during the experimental day when immediate predation risk was mimicked (FS). Dawn is a period of time when predation risk peaks as both nocturnal and diurnal predators use this time frame to hunt. The early morning (6.00h till 9.00h) shows the most overlap with the time frames at which African wild dogs (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995) and other predators like lions (Schaller 1972) and spotted hyenas (Holekamp et al. 1997, Drouet-Hoguet 2007) are active. Therefore, when mimicking immediate predation risk during this time frame kudus are likely to perceive predation risk as very high and adjust vigilance behaviour accordingly.

Individual vigilance levels of impalas were higher at waterholes inside Hwange National Park compared to waterholes in the buffer zone outside the park. As vigilance has generally been found to decrease with an increase in herd size (Roberts 1996, Burger 2001) the found differences could simply be due to the fact that the impala herds of which the focals were taken were larger inside Hwange National Park, but without enough variation in group size between locations to find a significant overall effect of herd size. Another factor that is likely to contribute is a possible difference in predation pressure inside and outside Hwange National Park. The proportion of time individual impalas spent vigilant in the buffer zone is similar to the highest vigilance level inside the park when immediate predation risk was mimicked (FS), suggesting that impalas in the buffer zone experience a constant high predation risk. As lion densities are similar inside and outside the park (Elliot 2007), and spotted hyenas within the Hwange system predominantly scavenge (Drouet-Hoguet 2007), these predators are unlikely to contribute to differences in predation risk. Spoor densities indicate that leopards and cheetahs are more abundant outside compared to inside Hwange National Park (Elliot 2007). As for both species an important part of the diet consists of small ungulates like impalas (Kruuk and Turner 1967, Fitzgibbon 1988, Balme et al. 2007), it is possible that the higher abundance of these predators in the buffer zone results in a higher perceived predation risk at waterholes outside the park.

For both kudus and impalas, the increase in vigilance when predation risk was high was largely due to an increase in high quality vigilance. Kudus showed an increase in high quality vigilance when immediate predation risk was mimicked and during time frames at which predation risk was likely to be high. Although impalas did not adjust their vigilance level in response to the experimental treatment, high quality vigilance was increased in situations where predation risk was likely to be perceived as high. High quality vigilance detracts from all other activities whereas low quality vigilance is used to monitor the surrounding during spare time and therefore likely to be less costly. These results suggest that costly behavioural adjustments to predation risk are likely to be made in the presence of immediate predation risk when the chances of survival directly depend on predator detection.

Apart from predation risk, factors like herd size and distance to cover are known to affect vigilance behaviour (Whittington and Chamose 1995, Roberts 1996, Frid 1997, Burger 2001). Vigilance generally decreases with an increase in herd size (Roberts 1996, Burger 2001), or the presence of other herbivores (Morse 1977, Fitzgibbon 1990, Périquet et al. 2010). For impalas the proportion of the herd engaged in head down activities increased with an increase in herd size. This suggests that a dilution effect allows more individuals to be engaged in non vigilant, risky, behaviour. Herd size and the presence of other herbivores affected total individual vigilance behaviour of kudus and the proportion of the kudu herd engaged in vigilant behaviour but did not affect the proportion of time individuals spent high quality vigilant. Previous studies have shown that non vigilant animals tend to react slower and as a consequence are more likely to be killed upon attack by a predator (Fitzgibbon 1988, Krause and Godin 1996, Hilton et al. 1999). This indicates that in the presence of immediate predation risk, individuals are likely to benefit by a vigilant response regardless of herd size or the presence of other herbivores. It is therefore possible that high quality vigilance depends very little on other factors whereas total vigilance, of which a significant proportion is represented by routine vigilance, may be influenced by herd size and the presence of other herbivores.

For kudus the proportion of time individuals spent vigilant, and the proportion of the herd engaged in vigilant behaviour increased with an increase in visibility. Cover can either serve as a protection (Scheel 1993, Whittington and Chamose 1995, Matson et al. 2005) or an obstruction (Underwood 1982, Frid 1997). For a browsing species like kudu, cover is more likely to serve as a protection and therefore likely to show a positive relationship with vigilance behaviour. For both kudus and impalas the time animals spent drinking at the waterhole increased with an increase in visibility. For kudus this is likely to be the result of the higher amount of time individuals spent vigilant resulting in animals spending less time drinking and therefore needing more time at the waterhole to meet their water requirements. Although studies of foraging behaviour have found that impalas spend more time vigilant when foraging far from cover (Matson et al. 2005), in this study vigilance behaviour of impalas was not found to be significantly related to visibility and therefore does not explain the increase in time spent drinking at the waterholes. For both kudus and impalas the time spent drinking increased with an increase in herd size. Although some studies have found that larger groups remain at waterholes longer (Burger and Gochfeld 1992), the increase with herd size found in this study is more likely to be due to the method used with time spent drinking measured as the difference in time between when the first individual started drinking and the last individual stopped drinking.

Some herbivores have been shown to adjust the time frames at which they visit the waterhole according to predation risk or completely avoid risky waterholes (Valeix et al. 2009[a]). The number of herds visiting the waterhole during the experimental days did not differ, indicating that kudus and impalas did not avoid risky waterholes. When immediate predation risk was mimicked (FS), both species seemed to adjust their time frame according to predation risk with less herds visiting the waterholes during the early morning and late afternoon, the time periods at which African wild dogs are likely to be hunting. Overall kudus spent less time drinking at the waterholes in the late afternoon which was largely due to a decrease in late afternoon drinking time during the second (FS) and third (F) experimental day (Figure 5). Instead of increasing vigilance levels during the more predator sensitive hours of the days when African wild dog presence was mimicked it is possible that kudus reduce the time they spend in the open areas by reducing their drinking time. In the mornings this trade off might be different as the need to access water might be more urgent with the hot hours of the day ahead, meaning that instead of reducing time spent drinking kudus increased their vigilance level.

In the buffer zone outside Hwange National Park a higher proportion of impalas in the herd was engaged in head down activities. This might seem contradictory to the findings of the focals, which showed that at the individual level impalas spent a greater proportion of their time vigilant outside the National Park, but is likely to be the result of sample sizes and the method used. Firstly, herd sizes for impala focals were larger inside compared to outside Hwange National Park while herd sizes for the impala scans were similar. Secondly, previous research has shown that herbivores spent a higher proportion of their time vigilant while approaching the waterhole, this level of vigilance has been found to be lower during the drinking and departure phase (Périquet et al. 2010). In the present study the individual vigilance levels include vigilance of focal individuals in the approach phase and the start of the drinking phase which are likely to be the phases where vigilance levels peak. The scans of the herd are taken during all three phases and could therefore on average show a different result.

Prey seemed to perceive immediate African wild dog presence as a high predation risk, especially at hours of the day when these predators are normally active, and adjusted their behaviour accordingly. To what extend the behavioural adjustments could affect African wild dogs hunting efficiency is difficult to predict. When habitat selection is viewed as an optimal foraging process with predators preferentially using habitat in which they yield the highest rate of energy, the differences found in anti-predator behaviour inside and outside Hwange National Park may affect habitat choice depending on the hunting method used. Unlike stalking predators, opportunistic predators might not have time to select non vigilant individuals (Cresswell et al. 2003). African wild dogs have been described to use both a stalking and an opportunistic hunting technique (Reich 1981, Fanshawe and Fitzgibbon 1993). The higher individual vigilance level of impalas outside the park during the approach and start of the drinking phase could result in early detection of an approaching African wild dog. Especially when a stalking hunting technique is used, the overall higher proportion of impalas in the herd engaged in head down activities outside the park could on the other hand benefit African wild dogs as there are fewer individuals in a position to detect their approach. Direct observations of prey selection in relation to prey behaviour in the different areas is needed to determine in which way the differences in prey behaviour are likely to affect African wild dog hunting efficiency.

Acknowledgement

The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. In addition we would like to thank the Hwange National Parks and Wildlife Management Authority, Forestry Commission, Hwange Safari Lodge and Touch the Wild for allowing us access onto their premises and supporting our fieldwork. We thank the staff of the Painted Dog rehabilitation centre for collecting African wild dog faeces. We wish to thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation, the Painted Dog Conservation project and the CNRS HERD programme with funding from the ANR FEAR (ANR-08-BLAN-0022).

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Chapter 4

Testing the risk and costs of kleptoparasitism for African wild dogs inside and outside a protected area

Chapter 4

Testing the risk and costs of kleptoparasitism for African wild dogs inside and outside a protected area

Ester van der Meer, Mkhalalwa Moyo, Gregory S.A. Rasmussen, Hervé Fritz

Abstract

The energetic output of hunting African wild dogs (*Lycaon pictus*) is extremely high. Therefore survival and reproductive success depend on the ability to secure prey but also on minimising foraging costs. African wild dogs often co-exists with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), these competitors can seriously increase foraging costs by kleptoparasitism. In this study we empirically and experimentally assessed the risk and costs of kleptoparasitism for African wild dogs inside Hwange National Park, where spotted hyena densities are high, and outside the park, where spotted hyena densities are lower. Lion densities within the study area have been fluctuating. The risk and costs of kleptoparasitism were determined by comparing direct observations during hunt follows of radio collared African wild dog packs and by the use of experimental call ups with African wild dog sounds inside and outside Hwange National Park. The risk of kleptoparasitism was found to be significantly higher inside the park. With the time it took lions and spotted hyenas to get to the kill site during African wild dog hunts being longer outside the park, allowing the African wild dogs a longer carcass access time. The found differences in risk and costs of kleptoparasitism could contribute to African wild dog habitat preference for the buffer zone outside Hwange National Park. As habitat choice in and around protected areas is often related to the possibility of exposure to an 'edge effect', interspecific competition should be considered in the conservation strategy of African wild dogs even when the pressure of lions and spotted hyenas is relatively low.

Key words: *African wild dog, kleptoparasitism, predator competition, foraging efficiency, habitat choice, interspecific competition, hyena, lion*

Status: accepted (*Behavioral Ecology*)

Introduction

In systems where species forage in the presence of others they may use the opportunity to steal resources from other successful foragers rather than spending time to secure resources themselves (kleptoparasitism) (Hamilton 2002, Broom and Ruxton 2003). In general kleptoparasitism is predicted to increase with a high density of hosts relative to prey and increasing food item value and handling time (Ruxton and Moody 1997, Hamilton 2002, Broom and Ruxton 2003). Another factor that affects the likelihood of kleptoparasitism is search efficiency. When competitors differ in their ability to search for food those with the lower search efficiency are more likely to use kleptoparasitism as a strategy to obtain food (Hamilton 2002). Kleptoparasitizing a competitor might not always be cost efficient as challenging a competitor takes time that could otherwise be spent searching for undiscovered food. But if there is a strong asymmetry in size or fighting ability the likelihood of successfully stealing food from a weaker competitor is increased and the benefits of kleptoparasitism may become higher than of searching for food (Broom and Ruxton 1998, Creel 2001, Hamilton 2002). Diet composition is likely to affect the benefits of kleptoparasitism. For species feeding on static food items like plants, the main costs of foraging are related to locating food items (Shipman and Walker 1989). Therefore kleptoparasites are likely to benefit by a reduction in search time. For species feeding on mobile food items like vertebrate prey, the main costs of foraging are related to capturing prey (Shipman and Walker 1989). Especially large carnivores experience relatively high hunting costs with long high speed chases and high costs of capturing and killing prey (Carbone et al. 2007). Therefore kleptoparasites are not only likely to benefit by a reduction in search time but also by avoiding the costs of chasing and killing prey.

Kleptoparasitism has been documented for many different types of animals, such as birds (Brockmann and Barnard 1979, Skorka and Wojcik 2008), fish (Webster and Hart 2006) and mammals (Carbone et al. 1997, Gorman et al. 1998). One of the mammals regularly affected by kleptoparasites is the African wild dog (*Lycaon pictus*), which often co-exists with larger carnivores such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). African wild dog hunting success ranges from 44% up to as high as 91% (for an overview see Creel and Creel 1998), which contrasts with the lower hunting success of spotted hyenas (25-30%; Holekamp et al. 1997) and lions (27-30%; Funston et al. 2001). The high hunting efficiency of African wild dogs compared to lions and spotted hyenas and their smaller body mass make them vulnerable for kleptoparasitism by these bigger carnivores. Although lions and spotted hyenas largely rely on hunting and scavenging to secure food, both are known to steal kills from African wild dogs (Estes and Goddard 1967, Reich 1981, Creel and Creel 1995; Carbone et al. 1997, Gorman et al. 1998, Drouet-Hoguet 2007). Data from different ecosystems show that lions and/or spotted hyenas affect African wild dogs indirectly by excluding them from habitat with high prey densities (Mills and Gorman 1997, Creel 2001) or directly by killing (Reich 1981, Ginsberg et al. 1995, van Heerden et al. 1995, Woodroffe et al. 1997) and through kleptoparasitism (Estes and Goddard 1967, Reich 1981, Carbone et al. 1997, Gorman et al. 1998, Creel 2001).

African wild dogs are efficient hunters that rely on high hunting success rates at regular intervals. They use a widely foraging strategy which comes with the benefit of increasing the likelihood of encounter and thus ensuring prey capture, but also comes with significant energetic costs (Huey and Pianka 1981). The energetic output of hunting African wild dogs is extremely high (Gorman et al. 1998, Rasmussen et al. 2008), with more than 1500KJ burnt per 100 meter run (Rasmussen 2009). Not only does the survival and reproductive success of African wild dogs largely depend on its ability to secure prey, foraging in itself is costly and therefore minimising foraging costs positively affects survival (Rasmussen et al. 2008). Lions and spotted hyenas interfere with this minimalisation and can seriously increase foraging costs by kleptoparasitism (Gorman et al. 1998).

In this study we empirically and experimentally assessed the risk and costs of kleptoparasitism for African wild dogs inside a protected area (Hwange National Park), where spotted hyena densities are high (Elliot 2007), and in the buffer zone outside the protected area where spotted hyena densities are lower (Elliot 2007). Due to sport-hunting lion densities within the study area have been fluctuating (see method). We determined the risk and costs of kleptoparasitism by comparing direct observations of kleptoparasitism during African wild dog hunts and by the use of experimental call ups with African wild dog sounds in areas inside and outside Hwange National Park.

Method

Study area

Hwange National Park is situated in the northwest of Zimbabwe (19°00'S, 26°30'E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the National Park is designated for photographic safaris and trophy hunting. Most of this land is either privately owned or state owned and managed by Forestry Commission. Over the years spotted hyena densities in the study area have been stable and densities have been estimated to be around 11.3 hyenas/100km^2 in the area inside the National Park and 5.5 hyenas/100km^2 in the buffer zone outside the National Park (Salnicki 2004, Drouet-Hoguet 2007, Elliot 2007). In 2005 the lion density inside Hwange National Park was estimated to be 2.7 lions/100km^2 while, due to sport-hunting, the lion density outside the park was estimated to be as low as 0.06 lions/100km^2 (Davidson 2009). In 2007 the lion density inside Hwange National Park was estimated to be around 2.6 lions/100km^2 and the lion density in the buffer zone had recovered to 2.2 lions/100km^2 due to a moratorium (Elliot 2007, Davidson 2009).

Species

African wild dogs are medium sized social canids, forming packs of up to twenty adults and their dependent offspring (Creel and Creel 1995, Woodroffe et al. 1997). They are crepuscular with hunts being most common at dusk and dawn or when sufficient moonlight is available (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Fuller et al. 1995, Rasmussen 2009). They hunt by sight sound and smell for small to large antelopes, with impalas (*Aepyceros melampus*), kudus (*Tragelaphus strepsiceros*) and duikers (*Sylvicapra grimmia*) being their main prey in and around Hwange National Park (Rasmussen 2009). Previous research has shown that there was no difference in territory size, foraging distance and diet composition of African wild dogs inside and outside the National Park, indicating that prey availability is similar (van der Meer et al. unpublished manuscript (chapter 2)).

African wild dogs have large territories, which on average range between 423 and 1318 km^2 (Woodroffe et al. 1997). With fewer than 8000 individuals left in the wild, African wild dogs are classified as endangered and consequently rank high for conservation (Hunter et al. 2010). Over the years their numbers in the Hwange area have declined. In 1997 it was estimated that African wild dog densities in and around Hwange National Park ranged between 150 and 225 individuals (Rasmussen 1997, Woodroffe et al. 1997). More recent information suggests that there are approximately 50 to 70 individuals left in and around Hwange National Park, an area that covers 20 000 km^2 (Zimbabwe Parks and Wildlife Management Authority 2009, Blinston 2010).

Hunt follows

Data from 22 radio collared African wild dog packs were collected by G.S.A. Rasmussen between 1991 and 2002, with a study duration of 29.5 ± 20.1 months (mean ± SD) per pack. As soon as a pack had been located it was monitored non-stop from a distance of ≥ 50m for as long as practically feasible (max 28 days). The activity of the packs was continuously monitored visually or from motion sensors incorporated in the radio collars and recorded at 5 min scan intervals. Whenever a change in activity mode or direction occurred location fixes were taken by using triangulation or visual observations and a GPS unit. When kills were made the number of African wild dogs feeding on the carcass, feeding time, the time it took before kleptoparasites arrived at the kill (lapse time) and the outcome of the defence of the kill were observed and recorded. As feeding time can differ per individual, it was measured as the time the pack had access to the carcass in cases where the kill was kleptoparasitized, successfully defended or when no kleptoparasites were present. We categorised the data into events inside the National Park and events in the buffer zone outside the National Park. Being kleptoparasitized was defined as having the carcass stolen by lions or spotted hyenas within 60 minutes after the actual kill. After this time, irrespective of pack size, all African wild dogs within a pack would either be satiated or the carcass would be finished.

Call ups

As the average pack size in our study area is approximately four individuals per pack and impalas are a main part of the diet a 2 minutes recording of four African wild dogs killing and eating an impala was used to call up lions and spotted hyenas. In total we selected 48 call sites along the northern edge of Hwange National Park; 24 inside the National Park, and 24 in the buffer zone outside the National Park. Lions and spotted hyenas are known to respond to call ups from a range varying between 2.5 and 3.2 km (Ogutu and Dublin 1998, Mills et al. 2001). Although it is possible that the sounds we used are less of a stimulus and therefore have a smaller range than the sounds of kills of larger prey species, hyena interactions and hyena-lion interactions that are generally used during call up sessions to estimate population densities, we decided to be conservative and situate call sites at least 7 km apart in order to avoid attracting the same animal twice. We called lions and spotted hyenas up at 05:30h in the morning and 18:00h in the evening, the time frames at which African wild dogs normally hunt.

We parked the car at an open spot on the road and played the sound fragment at maximum volume in the north, east, south and west direction. Sounds were played at high amplification with two 100W speakers connected to a 250W amplifier, powered by the vehicle’s

12V battery. Each 8 min call up session was followed by a 5 min pause. Under normal conditions the average feeding time of African wild dogs in our study area is around 30 min (Table 1). Therefore we repeated the 8 minutes session three times. After the third time another 26 minutes were spent in silence at the call site to allow for late responses. In total we spent 60 minutes at each call site. After a period of 60 minutes responses by kleptoparasites are unlikely to result in a significant loss of the kill as in a natural situation by then all African wild dogs in a pack will either be satiated or the carcass will be finished.

Species, time of response and number of animals responding were noted. Call ups were carried out with a minimum of three people to be able to monitor both the vocal and visual responses in all directions. As in general there were just one or two animals responding it was not difficult to keep track of the animals and avoid double counting. If an animal responded vocally and was thereafter seen at the kill site only the time of the visual response was recorded. After each session we checked the area within a range of 150m around the call up station for spoor.

As the time at which the responding animal was seen and the distance at which the sound travels could be influenced by vegetation density each call up was followed by a vegetation monitor to determine bush and tree densities following the method as described by Walker (1976). An imaginary cross was placed on top of the car, four vegetation plots were placed along those four lines at 50m from the car. Each plot consisted of a 10x10m square with a 5x5m square inside. Within the 10x10m plot the number of trees, the number of stems, the diameter of the stems and the total height, stem height, long canopy diameter and short canopy diameter of each tree were measured. Within the 5x5m plot the number of shrubs and the height and long and short diameter of each shrub were measured. A 1x1m square was randomly thrown three times to measure grass height. The following formulas were used to determine shrub volume and tree canopy volume: shrub volume = $\pi/4$ x long diameter x short diameter x height of shrub, tree canopy volume = $\pi/4$ x long diameter x short diameter x (tree height-stem height). At each plot we determined visibility in the north, east, south and west direction by having one observer sitting in the middle of the plot and a second person walk away with a Garmin GPS to measure the distance at which this person went out of sight for the observer.

As wind speed and light strength could potentially affect the response of lions and spotted hyenas, we measured wind speed with the use of a Silva wind meter (Silva Sweden AB, Sollentuna, Sweden), light strength was determined using a digital lux meter (LX1010B) (Precisions Mastech Enterprises, Kwun Tong Kowloon, Hong Kong).

Table 1. Feeding time with and without lions and/or spotted hyenas present, n=492, 191 kill sites inside Hwange National Park, 301 kill sites outside Hwange National Park (HNP).

Feeding time (min)	**Hyena**		**Lion and/or Hyena**	
mean ± SE	Inside HNP	Outside HNP	Inside HNP	Outside HNP
Kleptoparasitized	11.06 ± 3.61	18.71 ± 7.78	9.67 ± 4.48	18.71 ± 7.78
Defended	30.64 ± 5.64	41.25 ± 6.25	30.64 ± 5.64	41.25 ± 6.25
Not present	29.00 ± 1.92	31.08 ± 1.23	29.00 ± 1.92	31.08 ± 1.23

Statistical analysis

Hunt follows

As there was no or a very limited response of lions in the buffer zone outside Hwange National Park, we performed analyses for lions and spotted hyenas together or for spotted hyenas separately. We used a binary logistic regression model to calculate the probability of presence of lions and/or spotted hyenas. To identify the factors influencing the presence of lions and/or spotted hyenas we used a backwards step-wise selection procedure based on the likelihood ratio with successive removal of variables for which $P > 0.05$. For the analysis of successful and failed kleptoparasitism during African wild dog hunts we only selected cases where lions and/or spotted hyenas responded within the first 60 minutes. The variables for the hunt follows were; inside or outside Hwange National Park, time of hunt and African wild dog pack size. The interactions between pack size and inside or outside Hwange National Park, and time of hunt and inside or outside Hwange National Park were also taken into account. We used a similar procedure to analyse the probability of success of defence of the kill when lions and/or spotted hyenas were present during African wild dog hunts, with the variables; inside or outside Hwange National Park, African wild dog pack size and the interaction between the two.

We analysed lapse time with the use of a backwards generalized linear model with a gamma distribution. Two full models were built with an identity link or a log link. Based on the AICC values we decided that the generalized linear model with an identity link and maximum likelihood estimates as the scale parameter method was the best fitting model. Variables used in the analysis were; inside or outside Hwange National Park, time of hunt, African wild dog pack size. We also took the interaction between inside or outside Hwange National Park and time of hunt, and inside or outside Hwange National Park and pack size into account.

We used a linear regression model with a step-wise backwards procedure to determine the relationship between number of spotted hyenas present and African wild dog pack size. Variables added to the model were; African wild dog pack size and inside or outside Hwange National Park.

It has been estimated that African wild dogs have a stomach capacity of 9 kg (Creel and Creel 1995, Pribyl and Crissey 1999). The consumption rate of African wild dogs is likely to be affected by previous consumption and therefore African wild dogs might not always be able to consume 9 kg. As there was no information available about previous consumption we nevertheless used 9 kg as a baseline to see whether African wild dogs would have potentially met their maximum stomach capacity or not, this measure was used to quantify the quality of the kill. In order to be able to calculate whether the stomach capacity of a pack was met or not met for the denning season we calculated the maximum capacity by multiplication of the number of adults and yearlings in a pack times nine kilograms, for the nomadic season we added the number of pups times nine kilograms divided by two to be conservative (following Creel and Creel 1995 and Rasmussen et al. 2008). We obtained prey masses, measured as the total body weight, from Rasmussen et al. (2008). The maximum stomach capacity of a pack was subtracted from the prey mass, if this resulted in a negative number the pack was said not to have met its stomach capacity, if this resulted in a positive number the pack was said to have potentially met its stomach capacity. As there were a large number of cases where prey mass had not been estimated and therefore it could not be determined whether the stomach capacity had been met or not, we used a separate logistic regression model with only the cases where prey mass was known to calculate the probability of presence of lions and/or spotted hyenas in relation to whether the stomach capacity of the African wild dogs within a pack was met or not met. Backward variable selection was used with successive removal of non-significant variables. We used a nonparametric point bi-serial correlation in order to establish whether differences in lions and/or spotted hyenas presence when the stomach capacity of the African wild dogs was potentially met or not met were related to African wild dog pack sizes and/or prey masses.

Call up experiment

Similarly to the hunt follows, we performed analysis for lions and spotted hyenas together or for spotted hyenas separately. We used a binary logistic regression model to calculate the probability of presence of lions and/or spotted hyenas. To identify the factors influencing the presence of lions and/or spotted hyenas we used a backwards step-wise selection procedure based on the likelihood ratio with successive removal of variables for which $P > 0.05$. For the call ups we made a selection of vegetation variables based on bivariate Pearson’s correlations. As shrub measurements were strongly correlated with visibility, only visibility was used in the analysis. We chose canopy volume as the variable to represent trees as there was no correlation between canopy volume and visibility but canopy volume was significantly correlated with all other tree measurements. The variables used in the analysis of the experimental call up response were therefore; inside or outside Hwange National Park, time of call up, wind speed, light strength, tree canopy volume, grass height, visibility. Due to differences in land use animals in the areas outside Hwange National Park are more likely to be exposed to human activity which could possibly result in a shift in activity frame or a change in behaviour and therefore could potentially affect the response to the call ups. To test for possible differences in response related to differences in land use we also took the interactions inside or outside Hwange National Park and time of call up, visibility or light strength into account.

We analysed the lapse time during the experimental call ups for both lions and spotted hyenas together and spotted hyenas separate and used a backwards linear regression model with the variables; inside or outside Hwange National Park, time of call up, wind speed, light strength, tree canopy volume, grass height and visibility.

All statistical analyses were performed with SPSS software for MS Windows release 16.0 (SPSS Inc, Chicago, USA).

Results

Risk of kleptoparasitism

Both the hunt follows and the call up experiment showed that the risk for African wild dogs to encounter lions and/or spotted hyenas was significantly higher inside Hwange National Park. The likelihood of presence of lions and/or spotted hyenas at an African wild dog kill sites was higher inside the National Park ($B=1.23$, $SE=0.32$, $p<0.001$, $Wald=14.64$) (Table 2). There was a non significant tendency for an increase in the likelihood of lion and/or spotted hyena presence with an increase in pack size ($B=0.09$, $SE=0.05$, $p=0.078$, $Wald=3.11$). Time of hunt or the interactions between the variables and inside or outside Hwange National Park did not have a significant effect (all $p>0.260$). We found a similar result for spotted hyenas only, with the likelihood of presence of spotted hyenas being higher inside Hwange National Park (B=0.96, SE=0.33, p=0.004, Wald=8.48) (Table 2) and a non significant tendency for an increase in the likelihood of spotted hyena presence with an increase in pack size (B=0.10, SE=0.05, p=0.058, Wald=3.59). Time of hunt or the interactions between the variables and inside or outside Hwange National Park did not have an effect (all p>0.177).

During the call ups there was a significantly higher response of lions and/or spotted hyenas inside Hwange National Park (B=2.26, SE=0.72, p=0.002, Wald=9.81) (Table 3). An increase in wind speed resulted in a non significant tendency to decrease the likelihood of response (B=-0.36, SE=0.20, p=0.071, Wald=3.27). We found no significant effect for time of call up, light strength, tree canopy volume, grass height, visibility or the interaction between inside or outside the National Park and time of call up, visibility or light strength (all p>0.115).

If only spotted hyena responses were taken into account we found no differences in the likelihood of response inside or outside Hwange National Park. Variables entered in the model were inside or outside the National Park, time of call up, wind speed, light strength, tree canopy volume, grass height, visibility and the interactions between inside or outside Hwange National Park and time of call up, visibility or light strength (all p>0.118).

Table 2. Number of times lions and/or spotted hyenas were present at African wild dog kill sites, n=492, 191 kill sites inside Hwange National Park, 301 kill sites outside Hwange National Park (HNP).

	Hyena		**Lion**		**Lion and/or Hyena**	
	Inside HNP	Outside HNP	Inside HNP	Outside HNP	Inside HNP	Outside HNP
Presence	13.09% (n=25)	5.65% (n=17)	3.14% (n=6)	0 (n=0)	16,23% (n=31)	5.65% (n=17)
Kleptoparasitized	6,28% (n=12)	2,66% (n=8)	3.14% (n=6)	0 (n=0)	9.42% (n=18)	2.66% (n=8)
Defended	6,80% (n=13)	2,99% (n=9)	0 (n=0)	0 (n=0)	6.80% (n=13)	2.99% (n=9)
Mean lapse time (min) ± SE	10.84 ± 2.83	18.80 ± 4.32	14.40 ± 6.38	0 .	11.33 ± 2.57	18.80 ± 4.32
Mean number ± SE	2.73 ± 0.55	2.75 ± 0.55	. .	. .	. .	. .

Table 3. Response call up experiment, n=48, 24 call sites inside Hwange National Park, 24 call sites outside Hwange National Park (HNP).

Species responding	**Response inside HNP (nr)**	**Mean response inside HNP (nr) ± SE**	**Mean lapse time inside HNP (min) ± SE**	**Response outside HNP (nr)**	**Mean response outside HNP (nr) ± SE**	**Mean lapse time outside HNP (min) ± SE**
Hyena	9	1.67 ± 0.29	30.11 ± 4.10	5	1.00 ± 0.00	32.40 ± 3.54
Lion	7	1.86 ± 0.40	13.57 ± 3.21	1	1.00 .	41.00 .
Jackal	9	1.78 ± 0.28	8.77 ± 3.71	9	1.67 ± 0.17	21.33 ± 5.11
Kite	9	1.30 ± 0.26	16.89 ± 3.80	9	1.10 ± 0.19	12.22 ± 3.10
African wild dog	1	2.00 .	54.00 .	2	2.50 ± 0.50	42.00 ± 5.00
Leopard	0	0.00 .	0.00 .	1	1.00 .	28.00 .

Costs and circumstances

The presence of lions and/or spotted hyenas did not necessarily mean that African wild dogs lost their prey, as there was always a chance that they successfully managed to defend their kill. None of the variables added in the logistic regression model significantly affected the likelihood of the success of defence of a kill, whether it was tested for lions and/or spotted hyenas (all p>0.173) or spotted hyenas separately (all p>0.361). If looked at the percentage of successful defences and the percentage of cases where African wild dogs were kleptoparasitized there was basically a 50-50 chance that they either lost or successfully defended their kill when spotted hyenas were present at the kill site (Table 2). When lions were present African wild dogs always got kleptoparasitized (Table 2).

Lapse time of lions and spotted hyenas was shorter inside Hwange National Park (B=-11.30, SE=4.90, p=0.021, Wald=5.32) (Table 2). The time of day a hunt took place significantly affected the amount of time it took before these kleptoparasites arrived, with a longer lapse time during the morning hunts than during hunts that took place at night when there was sufficient moonlight (B=14.35, SE=4.57, p=0.002, Wald=9.86). African wild dog pack size, and the interaction between inside or outside Hwange National Park and time of hunt, and inside or outside Hwange National Park and pack size did not affect lapse time (all p>0.143). If only spotted hyenas were taken into account similar results were found, with a shorter lapse time inside the National Park (B=-14.47, SE=4.22, p=0.001, Wald=11.75) (Table 2), and a longer lapse time during the morning hunts than during hunts that took place at night when there was sufficient moonlight available (B=15.32, SE=4.41, p=0.001, Wald=12.08). African wild dog pack size, and the interaction between inside or outside Hwange National Park and time of hunt, and inside or outside Hwange National Park and pack size did not affect spotted hyena lapse time (all p>0.153). The lapse time for the experimental call ups for lions and spotted hyenas together showed a non significant tendency to be longer outside Hwange National Park (Mean_{in}±SE=21.00±2.99, Mean_{out}±SE=32.40±3.54, B=11.40, SE=5.61, p=0.057, t=2.03). For spotted hyenas separate there was no difference in lapse time inside or outside Hwange National Park (B=7.28, SE=4.65, p=0.149, t=1.57) (Table 3). In both cases lapse time was not affected by time of call up, visibility, grass height, canopy volume or wind speed (lions and/or spotted hyenas; all p>0.216, spotted hyenas; all p>0.149). Light strength did not affect lapse time when lion and spotted hyena responses were combined (B=-0.00, SE=0.00 , p=0.825, t=-0.23), but did seem to affect lapse times for spotted hyenas only, with a stronger light strength resulting in a longer lapse time (B=0.002, SE=0.001, p=0.048, t=2.21).

The number of spotted hyenas interacting, was significantly related to African wild dog pack size, with an increase in number of spotted hyenas interacting with an increase in African wild dog pack size (Figure 1) (Mean±SE=2.74±0.33, B=0.46, SE=0.05, p<0.001, t=8.46), inside or outside Hwange National Park did not affect the number of spotted hyenas interacting (B=-0.08, SE=0.48, p=0.872, t=-0.16). When tested without the extreme of a pack of twenty four African wild dogs versus thirteen spotted hyenas a similar result was found (B=0.31, SE=0.072, p<0.001, t=4.28). There was a higher likelihood of lions and/or spotted hyenas being present at the kill when the stomach capacity of the African wild dogs would have been met (B=-0.73, SE=0.35, p=0.038, Wald=4.32). When analysed for spotted hyenas only, the same result was found (B=-0.73, SE=0.36, p=0.043, Wald=4.10). This either indicates that the likelihood of lion and/or spotted hyena presence is higher when relatively small packs kill an average sized prey or when averaged sized packs kill big prey. We found a significant, correlation between lion and/or spotted hyena presence and prey mass (lions and/or spotted hyenas; p=0.016, r^2=0.01, spotted hyenas; p=0.012, r^2=0.01) while there was no correlation between lion and/or spotted hyena presence and pack size (lions and/or spotted hyenas; p=0.231, r^2=0.00, spotted hyenas; p=0.172, r^2=0.00).

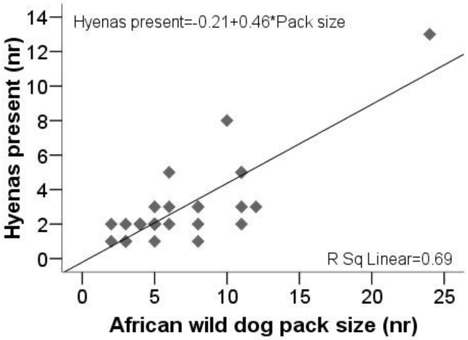

Figure 1. Number of spotted hyenas present at African wild dog kill sites in and around Hwange National Park in relation to African wild dog pack size.

Discussion

In this study we found that the risk of kleptoparasitism is significantly higher inside Hwange National Park. For spotted hyenas, for both the hunt follows and the call ups (Table 4), this risk seemed to be directly related to densities. During the hunt follows as well as the call ups virtually no responses of lions were noted outside Hwange National Park. At the time of the hunt follows the bias in response rate could have been the result of sport-hunting in the buffer zone outside Hwange National Park which resulted in low densities of lions and a female bias in adult sex ratio (Loveridge et al. 2007, Davidson 2009). Previous research has shown that adult male lions tend to obtain most of their food by scavenging from kills of lionesses and other predators (Scheel and Packer 1991), which is in accordance with our finding that only male lions responded to the call up sessions (no data on sex of lions responding during the hunt follows were available). However, the call ups took place after a moratorium was implemented and lion densities were recovering, and close to equal inside and outside Hwange National Park (Elliot 2007). Although lion and spotted hyena densities have been found to be positively related (Creel and Creel 1996, Mills and Gorman 1997), lions and spotted hyenas are known competitors (Funston et al. 1998). With spotted hyena densities inside the National Park being double compared to outside the National Park (Elliot 2007), the competition rate between lions and spotted hyenas will inevitably be higher inside Hwange National Park which could possibly sensitize lions up to a point where they are overall more likely to respond to potential competitors. Prey density and distribution might also play a role as kleptoparasitism is generally considered to be lower with an increase in prey density (Broom and Ruxton 1998, Hamilton 2002).

Table 4. Percentage of the population responding to call ups, densities based on Elliot 2007. Area covered inside Hwange National Park (HNP), 859.5 km^2, area covered outside Hwange National Park, 844.7 km^2.

Species	Density inside HNP per 100 km^2	Total present inside HNP call up area	Nr responding to call ups	% Population responding to call ups	Density outside HNP per 100 km^2	Total present outside HNP call up area	Nr responding to call ups	% Population responding to call ups
Lion	2.6	22.347	13	58.17	2.2	18.583	1	5.38
Hyena	11.3	97.124	15	15.44	5.5	46.459	5	10.76

Although spotted hyenas have been found to kill African wild dogs (Creel and Creel 1998), the main risk of encountering spotted hyenas, is related to kleptoparasitism. Lions on the other hand are known to be a common cause of death for African wild dogs (Mills and Gorman 1997, Creel and Creel 1998). Due to a strong positive relationship between pack size, survival and reproduction (Creel and Creel 2002, McNutt and Silk 2008), in small packs the loss of an individual can be detrimental for an entire pack of African wild dogs (Courchamp and Macdonald 2001, Rasmussen 2009). The fact that African wild dogs always lost their prey when encountering lions might be due to the fact that the risk of challenging a lion is not reduced to prey loss but might mean losing an individual and therefore the potential costs are too high to seriously attempt to fight.

Lions and spotted hyenas were more often present at kills where the stomach capacity of African wild dogs of 9 kg (Creel and Creel 1995, Pribyl and Crissey 1999) would have potentially been met, which seemed to be related to bigger prey rather than smaller pack sizes. This in itself is not surprising as with an increase in prey size, it is generally found that handling time and therefore the risk of kleptoparasitism increases as well (Ruxton and Moody 1997, Nilsson and Brönmark 1999, Hamilton 2002). There is a maximum to this increased risk as, according to the 'apple model' of Broom and Ruxton (2003), the longer the prey has been handled the less value it will have and therefore individuals will only challenge when there is sufficient food remaining. The period of time where sufficient food remains for lions and spotted hyenas to seriously challenge African wild dogs will inevitably be longer for bigger prey than for smaller prey. It will therefore be more profitable to kleptoparasitize on bigger prey items.

Lapse time during morning hunts was found to be shorter than during moonlight hunts. This most likely has to do with the fact that, with lions and spotted hyenas being primarily nocturnal (Grinnell et al. 1995, Mills et al. 2001), there is a bigger overlap in activity time for lions, spotted hyenas and African wild dogs during the night compared to the morning. During the call ups spotted hyena lapse time was found to increase with an increase in light strength. Stronger light strengths occurred late in the morning or early in the evening, the longer lapse time associated to it might mean that these periods of time were on the margins of the temporal activity frames of the spotted hyenas and it therefore took longer before there was a response. The likelihood of a response during the call ups showed a tendency to be negatively related to wind speed, this is likely to be due to wind speed affecting the range and direction at which the call up sounds travel.

For spotted hyenas minimum lapse time during the hunt follows was zero minutes indicating that spotted hyenas, as described in other studies (Estes and Goddard 1967, Reich 1981, Creel 2001, Rasmussen et al. 2008), start following hunting African wild dogs before they actually make the kill. As it might be easier for spotted hyenas to keep track of a big pack of

African wild dogs compared to a small pack, this following behaviour could also explain why there was a tendency for bigger packs to experience a higher risk of kleptoparasitism. During the call ups the average lapse time was found to be longer than during the hunt follows. During the call ups the spotted hyenas do not have the benefit of being able to follow the hunt from an early stage though, and might therefore still need to travel a considerable distance to get to the call site which inevitably results in a prolonged lapse time. In four cases during hunt follows inside the National Park spotted hyenas were actually observed to interfere with the chase, lions on the other hand were never observed to interfere with the chase. It is possible that, due to the small to medium prey sizes of African wild dogs, the benefits of kleptoparasitism for lions are relatively less compared to spotted hyenas and that, unlike for spotted hyenas, where kleptoparasitism appears to be an active strategy to obtain food, for lions kleptoparasitism is more of an opportunistic event where, if they accidentally run into a pack of African wild dogs they will steal the kill.

It took lions and/or spotted hyenas longer to get to a kill site outside Hwange National Park. As, after killing the prey by disembowelling it, African wild dogs devour their prey as quickly as possible, this allows them more time to consume a substantial part of the prey themselves before being kleptoparasitized. Generally hyenas seem to locate African wild dog kills more quickly in open habitat (Creel and Creel 1996, 1998). Although vegetation density did not have an effect on the response time of lions and/or spotted hyenas during the call up sessions it is possible that it does influence the response time during the hunt follows as vegetation density is likely to affect the ease with which spotted hyenas are able to follow a hunting pack of African wild dogs. It is therefore possible that the found differences in lapse time reflect differences in vegetation density inside and outside Hwange National Park.

It has to be kept in mind that the small sample sizes, especially when testing for interactions, imposes limitations. This is largely due to the limitations in following hunts in thick bush and the large number of hunts and call ups that need to be documented to be able to describe kleptoparasitism. Despite these limitations we do feel some conclusions can be drawn.

Studies by Creel and Creel (1996) and Mills and Gorman (1997) have shown that African wild dogs try to avoid competition with lions and spotted hyenas by utilising habitats in which lion and spotted hyena densities are low, even when this might mean moving into an area with lower prey density. Like for other carnivore species, most of the mortality of African wild dogs occurs when they range beyond reserve boundaries into border areas where, because of a so called ‘edge effect’, they get increasingly exposed to human activity resulting in mortality (Woodroffe and Ginsberg 1998, Woodroffe et al. 2004). Previous research has shown that, over the years African wild dogs in Hwange National Park, moved closer to or crossed the National Parks border increasingly exposing themselves to such an ‘edge effect’ (van der Meer et al. submitted (chapter 1)). One of the factors contributing to this movement could be competition with lions and spotted hyenas. In other African ecosystems spotted hyena presence at African wild dog kills varied between 18% (Selous, Tanzania) and 86% (Serengeti, Tanzania), when spotted hyenas were present the occurrence of kleptoparasitism varied between 0% (Kruger, South Africa) and 86% (Serengeti, Tanzania) (Creel and Creel 1998). Although compared to these numbers the pressure of kleptoparasitism inside and outside Hwange National Park might not be extraordinary high, the differences in risk and costs of kleptoparasitism might nevertheless affect African wild dog habitat choice. Within Hwange National Park African wild dogs lost their prey once out of every eleven hunts whereas in the buffer zone outside the National Park they lost their prey once out of every thirty eight hunts. Based on the model of Gorman et al. (1998), inside Hwange National Park African wild dogs have to approximately spent an additional 5 hours hunting to compensate for kleptoparasitism while outside the National Park this is an additional 3.5 hours. On top of that, when the kill is being kleptoparasitized African wild dogs have an approximately eight minutes longer feeding time outside the National Park (Table 1). For African wild dogs, for which the 'normal' 3.5 hours hunting each day already brings them close to their physiological limits (Gorman et al. 1998), these difference in risk and costs of kleptoparasitism could influence habitat choice for the buffer zone outside Hwange National Park.

Like in and around Hwange National Park habitat choice of African wild dogs in and around protected areas, due to differences in land use, is often related to the possibility of exposure to an 'edge effect' (human activity resulting in mortality) (Woodroffe et al. 1997). Even when the pressure of kleptoparasitism seems to be relatively low interspecific competition is likely to play a role in habitat selection of African wild dogs and should therefore be taken into account in the conservation strategy of the species.

Acknowledgement

The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. In addition we would like to thank the Hwange National Parks and Wildlife Management Authority, Forestry Commission, Wilderness safaris, Hwange Safari Lodge, Touch the Wild, and the various farmers within the Gwaai Intensive Conservation Area for allowing us access onto their premises and supporting our fieldwork. We thank Evelyne Gevaert, Pieter Huisman, Ian Chattington and Hans Dullemont for providing the necessary equipment. We thank all people that participated in the field work, especially the students and staff of the CNRS HERD programme. We wish to thank Simon Chamaillé-Jammes and Marion Valeix for their fruitful comments on previous drafts. We also like to thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation and the Painted Dog Conservation project.

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Chapter 5

Characteristics of African wild dog den sites selected under different interspecific predation pressures

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Ester van der Meer, Jealous Mpofu, Hervé Fritz

Abstract

To successfully reproduce many carnivorous mammals need access to suitable den sites. Den site selection is often based on fitness related factors like food availability, escape from predators and shelter from extreme weather conditions. African wild dogs are cooperative breeders that use a den to give birth to their offspring. They often co-exist with lions and spotted hyenas which are known to kill African wild dog pups. In this study we looked at the vegetation characteristics and distribution of roads and waterholes around den sites in areas with high and low lion and spotted hyena densities. Overall, den sites were predominantly situated in closed vegetation with little visibility, suggesting that regardless of predation pressure African wild dogs place their dens in vegetation that is likely to provide protection from predators. Surprisingly these results were less pronounced in the high predator density area. It has to be kept in mind though that in the high predator density area closed vegetation is likely to be a limiting resource as there was virtually none available, African wild dogs nevertheless managed to place 40.0% of their den sites in closed vegetation. In the high predator density area den sites were less often placed within 2 km from waterholes which could be an adaptation to reduce encounter rates with lions as these predators utilise areas within 2 km from waterholes to hunt. With the scarcity of preferred vegetation, African wild dogs in the high predator density area have to expose themselves to a higher predation risk or leave the area. As the high predator density area is based in a National Park and the low predator density area in the buffer zone outside the park, where African wild dogs experience a high human induced mortality rate, this can have serious conservation implications.

Key words: *African wild dog, den site selection, interspecific competition, intraguild predation, vegetation characteristics, limiting resource, lion, hyena*

Status: unpublished manuscript

Introduction

Carnivore ecology is not only affected by predator prey interactions but also by competition between predators. Interspecific competition between carnivores is either based on exploitation competition, interference competition, or both. Exploitation competition is related to diet overlap, where a prey item consumed by one predator cannot be consumed by another (Linnell and Strand 2000, Caro and Stoner 2003). Interference competition involves interactions between carnivores and can have various effects, like the loss of kills (Cooper 1991, Carbone et al. 1997), exclusion from preferred habitat (Durant 1998, Creel 2001) or interspecific killing (Palomares and Caro 1999). Interspecific killing can have important implications at a population level, for example interspecific killing is one of the main natural causes of African wild dog mortality (Woodroffe et al. 2004) and responsible for a high percentage of cheetah (*Acinonyx jubatus*) cub mortality (Laurenson 1994).

Habitat selection theory predicts that individuals select habitat where, depending on the activity they need to perform, they maximize their fitness. For many carnivorous mammals access to suitable den sites is crucial for successful reproduction and likely to affect population recruitment (Fernández and Palomares 2000, Norris et al. 2002, Richardson et al. 2007). As interspecific killing can affect survival of offspring (Laurenson 1994, Woodroffe et al. 2004) it is likely that interspecific competition plays a role in den site selection by carnivores. Den site selection has indeed been shown to be based on escape from predators (Pruss 1999, Hwang et al. 2007, Lesmeister et al. 2008, Ross et al. 2010), and while some studies have shown no effect of vegetation and visibility on den site selection (Theuerkauf et al. 2003), others show that den sites are selected based on vegetation characteristics and its related visibility as both are likely to affect safety from predators (Zoellick et al. 1989, Fernández and Palomares 2000, Arjo et al. 2003). Safety from predators is not the only factor determining den site selection; factors like food availability (Eide et al. 2001, Szor et al. 2008), shelter from extreme weather conditions (Eide et al. 2001, Richardson et al. 2007, Szor et al. 2008, Herr et al. 2010) and spatial distribution of water sources, roads and human settlements have also been found to play a role (Theuerkauf et al. 2003, Hwang et al. 2007).

African wild dogs (*Lycaon pictus*) are one of the mammalian carnivores that make use of a den to give birth to its offspring (Woodroffe et al. 2004). African wild dogs often coexist with other carnivores such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Interspecific competition with these larger carnivores has been found to affect both the distribution and the abundance of African wild dogs (Reich 1981, Creel and Creel 1996, Mills and Gorman 1997, Creel 2001). One of the reasons for the negative correlation between African wild dog densities and lion and spotted hyena densities is that African wild dogs are regular victims of interspecific killing by these larger carnivores. Lions are a major cause of African wild dog mortality and are known to kill both adults and pups (Reich 1981, Woodroffe et al. 2004). Spotted hyenas have been reported to disturb den sites and kill African wild dog pups (Creel and Creel 1998, Woodroffe et al. 2004, Painted Dog Conservation project; unpublished data). It is therefore likely that interspecific competition with lions and spotted hyenas plays a role in African wild dog den site selection. African wild dog dens in Selous (Tanzania) seemed to indeed be located in thickets to avoid encounters with other carnivores (Creel and Creel 2002) and dens in Pilanesberg (South Africa) were located in steep terrain with low lion densities (van Dyk and Slotow 2003).

As far as we know there are no detailed studies that have looked at African wild dog den site characteristics. In this study we tried to get an insight in which criteria African wild dogs used to select a den by comparing vegetation characteristics of den sites with random sites, and by looking at spatial distribution of factors like distance to roads and waterholes. To be able to determine whether interspecific competition with lions and spotted hyenas affects these criteria, den sites and random sites were studied in an area with relatively high and an area with relatively low densities of these larger carnivores.

Method

Study area

Hwange National Park is situated in the northwest of Zimbabwe (19°00’S, 26°30’E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. October is the hottest month with a mean daily temperature of 33.2 °C, and July is the coldest month with a mean daily temperature of 4.1 °C. The mean annual temperature is 20.3 °C. During the cool dry season (May to August) frost occasionally occurs.

Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside Hwange National Park is designated for photographic safaris and trophy hunting. Most of this land is either privately owned or state owned and managed by Forestry Commission. The vegetation is classified as typical southern African wooded savannah with patches of grassland (Rogers 1993). The mixed woodlands and bushlands in the study area are dominated by *Baikiaea plurijuga* Harms, *Terminalia sericea* Burch. ex DC., *Combretum* spp., *Acacia* spp. and *Burkea africana* Hook. Prey species present in the study area include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*).

Predator densities

Lions and spotted hyenas occur in the study area. The lion population has been fluctuating due to sport-hunting followed by a moratorium. In 2005 lion densities inside Hwange National Park were 2.7 lions/100km^2 while, due to sport-hunting, lion densities outside the park were as low as 0.06 lions/100km^2 (Davidson 2009). Over the years spotted hyena densities in the study area have been stable and densities have been estimated to be around 11.3 hyenas/100km^2 in the area inside the National Park, and 5.5 hyenas/100km^2 in the area outside the National Park (Salnicki 2004, Drouet-Hoguet 2007, Elliot 2007). In 2004 it was estimated that African wild dog densities in and around Hwange National Park were 1.5 African wild dogs/100km^2 which is around 225 individuals (Woodroffe et al. 2004). More recent information suggests that there are approximately 50 to 70 individuals left (Zimbabwe Parks and Wildlife Management Authority 2009, Blinston 2010).

Study species

African wild dogs are carnivorous cooperative breeders that live in packs. Within a pack usually only the alpha pair reproduces while the other pack members help care for the pups (Frame et al. 1979, Reich 1981, Malcolm and Marten 1982). Litter sizes average ten to eleven pups (Fuller et al. 1992). The alpha female gives birth to the pups in an underground den where they remain the first three months of their life. Dens are often old aardvark (*Orycteropus afer*) dens, sometimes modified by warthog (*Phacochoerus aethiopicus*) or spotted hyenas (Woodroffe et al. 2004). During early lactation the alpha female is confined to the den, other pack members feed the female by regurgitating food. When the pups start feeding on solid food the pack members regurgitate for the pups as well (Malcolm and Marten 1982). The alpha female can start taking part in the hunts three weeks after parturition. The pups will be restricted to the den for another two months. When the pack goes hunting a 'baby-sitter' may be left behind to take care of the pups and chases predators away from the den (Malcolm and Marten 1982).

Protocol

Location of natal dens was carried out by radio tracking African wild dog packs in the framework of wider research on the ecology of African wild dogs by the Painted Dog Conservation project. The most recent den sites, all known African wild dog dens identified between 2001 and 2006, were used in this study. Vegetation studies were carried out in 2007 between May and June, the months during which African wild dogs in the Hwange system generally give birth (Rasmussen 2009). Ten den sites inside Hwange National Park, an area with relatively high predator densities, and ten den sites outside the park, an area with relatively low predator densities, were used in this study to be able to compare vegetation characteristics in areas with high and low predator competition. We also selected twenty random sites inside Hwange National Park and twenty random sites outside Hwange National Park in order to be able to make a comparison and determine which characteristics the African wild dogs use in their den selection. Per den site two random sites were selected at a minimum random distance of five and a maximum random distance of twenty kilometres in the north, northeast, east, southeast, south, southwest, west or northwest direction of the den site.

Vegetation characteristics were determined based on the method as described by Walker (1976). At each den site and random site a plot was set consisting of a 10x10m square enclosing a 5x5m square. Tree characteristics were measured within the 10x10m square, shrub characteristics were measured within the 5x5m square, and grass characteristics were measured by randomly throwing a 1x1m square three times within the 10x10m square. Tree characteristics measured were tree height, canopy cover, stem density, stem surface and tree density. Shrub characteristics measured were shrub height, volume and density. For grasses grass height was measured. Canopy cover was determined by measuring and multiplying the long and short diameter of the canopy. Stem density was determined by counting the number of stems including dead stems taller than two meter and regardless of whether one tree consisted of several stems, while tree density was determined by counting the number of trees only. Stem surface was calculated using the formula: stem surface = $\pi \times (\text{diameter}/2)^2$. Shrub density was determined by counting the number of shrubs within the plot. Shrub volume was determined by measuring the height, the short and the long diameter and using the formula: shrub volume = $\pi/4$ x long diameter x short diameter x height of shrub.

Visibility was estimated by positioning a seated observer at the centre of each plot at an eye level of 75 cm above ground, simulating an African wild dog's eye height. A second person walked away from the observer in each of the major compass directions (North, South, East and West) until the observer could no longer view him, and then whistled. After whistling the second person started walking back towards the observer. As soon as the person was seen the observer whistled, the person walking stopped and recorded the distance between himself and the observer using the Garmin GPS. At the den sites, the dominant vegetation species was recorded and the type of vegetation classified as open, medium or closed and bushland, woodland or grassland. Woodland was described as habitat dominated by trees with trees ≥ 3m and less than 15m distance between neigbouring trees. Bushland was described as habitat dominated by shrubs and a distance > 30m in between trees. Grassland was described as habitat dominated by grass and a distance of > 30m between shrubs and/or trees. Closed habitat was characterized by a visibility ≤ 25m, medium habitat by a visibility >25m but ≤ 50m, and open habitat by a visibility > 50m.

All of these measurements were repeated by setting up plots 50 meters from the den site or random site into the North, East, South and West direction. In other words, the measurement of vegetation characteristics and visibility around the den sites and random sites used in the analysis consists of the average of the measurements of five plots. Distance of the den sites to the nearest road and waterhole were calculated with the use of ArcGis® version 9.3.

Statistical analysis

A general linear model was used in order to test whether there were differences in visibility, shrub height, shrub density, tree height and distance to the nearest road and waterhole between den sites and random sites overall, den sites and random sites in the high predator density area and den sites and random sites in the low predator density area. As shrub volume, stem surface, stem density, tree density and canopy cover did not follow the normality assumption a Mann-Whitney U test was used to test for differences between den sites and random sites overall, between den sites and random sites in the high predator density area and den sites and random sites in the low predator density area.

General linear models were also used to test for differences in visibility, shrub height, shrub density, tree height and distance to the nearest road and waterhole between den sites in the high and low predator density area and, in order to see what type of vegetation is available, random sites in the high and low predator density area. Mann-Whitney U tests were used to test for differences in volume, stem surface, stem density, tree density and canopy cover between den sites in the high and low predator density area and random sites in the high and low predator density area.

Previous research has shown that lions within the Hwange system select areas within 2 km of waterholes to hunt (Valeix et al. 2009[b]). Historically a large percentage of African wild dog kills is also made within 2 km of waterholes (Table 1). In order to see whether African wild dog dens were generally placed within a range of 2 km from waterholes, distances to the nearest waterhole were categorized into distances within 2 km from a waterhole and distances more than 2 km from a waterhole. Distance to the nearest waterhole was then analysed by displaying the frequencies in a contingency table and using a Pearson's chi-square test to see whether den sites were placed closer to waterholes than random sites, this analysis was performed for den sites and random sites in general, den sites and random sites in the high and low predator density area separately, den sites in the high and low predator density area and random sites in the high and low predator density area.

As sample sizes were small, no statistical analysis was performed on dominant vegetation species and the landscape type around the den sites. These variables were described according to their occurrence. All statistical analyses were performed using SPSS software for MS Windows release 16.0 (SPSS Inc, Chicago, USA).

Table 1. Distance of kills, and percentage of kills within different distances, from the nearest waterhole.

Species	Mean distance ± SE	0-1 km	1-2 km	2-3 km	>3 km
Duiker	2.85 ± 0.08 km	24.2% (n=16)	24.2% (n=16)	7.6% (n=5)	43.9% (n=29)
Kudu	2.21 ± 0.22 km	36.5% (n=42)	27.8% (n=32)	11.3% (n=13)	24.3% (n=28)
Impala	1.18 ± 0.28 km	50.6% (n=79)	39.1% (n=61)	5.1% (n=8)	5.1% (n=8)
Total	1.86 ± 0.11 km	40.7% (n=137)	32.3% (n=109)	7.7% (n=26)	19.3% (n=65)

Results

Overall, visibility around den sites was lower than around random sites ($\text{Mean}_{den}\pm\text{SE}=26.68\pm2.15$, $\text{Mean}_{rnd}\pm\text{SE}=41.85\pm3.65$, $F_{(1,59)}=7.89$, p=0.007, $r^2=0.12$). Accordingly, in the low predator density area visibility around den sites was lower than around random sites ($\text{Mean}_{den}\pm\text{SE}=22.99\pm1.79$, $\text{Mean}_{rnd}\pm\text{SE}=39.52\pm4.23$, $F_{(1,29)}=7.21$, p=0.012, $r^2=0.21$) (Figure 1). Although mean values were consistent with the overall pattern, visibility between den sites and random sites in the high predator density area did not significantly differ ($\text{Mean}_{den}\pm\text{SE}=30.38\pm3.64$, $\text{Mean}_{rnd}\pm\text{SE}=44.19\pm6.05$, $F_{(1,29)}=2.38$, p=0.134, $r^2=0.08$) (Figure 1). There was a non significant tendency for higher visibility around den sites in the high predator density area compared to den sites in the low predator density area ($F_{(1,19)}=3.32$, p=0.085, $r^2=0.16$). There was no difference in visibility around random sites in the high and low predator density area ($F_{(1,39)}=0.40$, p=0.529, $r^2=0.01$).

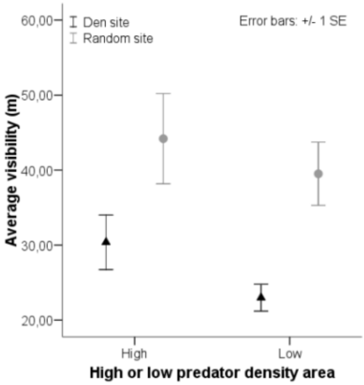

Figure 1. Visibility at den and random sites in a high or low predator density area.

Overall, den sites were more often placed in closed vegetation and less often in open vegetation than random sites ($\chi^2=11.21$, p=0.004) (Table 2). In the high predator density area den sites were more often placed in closed vegetation and less often in open vegetation than random sites ($\chi^2=9.38$, p=0.009) (Table 2). In the low predator density area there was a non significant tendency for den sites to be more often placed in closed vegetation and less often in open vegetation than random sites (χ^2=5.08, p=0.079) (Table 2). There was no difference in vegetation type between den sites in the high and low predator density area (χ^2=2.32, p=0.314) (Table 2). Random sites in the high predator density area were less often placed in closed vegetation than random sites in the low predator density area (χ^2=7.11, p=0.029) (Table 2).

Table 2. Vegetation type around den sites and random (rnd) sites in a high and low predator density area.

Vegetation	**General**		**High density area**		**Low density area**	
type	Den site	Rnd site	Den site	Rnd site	Den site	Rnd site
Closed	55.0% (n=11)	15.0% (n=6)	40.0% (n=4)	0.0% (n=0)	70.0% (n=7)	30.0% (n=6)
Medium	40.0% (n=8)	62.5% (n=25)	50.0% (n=5)	75.0% (n=15)	30.0% (n=3)	50.0% (n=10)
Open	5.0% (n=1)	22.5% (n=9)	10.0% (n=1)	25.0% (n=5)	0.0% (n=0)	20.0% (n=4)

There were no overall differences in shrub height, shrub volume, shrub density, tree height, stem surface, stem density, tree density, canopy cover and grass height between den sites and random sites (all p>0.260). In the high predator density area there was a non significant tendency for shrub density to be higher at den sites than at random sites ($Mean_{den}$±SE=0.80±0.16, $Mean_{rnd}$±SE=0.52±0.08, $F_{(1,29)}$=3.11, p=0.089, r^2=0.10), no such tendency was found in the low predator density area ($Mean_{den}$±SE=0.53±0.18, $Mean_{rnd}$±SE=0.67±0.23, $F_{(1,29)}$=2.52, p=0.124, r^2=0.08). In the low predator density area there was a non significant tendency for tree height to be smaller at the den sites than at the random sites ($Mean_{den}$±SE=435.20±41.86, $Mean_{rnd}$±SE=532.65±30.86, $F_{(1,29)}$=3.41, p=0.075, r^2=0.11), no such tendency was found in the high predator density area ($Mean_{den}$±SE=385.20±40.96, $Mean_{rnd}$±SE=375.17±32.98, $F_{(1,29)}$=0.03, p=0.857, r^2=0.00). Shrub height, shrub volume, stem surface, stem density, tree density, canopy cover and grass height did not differ between den sites and random sites in the high predator density area (all p>0.228). There was no difference in shrub height, shrub volume, stem surface, stem density, tree density, canopy cover and grass height between den sites and random sites in the low predator density area (all p>0.215).

Den sites in the high predator density area showed a non significant tendency to have a lower shrub height ($Mean_{high}$±SE=55.11±5.82, $Mean_{low}$±SE=67.77±3.26, $F_{(1,19)}$=3.61, p=0.074, r^2=0.17), lower stem density ($Mean_{high}$±SE=0.12±0.07, $Mean_{low}$±SE=0.08±0.04, U=27.00, z=-1.74, p=0.089) and lower tree density ($Mean_{high}$±SE=0.05±0.02, $Mean_{low}$±SE=0.03±0.01, U=25.00, z=-1.89, p=0.063) than in the low predator density area. Shrub volume, shrub density, tree height, stem surface, canopy cover and grass height did not differ (all p>0.143).

In general, tree height ($Mean_{high}$±SE=375.17±32.98, $Mean_{low}$±SE=532.65±30.86, $F_{(1,39)}$=12.16, p=0.001, r^2=0.24) and canopy cover ($Mean_{high}$±SE=8728.46±2259.46, $Mean_{low}$±SE=15880.70±3410.59, U=123.00, z=-2.08, p=0.038) were lower at random sites in the high predator density area than in the low predator density area. At the random sites there was a non significant tendency for shrub volume ($Mean_{high}$±SE=194199.70±41149.46, $Mean_{low}$±SE=314707.00±54281.56, U=135.00, z=-1.76, p=0.081) and stem surface ($Mean_{high}$±SE=17.48±4.89, $Mean_{low}$±SE=24.29±5.45, U=138.00, z=-1.68, p=0.096) to be smaller and grass height to be taller in the high predator density area ($Mean_{high}$±SE=26.14±3.44, $Mean_{low}$±SE=18.19±2.33, $F_{(1,39)}$=3.66, p=0.063, r^2=0.09). Shrub height, shrub density, stem density and tree density did not differ between random sites in the high and low predator density area (all p>0.123).

When taking descriptive factors such as dominant species into account it seems that a relative high proportion of the den sites in the high predator density area were situated in Zambezi teak habitat (Table 3). Especially in the low predator density area a relative high proportion of the den sites was situated in woodland (Table 4). There was no difference in distance to the nearest road between den sites and random sites in general ($Mean_{den}$±SE=0.71±0.18, $Mean_{rnd}$±SE=0.79±0.12, $F_{(1,59)}$=0.17, p=0.685, r^2=0.23), den sites and random sites in the high predator density area ($Mean_{den}$±SE=1.07±0.31, $Mean_{rnd}$±SE=1.16±0.21, $F_{(1,29)}$=0.07, p=0.797, r^2=0.00) and den sites and random sites in the low predator density area ($Mean_{den}$±SE=0.35±0.13, $Mean_{rnd}$±SE=0.41±0.21, $F_{(1,29)}$=0.23, p=0.637, r^2=0.01). In the high predator density area both den sites ($F_{(1,19)}$=4.60, p=0.046, r^2=0.20) and random sites ($F_{(1,19)}$=11.74, p=0.001, r^2=0.24) were placed further from roads than in the low predator density area.

There was also no difference in distance to the nearest waterhole between den sites and random sites in general ($Mean_{den}$±SE=1.97±0.24, $Mean_{rnd}$±SE=1.80±0.20, $F_{(1,59)}$=0.27, p=0.606, r^2=0.01), den sites and random sites in the high predator density area ($Mean_{den}$±SE=2.02±0.20, $Mean_{rnd}$±SE=1.90±0.33, $F_{(1,29)}$=0.07, p=0.796, r^2=0.00) and den sites and random sites in the low predator density area ($Mean_{den}$±SE=1.92±0.46, $Mean_{rnd}$±SE=1.69±0.07, $F_{(1,29)}$=0.22, p=0.644, r^2=0.01). No difference was found in distance to the nearest waterhole between den sites in the high and low predator density area ($F_{(1,19)}$=0.05, p=0.834, r^2=0.00) or random sites in the high and low predator density area ($F_{(1,19)}$=0.25, p=0.634, r^2=0.01).

With 35.0% of the den sites and 62.5% of the random sites situated within 2 km from a waterhole, den sites were less often placed within 2 km from a waterhole than random sites (χ^2=4.05, p=0.044). This overall difference was mainly due to the fact that den sites in the high predator density area were less often placed within 2 km from a waterhole than random sites (χ^2=4.29, p=0.038). In the high predator density area 20.0% of the den sites and 60.0% of the random sites were placed within 2 km from a waterhole. No such difference was found in the low predator density area (χ^2=0.63, p=0.429), where 50.0% of the den sites and 65.0% of the random site were placed within 2 km from a waterhole. There was also no difference in the number of den sites in the high and low predator density area (χ^2=1.98, p=0.160) and the number of random sites in the high and low predator density area (χ^2=0.11, p=0.744) placed within 2 km from the waterhole.

Table 3. Description of dominant species of vegetation at den sites in a high and low predator density area.

	High density area	**Low density area**
Mixed	20% (n=2)	50% (n=5)
Zambezi teak (*Baikiaea plurijuga)*	70% (n=7)	30% (n=3)
Terminalia (*Terminalia sericea*)	10% (n=1)	0
Sand camwood (*Baphia massaiensis*)	0	10% (n=1)
Mopane (*Colophospermum mopane*)	0	10% (n=1)
Sickle bush (*Dichrostachys cinerea*)	0	0
Combretum (*Combretum zeyheri*)	0	0
Msasa (*Brachystegia spiciformis*)	0	0
Ordeal tree (*Erythrophleum guineense)*	0	0

Table 4. Description of landscape type at den sites in a high and low predator density area.

	High density area	Low density area
Grassland	0	0
Bushland	40% (n=4)	20% (n=2)
Woodland	40% (n=4)	80% (n=8)
Mixed	20% (n=2)	0

Discussion

We are aware of the limitations imposed by the small sample size on defining criteria used by African wild dogs to find den sites. However, in this study we used all the known African wild dog dens, and would like to stress the impossibility to have a large sample size for a species that exists in such low numbers and breeds cooperatively, and would nevertheless like to draw some prudent conclusions.

In this study we found that overall, visibility around den sites was smaller than around random sites. Den sites in the low predator density area were placed in vegetation with significantly less visibility than random sites. Although this difference was not significant for den sites in the high predator density area, a similar pattern was found. When looked at vegetation type it was found that, despite the fact that there is little closed vegetation available, den sites were relatively often placed in closed vegetation (Table 2). Even in the high predator density area where there was virtually no closed vegetation available African wild dogs still managed to place 40.0% of their den sites in closed vegetation. Den sites in the high predator density area showed a non significant tendency to be placed in vegetation with lower shrub height, lower stem density, lower tree density and higher visibility compared to den sites in the low predator density area which could explain why the difference in visibility between den sites and random sites was found to be non significant in the high predator density area. These non significant differences are consistent with differences in distribution over the vegetation categories; in the high predator density area more den sites were found in open and medium vegetation and less den sites in closed vegetation compared to den sites in the low predator density area (Table 2). This inevitably results in lower averages of vegetation characteristics that are likely to define closed, medium or open vegetation like shrub height and stem and tree density.

Escape from predators has been shown to play an important role in den sites selection (Pruss 1999, Hwang et al. 2007, Lesmeister et al. 2008, Ross et al. 2010).While some studies have found that carnivores select dens with low surrounding vegetation in order to allow for an early detection of approaching predators (Zoellick et al. 1989), others have shown a preferential choice for den sites with dense and high surrounding vegetation that provides concealment from predators (Fernández and Palomares 2000, Creel and Creel 2002, Arjo et al. 2003). The non significant tendency of den sites in the high predator density area to have lower shrub heights, stem densities and tree densities compared to den sites in the low predator density area might suggest a random choice for open den sites in the high predator density area. However these differences are more likely to be a side effect of the vegetation types in which the den sites were found than the result of a selection process. This is supported by the fact that in the high predator density area, even though closed vegetation might not be as closed as in the low predator density area, the location of den sites is strongly biased towards closed vegetation. The significant differences in visibility and vegetation type and the fact that even when closed vegetation was virtually absent den sites were still found in this type of vegetation, points towards an overall strong selection for closed vegetation with little visibility.

In the high predator density area there also seemed to be a preference for areas with Zambezi teak (*Baikiaea plurijuga*) as a dominant species. The selection of Zambezi teak dominated habitat for a den site might be an adaptation to a high predation risk. Herbivores generally do not occur in large numbers in Zambezi teak habitat (Ben-Shahar 1996), as Zambezi teak is unpalatable (Holdo 2003, 2007). When herbivore densities are low it is likely that predator densities are reduced as well therewith possibly decreasing encounter rates.

African wild dogs showed a similar pattern in their den site preference in the high and low predator density area suggesting that the strength of predation risk has little effect. Although predator densities in the low predator density area are relatively lower than in the high predator density area there is nevertheless a predation risk present. African wild dogs have high energetic costs of gestation (Creel and Creel 1991), with these high reproductive costs it is likely that even when predation risk is relatively low African wild dogs try to maximize their fitness by choosing a den that will provide optimal protection for their offspring. It is therefore possible that no striking differences were found between vegetation characteristics of den sites in the high and low predator density area. It also has to be kept in mind that African wild dogs do not always dig a den themselves and regularly seem to make use of old aardvark dens (Woodroffe et al. 2004). Therefore den site selection by African wild dogs might partly reflect den site preference by aardvark, a species that is likely to experience a different selection pressure. An additional factor might be that den site selection has not only been found to be based on protection from predators (Pruss 1999, Hwang et al. 2007, Lesmeister et al. 2008, Ross et al. 2010), but also on other factors like shelter from extreme weather conditions (Eide et al. 2001, Richardson et al. 2007, Szor et al. 2008, Herr et al. 2010). Closed vegetation might provide relatively good protection to the sunny days and cold nights as found during the reproductive months in the study area. With weather conditions in the high and low predator density area being the same den site selection based on shelter from weather conditions is expected to follow a similar pattern.

Spatial distribution of water sources, roads and human settlements has also been found to play a role in den site selection (Theuerkauf et al. 2003, Hwang et al. 2007). African wild dogs are known to often use roads to travel and rest (IUCN/SSC 2007). Reich (1981) described how African wild dogs prefer road-foraging; they regularly followed the course of the road and even used roads as part of their hunting strategy. Other predators, like lions, have also been found to have a habit of travelling along roads (Chardonnet 2002). On average African wild dog den sites were placed less than 1 km from a road but the average distance to the road did not differ from those of the random sites. In the high predator density area both den sites and random sites were placed further away from roads than in the low predator density area. These findings suggest that distance to the road is directly related to the available road network rather than a selection criterion used to choose a den.

Another important factor in den site selection is food distribution (Eide et al. 2001, Szor et al. 2008). In arid and semi-arid savannah systems large herbivores are generally more abundant in the vicinity of waterholes (du Toit 2003, Redfern et al. 2003, Valeix et al. 2009[a]). An aggregated distribution of prey inevitably affects the movements of predators. African wild dogs in the study area predominantly predated on impalas (38.9% of the diet), kudus (31.2% of the diet) and duikers (15.0% of the diet) (van der Meer et al., unpublished manuscript (chapter 2)).

Historically 73.0% of the impala, kudu and duiker kills were made within 2 km from a waterhole (Table 1). It would therefore be expected that den sites are found relatively close to waterholes. Although on average den sites were situated within 1.97 km from a waterhole this distance did not differ significantly from the distance of random sites to waterholes, indicating that with the vast amount of waterholes in the study area, sites are inevitably placed close to a waterhole. Aggregation of prey around waterholes does not only affect African wild dogs but also the movement of their competitors. Lions within the Hwange system have been found to reduce their search effort by selecting areas within 2 km from a waterhole to hunt (Valeix et al. 2009[b]). With both lions and African wild dogs utilising the area within 2 km from a waterhole to forage it is likely that spotted hyenas, which often scavenge on kills made by lions (Drouet-Hoguet 2007) and are known to steal kills from African wild dogs (Reich 1981, Carbone et al. 1997, Creel 2001, van der Meer et al. accepted (chapter 4)), can be regularly found within this 2 km radius as well. When distances of den sites to the waterhole were categorized in distances ≤ 2 km or > 2 km it was found that African wild dog dens in the high predator density area were more often placed further than 2 km away from a waterhole than random sites which could be an attempt to reduce encounters with lions and spotted hyenas.

It seems that, as suggested by Creel and Creel (2002), African wild dogs predominantly tried to minimise predation risk by selecting den sites in closed vegetation with little visibility. Contrary to what would be expected, this selection was less pronounced in the high compared to the low predator density area. In the high predator density area there was virtually no closed vegetation available (Table 2), African wild dogs still managed to place 40.0% of their den sites in closed vegetation, this suggests that this type of vegetation is scarce and might therefore be a limiting resource. Without the possibility to access preferred den sites, African wild dogs have the choice to either expose themselves to a higher predation risk which could negatively affect their reproduction and recruitment, or leave the high predator density area. Previous studies have indeed shown that over the years African wild dogs in and around Hwange National Park moved into the low predator density area (van der Meer et al. submitted (chapter 1)). As the high predator density area is based within Hwange National Park and the low predator density area in the buffer zone outside the park where, thanks to a so called 'edge effect' (Woodroffe and Ginsberg 1998), African wild dogs get increasingly exposed to human activity resulting in mortality (van der Meer et al. submitted (chapter 1)), this can have far reaching implications and should be taken into account in the conservation strategy of this endangered species.

Acknowledgement

We wish to thank Dr. G.S.A. Rasmussen for providing data on African wild dog kill sites. The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. We would like to thank the Hwange National Parks and Wildlife Management Authority, Forestry Commission, Hwange Safari Lodge, Touch the Wild, and the farmers within the Gwaai Intensive Conservation Area for allowing us access onto their premises and supporting our fieldwork. We especially thank Gracious Njamba and Ntandokazulu Khumalo for their participation in the field work. We thank Hans Dullemont for providing equipment. We wish to thank Simon Chamaillé-Jammes and Marion Valeix for their fruitful comments on previous drafts. We also thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation and the Painted Dog Conservation project.

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Chapter 6

Differences in energetic costs and interspecific competition ecologically trap African wild dogs outside a protected area

Chapter 6

Differences in energetic costs and interspecific competition ecologically trap African wild dogs outside a protected area

Ester van der Meer, Gregory S.A. Rasmussen, Hervé Fritz

Abstract

Habitat selection can be viewed as an optimal foraging process with animals preferentially using habitat in which they yield the highest rate of energy. Viewed in this framework, the optimal choice of habitat for a predator will depend on the availability of prey and the foraging efficiency in each habitat. Another factor likely to play a role in habitat selection is predator competition. African wild dogs in Hwange National Park seem to prefer to establish territories in the buffer zone outside the park, even though human induced mortality in the buffer zone exceeds natality. Here we use an energy cost-benefit approach in order to try and explain the observed habitat selection. Data from hunt follows of 22 VHF collared African wild dog packs were used to determine energetic gain and losses inside Hwange National Park and the buffer zone outside the National Park. African wild dogs inside Hwange National Park seem to gain less energy than African wild dogs in the buffer zone outside the park leaving them with less energy available for reproduction which is reflected by the smaller relative number of pups within packs inside the National Park. Based on these findings African wild dogs in the Hwange system seem to have been caught in an ecological trap where formerly reliable ecological cues are no longer associated with an adaptive outcome due to human induced mortality. As ecological traps can cause extirpation of a population they have obvious management implications. In order to protect the African wild dogs conservation efforts should reach beyond the boundary of the protected area and focus on mitigating the ‘edge effect’ in the buffer zone surrounding Hwange National Park.

Key words: *African wild dog, habitat selection, ecological trap, foraging efficiency, interspecific competition, energetic requirements, intraguild predation, reproduction*

Status: unpublished manuscript

Introduction

Optimal foraging theory proposes that behavioural decisions by foragers are based on costs and benefits and shaped by natural selection. An individual's fitness is therefore directly related to its behaviour while foraging (Pyke 1984). Various foraging parameters will affect the fitness of a foraging animal, the main parameters being the amount of energy obtained from the food item, and time spend searching for food and handling the food item (Pyke 1984). Habitat selection can be viewed as an optimal foraging process with animals preferentially using habitat in which they yield the highest rate of energy (Rosenzweig 1991). Viewed in this framework, the optimal choice of habitat for a predator will depend on the density of prey and the search efficiency in each habitat (Fryxell 1997, Morris 2003).

Predators indeed select habitat according to prey densities (Litvaitis et al. 1986, Murray et al. 1994, Spong 2002, McCarthy et al. 2005). Higher densities of prey are generally believed to result in a higher search efficiency due to higher encounter rates (Norberg 1977, Draulans 1987). For a predator, searching for prey is not the only component of foraging though; chase and capture of prey are an essential part as well. An increase in activity results in an increase in metabolic rate (Norberg 1977, Carbone et al. 2007). Chasing prey, which is a period of maximum increased activity, is therefore likely to significantly affect the energetic costs of foraging. If a predator is able to approach its prey at a closer distance this generally reduces chase distance and increases the likelihood of a kill (Reich 1981, Fitzgibbon 1988, Hilton et al. 1999). Several studies have shown that, regardless of prey densities, predators preferred habitat in which, due to specific biotic or abiotic landscape attributes, prey was easier to catch (van Dyk and Slotow 2003, Rhodes and Rhodes 2004, Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007). The ease with which predators are able to catch prey should therefore be taken into account when looking at habitat selection.

Another factor likely to play a role in habitat selection is interspecific competition. Predator-prey studies are often based on a three trophic level system where predators forage free from predation risk, while in fact predator-prey interactions regularly take place at a four trophic level system in which intermediate predators face a trade off between obtaining food and being safe (Mukherjee et al. 2009). In systems where predators forage in the presence of others, top predators may use the opportunity to steal resources from smaller predators rather than spending time to secure resources themselves (kleptoparasitism) (Broom and Ruxton 1998, Creel 2001, Hamilton 2002). This will interfere with the foraging efficiency of the intermediate predator. Intraguild predation also occurs, and generally results in the death of one of the contenders (Caro and Stoner 2003). Due to these expensive costs, interference competition between intermediate and top predators is likely to have direct effects on habitat choice. Smaller predators have indeed been shown to avoid larger carnivores in both space and time (Mills and Gorman 1997, Durant 1998, Fedriani et al. 1999, Linnell and Strand 2000, Creel 2001, van Dyk and Slotow 2003).

Although, when population densities are low, habitat choice in theory should increase the fitness of a species this is not always the case. Animals rely on environmental cues to assess habitat quality in order to choose a suitable habitat. When, due to natural or human induced changes, these formerly reliable cues are no longer associated with an adaptive outcome, animals are likely to make a maladaptive habitat choice (Kolbe and Janzen 2002, Kristan 2003). When an animal shows a preferential choice for a habitat in which its reproductive success or adult survival is less than in other available habitat it is said to have been caught in an ecological trap (Kokko and Sutherland 2001, Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006, Pärt et al. 2007). Ecological traps are different from classic mortality sink systems. In a mortality sink, habitat choice is advantageous and animals only move into habitat in which there is no recruitment because there is not enough high quality habitat available. In an ecological trap, habitat choice is disadvantageous as animals living in high quality habitat choose to be in low quality habitat and migrate to replace dead conspecifics (Kristan 2003, Battin 2004). Within an ecological trap, sink populations can be temporarily sustained by the source before resulting in a rapid collapse of the whole system (Kristan 2003).

African wild dogs in Hwange National Park seem to prefer to establish territories in the buffer zone outside the National Park, even though by doing so they get increasingly exposed to human activity resulting in mortality (van der Meer et al. submitted (chapter 1)). In this study we use an energy cost-benefit approach in which we take foraging efficiency and interspecific competition into account in order to try and explain the observed habitat selection pattern. The energetic output of hunting African wild dogs is extremely high (Gorman et al. 1998, Rasmussen et al. 2008). Not only does the survival and reproductive success of African wild dogs largely depend on their ability to secure prey, foraging in itself is costly and therefore minimising foraging costs will positively affect survival (Rasmussen et al. 2008). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) interfere with this minimalisation and can seriously increase foraging costs through kleptoparasitism (Gorman et al. 1998, van der Meer et al. accepted (chapter 4)). It is therefore likely that both foraging efficiency and interspecific competition play a role in habitat selection by African wild dogs.

Territory sizes have often been found to be negatively related to the abundance of resources and the local density of conspecific competitors (see Adams 2001 for a review). As both factors could play an additional role in habitat selection of African wild dogs, we analysed territory sizes inside and outside Hwange National Park to test for possible differences in these variables. Based on the energy cost-benefit calculations we tried to determine whether or not the ecological cues likely to be used for habitat selection lead to a maladaptive habitat choice leaving the African wild dogs in the Hwange system ecologically trapped.

Method

Study area

Hwange National Park covers approximately 15 000 km^2 in the northwest of Zimbabwe (19°00'S, 26^{o}30'E). The Hwange region is classified as semi-arid. Over the last century mean annual rainfall has been 606 mm, with a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Prey species present include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*). Lions and spotted hyenas occur in the study area. The lion population has been fluctuating due to sport-hunting followed by a moratorium. In 2005 lion densities inside Hwange National Park were 2.7 lions/100km^2 while, due to sport-hunting, lion densities in the buffer zone outside the park were as low as 0.06 lions/100km^2 (Davidson 2009). Over the years spotted hyena densities have been stable and densities are estimated to be around 11.3 hyenas/100km^2 in the area inside the National Park and 5.5 hyenas/100km^2 in the area outside the National Park (Salnicki 2004, Drouet-Hoguet 2007, Elliot 2007).

Data were collected along the northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral area. Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the park is designated for trophy hunting and photographic safaris. Most of this land is privately owned or state owned and managed by Forestry Commission. The main tar road from Bulawayo to Victoria Falls runs through part of the study area.

Species

African wild dogs are medium sized obligate co-operators that live in packs of up to twenty adults and their dependent offspring (Creel and Creel 1995, Woodroffe et al. 1997). They are crepuscular, with hunts being most common at dusk and dawn and when sufficient moonlight is available (Fanshawe and Fitzgibbon 1993, Creel and Creel 1995, Rasmussen 2009). They hunt by sight sound and smell for small to large antelopes, with impalas (*Aepyceros melampus*), kudus (*Tragelaphus strepsiceros*) and duikers (*Sylvicapra grimmia*) being their main prey in and around Hwange National Park (Rasmussen 2009). African wild dogs have large territories, which on average range between 423 and 1318 km^2 (Woodroffe et al. 1997). With fewer than 8000 individuals left in the wild, African wild dogs are classified as endangered and consequently rank high for conservation (Hunter et al. 2010). Over the years their numbers in the Hwange area have declined. In 1997 it was estimated that African wild dog densities in and around Hwange National Park ranged between 150 and 225 individuals (Rasmussen 1997, Woodroffe et al. 1997). More recent information suggests that these days there are approximately 50 to 70 individuals left in and around the National Park (Zimbabwe Parks and Wildlife Management Authority 2009, Blinston 2010).

Hunt follows

Data from 22 radio collared African wild dog packs were collected by G.S.A.Rasmussen between 1991 and 2002, with a study duration of 29.5 ± 20.1 months (mean ± SD) per pack. As soon as a pack had been located it was monitored non-stop from a distance of ≥ 50m for as long as practically feasible (max 28 days). The number of adults, yearlings and pups in a pack was recorded and the activity of the pack was continuously monitored visually or from motion sensors incorporated in the radio collars, and recorded at 5 min scan intervals. Whenever a change in activity mode or direction occurred location fixes were taken by using triangulation or visual observations and a GPS unit. A hunt period was defined as the period from rest to rest within which the African wild dogs were actively searching for prey. Total distance travelled was the sum of all inter-fix distances during the period from rest to rest within which there was an active search for prey. Foraging distance is the sum of all inter-fix distances until a pack encountered prey and started a chase or started resting again for a period of > 30min. A chase was defined as the high speed pursuit of prey, chase distance was defined as the sum of all inter-fix distances during a chase and a chase was considered successful when resulting in a kill. Only verified kills were included in the analysis. Previous analyses based on cross sections and scale patterns of hairs extracted from faeces have confirmed that visual observations provided a reliable indicator for the consumption of smaller prey species (Rasmussen et al. 2008).

When kills were made the number of African wild dogs feeding on the carcass, feeding time, the time it took before kleptoparasites arrived at the kill (lapse time) and the outcome of the defence of the kill were observed and recorded. As feeding time can differ per individual, feeding time was measured as the time the pack had access to the carcass in cases where the kill was kleptoparasitized, successfully defended or when no kleptoparasites were present. Hunt follows were classified as hunts inside the National Park or hunts outside the National Park. Being kleptoparasitized was defined as having the carcass stolen by lions and spotted hyenas within 60 minutes after the actual kill. After 60 minutes, irrespective of pack size, all African wild dogs within a pack would either be satiated or the carcass would be finished. In total 461 kills were recorded, 191 inside the National park and 270 in the buffer zone outside the park. It was possible to determine chase distances for 229 of these hunts, 72 inside the National Park and 157 outside the park.

Statistical analysis

Mean per capita costs and benefits

To test whether there were significant differences between the different costs and benefits inside and outside Hwange National Park, per capita daily energetic values for chasing, walking, resting, the loss due to kleptoparasitism and the energetic gain were calculated inside and outside the park. Based on the model of Rasmussen et al. (2009) the kilometres chased was multiplied by 15 146 kilojoules. The method used to measure chase distances does not make an allowance for zigzagging, therefore, in accordance with Rasmussen et al. (2008), chase distances were multiplied by 1.3. In order to be able to calculate the amount of energy spent walking, walking time was calculated by subtracting the chase distance from the total distance travelled and dividing this number by a walking speed of 8.37 km/h (Rasmussen et al. 2008). Energy spent walking per hour was calculated by the use of the following equation:

$$\text{Energy spent walking} = M_d*(10.7*M_d^{-0.316}*V_w+6.03*M_d^{-0.303})*3.6 \qquad \text{(Taylor et al. 1982)}$$

With a body mass (M_d) of 25 kg and a walking speed (V_w) of 8.37 km/h the amount of energy spent walking was calculated at 3119.40 kilojoules per hour. Time spent walking was multiplied by this value to calculate the total amount of energy spent walking. The amount of kilojoules spent resting was calculated by subtracting the total time spent active from 24 hours and multiplying this number by 217.5 kilojoules (Gorman et al. 1998).

The carcass energetic value for a given kill was determined based on the model of Rasmussen et al. (2008). This value was divided by prey mass to give the energetic value in amount of kilojoules per kilogram. A stomach capacity of 9 kg was used to determine the amount of energy gained (Creel and Creel 1995, Pribyl and Crissey 1999). The per capita amount of kilograms consumed was calculated by dividing prey mass by the total number of adults and yearlings plus the number of pups divided by two during the nomadic season (following Creel and Creel 1995), and the number of adults and yearlings during the denning season when pups are too small to follow the pack and food is regurgitated by the adults and yearlings upon return to the den. If the amount of kilograms consumed exceeded the stomach capacity the value was set to 9 kg. The amount of kilograms consumed per African wild dog was multiplied by the amount of kilojoules per kilogram to give the per capita amount of kilojoules gained.

The loss due to kleptoparasitism was determined by calculating the per capita intake for the given pack size and time before kleptoparasites stole the kill (tk) by using the equation:

$$\text{Carcass intake} = (CEV/N)*(1-e^{-6608(N/CEV)tk}) \qquad \text{(Carbone et al. 2005)}$$

With N being the number of African wild dogs feeding, and carcass energetic value (CEV) for the relevant pack sizes being based on the values as determined by Rasmussen et al. (2008). When stomach capacity became a limiting factor the potential intake was taken as the stomach capacity (9 kg) multiplied by the energetic value per kilogram for a carcass of the size taken by respective pack size rather than the energetic value of the total carcass. The per capita carcass intake was subtracted from the amount of kilojoules an African wild dog could have been gained from the carcass to give the amount of per capita kilojoules lost due to kleptoparasitism.

As the number of adults and yearlings in a pack, the number of hunt periods per day, kilojoules gained per African wild dog by killing prey and the amount of kilojoules spent per African wild dog on chasing and resting did not follow the normality assumption, Mann-Whitney U tests were used to test for differences inside and outside Hwange National Park. A t-test was used to test for differences in the amount of kilojoules an African wild dog lost due to kleptoparasitism and walking inside and outside the park. To test for possible differences due to differences in hunting success a Mann-Whitney U test was performed for kilojoules gained per African wild dog for chases with a known outcome inside and outside Hwange National Park.

Per capita costs and benefits in relation to pack size

Calculations per pack were based on the average chase distances, average time spent walking and resting, the relative risk of kleptoparasitism and the average amount of kilojoules gained based on the calculation as described above. Costs and benefits were calculated per year for the denning and the nomadic season, with packs ≤ 5 denning 112 days and packs > 5 denning 81 days (Rasmussen et al. 2008). The average number of hunt periods per day was multiplied by 365 to determine the total number of hunts per year. Based on the percentage of successful and failed chases the total number of successful and failed hunts per year was calculated. Because failed chases are generally shorter than successful chases (van der Meer et al. unpublished manuscript (chapter 2)), chase distance was calculated for successful and failed chases separately following the method as described above. The amount of kilojoules used during successful and failed chases was multiplied by the number of successful and failed chases during the denning and the nomadic season inside and outside Hwange National Park. The yearly costs of chasing inside and outside the park were calculated by adding the costs of failed and successful chases for the denning and the nomadic season.

The amount of energy spent walking was calculated by multiplying the average time spent walking by 3119.40 kJ. This number was multiplied by the total number of hunts during the nomadic and denning season inside and outside Hwange National Park. The yearly costs of walking inside and outside the park were calculated by adding the costs of walking for the denning and the nomadic season.

The total activity time during a hunt was multiplied by the number of hunts per day and subtracted from 24 hours to give the number of hours spent resting per day. The number of hours per day spent resting was multiplied by 217.5 kJ (Gorman et al. 1998). The yearly energetic costs of resting were calculated inside and outside the National Park by adding the costs of resting for the denning and the nomadic season.

The likelihood of kleptoparasitism is 9.42% inside and 2.66% outside Hwange National Park, the likelihood of kleptoparasitism and the success of defence of the kill are not significantly related to African wild dog pack size (van der Meer et al. accepted (chapter 4)). Therefore the number of hunts kleptoparasitized was calculated by multiplying the number of successful hunts during the denning and the nomadic season by 0.0942 inside and 0.0266 outside the park. Kleptoparasites are more often present when a kill would have satiated the pack (van der Meer et al. accepted (chapter 4)). Therefore the energetic loss when a kill was kleptoparasitized was calculated based on the maximum per capita carcass energetic value for the relevant pack size as described by Rasmussen et al. (2008), taking into account a stomach capacity of 9 kg. Figures for per capita carcass intake for the denning and nomadic season, per hunt period in relation to pack size and time before kleptoparasites arrived at the kill site, 11.33 minutes inside and 18.80 minutes outside Hwange National Park (van der Meer et al. accepted (chapter 4)), were obtained by using the formula as described above. The per capita intake was subtracted from the maximum possible intake to calculate the per capita energetic loss when kleptoparasitized. The per capita energetic loss was multiplied by the number of kleptoparasitized hunts per year, and the yearly costs of kleptoparasitism inside and outside the park were calculated by adding the costs of kleptoparasitism for the denning and the nomadic season.

The average amount of kilojoules gained per African wild dog was multiplied by the number of successful hunts per year per season to calculate the amount of kilojoules gained per African wild dog during the nomadic and the denning season inside and outside Hwange National Park. The total yearly gain was calculated by adding the gain during the denning season and the gain during the nomadic season. The total energetic costs per year were the sum of the yearly costs of chasing, walking and resting, plus the additional costs due to kleptoparasitism. These total costs were subtracted from the yearly gain and divided by 365 days to get a figure for the per capita daily energetic net rate of energy intake for a given pack size.

Territory sizes

All GPS fixes from the hunt follows and individual sightings were plotted in ArcGis® version 9.3. To avoid a bias, an average position per day was used and only packs with more than fifty points a year and a minimum of one point a week were included in the analysis. For the analysis we remained with eight territories inside and fifteen territories outside Hwange National Park. We used the 95% fixed Kernel method (Worton 1989) to determine territories inside and outside Hwange National Park. A Mann-Whitney U test was used to compare territory sizes inside and outside the park. In order to be able to compare territories with the existing literature 95% Minimum Convex Polygons (MCP) were used to describe the maximum used space. A t-test was used to compare the average area covered inside and outside the Hwange National Park.

Reproductive success

As reproductive success is directly related to pack size we controlled for the number of adults and yearlings in a pack be dividing the number of pups by the number of adults plus yearlings. A Mann-Whitney U test was used to test for differences in the relative number of pups within a pack inside and outside Hwange National Park.

Results

Mean per capita costs and benefits

There was no significant difference in the number of hunt periods per day (Mean$_{In}$±SE=1.58±0.06, Mean$_{Out}$±SE=1.68±0.05, U=6820.00, z=-1.38, p=0.169) and the number of adults and yearlings in a pack (Mean$_{In}$±SE=5.81±0.11, Mean$_{Out}$±SE=5.51±0.08, U=340015.00, z=-1.72, p=0.085) inside and outside Hwange National Park. The amount of kilojoules gained per African wild dog did not differ inside or outside Hwange National Park (Mean$_{In}$±SE=42349.06±2874.84, Mean$_{Out}$±SE=42596.89±2497.07, U=31458.00, z=-0.07, p=0.944). When tested only for kills of which the chase was observed, no difference was found either (Mean$_{In}$±SE=44136.67±2417.57, Mean$_{Out}$±SE=42713.10±1711.66, U=1806.00, z=-0.59, p=0.557).

There was a tendency for the amount of kilojoules an African wild dog spent on chasing to be higher inside Hwange National Park (Mean$_{In}$±SE=12790.80±1873.22, Mean$_{Out}$±SE=9696.57±1258.56, U=4840.00, z=-1.77, p=0.076). The amount of kilojoules spent on walking (Mean$_{In}$±SE=2437.91±593.21, Mean$_{Out}$±SE=3142.91±582.27, t$_{(16)}$=-0.85, p=0.409) and resting (Mean$_{In}$±SE=4709.38±16.52, Mean$_{Out}$±SE=4694.19±12.04, U=19865.50, z=-1.08, p=0.278), did not differ inside or outside the park. There was a tendency for the amount of kilojoules lost to kleptoparasites to be higher inside Hwange National Park (Mean$_{In}$±SE=26167.12±5283.82, Mean$_{Out}$±SE=13611.96±4537.32, t$_{(24)}$=1.93, p=0.066).

In order to be able to calculate the difference in the amount of kilojoules gained inside and outside Hwange National Park the per capita amount of kilojoules spent on chasing, walking and resting and the kilojoules lost due to kleptoparasitism were subtracted from the kilojoules gained. The amount of kilojoules lost due to kleptoparasitism was calculated per hunt based on the respective likelihood of being kleptoparasitized (van der Meer et al. accepted (chapter 4)), by multiplying the mean amount of kilojoules lost by 0.0942 inside and 0.0266 outside the park. On average the net rate of per capita energy intake per hunt for an African wild dog inside Hwange National Park was 19946.03 kJ which is 4755.11 kJ (19.25%) less than the gain outside the park where on average the net rate of per capita energy intake per hunt was 24701.14 kJ.

Per capita costs and benefits in relation to pack size

Table 1 gives an overview of the costs and benefits inside and outside Hwange National Park.

Table 1. Mean daily energetic per capita costs and benefits in relation to pack size (AdYY) for African wild dogs inside and outside Hwange National Park (HNP), all values given in kilojoules.

Pack	**Inside HNP**					
size	Gain	Chase	Walk	Rest	Klepto	**Intake**
2	.	.	.	.	.	.
3	34603.77	-27116.19	-2754.17	-4574.34	-1094.64	**-3254.56**
4	39154.35	-29302.24	-2964.29	-4514.35	-981.97	**-1137.52**
5	37628.01	-33186.47	-2648.30	-4385.96	-711.88	**-3746.22**
6	.	.	.	.	.	.
Pack	**Outside HNP**					
size	Gain	Chase	Walk	Rest	Klepto	**Intake**
2	57891.03	-33265.28	-2335.79	-4367.87	-125.25	**13012.44**
3	48820.95	-24866.99	-3143.58	-4386.92	-117.71	**12895.16**
4	52258.58	-25689.74	-4284.98	-4454.97	-107.96	**15242.41**
5	50402.79	-18515.36	-3462.33	-4367.64	-120.33	**22654.79**
6	37592.56	-17054.85	-4372.24	-4539.64	-91.14	**10531.07**

Regardless of pack size, African wild dogs inside Hwange National Park on average lost energy while in the buffer zone outside the park individuals gained energy (Figure1). This seems to be mainly due to a lower energetic gain and higher chase expenses inside the park (Table 1).

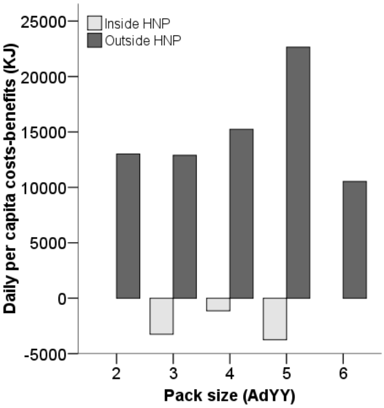

Figure 1. Daily per capita energetic costs and benefits in relation to pack size inside and outside Hwange National Park (HNP).

Territory sizes

Based on the 95% fixed Kernel method sizes of territories inside Hwange National Park were on average 126.07 km^2 ± 52.41 (Mean±SE), outside the park sizes of territories were on average 199.66 km^2 ± 127.76 (Mean±SE). There was no significant difference between territory sizes inside and outside Hwange National Park (U=55.00, z=-0.32, p=0.776). Based on the 95% Minimum Convex Polygons the sizes of areas covered were on average 528.17 km^2 ± 63.92 inside the park, and 389.00 km^2 ± 50.61 outside the park. There was no significant difference between sizes of areas covered inside and outside Hwange National Park ($t_{(15)}$=1.71, p=0.108).

Reproductive success

The relative number of pups within a pack was significantly lower inside Hwange National Park (Mean_{In}±SE=1.31±0.03, Mean_{Out}±SE=2.02±0.06, U=81162.50, z=-5.74, p<0.001) (Figure 2).

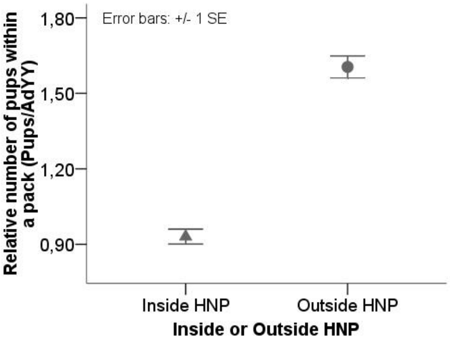

Figure 2. Relative number of pups within a pack, inside and outside Hwange National Park (HNP).

Discussion

Although the energetic calculations made in this study are by no means flawless as they do for example not take into account the likelihood of a 'baby-sitter' staying behind to guard the pups during the denning season, they do give an indication of the differences in energetic costs and benefits inside and outside Hwange National Park. From both the general analyses and the analyses per pack size it seems that even though the differences between energy spent on the individual activities inside and outside Hwange National Park are relatively small and not significant, the cumulative differences are considerable. African wild dogs inside Hwange National Park gained less energy than those in the buffer zone outside the park which means packs had less energy available for reproduction which is reflected by the smaller relative number of pups within packs inside the National Park. This is in accordance with foundation ecological theory, suggesting a life history trade-off with high rates of production when there are 'energy subsidies' that reduce the costs of maintenance (Odum 1971). If habitat selection is viewed as an optimal foraging process where animals preferentially use habitats in which they yield the highest rate of energy (Rosenzweig 1991), the observed differences in energy intake and reproductive success are likely to explain the preferred establishment of territories in the buffer zone outside Hwange National Park.

The size of the areas covered by African wild dogs in the Hwange system (Mean±SE=437.41±41.41), was similar to territory sizes reported in other African countries (Woodroffe et al. 1997). As an animal's movements are likely to reflect its response to resource distribution, it has been suggested that territory size can be used as a surrogate measure for resource distribution (Grant et al. 1992). The finding that there was no difference in territory sizes and the average amount of kilojoules gained per African wild dog did not significantly differ inside and outside Hwange National Parks suggests there is no difference in prey availability. This is in accordance with previous research which showed that foraging distance, the distance before prey was encountered, was not different inside compared to the buffer zone outside Hwange National Park (van der Meer et al. unpublished manuscript (chapter 2)). Although African wild dogs do not actively defend their territorial boundaries (Grant et al. 1992), their territories have been found to be spatially exclusive and in cases where overlap between packs occurred there was strong temporal avoidance (Parker 2010). Due to the low population densities of African wild dogs in and around Hwange National Park, the local density of conspecific competitors is unlikely to be a major determining factor in habitat selection. As territory sizes did not differ it seems that, even if local density of competing African wild dogs would play a role, intraspecific competition was similar inside and outside Hwange National Park and therefore factors other than prey availability and competition with conspecific neighbours determine the preference of African wild dogs to establish territories in the buffer zone outside the National Park.

An animal establishing a territory might not be able to predict the costs and benefits the territory will provide. Little is known about the actual processes that determine territory establishment in free living animals. Stamps (1999) proposed a learning based model of territory establishment for mobile animals that settle in large, vacant patches of spatially heterogeneous, temporally predictable habitat. This model describes the establishment of territories as a learning based process driven by positive and negative experiences. Positive experiences are believed to enhance the attractiveness of the area compared to a novel area of similar quality, and to increase the probability that animals return to the area in the future. Negative experiences in the form of aggressive interactions reduce the attractiveness of the area because they are costly to the competitors and are an indication that aggressive interactions may be expected in that area in the future. The probability of the use of an area is determined by its attractiveness relative to other areas. This attractiveness can vary as a function of habitat characteristics and familiarity with the area.

Although aggressive interactions between competitors in habitat selection models are generally viewed as intraspecific interactions the model could also apply to interspecific interactions between competing species. Lions and spotted hyenas are known competitors of African wild dogs (Carbone et al. 1997, Creel and Creel 1998, Creel 2001, Woodroffe et al. 2004).Whilst in this study it was found that the energetic loss due to kleptoparasitism is relatively little, the risk of encounters with lions and spotted hyenas is not limited to the potential loss of a kill. Encounters with these competitors increase the risk of injury due to aggressive interactions and the risk of intraguild predation. Lions are a major cause of African wild dog mortality and are known to kill both adults and pups (Woodroffe et al. 2004). Spotted hyenas have been reported to disturb den sites and kill African wild dog pups (Creel and Creel 1998, Woodroffe et al. 2004, Painted Dog Conservation project; unpublished data). Especially in small packs of African wild dogs the loss of a single individual can, due to a strong positive relationship between pack size, survival en reproduction (Creel and Creel 2002, McNutt and Silk 2008), be detrimental for an entire pack of African wild dogs (Courchamp and Macdonald 2001, Rasmussen 2009).

During the time of the study lion and spotted hyena densities were likely to be higher inside than outside Hwange National Park (see method) which is expected to increase the encounter rate of these predators. Lions and spotted hyenas were present at 1 out of every 6 kills made by African wild dogs inside Hwange National Park, compared to 1 out of every 18 kills in the buffer zone outside the National Park (van der Meer et al. accepted (chapter 4)). African wild dog mortality known to be caused by lions and spotted hyenas was found to be almost twice as high inside Hwange National Park compared to the buffer zone outside the National Park (van der Meer et al. submitted (chapter 1)). As both lions and spotted hyenas are territorial carnivores that actively defend their territories against intruders (Drouet-Hoguet 2007, Davidson 2009), aggressive interactions in an area at one time are likely to give information about the chances of encountering lions and spotted hyenas in the same area at a later time. Viewed in a learning based territory establishment framework it is therefore possible that encounters with lions and spotted hyenas, especially when African wild dog pack sizes are small, serve as negative experiences reducing the likelihood that African wild dogs return to the area.

African wild dogs inside Hwange National Park experience a lower hunting success and chase their prey over longer distances before they are able to make the kill (van der Meer et al. unpublished manuscript (chapter 2)). The higher chase expenditure found in this study inside the National Park reflects these differences in chase distances. Inside the park African wild dogs spent 3094.23 kilojoules more on the chase compared to outside Hwange National Park, which represents 15.51% of the net rate of energy intake inside the National Park. Although not significant, this difference is considerable. Despite the fact that the encounter rate of prey seems to be similar inside and outside Hwange National Park prey seems to be more catchable outside the park, which has been suggested to be related to differences in vegetation type (van der Meer et al. unpublished manuscript (chapter 2)). A higher catchability of prey is, from an African wild dog's perspective, likely to be viewed as a positive experience. Based on a learning based territory establishment model prey catchability and competition with other carnivores could well be driving forces behind the selection of habitat outside Hwange National Park.

Various studies suggest that predators preferentially use habitats in which they gain the highest rate of energy (Rosenzweig 1991). When calculated per pack size the differences in energy intake inside and outside Hwange National Park are high up to the point where packs on average do not gain energy inside Hwange National Park. From an ecological point of view the establishment of a territory in the buffer zone outside the National Park therefore seems to be the right fitness enhancing choice. However, moving out of the protected area comes with unaccounted risks in the form of an increased exposure to human activity resulting in mortality. From 1989 up to 2010, 327 African wild dogs were reported dead. To put this into perspective and indicate the significance of this loss; the population at the start of this period was estimated to be between 100 and 150 individuals only (Childes 1988). The majority of the deaths, 71.6%, occurred in the buffer zone outside Hwange National Park and were caused by humans (68.0%). The odds of mortality caused by humans were 46.71 times higher outside the National Park indicating an 'edge effect' in the buffer zone outside the National Park. African wild dogs with a territory outside Hwange National Park produced more pups but, due to this 'edge effect', the likelihood of mortality also became significantly higher resulting in mortality exceeding natality and no recruitment outside the National Park (van der Meer et al. unpublished manuscript (chapter 1)).

Based on these findings African wild dogs in the Hwange system seem to have been caught in an ecological trap where formerly reliable ecological cues are no longer associated with an adaptive outcome due to human induced mortality. As ecological traps can cause extirpation of a population (Delibes et al*.* 2001, Kokko and Sutherland 2001, Gilroy and Sutherland 2007), they have obvious management implications, especially while African wild dogs have become one of Africa's most endangered carnivores and consequently are red listed by the International Union for the Conservation of Nature (IUCN) as an endangered species (McNutt et al. 2008). This study shows that it is important to take habitat characteristics that are likely to affect prey catchability into account in the conservation strategy of the African wild dogs as these characteristics, and not just prey availability in itself, might determine whether a habitat is suitable for African wild dogs or not. It is also important not to underestimate the role lions and hyenas can play in habitat selection of African wild dogs, even when the pressure of kleptoparasitism seems to be relatively little.

Acknowledgement

The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management Authority are kindly acknowledged for providing the opportunity to carry out this research. In addition we would like to thank the Hwange National Parks and Wildlife Management Authority, Forestry Commission, The Hide, Hwange Safari Lodge, Lions den enterprises, Touch the Wild and the various farmers within the Gwaai Intensive Conservation Area for allowing us access onto their premises and supporting our fieldwork. We wish to thank Jealous Mpofu and Peter Blinston for their participation in the hunt follows. We also like to thank anonymous referees for their comments that helped to improve this paper. This study was supported by the Stichting Painted Dog Conservation and the Painted Dog Conservation project.

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Discussion

Testing the ecological
trap hypothesis
for
African wild dogs
in and around
Hwange National Park

Discussion

In this study we found that over the years African wild dog packs either showed a decrease in the distance of their territory to the Hwange National Park border or crossed the border and established territories in the buffer zone surrounding the National Park. In the buffer zone outside the National Park African wild dogs experienced a higher reproductive success but due to an ‘edge effect’, mortality exceeded natality resulting in no recruitment and packs falling apart in groups below the minimal pack size of six individuals necessary for successful reproduction (Courchamp and Macdonald 2001, Rasmussen et al. 2008). This has resulted in a decrease of the African wild dog population in the study area. Between 1989 and 2002 the full life history of twenty African wild dog packs in the study area was documented, fifteen of these packs extirpated of which eleven known to be due to human caused mortality. With an aggregation of waterholes (90%) and therewith prey along the northern boundary of Hwange National Park (Valeix 2006) it is probable that the largest part of the African wild dog population is also found along this northern boundary. Therefore the high level of anthropogenic mortality as documented in this study is likely to have largely contributed to the overall population decline in and around Hwange National Park. African wild dogs are known to occur in a wide range of habitats (Fanshawe and Fitzgibbon 1993, Mills and Gorman 1997, Creel and Creel 2002) and could therefore, in theory, be distributed throughout the biggest part of Hwange National Park. It is likely though that, due to a favourable waterhole and therefore prey distribution, African wild dogs will eventually be attracted to the northern boundary where they end up exposing themselves to a high risk of anthropogenic mortality when they start ranging beyond the Hwange National Park border into the buffer zone outside the park.

Within a classic source-sink system a source is described as high quality habitat where natality is larger than mortality and a sink is described as low quality habitat where natality is lower than mortality (Dias 1996). Based on this definition the area inside Hwange National Park is expected to be the source while the buffer zone outside the park is expected to be the sink. Within a source-sink system movement of animals into the sink is density dependent; surplus animals from the high quality source habitat are forced to migrate into the low quality sink habitat when there is not enough source habitat available (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996). The population density in Hwange National Park is so small that it is unlikely that African wild dogs migrating into the buffer zone outside the park are actually surplus animals forced to migrate into the sink. The fact that there are no differences in territory sizes inside and outside the National Park supports this assumption. Although African wild dogs do not actively defend their territorial boundaries (Grant et al. 1992), their territories have been found to be spatially exclusive and in cases where overlap between packs occurred there was strong temporal avoidance (Parker 2010). If the Hwange system would serve as a classic source-sink system, African wild dogs in the source habitat inside Hwange National Park are only likely to migrate into the sink habitat in the buffer zone outside the National Park when the African wild dog density inside the park has reached its maximum. It would therefore be expected that the National Park would be occupied at a higher density than the buffer zone resulting in smaller territory sizes inside the park due to a higher number of neighbouring packs.

Especially if source habitat is viewed as habitat with a high density of high quality patches where resources are more abundant it is to be expected to find smaller territory sizes inside Hwange National Park. As territory size is viewed as an indication of resource distribution (Grant et al. 1992) the finding that there was no difference in territory sizes inside and outside Hwange National Park suggests that there was no difference in prey availability. Although the lack of historical data on herbivore densities outside Hwange National Park makes it difficult to directly compare herbivore densities inside and outside the park, measurements on African wild dog hunting behaviour can be used for an indirect comparison. There was no difference in foraging distance, the distance travelled before encountering prey, inside or outside Hwange National Park, nor was there a difference in the number of hunt periods per day. Diet composition and the amount of kilojoules gained per African wild dog were also similar inside and outside the National Park. It can therefore be assumed that there were no differences in prey availability inside and outside the National Park. It also has to be kept in mind that, contrary to what would be expected based on a classic source-sink system, the favourable ecological conditions were in fact found in the sink habitat in the buffer zone outside the park.

Although prey availability does not seem to differ inside and outside Hwange National Park, foraging costs nevertheless differed substantially due to more successful chases and shorter chase distances in the buffer zone outside the National Park. African wild dogs use a widely foraging strategy which increases the likelihood of encountering prey but, compared to predators using a sit and wait strategy, comes with significant energetic costs (Huey and Pianka 1981). In addition to this costly strategy the energetic output of hunting African wild dogs is known to be extremely high (Gorman et al. 1998, Rasmussen et al. 2008). Therefore survival and reproductive success of African wild dogs does not only depend on the ability to secure prey but also on minimising foraging costs (Rasmussen et al 2008, Rasmussen 2009). The observed differences in hunting efficiency inside and outside Hwange National Park could therefore be one of the main reasons why African wild dogs prefer to leave the National Park. As no significant differences in body condition and prey anti-predator response to African wild dogs were found inside and outside Hwange National Park it is likely that the found differences in hunting efficiency are due to differences in landscape attributes. Inside Hwange National Park there was a higher likelihood for a kudu or impala kill to be made in high visibility habitat. Although some studies have found no effect of vegetation on the probability of African wild dogs making a kill (Fanshawe and Fitzgibbon 1993), others have shown that vegetation does affect hunting efficiency (Reich 1981). In habitat with low visibility, average flight distance of prey is smaller resulting in shorter chase distances (Reich 1981). Several other studies have shown that biotic and abiotic landscape attributes affect hunting efficiency and, regardless of prey abundance, predators selected habitat with specific landscape attributes that made prey easier to catch (van Dyk and Slotow 2003, Rhodes and Rhodes 2004, Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007). As vegetation seems to affect prey catchability it is likely that, based on differences in vegetation density resulting in a higher hunting efficiency, African wild dogs prefer to select habitat in the buffer zone outside the National Park.

Another factor likely to play a role in habitat selection by African wild dogs is interspecific interference competition with lions and spotted hyenas. Lions and spotted hyenas are known competitors of African wild dogs (Carbone et al. 1997, Creel and Creel 1998, Creel

2001, Woodroffe et al. 2004) and several studies have shown a negative relationship between lion and spotted hyena densities, and African wild dog densities (Mills and Gorman 1997, Creel 2001). During the time of the study lion and spotted hyena densities were likely to be higher inside than outside Hwange National Park which is expected to increases the encounter rate with these predators. It was found that lions and spotted hyenas were present at 1 out of every 6 kills made by African wild dogs inside Hwange National Park, compared to 1 out of every 18 kills in the buffer zone outside the National Park (van der Meer et al. accepted (chapter 4)). Interference competition between predators can have direct effects in the form of kleptoparasitism or intraguild predation (Caro and Stoner 2003). In the buffer zone outside the National Park the kills of African wild dogs were not only less often kleptoparasitized by lions and spotted hyenas, it also took these kleptoparasites longer to arrive at the kill site, allowing the African wild dogs to consume more of their kill themselves. Although, due to the long time it takes lions and spotted hyenas to arrive at the kill site, the loss translated in kilojoules is relatively little, the difference in encounter rates inside and outside the National Park could nevertheless affect African wild dog habitat choice. Lions and spotted hyenas are known competitors of African wild dogs (Carbone et al. 1997, Creel and Creel 1998, Creel 2001, Woodroffe et al. 2004). The risk of encounters with lions and spotted hyenas is not limited to the potential loss of a kill. Encounters with these competitors increase the risk of injury due to aggressive interactions and the risk of intraguild predation. Lions are a major cause of African wild dog mortality and are known to kill both adults and pups (Woodroffe et al. 2004). Spotted hyenas have been reported to kill African wild dog pups (Creel and Creel 1998, Woodroffe et al. 2004, Painted Dog Conservation project; unpublished data). Especially in small packs of African wild dogs the loss of a single individual can, due to a strong positive relationship between pack size, survival en reproduction (Creel and Creel 2002, McNutt and Silk 2008), be detrimental for an entire pack of African wild dogs (Courchamp and Macdonald 2001, Rasmussen 2009).African wild dog mortality known to be caused by lions and spotted hyenas was found to be almost twice as high inside Hwange National Park compared to the buffer zone outside the National Park (van der Meer et al. submitted (chapter 1)). Aggressive interactions in an area at one time are likely to give information about the chances of encountering lions and spotted hyenas in the same area at a later time. The higher encounter rate and mortality risk inside Hwange National Park are therefore likely to reduce the likelihood that African wild dogs return to the area.

For many carnivorous mammals access to suitable den sites is crucial for successful reproduction and likely to affect population recruitment (Fernández and Palomares 2000, Norris et al. 2002, Richardson et al. 2007). Den site selection is therefore seldom random but often based on fitness related factors like food availability (Szor et al. 2008), shelter from extreme weather conditions (Eide et al. 2001) and escape from predators (Pruss 1999, Hwang et al. 2007, Lesmeister et al. 2008, Ross et al. 2010). African wild dogs use a den to give birth to their offspring. As both lions and spotted hyenas are known to kill African wild dog pups (Creel and Creel 1998, Woodroffe et al. 2004, Painted Dog Conservation project; unpublished data) interspecific competition with these predators is likely to play a role in African wild dog den site selection. In this study we found that overall visibility at den sites was smaller than at random sites. Den sites outside Hwange National Park, where lion and spotted hyena densities were relatively low, were placed in vegetation with significantly less visibility than random sites. Although the difference for the den sites inside the National Park, where lion and spotted hyena densities were higher, was not significant a similar pattern was found. When looked at vegetation type it was found that despite the fact that there is little closed vegetation available den sites were relatively often placed in this type of vegetation. Even inside the National Park where there was virtually no closed vegetation present African wild dogs still managed to place 40.0% of their den sites in closed vegetation. It seems that African wild dogs tried to minimise predation risk by selecting den sites in closed vegetation with little visibility. Contrary to what would be expected, the preference for closed vegetation with little visibility was less pronounced inside the National Park where lion and spotted hyena densities were relatively high. It has to be kept in mind though that based on random sites it seems that inside the National Park there was virtually no closed vegetation available, which suggests that this type of vegetation is scarce and might therefore be a limiting resource. Without the possibility to select preferred den sites, African wild dogs have no other choice than to either expose themselves to a higher predation risk which could negatively affect their reproduction and recruitment or leave the high predator density area and move into the buffer zone outside Hwange National Park.

Habitat selection theory predicts that individuals select habitat where, depending on the activity they need to perform, they maximize their fitness. Based on the found information about the relationship between habitat preference and habitat quality in the Hwange system it seems that African wild dogs base their habitat selection on the right ecological cues. In the buffer zone outside Hwange National Park they experience a higher hunting efficiency, less competition with lions and spotted hyenas and better access to suitable den sites. As a result African wild dogs outside the National Park gain more energy and have a higher reproductive success. However, due to human induced changes that African wild dogs are unable to account for, these ecologically reliable cues are no longer associated with an adaptive outcome. The human activity in the buffer zone results in mortality exceeding natality, turning the buffer zone into a mortality sink. African wild dogs nevertheless make a maladaptive habitat choice and show a preference for this sink as they are unable to judge habitat quality accurately. In other words, African wild dogs in the Hwange system have been caught in an ecological trap. Within an ecological trap habitat choice becomes detrimental and is likely to result in a rapid collapse of the system and extirpation of the species involved as, unlike within a source-sink system where movement of animals into the sink is density dependent, a source population is not maintained due to a non-density dependent preference for the sink habitat (Kokko and Sutherland 2001). The fast decline in the African wild dog population in and around Hwange National Park supports the finding that the Hwange system serves as an ecological trap; in just five years time (2004-2009) the African wild dog population in and around Hwange National Park has been reduced with more than 75% (Woodroffe et al. 2004, Zimbabwe Parks and Wildlife Management Authority 2009). This fast reduction is likely to be the result of a collapse of the system due to a maladaptive habitat choice for a mortality sink, accelerated by a so called Allee effect, where population growth becomes negative when individuals become rare.

As ecological traps can cause extirpation of a population (Delibes et al. 2001, Kokko and Sutherland 2001, Gilroy and Sutherland 2007), they have obvious management implications. The rate at which extirpation takes place is determined by the initial population size. When population size is low ecological traps lead to rapid extirpation because no animal will use the less-preferred, but more suitable, habitat. An animal's ability to, behaviourally or evolutionary, adapt to a changing environment determines its vulnerability to an ecological trap. Time plays a vital role; the less time animals have to adapt to changes in the environment the more likely they are to make maladaptive habitat choices (Schlaepfer et al. 2002, Battin 2004, Gilroy and Sutherland 2007). The main cause of human induced mortality in the buffer zone is poaching with wire snares (van der Meer et al. submitted (chapter 1)). The deteriorating economy within Zimbabwe has resulted in a fast and massive increase in poaching within the buffer zone leaving the African wild dogs no time to adapt to this environmental change. It is discussable whether, if given the time, African wild dogs would ever be able to adapt to unnatural circumstances like poaching. Snares are not deliberately set for African wild dogs but they are indiscriminate and with their widely ranging behaviour African wild dogs run a high risk to accidentally get caught when they range beyond the park border. As snare lines are set up at random places in the bush and left for days before poachers come to collect their catch there are not many environmental cues that would allow African wild dogs to adapt their behaviour unless they are able to connect mortality to humans and completely refrain from moving into areas where there is any form or shape of human activity. It is more likely though that ecological cues increasing reproduction will remain to play a stronger role in habitat selection than cues related to human induced changes to the environment. Due to the rapid decline in African wild dog numbers the African wild dog population within the Hwange system can be classified as low which means there is not much time left to make the right management decisions to conserve the remaining packs. From a genetic point of view it might not be too late to restore the Hwange population as immigration of African wild dogs from other countries into Hwange National Park seems to occur and African wild dogs around the Victoria Falls Hwange National Park border regularly seem to cross into neighbouring countries. The recent set up of the Kavango-Zambezi Transfrontier Conservation area, of which Hwange National Park and its adjacent buffer zone form the Zimbabwean component, will further facilitate transboundary movement of the species.

If sink habitat acts as an ecological trap, conservation efforts can focus either on reducing the attractiveness of the trap by removing the erroneous cues that cause and organism to prefer poor quality habitat, increasing the quality of the trap habitat such that population growth rate becomes positive or by focussing on alternative habitat by introducing appropriate settlement cues to suitable but unoccupied areas (undervalued resources) (Donovan and Thompson 2001, Battin 2004, Gilroy and Sutherland 2007). As the cues at which African wild dogs within the Hwange system base their habitat choice are sound ecological cues that, in an undisturbed ecosystem, would lead to an adaptive outcome they can hardly be called erroneous. Making the buffer zone less attractive or making Hwange National Park more attractive would mean taking drastic measures to manipulate vegetation density and predator density while maintaining the same or a higher level of prey density. Manipulating an ecosystem is easier said than done as every step taken will inevitably affect not only the African wild dogs but the ecosystem as a whole. Additional research will be necessary to determine which factors affect vegetation density inside and outside Hwange National Park, what factors result in a high lion and spotted hyena density inside Hwange National Park and what potential impact manipulation of these variables could have. Apart from the fact that Hwange National Park and the surrounding buffer zone are not only an African wild dog sanctuary but harbour many other animal and plant species which faith has to be taken into account, by the time the answers to these complicated questions have been found the African wild dog population in and around

Hwange National Park will have probably extirpated. The same counts for the identification of alternative habitat and the introduction of appropriate settlement cues.

A quicker and more practical solution could be to simply prevent animals from migrating into the mortality sink by forcing them to stay in the source habitat. In other words, setting up a barrier that prevents African wild dogs to enter the buffer zone. As an actual physical fence will prevent other wildlife from entering the buffer zone where a large part of the land is designated to hunting and, to a lesser extent, photographic safaris it is unlikely that this measure will find support. As an alternative it might be possible to use a so called ‘biofence’ made of scent marks with chemicals subtracted from African wild dog urine (Marshall 2004). Olfactory communication by scent marks prevents African wild dogs to enter each other’s territory, applying artificial scent marks might serve as a natural barrier and prevent African wild dogs to enter ‘unwanted’ areas (Marshall 2004), like the buffer zone outside Hwange National Park. It has to be kept in mind though that if human induced mortality is eliminated, the buffer zone, based on ecological parameters, has the potential to be a more productive habitat than Hwange National Park. Increasing the quality of the trap habitat so that population growth becomes positive might therefore be the ultimate solution. The average litter size is almost twice as high outside the National Park which means that in order to ensure a fast recovery of the population it, from a conservation point of view, would make the most sense to expand conservation efforts beyond the borders of the protected area and focus on countering the human induced mortality in the buffer zone along the northern boundary of the National Park.

In the last century, direct persecution by humans has been an important cause of the decline in African wild dog numbers throughout Africa (Woodroffe et al. 1997). Even in National Parks, African wild dogs were shot and poisoned as vermin. Although shooting of African wild dogs is no longer a National Parks policy, human prosecution remains a problem as African wild dogs are often perceived as a pest which kills livestock, or competes with humans for wild ungulates in hunting areas (Woodroffe et al. 1997). In areas where natural prey remains, even at low densities, livestock depredation has been found to be uncommon (Rasmussen 1999, Woodroffe et al. 2005). However, in areas where wild prey is seriously depleted livestock depredation can be a problem (Woodroffe et al. 2005) which can be minimised by appropriate livestock husbandry (Rasmussen 1999, Woodroffe et al. 2005, Woodroffe et al. 2007). In areas where ranches are game fenced and predominantly used for cattle or consumptive wildlife utilisation ranchers generally show a negative attitude towards African wild dogs (Lindsey et al. 2005). In a study by Lindsey et al. (2005) some farmers perceived African wild dogs as animals that are a liability to farmers as they consume valuable wildlife and cause damage to fences while hunting, the majority of the farmers agreed though that African wild dogs are a natural component of a healthy ecosystem and tourists like to see African wild dogs. Many ranchers realised that African wild dogs had a potential ecotourism value and the most positive attitudes were found in areas where ranches belonged to conservancies and land use was dominated by ecotourism (Lindsey et al. 2005). In and around Hwange National Park livestock depredation by African wild dogs has been virtually absent (G.S.A. Rasmussen, Painted Dog Conservation project; pers. comm.), this has helped to promote a positive attitude towards the species. The commercial farms in the buffer zone outside the National Park are unfenced areas predominantly used for consumptive wildlife utilisation. Wildlife can move freely into these areas and shooting of African wild dogs has historically been a problem. In 1987 a national start to counter this problem was made when African wild dogs were afforded a special 'protected' status and shooting of African wild dogs became officially prohibited (Zimbabwe Parks and Wildlife Management Authority 2004).

This is not enough though, in order to protect the remaining population of African wild dogs in and around Hwange National Park poaching will need to be prevented. Due to the establishment of wildlife protected areas in colonial times and human encroachment in the areas surrounding these protected areas, the areas in which rural people are allowed to use wildlife and other natural resources have been restricted and, with the growing human population, utilisation of these resources has generally become unsustainable (Hulme and Murphee 2001). National parks and game reserves are historically managed without much consideration of rural people, and 'fences and fines' have been the traditional way to minimise human impact and discourage illegal activities like poaching. The rural communities surrounding protected areas often experience social and economic hardship and, due to restricted use of natural resources and human animal conflict, have generally developed a negative attitude and resentment towards nature conservation and the instituted systems of wildlife management (Hulme and Murphee 2001). The historical methods of wildlife management seem to be ineffective in curbing illegal activities like poaching, and frequently result in confrontational relationships with rural communities (Newmark and Hough 2000). More and more the former 'fences and fines' approach to conservation is viewed as anachronistic and counterproductive and conservationists try to socially and economically involve local communities in conservation programmes in order to create direct incentives to protect biodiversity (Newmark and Hough 2000, Hulme and Murphee 2001).

These so called integrated conservation and development projects have been implemented with varying results. For example, in Zambia an experimental project was set up to try and counter the high level of poaching of elephants and rhinos in an around the protected areas in the Luangwa Valley. Local people around the protected areas were involved in wildlife protection and management activities by training and employing local residents as wildlife management staff and setting up village wildlife counsels to provide advice and assistance. A sustained yield use of wildlife was adopted to invest revenues in community development and to make the program self supporting. As a result poaching dropped dramatically, local economies were improved and the attitude of local people towards wildlife management and conservation became more positive (Lewis et al. 1990). On the other hand, in Ranomafana National Park in Madagascar the hiring of poachers as national parks staff actually increased poaching because these new employees used their earnings to hire more people to expand their poaching operations (Ferraro et al. 1997). Within Zimbabwe, wildlife and other natural resources are generally protected from illegal activities by a 'fences and fines' approach but initiatives have been taken to involve the local communities in resource management. In the mid 1980's the Parks and Wildlife Management Authority in Zimbabwe designed an integrated conservation and development project named the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE). This programme has been implemented in all rural communities surrounding the nations protected areas, including the communities around Hwange National Park, and is seen as a long term programmatic approach to use wildlife and other natural resources to promote rural institutions and improve governance and livelihoods (Hulme and Murphee 2001, Taylor 2009). Although the programme faced some difficulties due to nationwide deteriorating socio economic conditions, and a number of assumptions underlying the success of CAMPFIRE as an innovative model for community based natural resource management still have to be met, CAMPFIRE confirms the concept that sharing responsibility and accountability can be very successful in promoting the collective and participatory management of natural resources (Taylor 2009).

Although integrated conservation and development projects like CAMPFIRE are great tools to promote collective and participatory management of natural resources on a broad scale, the improvement of the livelihoods of local communities near protected areas does not inevitably lead to long term viability of single species. In 1992 the Painted Dog Conservation project was established in order to ensure a more fine scaled species specific approach to protect the African wild dogs in and around Hwange National Park. With human induced carnage from snares, shooting and road kills accounting for most of the African wild dog mortalities, and early presentations showing prejudice and ignorance, it was clear that unless this situation was addressed the species could quickly become extirpated in the Hwange area. The emphasis of this private voluntary organisation has thus been to identify critical issues and use action and education to make a substantial long lasting contribution to the conservation of African wild dogs, the conservation of nature, and the lives of the local people by providing employment and education opportunities. Their rehabilitation facilities allow the Painted Dog Conservation project to deal with any eventuality concerning injured or orphaned African wild dogs or the translocation of entire packs from problem areas. With their anti poaching units they actively try to prevent poaching by carrying out daily anti poaching patrols. Since the first of these units was deployed in 2001 they have collected over 15 000 snares in the buffer zone along the northern boundary of Hwange National Park. In an attempt to improve local livelihoods and provide nutrition and food security the Painted Dog Conservation project is involved in the placement of boreholes and the establishment of communal gardens. Apart from action, education is important to raise awareness and prevent prejudice and ignorance. The Painted Dog Conservation visitor centre features an interpretive hall which teaches visitors about the Hwange ecosystem, the plight of the African wild dogs and the significance of biodiversity and nature conservation. On a yearly basis the sixth grade students of the local schools surrounding the study area visit the children’s bush camp where they learn about conservation concepts. Through the children’s bush camp and nature conservation clubs at schools, an emotional attachment to nature is promoted in hopes that it will lead to an attitude of caring for it.

Integrated conservation and development projects are highly vulnerable to political unrest and economic downturn (Newmark and Hough 2002). Due to deteriorating socio economic conditions within the area, it has been difficult to assess whether the community outreach programmes of the Painted Dog Conservation project have resulted in a quantitative improvement of the livelihoods of the targeted communities. However, the Painted Dog Conservation project has certainly managed to raise awareness and prevent prejudice and ignorance. The increased familiarity with African wild dogs and the Painted Dog Conservation project has resulted in a willingness of the local authorities and stakeholders to help and protect the species. Painted Dog Conservation has not only successfully lobbied for the species to be given special protection under the Parks and Wildlife Act, they have also been successful in securing the only prosecution against an individual for shooting an African wild dog. This seems to have resulted in shooting no longer being a major problem in the area. With the permission of the department of roads, road signs have been erected to alert motorists to the presence of African wild dogs utilizing the main roads around Hwange National Park. With the help of the local stakeholders and the Zimbabwe Republic Police a process has been started to bring down the speed limit on the roads directly surrounding the National Park from 80 km/h to 60 km/h. Road signs will be erected to inform motorists of the adjusted speed limit in the area. The Painted Dog Conservation anti poaching units, the Hwange Parks and Wildlife Management Authority, Forestry Commission and the Zimbabwe Rural Police collaborate to prevent poaching. In 2009 the fine for poaching an African wild dog has been set at 3000 USD (Trapping of Animals (Payment for Trapping of Wild Animals) Notice 2009). This has made it possible to effectively prosecute and sentence poachers, which is likely to serve as a deterrent to other likeminded offenders.

Although Africa has a long history with integrated conservation and development projects this approach generally has had limited success (Hulme and Murphee 2001). Often projects fail to achieving both conservation and development objectives and it has therefore been suggested that integrated conservation and development projects should be viewed as just one option out of a variety of options to conserve natural resources, and that alternatives should be actively explored and taken into account as well (Newmark and Hough 2002). The examples as mentioned above show that strictly from a conservation point of view a ‘fence and fine’ approach can help to provide adequate legal tools to protect a species. It seems that a combination of an integrated conservation and development approach and a ‘fences and fines’ approach is necessary to create the right conservation framework to try and prevent the African wild dogs in and around Hwange National Park from extirpation. As long as the livelihoods of local communities are not adequately improved subsistence poaching is likely to exist. Over the recent few years the Zimbabwean economy seems to be slowly recovering therewith creating a better ground for the protection of wildlife and other natural resources. However, with more than 3000 snares collected in 2010 (Blinston 2010), which is similar to the number of snares collected in 2009 (Blinston 2009), the problem of cable snare subsistence poaching remains. It is likely that, with an unemployment rate believed to be over 90%, the economic improvement has yet been too little to significantly improve local livelihoods and the provision of alternative sources of protein and income will remain necessary to prevent poaching. The legal tools to adequately protect the species are in place and continuing to create awareness and familiarising people with African wild dogs creates the right mindset to make it possible and acceptable to prosecute people that endanger the species. The main question is whether, with the extremely rapid decline in the Hwange African wild dog population over the past decade, there is enough time to be able to adequately improve livelihoods and create the right conservation framework up to a point where the African wild dog population in and around Hwange National Park will be restored…

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Acknowledgement

Testing the ecological
trap hypothesis
for
African wild dogs
in and around
Hwange National Park

Acknowledgement

Thank you mum and dad for giving me the opportunity to study, without my education I wouldn't be the person I am today,

Thank you Pascalle and Vera for making me believe in myself and science,

Thank you Greg for sharing your historical data base and helping me to define my conservation question,

Thank you Hervé for believing in me, together we've turned this into a fine piece of work,

Thank you Peter for your support, giving me the freedom to do whatever I deemed necessary doing, making sure we were fed even when food wasn't available and providing us with a place to call home,

Thank you Ron and Marianne for helping me to make this PhD happen,

Thank you Jealous for turning me into a bush girl and for all those unforgettable moments of which the memories will always last...

Thank you Gilbert and Last for making sure my car never let me down and always brought me home safe,

Thank you Frogs for spoiling me and helping me out whenever needed,

Thank you Xmas, Washington, JB and Clive for never even raising as much as an eyebrow whenever I asked you to collect something for my research, whether it was buckets full of wild dog faeces or bottles full of blood, you guys are great!

Thank you Mkhalalwa, Gracious, Justice, Kuhms, Wellington, Never, Birton, Simeon, and all the other National Parks rangers, members of the PDC Anti Poaching Unit and students, for making my research your research and helping me out in the field,

Thank you to all the staff of Painted Dog Conservation for helping me with whatever needed, whether it was making a copy, washing my clothes, repairing the toilet or clearing the grass around the house, without you my life would have been a lot more difficult,

Thank you Chris for giving me the opportunity to learn how to use ArcGIS,

Thank you Fred for helping me out with equipment and clothing,

Thank you Rob, also on behalf of the (de-snared) animals, for making sure I have my own dart kit and the best receiver ever, both have proven to be invaluable,

Thank you Volkert for enabling me to print my words on paper,

Thank you Nicole for always being interested and supportive,

Thank you Monique for sharing a passion,

Thank you Karin for not forgetting me, even though the distance between us became further our friendship only became stronger,

Thank you to all the family and friends who kept reading and responding to my bush mails, it made the Netherlands a bit closer to Zimbabwe,

Thank you Marion and Simon for your support and critical reviewing, your valuable input has been much appreciated,

Thank you Olivier for your helpful guidance in the world of statistics and vigilance,

Thank you Nolwenn for translating my words in French,

Thank you Gerwen, Rob and Barbara for being real life savers and helping me out with the vital ingredients for a PhD: data analyses and literature,

Thank you Roger and Jessica for teaching me the finer art of immobilising wildlife, it's always as much a privilege as a pleasure to work with you,

Thank you Peter and Judy for sharing 'the dream' with me whenever I was in search of the dogs,

Thank you Evelyne, Alison, Pim, Sem, Eric, Arndt, Saskia and Susanne for allowing me to use your beautiful pictures,

Thank you William, Perrine, Brent, Laurie, Nic, Martin, Greg, Catherine, Bruce, Wendy, Jane, Zeke, Andy, Jaëlle, Matt, Patrick, Alison, Eleonore, Elsa, Alice, Elodie, Marine, Bertrand, Pierrick, Florian, Stephanie, Claire, François, Hugo, Chloé, Marion, Nicolas, Monicah, Tawanda, Peter, Tsitsi, Kuku, Godfrey, Edwin, Bekhi, Sharon, Garry, Sandra, Janet and all the others who have shared stories, food and drinks and made sure I haven't completely lost the ability to be sociable,

Thank you Hans for your unconditional love and support, single we are silver, together we are gold!

Thank you all for your friendship, help and support!

Esther

"Elephant, giraffe, zebra, buffalo, lion, kudu, steinbuck, warthog, they are all there on show. The animals are doing their bit. The keepers of the kingdom are not."

-Keith Meadows-
Wankie
The story of a great game reserve
by Ted Davidson