

# Factors influencing African wild dog (*Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications

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PhD thesis



Photo: Craig Jackson

## Preface

Looking back, it is hardly surprising that I have pursued a career in wildlife research. For as long as I can remember, my parents have regularly taken my sisters and me on excursions to various wildlife reserves. Living less than 3km from the Kruger National Park certainly helped, and we frequented the park. Through my family's love and support, I have been able to pursue my childhood love of the African bush after leaving school and make it part of my career. I now get to visit and do fieldwork in places most people have to pay a lot of money to visit during their holidays! Many people have contributed to my PhD project, both directly and indirectly, and without their assistance, guidance and support I would not have been able to complete this thesis. I am truly grateful to everybody who played a part, and in particular I would like to thank:

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## Summary

Large carnivores are particularly susceptible to negative anthropogenic effects. As human populations continue to encroach on wildlife habitats, protected areas may become increasingly important for large carnivore conservation. The African wild dog (*Lycaon pictus*) occurs at low densities and ranges over wide areas where anthropogenic activities account for a large proportion of mortalities. However, conserving wild dogs within protected areas presents several challenges that conservation managers need to address. In particular, wild dog populations occurring within the relative safety of protected areas are prone to sources of mortality associated with edge effects, intra- and interspecific competition, while fragmentation threatens population viability.

Land use along protected area boundaries is often characterised by an abrupt transition. Within the boundaries carnivores are protected and valued, but outside are regarded as a threat to humans their domestic animals, leading to their persecution. In addition, these transitional zones are associated with other threats such as accidental deaths inflicted by motor vehicles, contraction of disease from domestic dogs (*Canis familiaris*), and wire snares set by bush meat hunters. Edge effects are a major problem in the conservation of wild dogs, yet limiting their ranging behaviour poses a seemingly insurmountable challenge. However, wild dogs are territorial and the scent marks of neighbouring packs directly influence their ranging behaviour as neighbouring packs are avoided since encounters can be potentially fatal. We found that targeted deployments of translocated foreign scent marks influenced the ranging behaviour of an otherwise free-ranging wild dog pack. When exploring unfamiliar areas near or outside the protected area boundary, exposure to foreign scent marks resulted in the pack covering significantly greater distances and moving in the direction of their frequented range inside the protected area. Unlike wire fences, scent marks present a biologically relevant cue which, once detected, elicits a behavioural response. With further experimentation and a greater understanding of wild dog territoriality operates, this technique has the potential to reduce wild dog ranging into conflict-prone landscapes alongside wildlife reserves.

For the scent mark technique to be an effective management tool, wild dog packs should ideally be repelled by the presence of foreign scent marks. Scent marks are used to communicate territorial boundaries yet all studies of wild dog territoriality have to date reported that the degree of territorial overlap between neighbouring packs varies hugely. Attempting to maximize the effectiveness of managing wild dog ranging behaviour using foreign scent marks would necessitate an understanding of why, in certain instances, wild dog territorial boundaries are apparently ignored resulting in extensive transgression. We found that inter-pack relatedness was extremely important; unrelated packs had very low levels of overlap and these were restricted to the peripheral parts of territories. In contrast, related dyads overlap significantly more and even intensively utilized parts of the range, where the probability of encountering a neighbouring pack is far higher, were found to overlap. Pack size had little effect between related neighbours, but in unrelated dyads there was a tendency for larger packs to overlap more onto the territories of smaller packs. While Intraspecific competition can result in mortality, all available evidence suggests that aggression is greatly reduced between related packs. Establishing a territory alongside close relatives may therefore extend exclusive fitness benefits from the intra-pack to inter-pack level. The natural spacing system thus has the potential to affect the number of packs a given protected area can accommodate, as well as survival parameters through variations in the intensity of intraspecific competition. The findings are therefore important for the management of the species, specifically in intensively managed populations. For the purposes of using translocated scent marks to create a biological barrier, it is therefore important to use foreign scent marks from unrelated individuals as scent marks from related packs may not illicit the desired behavioural response.

The effects of interspecific competition on wild dog populations are, however, usually far greater than intraspecific competition. Lions (*Panthera leo*) and, to a lesser degree, spotted hyenas (*Crocuta crocuta*) can have major effects on wild dog populations and in combination account for more than 50% of wild dog deaths. As the dominant carnivore, lion densities are positively correlated with prey availability. Spatial variations in lion densities are therefore associated with specific landscape types and low lion density habitats are exploited by wild dogs, facilitating coexistence. Lions do not prefer hilly, mountainous and other forms of rugged terrain. With their decreased risk of lion encounter, we found that wild dogs actively selected rugged terrain when denning. Since wild dogs only reproduce once per year, the success of the annual event has a large influence on pack and population viability. Den site selection thus forms a primary defense strategy against predation.

Wild dogs are also vulnerable to interspecific competition outside of the denning period when ranging widely across their territory. Habitat selection should therefore attempt to minimize the probability of risky encounters with lions and hyenas. As case in point is the reported local extinction of a studied population of wild dogs in the Serengeti National Park (SNP), Tanzania. Both disease and interspecific competition were identified as contributing factors, yet the ultimate cause of the extinction has never been identified. Over a twenty-five year period the population declined before finally disappearing entirely. Although not well documented, the wild dog population did persist in the eastern parts of the ecosystem. Since the habitat characteristics are very different in these parts, we hypothesized that certain ecological features affected the distribution and availability of competition refuges. Given the dramatic increase in lion and spotted hyena populations during the wild dog population decline, competition refuges may have become increasingly important to limit costly interspecific competition. A species distribution model was derived using occurrence records from the extant population within the ecosystem. We then used global positioning system (GPS) collar data from two wild dog packs recently reintroduced into SNP and overlaid the data onto the habitat suitability model. Habitat intensively utilized by wild dogs corresponded closely to habitat predicted as highly suitable, which was characteristically rugged. An analysis of movement data revealed that this habitat acted as competition refuges, the distribution of which was very limited within the SNP. However, habitat with an ability to provide wild dogs with respite from competition was abundant in the eastern parts of the ecosystem, where the population has managed to persist. The reported local extinction appears therefore to have instead been a range contraction; as lion and hyena populations increased, wild dogs were only able to survive in areas where they were not permanently exposed to high levels of competition. Topographic heterogeneity, and in particular patches of rugged terrain, are therefore important should wild dogs successfully coexist in the presence of lion and hyena populations.

While edge effects, intraspecific and interspecific competition are associated with protected areas and their immediate surroundings, many populations of wild dogs are located in geographically isolated populations. Population viability is greatly reduced in such instances. Wild dogs are, however, capable of dispersing long distances in the search of mates. In South Africa, the majority of wild dog populations occur in relatively small and geographically isolated populations. Most of these reserves have reached carrying capacity and a large proportion of the country's total population occurs outside protected areas. We identified five priority conservation areas where habitat was relatively intact and where wild dogs had been sighted on numerous occasions, inferring some degree of connectivity to a source population. We assessed connectivity using different methodologies and using a dataset of occurrence records for both dispersing and resident packs of wild dogs. Despite the use of potentially subjective cost layer, current flow analysis provided the best connectivity analysis with greater potential to be incorporated into management plans. Our study shows that using habitat selection data from animals in

resident populations, connectivity may be underestimated as dispersing individuals are often less habitat specific.

## List of papers

The PhD thesis consists of the following five papers:

- I. Jackson, C.R., McNutt, J.W. & Apps, P.J. 2012. **Managing the ranging behaviour of African wild dogs (*Lycaon pictus*) using translocated scent marks.** *Wildlife Research*, 39, 31–34.
- II. Jackson, C.R., Groom, R., Jordan, N.R. & McNutt, J.W. **The effect of relatedness and pack size on territory overlap in African wild dogs.** (submitted manuscript)
- III. Jackson, C.R., Power, R.J., Groom, R.J., Masenga, E.H., Mjinga, E.E., Røskft, E. & Davies-Mostert, H. **Heading for the hills: risk avoidance drives den site selection in African wild dogs.** (submitted manuscript)
- IV. Jackson, C.R., Masenga, E.H., Lyamuya, R., Robertson, M.P., Fossøy, F., Mjinga, E.E., Fyumagwa, R.D. & Røskft, E. **Living in the lion's den: the role of competition refuges for African wild dog survival in the Serengeti-Mara Ecosystem.** (manuscript)
- V. Jackson, C.R., Marnewick, K., Lindsey, P.A., Røskft, E. & Robertson, M.P. **Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa.** (manuscript)

## Introduction

Biodiversity is being lost at an unprecedented rate due to ever-increasing human populations. Among terrestrial mammals, carnivores represent some of the most endangered species (Ceballos et al. 2005; Schipper et al. 2008). Large mammalian carnivores are particularly vulnerable and, despite concerted efforts to conserve them, anthropogenic processes have driven a continual global decline of their populations (Karanth & Chellam 2009). Large carnivores are challenging to conserve due to their predatory behaviour, low population densities and large area requirements (Noss et al. 1996; Nowell & Jackson 1996; Woodroffe & Ginsberg 1998; Woodroffe 2000; Cardillo et al. 2005).

The effects of bottom-up processes on carnivore populations have been well documented (Creel et al. 2001) and highlight the importance of habitat loss and depleted prey bases for carnivore populations. Smaller patches of undisturbed habitat, resulting from habitat loss and fragmentation, increase the probability of carnivores encountering human settlements. This is exacerbated by their wide-ranging behaviour which, even when residing predominantly within protected areas, leads to heightened levels of contact with people (Woodroffe & Ginsberg 1998). Human intolerance of predatory behaviour, whether based on real or misconceived perceptions of risk they pose to livestock and humans, leads to direct persecution of carnivores (Treves & Karanth 2003). Anthropogenic sources of mortality also occur through indirect processes such as road traffic accidents or entrapment in wire snares set by bushmeat hunters (Woodroffe & Sillero-Zubiri 2012). A substantial proportion of mortality in many large carnivore populations is directly attributable to humans and their activities (Cardillo et al. 2004; Inskip & Zimmermann 2009).

Within ecosystems, interspecific competition – competitive interactions between co-occurring large carnivore species – is a top-down process which exerts strong selective pressures on guild members, influencing distributions and abundances (Palomares & Caro 1999; Creel et al. 2001; Caro & Stoner 2003; Ritchie & Johnson, 2009). Patterns of spatial and temporal avoidance, in addition to costly direct encounters, ultimately decrease a species' fitness (Creel & Creel 1996; Gorman et al. 1998; Linnell & Strand 2000) and heighten a species' likelihood of local or global extinction (Polis et al. 1989). Top order predators play a vital role in ecosystem regulation and, in their absence, top-down control may be lost with potential cascading effects ensuing (Ritchie & Johnson 2009).

African savanna ecosystems are characterised by a diverse array of large carnivores and these form a critical component of Africa's biodiversity (Winterbach et al. 2013). The large carnivore guild is comprised of lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*). Of these, the African wild dog is the most threatened species having been extirpated from 25 of the 39 countries they formally occurred in (Woodroffe et al. 1997). Wild dog populations are absent in most of west and central Africa, with large-scale declines in populations in east and southern Africa (Woodroffe & Ginsburg 1999). The majority of remaining populations are relatively small in size and fragmented in distribution (Woodroffe & Sillero-Zubiri 2012). The species is listed as Endangered by the International Union for the Conservation of Nature (IUCN) and the entire global population is estimated to comprise less than 1400 mature individuals (Woodroffe & Sillero-Zubiri 2012).

African wild dogs are obligate cooperative breeders and highly social group-living canids. Wild dogs generally disperse in search of mates as single-sex groups (McNutt 1996) and packs are therefore formed by an unrelated dominant pair together with their same-sex relatives (Frame et al. 1979; Girmin et al. 1997). The alpha male and alpha female typically monopolize breeding while the remainder of the

pack assist with pup rearing. The use of genetic techniques has, however, revealed that subordinates are afforded breeding opportunities more frequently than originally thought (Spiering et al. 2010). Reproduction occurs once a year and usually coincides with the dry season (Reich 1981; Maddock & Mills 1994; McNutt 1996). Wild dogs excavate dens, often modifying disused warthog burrows or hyena dens, and utilize these shelters until the pups are approximately three months old.

Pack size ranges widely in size but an average size may vary between approximately 8 – 13 individuals (Frame et al. 1979; Maddock & Mills 1994; Mills & Gorman 1997; Creel & Creel 2002). Wild dog packs establish and defend a relatively large territory, typically ranging from 200 – 700km<sup>2</sup> but often exceed 1000km<sup>2</sup> (Mills & Gorman 1997; Creel & Creel 2002; Parker 2009; Woodroffe 2011). As result, wild dogs occur at low densities even in healthy populations.

Their extensive ranging behaviour makes them difficult to conserve and the most common source of wild dog mortality is human-induced (Woodroffe et al. 2007). Most protected areas inhabited by wild dogs are unfenced, but even electrified game fences aimed at confining them are often ineffective. In South Africa, for example, reintroduced wild dog packs escaped from 78% of the nine fully-fenced meta-population reserves (Davies-Mostert et al. 2009). Their wide-ranging behaviour brings them into contact with humans, where their predatory habitats are not tolerated by livestock owners (Lindsey et al. 2005). It is estimated that approximately 60% of adult wild dog deaths, both inside and outside protected areas, are linked to human activities (Woodroffe & Ginsburg 1999). Diseases, such as rabies and canine distemper virus, have resulted in the death of entire populations and these are usually contracted from domestic dogs (Woodroffe & Ginsburg 1999; Goller et al. 2010). Snares and road traffic accidents are also another major cause of wild dog mortality.

In order to support viable populations, wild dogs consequently require extensive protected areas free from negative anthropogenic processes. Areas of adequate size are limited in availability and even then wild dog populations may be prone to decline and low population sizes. For example, the 20 000km<sup>2</sup> Kruger National Park in South Africa, roughly the size of Israel, currently supports a wild dog population of less than 200 individuals.

Although largely protected from negative anthropogenic effects, populations within protected areas may be severely limited by interspecific competition by other large carnivores (Woodroffe & Ginsburg 1999; Creel 2001). Among the members of the large carnivore guild, wild dogs are far smaller than their main competitors, lions and spotted hyenas (Creel & Creel 2002). Across several studied populations, lions account for as much as 43% of wild dog mortality while hyenas account for approximately 10% (Woodroffe & Ginsburg 1999). Compared to hyenas, lions impose a far greater risk and are avoided at all times (Webster et al. 2012). Data from large ecosystems indicate that wild dog densities are inversely correlated with lion and spotted hyena densities (Creel & Creel 1996). As a highly cooperative unit, wild dog packs are extremely efficient hunters and can utilise habitats with lower prey densities which are not favoured by lions (Mills & Gorman 1997). Their efficient cooperative hunting abilities thus facilitate spatial avoidance which promotes coexistence amongst the large carnivore species (Mills & Gorman 1997). Within smaller protected areas, habitat heterogeneity may be limited thereby restricting wild dogs' avoidance of dominant competitors. Although protected areas may reduce anthropogenic threats, interspecific competition may instead be a limiting factor and jeopardise wild dog population viability.

## Aims

As human populations continue to expand, protected areas will conceivably play an increasingly important role in the conservation of African wild dog populations. Protected areas, however, do not equate to a problem-free management solution (Davies-Mostert et al. 2009). Although protected areas may greatly reduce negative anthropogenic effects, wild dogs are particularly prone to edge effects as their wide ranging behaviour brings them into conflict with human communities, and the threats associated with them, surrounding protected areas (Woodroffe & Ginsberg 1998). Even when protected area's perimeters are fenced with electrified predator-proof fencing, wild dogs are notoriously difficult to contain, thus exposing them to anthropogenic sources of mortality (Davies-Mostert et al. 2009). While wire fences have no biological relevance to wild dogs, space use in free-ranging populations is largely determined by semiochemical communication relayed via scent marks (Parker 2009; Jordan et al. 2013). We therefore set out to determine whether translocated scent marks, from unrelated and unfamiliar wild dog packs, could be used to limit wild dog ranging behaviour to limit undesirable ranging into high-risk areas (PAPER I).

Using translocated scent marks as a potential management tool relies on the natural mechanisms of territorial behaviour that influence wild dog ranging behaviour. To optimize the effectiveness of the potential management technique, a thorough understanding of territorial behaviour is essential. All studies to date have reported huge variability in the degree of territorial overlap between neighbouring wild dog packs. For the purposes of managing wild dog ranging behaviour with translocated scent marks, it would, in most instances, be desirable to have no overlap; i.e. the scent marks should preferentially result in an about turn or a "hard boundary". Thus understanding the reported variability in territorial overlap is of vital importance for the effective use of translocated scent marks in management applications (PAPER II).

Protected areas aim to maintain intact ecosystems, and wild dogs need therefore to contend with larger, more dominant, carnivores. Lions and spotted hyenas pose particular threats, but their densities vary at the landscape level. Lion densities are positively associated with prey availability, which in turn are associated with certain landscapes rather than others. Hills, koppies (inselbergs) and mountainous terrain are not preferred lion habitats and by selecting these rugged habitat types, wild dogs can reduce the likelihood of encounter through spatial avoidance of lions. Suitable low-risk habitats could facilitate coexistence, and hence directly affect population viability, and the availability of such would be important during both reproduction (PAPER III) and general ranging behaviour (PAPER IV).

Finally, population viability is jeopardised when populations are geographically isolated from one another. This is particularly true for wild dog populations in South Africa. Wild dogs, however, have the ability to disperse several hundreds of kilometres, find mates and form a pack (Davies-Mostert et al. 2012). In addition to habitat providing connectivity between populations, identifying priority conservation areas based on their proximity and degree of connectivity to source populations is a vital conservation strategy (PAPER V).

In the papers presented in this thesis, my co-authors and I have investigated how various aspects of wild dog ranging behaviour and habitat selection might affect their conservation and management. The specific aims, results and conclusions are presented in the paper-specific summaries below.

## Summary of Papers

### Paper I

#### *Managing the ranging behaviour of African wild dogs (Lycaon pictus) using translocated scent marks*

Expanding human populations increase human-wildlife conflict and lead to abrupt transitions in land use along the boundaries of protected areas. Carnivores are frequently not tolerated immediately outside of protected areas due to conflict over livestock depredation and anthropogenic mortality is the most common source of wild dog mortality (Woodroffe et al. 2007). Conflict is exacerbated by wild dogs' wide-ranging behaviour and although most wild dog populations occur in unfenced areas, even electrified game fences aimed at confining predators are ineffective at containing wild dogs (Davie-Mostert et al. 2009). Effective management of wild dog ranging behaviour would assist protected areas in achieving their desired goals but efficient techniques are currently lacking.

Wild dog packs are territorial (Mills & Gorman 1997; Parker 2009; Woodroffe 2011) and demarcated by urine and faecal scent marks (Parker 2009). Infrequent direct encounters with neighbouring wild dog packs can have fatal consequences (Creel & Creel 2002) and promotes the avoidance of conspecific's territories. Wild dog packs inhabiting the peripheral parts of protected areas have no neighbours outside the boundary. In the absence of a neighbouring pack, the lack of scent marks may lead wild dog packs to range into human-dominated landscapes. Translocated scents marks, simulating the presence of a wild dog pack, may therefore deter wild dogs from leaving the safety of protected areas. Furthermore, single exposures to foreign scent marks may lead to packs rapidly vacating the immediate vicinity, and could be used to displace them from areas where their presence is undesirable.

In this paper, we aimed to investigate the effectiveness of using targeted scent mark deployments to signal an otherwise free-ranging wild dog pack to return to their frequented range within the safety of a protected area. The targeted scent mark deployments resulted in the focal pack moving in the direction of their frequented range, located within the protected area. Furthermore, the distance moved during the 24 hours following scent mark deployments was significantly greater than undisturbed daily distances. The pack's lengthy and directed movements were consistent with territorial avoidance. The detection of unfamiliar scent marks could chemically signal an imminent risk of an aggressive and potentially fatal encounter with conspecifics. Olfactory signals have been identified as having a potential role in wildlife management (Welsh & Müller-Schwarze 1989; Campbell-Palmer & Rosell 2010) but have rarely been applied to the conservation of free-ranging wildlife (Linklater 2004). We discuss the potential application thereof in the conservation of African wild dogs.

## Paper II

### *The effect of relatedness and pack size on territory overlap in African wild dogs*

Spacing patterns mediate competitive interactions between conspecifics and, by reducing costly intraspecific encounters, is a mechanism that ultimately increases fitness (Wilson 1975). Spacing patterns in many vertebrate populations are characterised by a home range, territory and/or core area (Mares *et al.* 1982). Many vertebrates are territorial, attempting to exclude conspecifics from specific areas of their range, yet the intensity with which core areas are defended may show some degree of plasticity. Explanations for observed variation have traditionally focused on fluctuations in population density as well as the availability of mates and resources (Both & Visser 2000; López-Sepulcre & Kokko 2005). Kin-clustering occurs when neighbouring individuals or groups have home ranges alongside close relatives. Tolerance may be greatly increased between close relatives and territorial defence relaxed (Walls & Kenwood 2001; Kitchen *et al.* 2005), thereby affecting patterns of territorial overlap.

Studies of African wild dog ranging behaviour have reported relatively large territories, yet the degree of overlap between neighbouring territories varied greatly in every studied population (Mills & Gorman 1997; Creel & Creel 2002; Parker 2009; Woodroffe 2011). Factors affecting this variability have not been investigated to date. We used global positioning system (GPS) collar data to determine the degree of territorial overlap between wild dog territories in two southern African populations. The effects of inter-pack relatedness and pack size on observed levels of overlap was assessed for each dyad.

Relatedness was found to be positively associated with the degree of territorial overlap. On average, unrelated packs had low levels of overlap which was restricted to the peripheral parts of territories where probability of encountering a neighbouring pack was relatively low. In contrast, peripheral overlap between related neighbours was significantly greater. Furthermore, many of the related dyads had overlap between more intensively utilised portions of their territories where the probability of conspecific encounter was far higher. Pack size did not influence the degree of overlap between related packs. In unrelated dyads, however, an effect of pack size was evident and larger packs overlapped more onto the territories of smaller packs.

Our findings are the first detailed study investigating factors effecting territorial overlap in wild dogs. Given the presence of kin-clustering and increased overlap between related packs, inclusive fitness benefits may be extended from the intra-pack to inter-pack level. The findings have direct implications for the management and conservation of the species, specifically in intensively managed populations.

## Paper III

### *Heading for the hills: risk avoidance drives den site selection in African wild dogs*

Habitat selection allows animals to increase their fitness (Thomas & Taylor 2006) and this may be particularly evident when breeding. Reproductive success underpins population persistence and consequently places a strong selective force on mechanisms and strategies which decrease juvenile mortality. Dens are important for successful reproduction in several carnivores (Moehlmann 1989; Smits et al. 1988) and den site location is carefully selected based on factors such as food availability (Pruss 1999; Arjo et al. 2003), shelter from extreme weather (Eide et al. 2001) or predator evasion (Ruggiero et al. 1998; Slough 1999).

Wild dog packs reproduce only once a year and the success thereof has strong effects on pack and population persistence (Malcolm & Martin 1982). Rates of mortality are highest during the first few months of life (Malcolm & Martin 1982) and lions account for a large proportion of pup deaths (Woodroffe & Ginsburg 1999). Packs are based around a den for approximately three months (Malcolm & Martin 1982) but little is known about den site selection. By selecting den sites in habitat with a lower probability of lion encounter, den site selection has the potential to increase reproductive success. Spatial variation in lion densities are largely driven by prey availability which in turn are associated with specific habitat types. Hilly, mountainous and rugged terrain are avoided by lions yet favoured by wild dogs (Mills and Gorman 1997; van Dyk & Slotow 2003). By exploiting such landscapes, wild dogs are able to spatially avoid lions and minimize the risk of potentially fatal encounters.

We hypothesized that rugged terrain should be selected by wild dogs during denning. We assessed the relationship between the distribution of 100 wild dog den sites and the occurrence of rugged terrain in four wild dog populations. A terrain ruggedness index (TRI) was derived and used to map terrain ruggedness within each study area. The characteristics of actual and potential (random) den sites were contrasted in order to determine whether wild dogs select terrain that is more rugged than that which is available on average. Our hypothesis was supported and we found that the distribution of wild dog dens was strongly associated with rugged terrain. The probability of encountering lions is lowest in rugged areas and we postulate that risk avoidance drives den site selection. The presence of rugged terrain may therefore be an important factor affecting wild dog population viability and should therefore be taken into consideration in the species conservation and management. In this regard, the simple analysis used to assess terrain ruggedness may be useful to evaluate habitat suitability, particularly for potential reintroduction projects, across large landscapes.

## Paper IV

### *Living in the lion's den: the role of competition refuges for African wild dog survival in the Serengeti-Mara Ecosystem*

Top predators in terrestrial ecosystems are a highly interactive group of keystone species that can be adversely affected by other guild members (Caro & Stoner 2002; Ritchie & Johnson 2009). Intra-guild dynamics are influenced by processes such as harassment (Creel & Creel 1996), kleptoparasitism (Cooper 1991), intra-guild predation (Palomares & Caro 1999), and avoidance of competing predators (Fuller & Keith 1981). Wild dogs are considerably smaller than their main competitors, lions and spotted hyaenas, and their small size makes them particularly vulnerable to interspecific competition (Carbone et al. 2005). The gradual decline of the Serengeti National Park (SNP) wild dog population, which culminated in their local extinction, occurred concomitantly with a twofold increase in lion densities (Packer et al. 2005) as well as more than a 150% increase in the spotted hyena population (Hofer & East 1995). The lion and hyena densities, however, are not unlike those from other protected areas in Africa in which wild dogs have successfully persisted. Furthermore, wild dogs have persisted elsewhere in the same ecosystem where ecological characteristics were different to the former wild dogs study area. We hypothesized that, in the presence of moderate to high densities of top predators, environmental factors strongly influence the suitability of the SNP to support a viable wild dog population. In particular, a lack of competition refuges (Durant 1998) may expose wild dogs to unsustainably high levels of competition.

We developed a species distribution model (SDM) using occurrence records of wild dogs occurring within the greater Serengeti-Mara ecosystem. Ecological variables documented to drive variation in Serengeti lion densities were included in the SDM. Habitat predicted as highly suitable by the SDM closely matched habitat frequented by two recently reintroduced wild dog packs. The ecological characteristics of highly suitable habitat were identified and, by analysing movement data of the free-ranging packs, we show that these areas represent competition refuges for wild dogs. The SDM indicated the scarcity of competition refuges within SNP, particularly within the former 3000 km<sup>2</sup> study area where wild dogs were studied from 1967 – 1992 (Frame et al. 1979).

Although reported as locally extinct, recent evidence indicates that the wild dog population has in fact persisted. Our results indicate that the most probable ultimate cause of wild dog disappearance involved a range contraction into more suitable habitat following increased levels of interspecific competition. In the presence of interspecific competition, the suitable habitat characterised by rugged terrain provided the wild dog population with respite from competition and have persisted here until present. More than 20 years after their supposed “extinction”, we show that the wild dog study area was located in suboptimal habitat. By restricting research activities to plain-like areas, the surviving component of the population went undetected in the hilly eastern parts of the ecosystem. This study provides a unique insight into spatially explicit factors affecting intra-guild coexistence which are not considered in conservation planning for the endangered African wild dog.

## Paper V

### *Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa*

Identifying and maintaining connectivity between key habitats has become increasingly important in conservation planning (e.g. Wilcove et al. 1998; Fahrig 2003; Cushman 2006). Various techniques are used to assess the degree of connectivity between habitat patches, yet the validity and biological relevance of these methods are debated (Beier et al. 2008; Cushman et al. 2009; Richard & Armstrong 2010; Carroll et al. 2012). Identifying connectivity networks based on empirical observations of dispersing individuals is ideal (Hilty and Merenlender 2004; Graves et al. 2007), yet disperser-specific data is lacking for most species of conservation concern (Fagan & Calabrese 2006). Consequently, models are regularly based on studies of habitat selection by individuals in resident populations, even though dispersers may not require habitat which supports permanent residence.

To evaluate the effectiveness of different methodologies and the potential effect of non-disperser-specific occurrence records, we used a database of African wild dog (*Lycaon pictus*) occurrence records in north-eastern South Africa (n = 576). Ecological niche models (ENM) for wild dogs packs and dispersers were developed and connectivity was also assessed using least cost path (LCP) and current flow models. Model outputs were further validated using occurrence records (n = 339) for cheetah (*Acinonyx jubatus*), another carnivore of conservation concern.

The ENM for resident wild dog packs identified large but isolated patches of suitable habitat, while the disperser model had greater suitability values for areas in between highly suitable patches. When disperser-specific data was excluded, models omitted large areas which were confirmed to have provided connectivity. Modelling techniques using a potentially subjective cost layer have been criticised, but the current flow model outperformed the other connectivity techniques and its predictions are meaningful for conservation planning. Five priority conservation areas for wild dogs were identified based on habitat suitability, proximity and connectivity to source populations, and records of wild dog occurrence.

The general lack of disperser-specific data promotes the use of habitat data recorded from resident individuals in connectivity analyses. The debated shortcomings of these frequently employed techniques are illustrated by our comparative study and their potential effects on conservation management are highlighted. Although assessments of habitat connectivity using current flow methodology require a potentially subjective cost layer, this technique was particularly effective at identifying habitats facilitating connectivity.

## Conclusion and perspectives

In the five papers presented here, my co-authors and I have furthered our understanding of how specific factors affect wild dog habitat selection and ranging behaviour. Firstly, we illustrated how targeted scent mark deployments can potentially be used as a management tool to limit wild dog ranging behaviour. Subsequent to our study, the potential merit of using scent marks as a management tool was also investigated with wolves (*Canis lupis*) and showed similar promise (Ausband et al. 2013). Although we used scent marks in an attempt to repel wild dogs from designated risk-prone areas, they could also be used as an attractant to dispersers. Dispersing groups of wild dogs are capable of travelling hundreds of kilometres, actively searching for mates (Davies-Mostert et al. 2012). In modern landscapes, wild dog populations are often small and fragmented. Dispersing individuals thus have a low probability of finding mates and, while ranging widely in search of mates, they face a high risk of human-induced mortality. If detected, wild dog scent marks deployed in an area otherwise devoid of any chemical cues would signal the apparent presence of a wild dog pack, i.e. potential mates. This prospect is supported by an observation of dispersing wild dogs which closely followed a deployed scent trail, comprised of translocated scent marks, for approximately 30km in the Northern Tuli Game Reserve, Botswana (Jackson et al., unpublished data). When two or more wild dog populations are separated by mixed land uses types, translocated scent marks may have the potential to direct and channel dispersing wild dogs through safer habitat and towards other populations and reduce the mate-finding Allee effect (Somers et al. 2008).

Wild dog packs are highly social and the inclusive fitness benefits afforded to non-breeding pack members has been documented (Malcolm & Marten 1982). Our analysis of factors affecting territorial overlap indicated the importance of relatedness; related packs overlapped considerably, even among frequented areas where the probability of encounter is far higher. These results indicate that inclusive fitness benefits may also arise when related packs occupy territories alongside one another. Pack size is only of significance between unrelated neighbours, where larger packs overlap more onto the territories of smaller packs. Wild dog packs, rather than individuals, are the functional unit of wild dog populations and this natural spacing pattern, with increased overlap, is important to consider in intensively managed populations of the endangered species. These results also indicate that translocated scent marks deployed in an attempt to manage wild dog ranging should not originate from related packs.

Wild dogs' avoidance of lions and hyenas, and the inverse relationship in their densities, has been well documented. There has, however, been a lack of information identifying which habitat characteristics are preferred by wild dogs and, more specifically, what constitutes competition refuges. Since interspecific competition is a major limiting factor for wild dogs, it is somewhat surprising that this relationship has not been investigated thoroughly before. We found that rugged terrain played an important part in the avoidance of dominant carnivores, both during reproduction and general ranging behaviour. Such habitat is not favoured by lions and hyenas and functions as competition refuges.

The importance of competition refuges is illustrated by the work on wild dogs in the Serengeti-Mara ecosystem where, despite reports to the contrary, wild dogs have persisted but only in rugged areas. Our model accurately predicted habitat which provides refuge from competition and illustrated how the former study area, where wild dogs were studied for 25 years, was characterised by low quality habitat. The paper also highlights that, in the presence of competition, a large protected area with an abundance of prey may not necessarily be ideal for wild dog conservation. Although wild dogs are classified as habitat generalists, when confronted with interspecific competition they are by necessity driven to be habitat specialists. Conservation planning should therefore ensure that protected areas incorporate adequate habitat types and heterogeneity such that spatial avoidance of competition is avoided.

In South Africa, a large proportion of the national wild dog population occurs outside of protected areas. We identified the most ecologically viable areas that were well connected to source populations as priority conservation areas. Since these areas are ecologically intact, land use is currently the major limiting the suitability of the areas for wild dog conservation. Land use planning is thus of major importance in conservation planning. The evaluation of habitat connectivity techniques, as well as the use of disperser-specific data provided insights into the field of connectivity analysis. Since connectivity is becoming increasingly important for wildlife populations in general, it is important that the methods used to assess connectivity provide realistic and biologically relevant results. By using occurrence data from resident populations, where habitat requirements need to support permanent residence, we showed that habitat which does in fact provide connectivity for dispersing individuals is not identified as such. The current flow model accurately incorporated both disperser and resident pack records, highlighting the performance and potential merit of this technique in connectivity assessments.

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## PAPER I

## Managing the ranging behaviour of African wild dogs (*Lycaon pictus*) using translocated scent marks

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### Abstract

**Context.** Conflict between large carnivores and livestock outside the boundaries of wildlife areas frequently results in losses to both livestock and predator populations. The endangered African wild dog (*Lycaon pictus* Temminck, 1820) is wide ranging and unrestricted by conventional fences, thereby posing a major challenge to conservation managers. Wild dogs are territorial and communicate residence using scent marks. Simulating the presence of other wild dogs using translocated foreign scent marks may therefore represent a means to manage wild dog ranging behaviour.

**Aims.** To investigate the effectiveness of using targeted scent-mark deployments to signal a wild dog pack to return to their frequented range within the safety of a protected area.

**Methods.** We report on the ranging behaviour of a wild dog pack reintroduced into a wildlife area in Botswana with no recent history of resident wild dogs. We describe daily movements by the free-ranging introduced pack and compare these to moves following targeted deployment of scent marks when the wild dog pack had ranged close to or outside the boundaries of the protected area.

**Key results.** Targeted foreign scent-mark exposure resulted in the pack moving closer to the geometric centre of its range. The mean distance travelled the day after exposure was significantly greater than the distance travelled the previous day and the mean daily distance moved during the study period.

**Conclusions.** Targeted exposure to foreign scent marks proved to be a viable alternative to recapturing dogs that had ranged beyond the boundaries of the wildlife area.

**Implications.** This novel approach to managing free-ranging carnivores utilises biologically relevant signals and holds potential not only for the conservation of African wild dogs, but also for other territorial species.

**Additional keywords:** bioboundary, chemical communication, human–wildlife conflict, scent marking, semiochemical, territoriality.

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### Introduction

Human–wildlife conflict intensifies as human populations expand into areas bordering protected areas. Abrupt transitions in land use at the boundaries of protected areas can have severe consequences for wildlife populations, particularly for large carnivores deemed a threat to livestock and sometimes to humans. The African wild dog (*Lycaon pictus*), one of Africa's most endangered large carnivores (IUCN 2010), exists at low densities even in healthy populations, ranges widely outside protected areas, and is negatively affected by conflict with livestock farmers.

Anthropogenic mortality is the most common source of wild dog mortality in most studied populations (Woodroffe *et al.* 2007). Most protected areas inhabited by wild dogs are unfenced, but even electrified game fences aimed at confining

them are often ineffective. In South Africa, reintroduced wild dog packs escaped from 78% of the nine fully fenced meta-population reserves, constituting the most common problem requiring management intervention (Davies-Mostert *et al.* 2009). Confining socially established packs of wild dogs within a reserve's boundaries is the most important determinant in the success of a reintroduction (Gusset *et al.* 2008). Recapturing escaped wild dogs is both difficult and costly, while the alternative, leaving them to return on their own, can result in livestock losses and extermination of wild dogs by farmers. There is a need for a means of keeping wild dogs inside protected areas that is more effective than conventional or electric fencing.

Wild dog packs are territorial (Mills and Gorman 1997; Parker 2009; Woodroffe 2011) and territories are demarcated with urine

and faecal scent marks that influence neighbouring packs' movements (Parker 2009) and are presumed to communicate territorial residence. Infrequent direct encounters with conspecifics can have fatal consequences (Creel and Creel 2002) and neighbouring territories are thus avoided.

Packs at the edges of protected areas have no neighbours outside the protected area and if the absence of neighbours' scent marks leads them to expand their home ranges into human-dominated landscapes, then using translocated scent marks to create artificial wild dog territory boundaries at the periphery of protected areas may be a means of keeping wild dogs inside protected areas.

In addition, if wild dog packs avoid potentially lethal encounters by moving out of areas where they detect other packs' scent, single exposures to translocated foreign scent marks could be used to move dogs out of areas where their presence is, for whatever reason, undesirable. Here, we report on a test of such an application of translocated scent marks to manage the ranging behaviour of an otherwise free-ranging pack of wild dogs reintroduced into the Northern Tuli Game Reserve, a mostly unfenced private game reserve in eastern Botswana.

## Materials and methods

### Study area

The Northern Tuli Game Reserve (NTGR) in eastern Botswana borders South Africa and Zimbabwe (Fig. 1). The NTGR consists of 720 km<sup>2</sup> of private land formerly used for commercial farming. The western boundary is game fenced, and a poorly maintained fence runs through the southern section (total fence length ~86 km; Fig. 1). Wild dogs and other species of large carnivores including lions and cheetahs frequently move through these fences (C. R. Jackson, pers. obs.). The south-western, eastern and northern boundaries are unfenced (~71 km). There is no recent (past 40 years) evidence

of resident wild dogs in the NTGR before the reintroduction of the pack of 18 dogs that were the subject of the present study. The pack originated from a perimeter-fenced national park in South Africa, from which they had escaped at least 13 times between May 2003 and April 2007 (Davies-Mostert *et al.* 2009). After predation on livestock and the killing of some wild dogs by farmers, the remainder of the pack was recaptured in May 2007 and moved to the NTGR. They were released into the NTGR in April 2008.

### Scent-mark translocations

Naturally voided wild dog urine and faeces were collected from a free-ranging pack in a radio-collared study population in northern Botswana. Collected samples included some substrate soil and vegetation, and each was catalogued, sealed in aluminium foil and frozen. These were transported frozen, then defrosted and redistributed in the NTGR. Targeted scent-mark deployments were performed when GPS fixes, sightings or VHF tracking (below) showed that the pack had ranged close to or outside the NTGR boundary, and into or close to areas where livestock farmers posed a threat. In all, 3–26 (mean = 12) thawed scent marks were distributed at distances ranging between 50 and 200 m from the resting dogs, taking wind strength and direction into account, and without disturbing them from their resting position. Following distribution of scent marks, the wild dogs were observed from a distance and/or located the following day.

### Analysis

Pack locations were acquired from GPS collars or from direct observations using VHF-radio-tracking. During the study period, one to two wild dogs were fitted with GSM-GPS collars (four to six fixes per collar per day) and an additional one to two animals with VHF collars; the number at any given time varied as a result of collar failure, dispersal events or mortalities. Pack size varied between 14 and 28 individuals. The minimum distance moved in 24 h was estimated from the distance between consecutive daily resting locations (DRL), calculated using ArcGIS 9.2 (ESRI, Redlands, CA). Statistics for undisturbed daily distances were calculated from GPS collar data for 408 non-denning days between 28 September 2008 and 28 February 2010 when no darting or scent deployments took place. The annual ~3-month denning period was excluded because the dogs return daily to the den (21 June–27 September 2008 and 9 June–17 September 2009).

To assess the effect of foreign scent marks on the pack's movement patterns, the distances moved after scent-mark deployments were compared with (1) overall undisturbed daily distances and (2) undisturbed daily distances in the 24 h before scent marks were deployed. To test whether human activity near the dogs, rather than the scent marks themselves, could account for the changes in distances moved, we compared distances moved following human disturbance when wild dogs were darted to remove snares or fit radio-collars, a far more invasive form of disturbance, with the undisturbed movements and movements after scent deployments.

Directions of travel in the 24 h following scent-mark deployment were categorised as towards or away from the

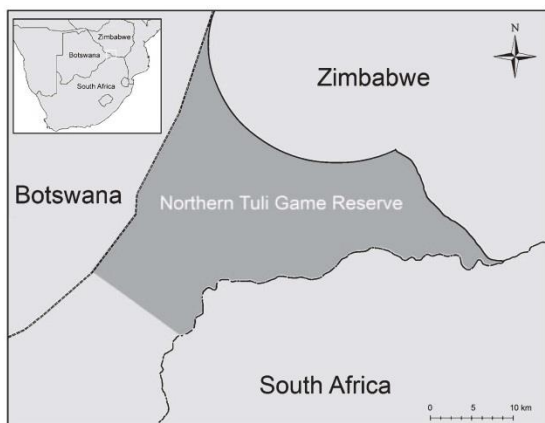


**Fig. 1.** The location of the Northern Tuli Game Reserve (NTGR) in eastern Botswana. A poorly maintained fence runs the length of the border between Botswana and South Africa. A game fence delineates the boundary of the NTGR and Tuli Block to the west (dashed line). There are no fences along the NTGR's boundary with Zimbabwe, or along the reserve's south-western boundary.

geometric centre of the cumulative set of daily resting locations ( $n=408$ ) according to whether the wild dogs' DRLs 24 h after scent deployment were closer to the centre or further from it than their DRLs when scent was deployed. Non-parametric Mann–Whitney rank sum tests were used to analyse distances moved while the direction of movements was analysed using a binomial test. In addition to mean values, median values are provided for each group because of the small sample sizes.

## Results

The wild dog pack was exposed to a targeted deployment of translocated scent marks on 10 occasions. On eight occasions, the focal pack had been ranging in the absence of any fresh foreign scent marks for several days previously. Two additional trials followed a first set of scent marks deployed 24 h earlier. Seven of the eight independent scent-mark deployments were followed by the pack moving closer to the geometric centre of the cumulative locations ( $P=0.035$  binomial, ( $P=0.5$ )). After one trial exposure, the pack moved 4.6 km, but headed away from the geometric centre. They were exposed again 24 h later to another set of scent marks and then moved 6.0 km, with the subsequent DRL closer to the geometric centre. The net effect of the two deployments was to move the dogs 2.3 km closer to the geometric centre.

For all 10 scent-mark deployments, the distance moved in the subsequent 24 h (mean = 7.21 km, median = 6.15 km) was significantly greater than both the distance moved in the preceding 24 h ( $P=0.015$ ; mean = 3.44 km, median = 3.17 km) and the mean daily distance moved throughout the study period ( $P=0.004$ ; mean = 4.05 km, median = 3.69 km), and was greater, although not significantly, than the distances moved 24 h after darting disturbance ( $P=0.058$ ; mean = 3.91 km, median = 3.6 km) (Fig. 2). The greatest daily distance moved during the study period (15.2 km) followed a targeted scent-mark exposure, after the dogs had moved only 2.1 km the previous day.

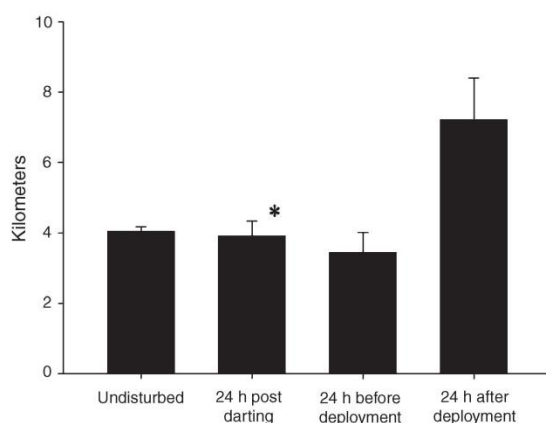


**Fig. 2.** Mean daily distances ( $\pm$ s.e.) moved by the pack of African wild dogs throughout the study period ( $n=408$ ), and comparison of distance before and after being exposed to translocated foreign scent marks during 10 experimental trials. \*Disturbance ( $n=4$ ) does not include denning-season immobilisations ( $n=5$ ), following which distances moved = 0 km.

In contrast to the distances moved following exposure to scent marks, distances moved in the 24 h before scent-mark deployments did not differ significantly from the undisturbed daily distances ( $P=0.720$ , Mann–Whitney rank sum). Disturbance during darting had no effect on distance moved ( $P=0.817$ , Mann–Whitney rank sum) (Fig. 2). When disturbed at the den, wild dogs may move to a new den (Kühme 1965), yet darting during the denning season ( $n=5$ , not included above) did not result in any evidence of disturbance or den relocation (Kühme 1965).

On one occasion, we observed the investigation of foreign scent marks. This occurred just before the first denning period after reintroduction in 2008. Both  $\alpha$  and  $\beta$  females were heavily pregnant and when located 1.9 km outside the NTGR, the pack was resting alongside a freshly excavated warthog burrow that appeared to have been selected as a den. After the wild dogs had moved to a new resting spot ~50 m away, six dominant-pair urine overmarks (the  $\alpha$  pair characteristically urinate on top of one another's faeces and urine) and one faecal sample from a subadult male were placed at the entrance to the burrow. Within 2 min, the first dogs directly approached the scent marks with heads held low, sniffing. Within the following 2–3 min, the rest of pack followed and also investigated the foreign marks. Immediately thereafter, the twittering greeting call (Webster *et al.* 2010) was heard. This was at 1000 hours, when wild dogs typically rest (Fuller and Kat 1990; Woodroffe 2011); however, on this occasion the entire pack moved off. The pack moved 2 km north-west during the subsequent 45 min, heading towards the geometric centre inside the NTGR. The following day, the pack was back inside the reserve (6.8 km from previous DRL), and we deployed a further three urine marks. The pack moved 10.8 km and 2 days after the second deployment the  $\alpha$  female gave birth 23.5 km (straight-line distance) from the initial den site. This observation supports the link between the detection of foreign scent marks and a subsequent behavioural response.

## Discussion

Scent-mark trials with a reintroduced African wild dog pack habituated to human proximity consistently resulted in the pack moving in the direction of their familiar territory inside the protected area in the following 24 h. The mean daily distance moved following scent-mark deployment was almost double the mean daily distance moved when undisturbed. If the effects of scent-mark deployment were due to disturbance *per se* rather than a response to the scent marks, then disturbance due to darting should have had the same effects. In the absence of any such effects, we conclude that the significant differences in both the distance and the direction moved were in response to the translocated scent marks.

The introduced pack's lengthy movements in the direction of the geometric centre of their range are consistent with territorial avoidance of another wild dog pack. To an investigating pack, unfamiliar conspecific scent marks could provide the chemical signal that indicates an imminent threat of an aggressive and potentially fatal inter-pack encounter (Creel and Creel 2002).

From a management perspective, when wild dogs leave protected areas it is usually desirable that they return or be returned as soon as possible. Except on rare occasions when

escaped dogs are still close to the boundary of a protected area (Davies-Mostert *et al.* 2009), recapture has been the only method of recovering a wild dog pack alive once they left their protected wildlife area. Recapturing a free-ranging wild dog pack is difficult and expensive; it often involves a helicopter, a ground support team, veterinarians and several days (English *et al.* 1993). The option to signal wild dogs to return to the relative familiarity of a protected area using translocated foreign scent marks represents a significant advance in management techniques. Translocating scent marks could at the very least serve as a first option in dealing with escaped wild dogs. In addition, scent marks have the potential to displace wild dogs from hostile conflict conditions, such as livestock areas, more rapidly than mobilising a capture team. As a complement to the focussed deployments described here, biologically relevant boundaries, or bioboundaries, produced by distributing scent marks along the borders of wildlife areas to produce artificial territorial boundaries could help reduce losses resulting from conflict between wildlife species and livestock.

The use of olfactory signals has been identified as having management potential for numerous territorial species (see Welsh and Müller-Schwarze 1989; Campbell-Palmer and Rosell 2010), but has very rarely been applied to the conservation of free-ranging wildlife (Linklater 2004). Unlike costly game fencing (Bode and Wintle 2010) and other physical boundaries that have proven ineffective in restraining the free-ranging of wild carnivores, the use of scent marks exploits biologically relevant natural signals that predictably influence their ranging.

The targeted scent-mark deployments described here are the first that we know to have used naturally produced scent marks collected from free-ranging conspecifics. We believe that the use of species-specific semiochemistry for management of free-ranging wildlife merits further investigation with other territorial species.

### Acknowledgements

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## PAPER II

# The effect of relatedness and pack size on territory overlap in African wild dogs

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## Abstract

Spacing patterns mediate competitive interactions between conspecifics, ultimately increasing fitness by reducing costly encounters. Studies of space use in African wild dogs (*Lycaon pictus*) have reported relatively large territories, yet the degree of territorial overlap between neighbouring packs varied greatly in all study areas. Factors potentially affecting the degree of overlap, such as relatedness and pack size, have not been investigated. We used global positioning system (GPS) collar data from 21 wild dog packs to calculate the extent of territory overlap (20 dyads). On average, unrelated neighbouring packs had low levels of territorial overlap which was restricted to the peripheral 95% utilisation kernel regions in all but one dyad (mean overlap = 6.5%). Related neighbours had significantly greater levels of peripheral overlap (mean = 18.5%). Only one unrelated dyad included overlap between 75%-75% kernels, but no 50%-50% kernels overlapped. However, eight of the 12 related dyads overlapped between 75%-75% kernels (mean = 11.5%) and six between the frequented 50%-50% kernels (mean = 6.3%). The probability of encountering a pack in its 50% kernel was 4.93 times greater than in the 95% kernel, and 2.34 times greater than in the 75% kernel. Pack size had little effect on the extent of overlap between related dyads, but among unrelated neighbours, larger packs overlapped more onto the territories of smaller packs. All available evidence suggests that costly intra-specific aggression is greatly reduced between related packs. Consequently, the tendency for dispersing individuals to establish territories alongside relatives, where intensively utilised portions of ranges regularly overlap and result in significantly greater probabilities of encounter, may extend kin selection and inclusive fitness benefits from the intra-pack to inter-pack level. This natural spacing system can affect survival parameters and the carrying capacity of protected areas, having important management implications for intensively managed populations of this endangered species.

**Keywords:** carnivores, home range, kin clustering, philopatry, sex-biased dispersal, social structure, social tolerance, space use patterns

## Introduction

The spacing patterns of groups or individuals result from interactions between conspecifics and their environment and these patterns may vary within and between populations of the same species (Maher & Lott, 1995; White & Harris, 1994). Spacing mediates competitive interactions and is a mechanism that ultimately increases fitness by reducing costs linked to intraspecific encounters (Wilson, 1975). As a result, spacing in vertebrates is typically characterised by a home range, territory and/or core area (Mares et al., 1982). Territorial species attempt to exclude conspecifics from specific areas and these are advertised using auditory, visual or olfactory cues as well as aggressive interactions (Brown & Orrians, 1970). However, even highly territorial species may show some degree of plasticity with regards to the intensity with which core areas are defended, and explanatory factors for such variance have traditionally focused on fluctuations in population density and the availability of mates and resources (Both & Visser, 2000; López-Sepulcre & Kokko, 2005).

Species-specific patterns of natal philopatry and sex-biased dispersal promote distinctive genetic and social population structures. More specifically, patterns of dispersal in which dispersers establish themselves in close proximity to their place of birth result in kin-clustering; neighbouring individuals or groups share certain home range boundaries with close relatives. When potentially competing conspecifics are closely related individuals, tolerance may increase and aggressive territorial defence may be partially or entirely relaxed (Kitchen et al., 2005; Walls & Kenwood, 2001). In kin-selected populations, beneficial interactions among kin occur with sufficient frequency to be selected for, giving rise to cooperative behaviour (Hatchwell, 2010). While studies of inclusive fitness have typically focused on cooperation among related individuals within a group, kin-clustered spatial population organisation provides a mechanism for the evolution of cooperative behaviour between groups (Lambin et al., 2001).

Few studies have documented kin clustering within large carnivore populations (Moyer et al., 2006; Van Horn et al., 2004). The degree of relatedness among Swift foxes (*Vulpes velox*) explained the level of overlap tolerated by neighbouring territory holders; the more closely related neighbours had ranges that overlapped by as much as 54.77% and the highest levels of tolerance, even den sharing (Kitchen et al., 2005). Similarly, the degree of range overlap between adult female raccoons (*Procyon lotor*), brown bears (*Ursus arctos*) and Florida black bears (*Ursus americanus floridanus*) were positively associated with relatedness (Moyer et al., 2006; Ratnayeke, Tuskan & Pelton 2002; Støen et al., 2005).

African wild dog spatial organisation is characterised by packs establishing and defending a relatively large territory, typically ranging from 200 – 700km<sup>2</sup> (Creel & Creel, 2002; Mills & Gorman, 1997; Parker, 2009; Woodroffe, 2011a). Wild dog territories are advertised by urine and faeces which are deposited throughout their ranges and influence conspecific's movement and behaviour (Jackson, Apps & McNutt, 2012; Jordan et al., 2013; Parker, 2009). The degree of territorial overlap, however, varies greatly within populations and ranges from little or no overlap between neighbouring territories to extensive overlap comprising more than 50% in extent (Creel & Creel, 2002; Mills & Gorman, 1997; Woodroffe, 2011a). The underlying reason for this variation is not understood and there is no evidence linking it to prey density or availability (Mills & Gorman, 1997). The extent of wild dog territoriality is questionable given the extensive overlaps (Woodroffe, 2011a), but wild dogs are reasoned to be territorial based on the fact that their large territories result in infrequent encounters with neighbouring packs (Creel & Creel, 2002; Mills & Gorman, 1997; Woodroffe, 2011a). The definition of wild dog territoriality based on this explanation may be justifiable if overlap only occurred between peripheral parts of neighbouring home ranges. However, overlap has also been observed in far smaller “core areas”, the portion of a territory frequented by the resident pack (Creel & Creel, 2002; Woodroffe, 2011a). A disproportionately large amount of time is spent in the 50% contour “core area” which may comprise, on average, only 14% of

the total home range size (Creel & Creel, 2002) thus resulting in a far higher probability of encounter. Consequently, current reasoning does not completely and consistently explain observed patterns of space use and, in particular, extensive multiple-year territorial overlap in wild dog populations thus calling into question their designation as a territorial species.

African wild dogs are obligate cooperative breeders and packs are usually formed between a group of closely related males and an unrelated group of females, who are also closely related to one another (McNutt, 1996a). Reproduction is typically monopolized by the alpha pair and the inclusive fitness benefits afforded to the non-breeding helpers have been well documented (e.g. Malcolm & Marten, 1982). The high degree of relatedness between adults and offspring is hypothesised to provide the kin-selected mechanism facilitating such cooperation. Dispersing wild dogs tend to establish territories bordering natal packs and thus kin-clustering occurs within the population (Girman et al., 1997; McNutt, 1996a). As a result, some neighbouring packs would be closely related providing the potential for comparatively amicable inter-pack behaviour to arise. However, group size may be an important determinant in contests between social carnivores (McComb, Packer & Pusey, 1994). Wild dog pack sizes vary considerably (Creel & Creel, 2002) and may thus be a particularly important factor affecting the extent of territorial overlap.

Relatedness and pack size have never specifically been taken into account in studies documenting space use and territorial overlap in African wild dogs. Here we investigate how variations in territorial overlap may be explained by kin relatedness and group size between neighbouring packs.

## **Materials and methods**

### *Study areas*

We used data from two long-term wild dog research projects in southern Africa. The first population is located in Botswana's Moremi Game Reserve (Botswana population), at the eastern end of the Okavango Delta, and has been studied continuously since 1989. The second population is located in the Savé Valley Conservancy (SVC) in south eastern Zimbabwe (Zimbabwe population) and has been studied since 1996. Both study areas are semi-arid African savanna ecosystems largely dominated by mopane (*Colophospermum mopane*) shrub or woodland. The study area of the Botswana population (ca. 2600 km<sup>2</sup>; 19°31'S, 23°37'E; elevation ca. 950 m) is bordered by the Okavango Delta and includes the Moremi Game Reserve and Wildlife Management Areas. Further details can be found in McNutt (1996a). The study area of the Zimbabwe population (ca. 3340 km<sup>2</sup>; 20°36'S, 32°16'E; elevation ca. 600m) lies in the semi-arid south east of Zimbabwe, just north of the Gonarezhou National Park. Further details can be found in Lindsay et al (2008). The SVC supports between 10-12 packs of wild dogs each year.

### *Ethical note*

Packs were radiotracked from the air and/or from a vehicle, with one to four individuals in each pack fitted with GPS radiocollars with a VHF tracking pinger (Botswana: Vectronic Aerospace GmbH, Berlin, Germany, <280 g, 8 packs; Televilt TVP Positioning AB, Lindesberg, Sweden, <300 g, 4 packs; Zimbabwe: African Wildlife Tracking, Pretoria, South Africa, <640 g, 9 packs). Collar weights represented 0.6-1.16% of body weight for the Botswana population (based on weights in Smithers, 1983) while in Zimbabwe they were on average ca. 2.6% of collared animals' body weight. To fit collars, wild dogs were darted from a vehicle. Wild dogs in Botswana were darted using Telinect darting equipment (Telinect U.S.A., Inc., Agua Dulce, CA, USA), at a distance of less than 15m, with a mixture of ketamine HCl with xylazine and atropine (Osofsky et al., 1996). Animals in Zimbabwe were immobilized using Daninject equipment, darted at a distance <25m, with a mixture of ketamine and metatomidine. Reversal from anaesthesia in both study areas was achieved using yohimbine. Dosages were based on the weights of wild dogs

provided in Smithers (1983) and adjusted based on visual estimates of individual animal's body size. Immobilized animals were placed in shaded areas and, if required, cooled with water. Heart rates and temperatures were monitored throughout the 30-40min procedure during which collars were fitted. Wild dogs recovered fully from immobilization after ca. 1.5 hours and all individuals successfully rejoined their packs. Individuals were reimmobilized upon the expiry of radiocollars, which were either replaced or removed. As reported from other studies on African wild dogs (Woodroffe, 2001), we did not observe any negative effects from either the wearing of radiocollars or immobilisation procedures. Research was conducted under permit from the Botswana Department of Wildlife and National Parks as well as the Research Council of Zimbabwe and the Zimbabwe Parks and Wildlife Management Authority.

#### *Defining relatedness*

Wild dogs are individually identifiable using their unique tri-colour coat patterns. The long-term monitoring of both study populations included photographic records of each individual, as well as of dispersal and pack formation, and as a result pedigree data is available for a large proportion of the study packs. In this study, a pack was defined as a group containing at least one adult male and female forming a potential reproductive unit (cf. McNutt, 1996a; Malcolm, 1979). The mother of each litter was therefore easily identified, and she was the only female to nurse the pups. Using these criteria, mothers were known for all pups born during the current study. Importantly, immigration events leading to the formation of the packs followed in this study involved either unknown (and therefore not closely related) individuals from outside the study population or individuals of known origin that were not closely related to the opposite sex residents of the pack into which they immigrated. On the basis of these pedigree data, relatedness between packs was determined. As we did not conduct genetic analyses, we only considered female-based relatedness between neighbouring packs. Consequently, exact paternal relationships were irrelevant to the aims of this study. Familiarity, in addition to actual or perceived relatedness, is expected to be the underlying mechanism of inbreeding avoidance, and this is accounted for by the pedigree data.

Packs were defined as related when the alpha female in a given pack was the mother, daughter or sister to either of the dominant pair in a neighbouring pack. Since females are the more philopatric sex (McNutt, 1996a), the relationships between alpha females of neighbouring packs are of particular importance. If relatedness between two neighbouring packs was uncertain, they were excluded from analyses. Data from a total of 21 wild dog packs and 20 dyads (Botswana = 13 packs and 12 dyads; Zimbabwe = 8 packs and 8 dyads) were included in analyses described hereunder.

#### *Determination of home ranges and overlap*

Each pack was fitted with a minimum of one global positioning system (GPS) collar from which movement data was acquired. The number and times of daily GPS fixes varied between different periods and study areas. Wild dogs are active during the early morning and again during the late afternoon and early evening. To standardize methodology as far as possible yet still capture movement patterns, we selected two GPS locations per day. The first reading was taken during the early morning (05:00, 06:00 or 06:30) and the second location 12hours thereafter. Wild dogs spend approximately three months at a den each year. Annual denning periods were excluded from home range analyses to avoid introducing a spatial bias, as ranges are constricted to approximately 25% of annual ranges during this period (Pomilia et al., Submitted). Data used in analyses was collected from 2002 - 2003 and 2008 – 2012 in Botswana and during 2009 – 2013 in Zimbabwe.

Wild dog home ranges were evaluated using kernel density contours which allows different levels of spatial utilisation to be assessed (Seaman & Powell, 1996). The two daily GPS records were used to determine 95%, 75% and 50% utilisation contours. Ranges8 (version 2.8; Anatrack Ltd) was used to

calculate utilisation contours with default parameters selected for contour determination (“location density”), smoothing multiplier (“fixed multiplier” (1)), and matrix rescaling (“rescale to fit matrix”). The reference smoothing parameter (hRef), calculated from the standard deviation of rescaled x and y coordinates divided by the sixth root of the number of locations, was used in the kernel analysis.

Home ranges are dynamic and fluctuate over time. Using too short a time period for the assessment of overlap will result in an underestimation of home range size, while extensive durations may obscure temporal shifts in range boundaries and hence overlap between neighbours. Consequently, a four month period, excluding denning periods, was available and used for 20 of the 21 packs. Due to a lack of data for a single pack, which was bordered by one related and one unrelated pack, a two month time period was used.

Overlap between two neighbouring packs’ respective 95%, 75% and 50% contours were calculated using the overlap analysis function in Ranges8 (version 2.8; Anatrack Ltd). The pairwise overlap analysis calculates the extent that Pack A overlaps onto Pack B’s specific utilisation contour, as well as the extent that Pack B overlaps onto Pack A’s corresponding contour. The pack-specific overlap thus results in two values for each overlapping contour (Walls & Kenwood, 2001). The degree of overlap is expressed as the percentage of the focal pack’s total contour area overlapped by the neighbouring pack. Alternative methods of overlap calculation use the size of the overlapping area as well as the sum of the home range size for each of the two individuals or groups to derive a single overlap coefficient per dyad (Ratnayeke et al., 2002; Støen et al., 2005; Walls & Kenwood, 2001). While this single value has been found to be similar to the two values per dyad (Walls & Kenwood, 2001), it is dependent on the home range sizes of each member of a dyad. Since home range size varied greatly in our study, we chose to use the two separate values and not approximate a single overlap value for each dyad. This is likely to be the more biologically relevant value, as it more accurately reflects the degree and therefore potential ‘cost’ of overlap for each individual pack.

#### *Probability of encounter*

Since a disproportionately large proportion of a wild dog pack’s time is spent in the smaller core areas, an overlap of 10%, for example, between two packs’ 95%-95%, 75%-75% or 50%-50% kernels does not confer the same likelihood of encounter and is therefore also an important consideration. The 12 hourly GPS data and associated 50%, 75% and 95% kernel density estimator contours (described above) were used to derive a measure of the probability of encountering a neighbouring pack in any of its three defined kernels. For this purpose, the size of the each contour was calculated and the size of any smaller contours subtracted therefrom, to reveal the size of the specified contour alone (i.e. the size of the 75% kernel is subtracted from the 95% kernel and the 50% kernel is subtracted from the 75% kernel to reveal the 95% and 75% kernels, respectively). The number of GPS locations occurring within each of the exclusive kernels was then calculated and divided by the total number of GPS locations, thereby providing a percentage of total time spent in each of the three specified kernels. To account for the variations in the size of the three kernels, the percentage of total time was then divided by the size (km<sup>2</sup>) of each specific contour. By relating the proportion of total time spent in each contour with the size thereof, a comparative assessment of potential encounter rates in the three contours is facilitated.

#### *Identifying factors affecting the extent of overlap*

To investigate the factors affecting the percentage of a pack’s territory that overlapped with its neighbour, we ran a series of linear mixed effects models (LMEs) in the package ‘R’ (R Development Core Team, 2013). We included the identity of the focal pack as a random term to account for repeated measures. We used Akaike’s information criterion (AIC) to select the most plausible model from a set of credible options. A full model set was generated using the function ‘dredge’ in the MuMIn package

(Bartoń, 2012). Terms included in the models were relatedness (related or unrelated), pack-size ratio (the number of individuals in the focal pack [including all adults, yearlings and pups] divided by the number of individuals in the overlapped pack), and their two-way interaction. As the Akaike weight of the best model was  $<0.9$  and several models had deviance in the AIC lower than 7 units (Burnham et al., 2011; Grueber, 2011), we conducted model averaging using the MuMIn package (Bartoń, 2012). We selected the top models whose cumulative AIC weights were  $>0.95$  to construct model-averaged estimates of the parameters (Grueber, 2011).

## Results

### Range overlap

For related neighbours, mean overlap between 95% kernels was 18.54% ( $N = 24$ ; median + SD = 14.49%; SD = 12.4; range: 2.72 – 56.26%), whilst for unrelated neighbours it was 6.51% ( $n = 16$ ; median = 0.995%; SD = 10.65; range: 0.0058 – 36.7) (Fig. 1), a highly significant difference (Mann-Whitney Rank Sum Test;  $U = 66.0$ ;  $P < 0.001$ ).

Overlap between neighbouring packs' more intensively utilised 50% and 75% contours (i.e. overlap between 50%-50% and between 75%-75% contours) indicated that while only a single unrelated dyad overlapped between their respective 75% contours (5.1% and 13.63%), 8 of 12 related dyads overlapped between these kernels with a mean of 11.52% ( $n = 16$ ; median = 8.75; SD = 10.44; range: 0.22 – 37.59). Only related neighbours overlapped between their respective 50% contours (6 of 12), with a mean value of 6.31% ( $n = 12$ ; median = 6.25%; SD = 5.83; range: 0.103 – 17.74).

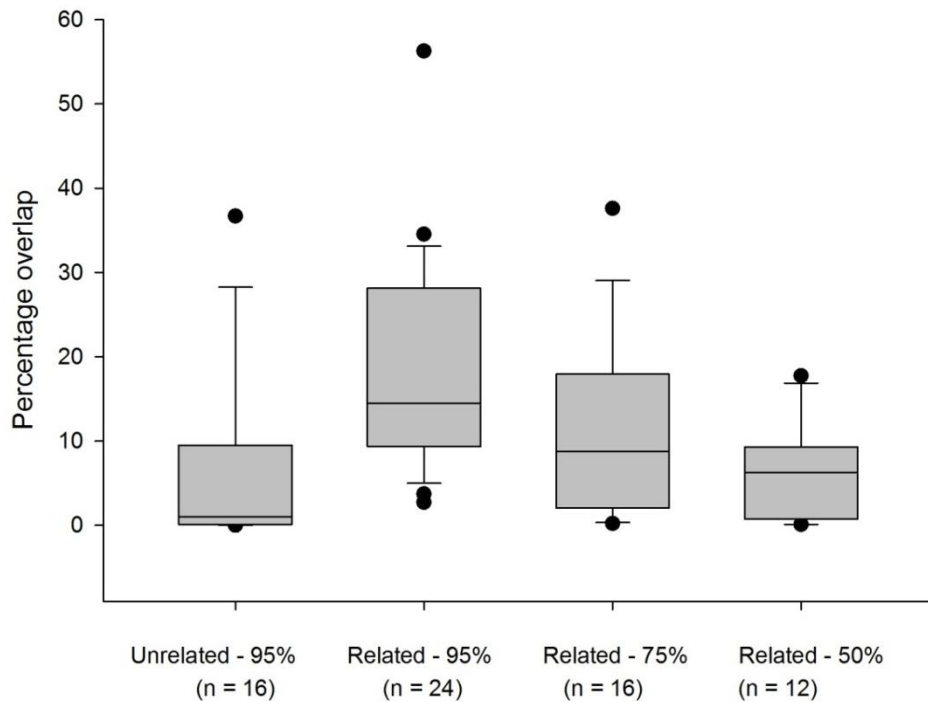


**Figure 1.** The extent of territorial overlap between neighbouring wild dog packs. Kernel density estimates of packs' 50%, 75% and 95% utilisation areas were determined and the extent of overlap determined for all dyads. Only one unrelated dyad overlapped between 75% contours and is therefore not shown, while no unrelated dyads overlapped between 50% kernels.

### *Probability of encounter*

An ANOVA indicated a significant difference between the values associated with each of the three kernel types ( $H = 26.5$ ,  $df = 2$ ,  $P = <0.001$ ). The pairwise multiple comparison procedure using the Turkey Test method revealed that each of the three groups were significantly different from one another ( $P = <0.05$ ). With a mean of 0.482 (SD = 0.351), the mean probability of encounter in the 50% kernel was 4.93 times greater than within the 95% contour (mean = 0.0976; SD = 0.061) and 2.34 times greater than within the 75% kernel (mean = 0.206; SD = 0.156; see Fig. 2).

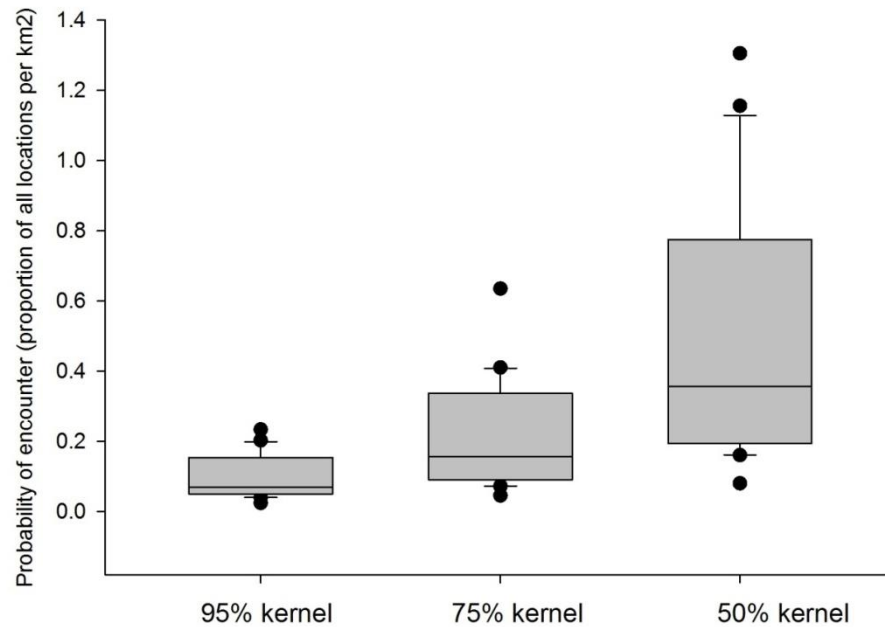


**Figure 2.** Estimated encounter probabilities within different home range density kernels. The proportion of GPS locations occurring in each of the three kernel density classes, indicating the proportion of time spent in each, were calculated for each pack ( $n = 20$ ) and divided by the size of the respective kernels ( $\text{km}^2$ ). The distribution and density of these records indicate that the mean probability of encountering a pack in its 50% kernel is 4.93 times greater than within its 95% kernel, and 2.34 times greater than the 75% contour.

### *Linear mixed effects model*

The mixed effects model revealed an interaction between relatedness and pack-size ratio (Tables 1 and 2). In unrelated dyads, an increase in pack-size ratio results in an increase in overlap; i.e. larger packs overlap more on smaller packs. In contrast, however, pack-size ratio has little effect between related packs and the predicted extent of overlap is relatively consistent (Fig. 3).

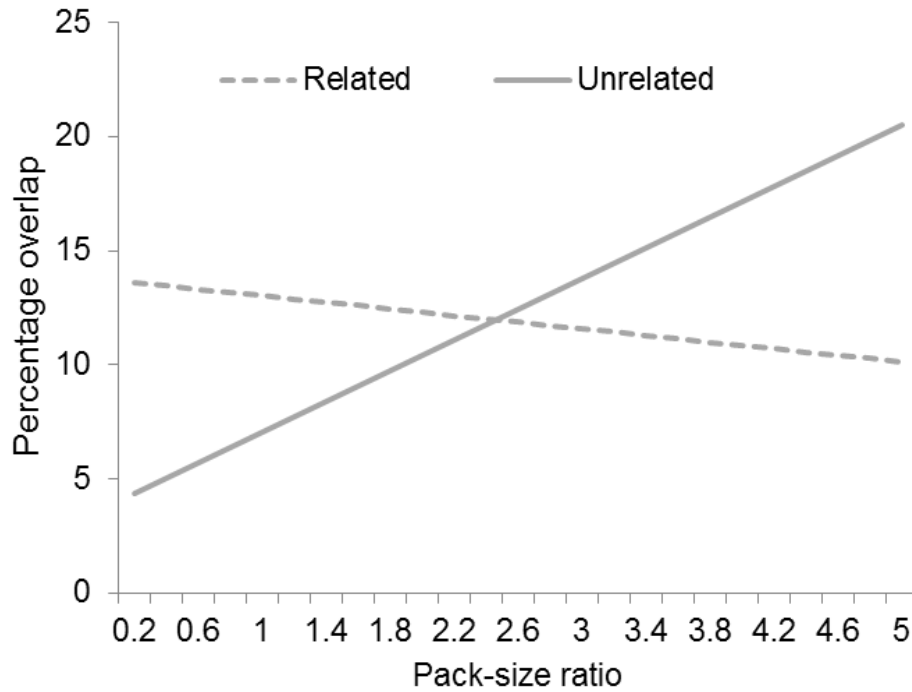


**Figure 3.** The effect of the interaction between relatedness and pack size ratio on the percentage of a pack's range that overlaps with that of a neighbouring pack (N=40). The range shown is identical to the analysed dataset.

**Table 1.** Linear Mixed Effects models investigating the factors affecting the percentage of a pack's range that overlaps with that of a neighbouring pack (N=40).

| Model | Description                                                   | k | AICc     | $\Delta_i$ | W <sub>i</sub> |
|-------|---------------------------------------------------------------|---|----------|------------|----------------|
| Basic | (Intercept)                                                   | 3 | 314.8167 |            |                |
| 1     | Pack-size ratio + Relatedness + Pack-size ratio * Relatedness | 6 | 305.02   | 0          | 0.62           |
| 2     | Pack-size ratio + Relatedness                                 | 5 | 306.04   | 1.02       | 0.38           |

Focal pack identity (N=19) was included as a random term. k = parameters,  $\Delta_i$  = AICc<sub>i</sub> - AICc<sub>min</sub>, w<sub>i</sub> = Akaike weights.

**Table 2.** Effects of each parameter from Table 1 on the percentage of a pack's range that overlaps with that of a neighbouring pack (N=40).

| Parameter                                            | Estimate | Std. Error | CI (2.5-97.5%) | Relative importance |
|------------------------------------------------------|----------|------------|----------------|---------------------|
| (Intercept)                                          | 3.7046   | 4.2076     | -5.125, 12.534 |                     |
| Pack-size ratio                                      | 2.3615   | 1.7261     | -1.261, 5.984  | 1                   |
| Relatedness (related) <sup>1</sup>                   | 10.0487  | 4.9649     | -0.373, 20.470 | 1                   |
| Pack-size ratio * relatedness (related) <sup>1</sup> | -0.2034  | 2.6753     | -5.824, 5.417  | 0.62                |

<sup>1</sup>unrelated was the reference category.

## Discussion

To date, studies of wild dog ranging behaviour have reported highly variable levels of territorial overlap (Creel & Creel, 2002; Mills & Gorman, 1997; Woodroffe, 2011a), which was also the case in our study. Factors affecting these large intra-population variations have previously not been investigated, most likely due to a lack of suitable data. Detailed multi-generation pedigree and ranging data are rare for wild dog populations, and while our sample sizes are relatively modest, they provide a unique insight into the spatial organisation of wild dog populations and the specific role of relatedness and pack size.

Our data indicate a strong positive relationship between the degree of territorial overlap between neighbouring packs and their relatedness to one another. Since the increased overlap and heightened probability of encounter is most likely facilitated by greater levels of mutual tolerance, kin facilitation (Hamilton, 1964) may be an important factor in the social ecology and space use patterns in African wild dog populations. The presence of related neighbouring packs is consistent with sex-biased dispersal where females are the more philopatric sex (McNutt, 1996a) and our results emphasise the matrilineal pattern of social organisation within African wild dog populations.

Although documented in other species (Moyer et al., 2006; Ratnayeke et al., 2002; Støen et al., 2005), studies of African wild dog ranging behaviour have never considered a flexible pattern of territorial space use based on relatedness. While peripheral overlap between related packs was nearly three times greater than unrelated dyads in this study, the stark contrast between overlap in the 50% and 75% contours of related and unrelated dyads is of particular importance. Since the probability of encountering a neighbouring pack within its 50% kernel is roughly five times greater than the 95% kernel, our data illustrate that unrelated neighbours avoid these areas entirely while more than half the related neighbours overlapped. Furthermore, more than 70% of related dyads overlapped between their 75% kernels where the likelihood of encounter is more than double that of the 95% kernel.

Our findings are further supported by data from other populations, such as a comprehensive study in the Selous Game Reserve, Tanzania (Creel & Creel, 2002). The maximum overlap between two core areas was 12% (derived from minimum convex polygons, not kernel density estimates), while the mean overlap between cores was only 0.5%. This extreme overlap occurred between two related packs (Creel & Creel, 2002), which provides strong evidence for the female link to space use and territorial overlap. Females typically establish territories closer to the natal pack (McNutt, 1996a) thereby promoting this 'budding' pattern of dispersal which is common in mammals (e.g. banded mongooses, Nichols et al., 2012). Furthermore, genetic work by Girman et al. (1997) indicated that dispersers frequently move into areas occupied by a high proportion of close relatives which would promote territory formation alongside kin. But why would dispersers preferentially move into areas with close kin?

Since relatives share a relatively high proportion of their genes, they are predicted to behave relatively more altruistically and less aggressively towards relatives (Hamilton, 1964). This process of kin selection can operate at low levels of relatedness where less apparent forms of cooperation, such as increased tolerance, are important (Wolf & Trillmich, 2008). Having close relatives as neighbours would facilitate the possibility that kin selection could be extended from the intra-pack to inter-pack, or population, level. Wild dogs are obligate co-operators with packs working cooperating during hunting (Creel & Creel, 1995), defence of kills (Carbone et al., 1997) and guarding young (Malcolm & Marten, 1982). Consequently, larger wild dog packs are more successful and raise a greater number of offspring (Creel et al., 1998; Malcolm & Marten, 1982; McNutt & Silk, 2008; Woodroffe 2011(b)). Intra-specific competition can result in high rates of mortality (Creel & Creel, 1998; 2002) thereby reducing a pack's fitness through reduced numbers of cooperative pack members. Tolerance of conspecifics may

therefore be positively related to the degree of kinship as in other species (e.g. the swift fox; Kitchen et al., 2005; though see McNutt, 1996b, and McNutt et al., 2008). Based on our results indicating a consistent positive relationship between relatedness and the degree of territorial overlap and associated probability of encounter, we hypothesise that this is mediated by kin-related tolerance. The indirect benefits accrued from residing in kin clusters may therefore be of fundamental importance and drive patterns of space use in African wild dog populations, as in other species (Moyer et al., 2006; Ratnayeke et al., 2002; Støen et al., 2005).

Our results also provide the first insight into the role of pack size in territorial overlap. Although levels of overlap were on average far lower between unrelated dyads, pack size was positively related to the degree of overlap, while having little influence on overlap between related packs. Larger packs tend therefore to overlap more onto smaller unrelated neighbours. Pack size may therefore not only be positively related to hunting efficiency, defence of kills, and pup guarding (discussed above), but may also influence a pack's intraspecific competitive abilities. In the presence of unrelated neighbours, larger packs may therefore range more widely. This is supported by observations of direct encounters between neighbouring wild dog packs in Selous Game Reserve, which resulted in the smaller pack being attacked and pursued by the larger pack in 11 of 13 instances (Creel & Creel, 2002).

#### *Management and conservation implications*

With relatively few large protected areas supporting wild dog populations, conservation efforts often need to focus on small protected areas. South Africa's meta-population, for example, has wild dog packs scattered across the country in several relatively small game reserves. Populations are managed intensively, particularly since natural levels of immigration are not adequate to sustain the geographically isolated populations, and periodic translocations are required (Mills et al., 1998). Current management of translocations actively avoid establishing new packs that have any close genetic links to existing meta-population packs within a given region. While based on important population genetic considerations, these management actions will negate the possible formation of natural space use patterns. In addition to potential effects on fitness and ultimately population viability, population densities could potentially be higher when neighbouring packs form through the natural process of female budding.

Hluhluwe-iMfolozi Game Reserve is a relatively small (900km<sup>2</sup>) meta-population reserve. Based on its size and the average wild dog home range size, it was reasoned that the reserve could support, at most, two to three packs (Maddock, 1999). After supporting only one to two packs for 20 years, the number grew to nine packs within eight years (Somers et al., 2008). Surprisingly, the sharp population increase followed a population crash between 1998 and 2000, when 83% (33/40) of the wild dogs disappeared, culminating in the fission of all three packs. The only remaining pack subsequently comprised only two wild dogs. Importantly, however, this pack persisted. With a few additional animals added to the reserve (two in 2001, eight in 2003), the rapid increase in the number of new packs is likely to have resulted in several related individuals in neighbouring packs. Indeed, Somers et al., (2008) state that three recorded dispersal events, all females, resulted in three new packs (up to 2004 only). These females joined unrelated males and neighbouring packs were thus related. The related packs would be expected to be more tolerant of one another and accommodate extensive spatial overlap, facilitating higher densities. By the end of 2009 the reserve supported 69 adult wild dogs per 1000km<sup>2</sup>, the highest recorded wild dog density (see review in Creel & Creel 2002; WAG minutes 26 November 2009), with the total population size being roughly equal to the population inhabiting the 20 000km<sup>2</sup> Kruger National Park (WAG minutes 26 November 2009).

Our hypothesis that closely related packs may result in higher wild dog population densities, is further supported by a study of a recovering free-ranging wild dog population in Kenya. Woodroffe (2011a) reported that as wild dog densities tripled over a nine year period, territory sizes remained the same, but the degree of overlap increased. Since wild dogs often settle in areas with a high proportion of close relatives (Girman et al., 1997), it is probable that the increased levels of overlap occurred between related packs.

Our results, in combination with the supporting evidence provided by the case studies, emphasize that managers of small wild dog populations should carefully consider the kin-related social population structure observed in free-ranging populations. These spacing patterns have the potential to affect population densities within protected areas and intra-specific rates of mortality. These factors are of great importance since they have direct implications for the number of animals that can be conserved within each protected area as well the local population viability of the endangered carnivore. While this may raise concerns about the genetic diversity of populations, it is only the females that need to be closely related between packs, as is the case in free ranging populations.

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## PAPER III

# Heading for the hills: risk avoidance drives den site selection in African wild dogs

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## Abstract

Compared to their main competitors, African wild dogs (*Lycaon pictus*) have inferior competitive abilities and interspecific competition is a serious fitness-limiting factor. Lions (*Panthera leo*) are the dominant large carnivore in African savanna ecosystems and wild dogs avoid them both spatially and temporally. Wild dog young are particularly vulnerable and suffer high rates of mortality from lions. Since lions do not utilize all parts of the landscape with an equal intensity, spatial variation in lion densities can be exploited by wild dogs both during their general ranging behaviour, but more specifically when they are confined to a den with vulnerable young. Since patches of rugged terrain are associated with lower lion densities, we hypothesized that these comparatively safe habitats should be selected by wild dog for denning. We investigated the relationship between the distribution of 100 wild dog den sites and the occurrence of rugged terrain in four wild dog populations located in Tanzania, Zimbabwe and South Africa. A terrain ruggedness index (TRI) was derived from a 90m digital elevation model and used to map terrain ruggedness at each site. We compared characteristics of actual and potential (random) den sites to determine how wild dogs select den sites. The distributions of wild dog dens were strongly associated with rugged terrain and wild dogs actively selected terrain that was more rugged than that available on average. The likelihood of encountering lions is reduced in these habitats, minimizing the risk to both adults and pups. Our findings have important implications for the conservation management of the species, especially when assessing habitat suitability for potential reintroductions. The simple technique used to assess terrain ruggedness may be useful to investigate habitat suitability, and even predict highly suitable denning areas, across large landscapes.

## Introduction

Habitat selection allows animals to select specific habitat attributes which allow them to increase their fitness (Thomas & Taylor 2006). This behavioural process may be particularly evident during the breeding season. Since reproductive success is vital for population persistence, it places a strong selective force on mechanisms and strategies to optimize the survival of young. Many mammalian carnivores require a den to successfully rear offspring (Moehlmann 1989; Smits et al. 1988). The location of den sites are therefore not randomly dispersed across a landscape but are instead often selected based on factors such as food availability (Pruss 1999; Arjo et al. 2003), shelter from extreme weather (Eide et al. 2001) or predator evasion (Ruggiero et al. 1998; Slough 1999).

Endangered African wild dogs (*Lycaon pictus*) live in highly social packs which cooperate to feed and protect the dominant alpha pair's offspring (Malcolm & Martin 1982). Wild dog packs reproduce once a year and spend approximately three months at a den before pups become mobile (Malcolm & Martin 1982). Larger packs are generally more reproductively successful than smaller ones and this is attributed to a greater hunting efficiency and defence of young and kills (Creel & Creel 1995; Courchamp & Macdonald 2001). The annual reproductive event is thus a vital component of wild dog ecology that strongly influences pack survival and population persistence.

Among the large African carnivores, wild dogs are far smaller than their main competitors, lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Creel & Creel 2002). Lions account for as much as 43% of wild dog mortality, 31% of which are pups (Woodroffe & Ginsburg 1999). Although hyenas steal wild dog kills (Carbone et al. 1997), they account for only 4% of adult and 6% of pup mortality (Woodroffe & Ginsberg 1999). Lions impose a far greater risk to wild dogs and are avoided whenever they are encountered or detected (Webster et al. 2012). Although wild dogs can rapidly cover large distances (spatial avoidance), this mechanism facilitating coexistence is negated during the denning period when packs are confined to den sites. Wild dog mortality rates are highest during the first few months of life (Malcolm & Martin 1982) and den site selection is thus an important driver of reproductive success.

Lion densities differ in space and as the dominant large carnivore their densities are positively correlated to prey density (Mills & Gorman 1997). Certain landscape features may therefore not be favoured by lions due to a lower abundance of preferred prey species (e.g. Mizutani 1999) or where topographical and vegetation characteristics make hunting more challenging for the ambush predators (van Dyk & Slotow 2003; Hopcraft et al. 2005). This causes a heterogeneous risk landscape allowing wild dogs to behaviourally mediate the risk of interspecific encounters by the selection of lower risk habitats. Consequently, wild dog densities tend to be inversely correlated to those of lions (Mills & Gorman 1997).

Variations in the two species' densities are strongly associated with specific habitat types. For example, in the Kruger National Park, South Africa, important prey species for lion, such as buffalo (*Syncerus caffer*), are associated with open savanna landscapes (Mills & Gorman 1997). These prey-rich landscape types were the most preferred habitat types for lions (Mills & Gorman 1997). In contrast, lions avoided hilly and mountainous terrain which were significantly more preferred by wild dogs and ranked as wild

dogs' most preferred habitat types (Mills & Gorman 1997). Not only were these rugged habitat types ranked as the least preferred by lions, but also by spotted hyenas (Mills & Gorman 1997). Patches of rugged terrain in the form of hills, ridges or inselbergs thus have the potential to provide wild dog populations with respite from interspecific competition (van Dyk & Slotow 2003).

Given the variation in risk based on habitat types, we hypothesized that wild dogs actively select rugged habitat for denning as part of their risk avoidance strategy. We tested our hypothesis with den site location data from four wild dog populations located in Tanzania, Zimbabwe and South Africa. Selected habitat features are those utilised disproportionately more often than their general availability (Manly et al. 2002). To assess whether wild dogs actively select rugged terrain in which to den, we created three random contrast locations per den site, located within the same study area. These locations provide an indication of available but unutilised habitat. Factors influencing den site selection are well studied in other large canids such as wolves (for e.g. Theuerkauf et al. 2003; Trapp et al. 2008; Kaartinen et al. 2010) but, excepting for a single recent study on wild dogs (van der Meer et al. 2013), are entirely lacking for the species. More specifically, the potential role of rugged terrain for successful reproduction in African wild dog populations has never been considered before and is of potential importance for the conservation management of this endangered carnivore.

## Methods

### *Study areas*

We used wild dog den site locations from four different ecosystems. The Loliondo Game Controlled Area (LGCA) is situated within the eastern part of the Serengeti Ecosystem in northern Tanzania and is bordered to the west by Serengeti National Park. The area is 4000 km<sup>2</sup> in size with a population of approximately 130 wild dogs in 8 – 10 packs (Masenga 2011). A large part of the LGCA landscape is undulating and hilly. Vegetation types vary greatly within LGCA and range from open woodland to short grass plains. Dominant species include *Acacia drepanolobium* on black cotton soils, high altitude forests of *Juniperus procera*, while the long grass plains are characterised by *Acacia gerardii*, *Rhus natalensis*, *Euclea divinorum*, and *Acacia hockii* tree species (Homewood et al., 2001).

The 3450 km<sup>2</sup> Savé Valley Conservancy (SVC) is situated in the semi-arid south-east of Zimbabwe and is largely dominated by mopane (*Colophospermum mopane*) shrub or woodland. There are at least 11 known wild dog packs in the SVC, totalling approximately 110 adult and yearling wild dogs. The wild dog population has been studied in the SVC since 1996.

Venetia Limpopo Nature Reserve (VLNR) is a 316 km<sup>2</sup> privately owned reserve located in Limpopo Province in the north of South Africa. The reserve is low-lying with a semi-arid climate and falls within the Limpopo rugged bushveld and Musina Mopane bushveld vegetation types of the savanna biome (Mucina & Rutherford 2006). The naturally occurring lion population remained relatively stable (~18 individuals) during the period of this study. A reintroduced population of wild dogs fluctuated between 11-27 individuals. The reserve is enclosed by 'predator-proof' electrified perimeter fencing.

The fourth study area, which fluctuated between 5 and 56 individuals in 1 - 6 wild dog packs, was located in Madikwe Game Reserve (MGR). The 620 km<sup>2</sup> protected area is situated in the semi-arid north-

west region of South Africa. It is located within the savanna biome and vegetation types are classified as Dwarsberg-Swartruggens Mountain Bushveld, Madikwe Dolomite Bushveld and Dwaalboom Thornveld (Mucina & Rutherford 2006).

#### *Den site location records*

Wild dogs often shift the location of their den during the course of the denning period. We only used the first den site locations each season, as this is selected prior to the birth of offspring. Selection of secondary den sites would be limited to some degree by the young pups which would often need to be carried by adults, thus potentially limiting the distance from the initial location. A total of 19 den sites (2005-2009) were used for LGCA, 57 den sites for SVC (2005-2013), 6 den sites for VLNR (2002-2007) and 18 den sites in MGR (1998 – 2013).

#### *Random contrast location*

To determine the extent of variation in terrain ruggedness and the types of habitat available to wild dog packs within each study area, three random locations were generated per known den site in ArcMap (ESRI, Redlands, CA, USA). Movement data (not shown) indicated that the vast majority of each study area was traversed by wild dog packs outside of the denning period. Thus the majority of study areas were theoretically available for denning, although at a finer scale suitable den sites would be required. Packs typically use burrows excavated by warthog *Phacochoerus africanus*, aardvark *Orycteropus afer* or other partly fossorial mammals (Creel & Creel 2002), or caves and crevices in rocky areas (van Dyk & Slotow 2003).

#### *Terrain ruggedness index*

To assess the distribution of rugged terrain we used a 90 m digital elevation model (DEM). A spatial filter was applied to determine the standard deviation around each focal grid cell. Since each grid cell value is altitude, neighbouring grid cells in flat areas have little or no difference in altitude. In rugged areas, neighbouring grid cells differ. This difference can be quantified by calculating the standard deviation around each grid cell to provide a terrain ruggedness index (TRI). For this analysis, we selected a grid cell neighbourhood of 3 x 3 grid cells (270m x 270m) around each focal grid cell from which the TRI value was calculated. The resulting TRI values reflect fine scale variation in altitudes, not absolute altitude values, and are therefore comparable across ecosystems despite variations between their regional mean altitudes. TRI values for all grid cells within a 100m, 250m, and 500m radius of den sites were extracted and contrasted with TRI values within the same radii from random contrast sites. A Kruskal-Wallis one way analysis of variance (ANOVA) on ranks was used to test for differences between the six groups within each study area. Dunn's method, a multiple comparison procedure, was used to identify specific groups that differed from one another (significance when  $P = <0.05$ ).

## **Results**

Wild dogs in all four populations consistently selected den sites in significantly more rugged terrain than what was available on average (ANOVA; MGR:  $H = 1038.142$ ,  $df = 5$ ,  $P = <0.001$ ; VLNR:  $H = 243.549$ ,  $df = 5$ ,  $P = <0.001$ ; LGCA:  $H = 938.108$ ,  $df = 5$ ,  $P = <0.001$ ; SVC:  $H = 657.126$ ,  $df = 5$ ,  $P = <0.001$ ). Within each study area, the multiple comparison indicated that TRI values around actual den sites were significantly

greater (Dunn's method,  $P = < 0.05$ ) than TRI values within equivalent distances from random contrast den sites.

The analysis revealed that the LGCA is, on average, the most rugged and undulating study area (Fig. 1). The TRI values were also relatively high in MGR. However, rugged terrain in MGR occurs in the form of ridges and hills which stand out from relatively flat surroundings (Viljoen & Moore 2007), while much of the LGCA is rugged and lacks large patches of even terrain. This is evident when contrasting the TRI values between actual and random dens (Fig. 1). In MGR, random sites had extremely low TRI values relative to the actual den sites. In LGCA the random sites are characterised by considerable ruggedness, yet the actual den sites are still located in significantly more rugged terrain.

Compared to LGCA and MGR, both VLNR and SVC had relatively low overall TRI values. The isolated nature and small size of rugged habitat patches in these study areas was also evident as the higher values, as indicated by the 90<sup>th</sup> percentile error bar, decrease considerably with increasing distance from the den sites. In MGR, den sites were frequently situated in foothills of large ridge structures. Consequently, as the radii around dens was increased from 100 m to 500 m, the skew in the data shifted to greater TRI values as a result of more of the rugged ridges being incorporated in the analysis.

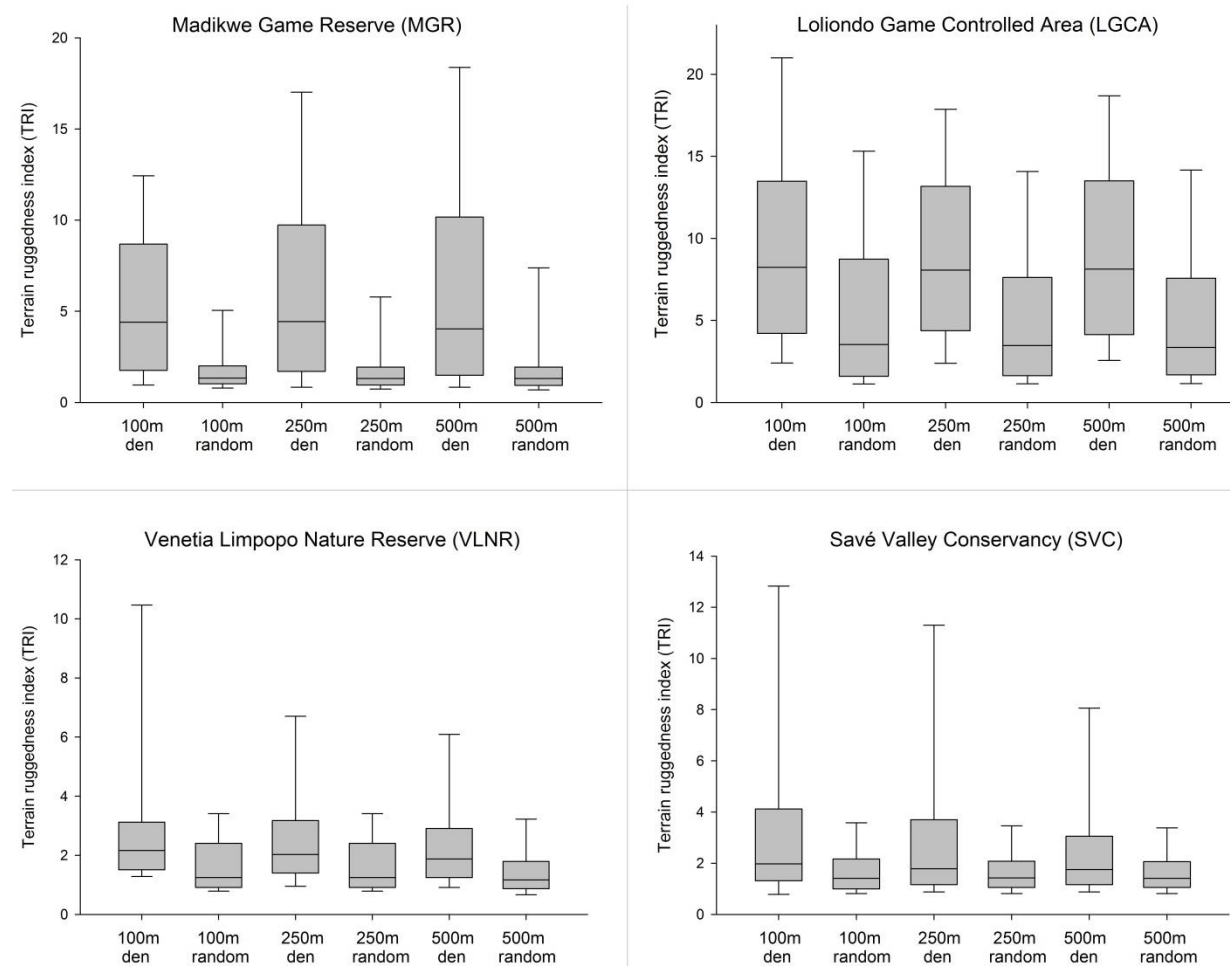


**Figure 1.** A boxplot showing the terrain ruggedness index values within 100m, 250m and 500m of wild dog dens (“den”) and random contrast locations (“random”) within each of the four study populations. Median values are indicated in the boxes while the error bars indicate the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Outliers not shown due to scaling of the graphs.

## Discussion

Since young wild dogs are particularly vulnerable to predation, den site selection is a primary defence mechanism and strategy to maximise reproductive success. Our results clearly illustrate that rugged terrain is selected by wild dog packs for the purpose of reproduction and the rearing of pups. We postulate that this is due to risk avoidance, as hilly and mountainous terrain are not preferred lion or spotted hyena habitats (Mills & Gorman 1997; van Dyk & Slotow 2003) and the probability of encountering these competitors are thus reduced in rugged terrain (van Dyk & Slotow 2003).

Wild dog packs accompanied by young pups are more likely to alarm call following exposure to lion roars than packs without young (Webster et al. 2012). Despite their apparent increased sensitivity to lion’s presence, these packs were found to move shorter distances in the hour after hearing lion roaring as the young seemingly restricted their ability to rapidly vacate the immediate vicinity (Webster et al. 2012). An area with low lion and spotted hyena density, as well as places of cover, would therefore be particularly favourable whilst raising pups (van Dyk & Slotow 2003). In contrast to a direct encounter in open habitat, it is reasonable to assume that wild dog pups would be far less exposed in rugged terrain and have a greater chance of evading predators. Once the pups become older, they may be left alone while the pack goes out hunting, making such habitat even more important.

After leaving their pride to give birth, lionesses seek dense cover to rear their cubs and may utilise hills (Hanby et al. 1995). However, they use the habitat for this purpose alone and may be disinclined to engage in any risk-prone interactions with other predators. Their use of similar rugged habitat for reproduction also indicates the potential safety that these habitats may afford vulnerable altricial offspring. Furthermore, since lionesses with young are the only portion of the lion population that periodically seek out and utilise rugged habitat, it further substantiates the argument that these habitats are generally safer with reduced levels of inter- and intra-specific competition.

### *Implications for conservation planning*

Wild dogs have evolved behavioural mechanisms that allow them to occur sympatrically with dominant carnivores. These mechanisms evolved in large heterogeneous landscapes where the density and distribution of competitors varied spatially and temporally. Wild dogs are particularly prone to anthropogenic threats, and protected areas are therefore of importance for their survival (Woodroffe & Ginsburg 1998). However, interspecific competition within protected areas may significantly inhibit conservation efforts for this endangered carnivore (Creel & Creel 1996). An understanding of competition refuges (Durant 1998), especially for reproduction, is thus of great relevance as these may be limited in relatively small protected areas. A simple analysis of terrain ruggedness would rapidly determine the extent of potential denning habitat within a given protected area, thereby assisting assessments of its suitability to conserve wild dogs. While it has been suggested that wild dog

reintroductions should not be conducted in reserves with high lion densities (Creel 2001; Creel et al. 2001), landscape heterogeneity may largely determine the degree to which the two species can coexist. A case in point is Pilanesberg National Park (PNP) in South Africa. Despite the small 572 km<sup>2</sup> reserve's lion population exceeding 140 lions at times, wild dogs survived on the reserve since their reintroduction in 1999 (van Dyk & Slotow 2003). PNP is located in an inactive volcanic crater and the reserve's topography is characteristically rugged. Dens were located in rugged areas that were known to be low lion density areas and, more specifically, lions were "not known to use the steep slopes... where dens were located" (van Dyk & Slotow 2003). An analysis of mean terrain ruggedness values within ten protected areas with resident wild dog populations revealed that PNP had the greatest TRI values (Jackson et al., unpublished data). Although LGCA had the greatest TRI values in this study, the mean terrain ruggedness in PNP is twice that of LGCA. Evidence therefore suggests that undulating terrain plays an important role in wild dogs' spatial avoidance of lions thereby facilitating sympatric coexistence of wild dogs and lions. Consequently, an assessment of topographic heterogeneity may be important in wild dog conservation planning, particularly during habitat assessments prior to potential reintroductions.

Here we have indicated, for the first time, the selection of rugged terrain for denning purposes in four populations of wild dogs, using a novel technique that has significant conservation applications. The simple technique used to devise the terrain ruggedness index may be useful to investigate habitat suitability, and even predict highly suitable denning areas, across large landscapes. The technique may also be applicable in the studies of other carnivores which have a strong association with rugged terrain, such as leopards (*Panthera pardus*; Steyn & Funston 2009). Future work may aim to establish the relationship between lion and wild dog densities at finer spatial resolutions and establish how the availability of rugged terrain may influence interspecific coexistence and relative densities of the two species.

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## PAPER IV

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## **Living in the lion's den: the role of competition refuges for African wild dog survival in the Serengeti-Mara Ecosystem**

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## Abstract

Factors driving population decline are usually complex, as exemplified by the local extinction of an African wild dog (*Lycaon pictus*) population in Serengeti National Park (SNP), Tanzania. Although disease and interspecific competition were contributing factors, the ultimate cause(s) were never identified. Despite occurring elsewhere in the Serengeti-Mara Ecosystem, the sizeable wild dog population has not recolonized the SNP. Lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) populations doubled during the two decades preceding the wild dogs' disappearance. Since wild dogs are a subordinate carnivore, we hypothesised that the spatial distribution and availability of competition refuges affected population viability. We used a species distribution model (SDM) to assess habitat suitability across the entire ecosystem. Global positioning system (GPS) collar data from two wild dog packs recently reintroduced into SNP indicated that intensively utilised habitats closely matched the distribution of habitat predicted as highly suitable by the SDM. We identified the characteristics of highly suitable habitat and show that such habitat represents competition refuges. The SDM revealed the scarcity of refuges in SNP and particularly within the former 3000 km<sup>2</sup> study area where wild dogs were studied from 1967 - 1992. Contrary to general belief, recent evidence indicates that the wild dog population never went extinct. Based on our results, we propose that the ultimate explanation of the wild dog disappearance involves a range contraction into more suitable habitat, following increased levels of interspecific competition. Here wild dogs were afforded respite from competition and have persisted until present. More than 20 years after their "extinction", we show that wild dog research was conducted in suboptimal habitat and that by restricting research to plain-like areas, the surviving component of the population went undetected.

## Introduction

Large carnivores are particularly vulnerable to anthropogenic threats in modern human-dominated landscapes (Woodroffe 2000). Having been extirpated from 25 of the 39 countries they historically occurred in (Woodroffe et al. 1997), African wild dogs epitomize the plight of such predators. Wide-ranging species require large areas to support viable populations (Woodroffe & Ginsburg 1999). As one of Africa's largest national parks, the prey-rich Serengeti National Park (SNP) in northern Tanzania might be regarded as an ideal location to conserve the endangered wild dog (Masenga 2011). However, the SNP wild dog population declined from 95 adults in 12 packs in 1970 (Frame et al. 1979) to local extinction in 1991-1992 (Ginsburg et al. 1995). The cause of their demise was extensively debated in the literature, particularly after it was proposed that stress induced by researcher's handling of the animals compromised wild dog's immune response to disease (Burrows et al. 1994). This was subsequently rejected on several accounts (Ginsburg et al. 1995, Creel et al. 1997) and the most parsimonious explanation of proximate factors suggested that both periodic outbreaks of disease and interspecific competition contributed significantly to their demise (Ginsburg et al. 1995).

Between 1975 and 1991, there were three occasions when the inter-annual wild dog population size crashed by more than 40% (Ginsburg et al. 1995). These rapid declines are characteristic of disease outbreaks and the presence of both canine distemper virus (CDV) and rabies in the ecosystem were confirmed (Alexander et al. 1992; Alexander & Appel 1994; Burrows et al. 1994; Munson 1994). With large litter sizes, wild dog populations have the potential to rapidly recover following population crashes (Woodroffe 2011), and disease alone is unlikely to have accounted for the long-term decline. Concomitant with the wild dog population decline, studies indicated that the lion population almost doubled (Packer et al. 2005) while the spotted hyaena population increased by 150% (Burrows et al. 1994). Lions steal wild dog kills and may account for up to 12% of adult and 31% of pup mortality (Woodroffe & Ginsburg 1999). Although hyenas kleptoparasitize wild dog kills, they account for only 4% of adult mortality and 6% of pup mortality (Woodroffe & Ginsburg 1999). Unlike hyenas, wild dogs actively avoid lions whenever they detect them and lions play a far greater role in limiting wild dog populations than hyenas (Webster et al. 2012). Wild dog densities are inversely correlated with those of lions and hyenas across many ecosystems (Creel & Creel 1996, Mills & Gorman 1997) and evidence suggests that interspecific competition was a significant factor in the demise of the SNP population (Ginsburg et al. 1995).

From an evolutionary perspective, the costs of interspecific competition are offset through morphological, behavioural and life history adaptations that facilitate niche partitioning, increasing fitness and promoting coexistence (Creel et al. 2001). These adaptations are, however, dependent on either the presence of temporal environmental fluctuations (Chesson & Warner 1981) or, more frequently, spatial heterogeneity (Chesson 1985). The SNP lion and hyena densities are similar to those from other protected areas in Africa (Packer et al. 2013) in which wild dogs have successfully persisted. If competition was in fact a significant factor underlying the gradual decline of the Serengeti wild dogs, it would suggest that mechanisms of coexistence were somehow impeded, increasing the species' vulnerability to interspecific competition and ultimately local extinction.

Elucidating potential processes limiting wild dog coexistence, specifically in a retrospective manner, is extremely challenging. Although poorly documented, wild dogs have persisted outside of the national park's boundaries yet within the greater Serengeti-Mara ecosystem (Marsden et al. 2012). Following the reintroduction of two wild dog packs into the SNP in 2012, a rare opportunity to gain an empirical insight into wild dog coexistence with large predators arose. Despite the presence of lions (Maddox 2003), disease (Goller et al. 2010) and additionally being persecuted by local communities (Masenga

2011), wild dogs have persisted in the adjoining Loliondo Game Controlled Area (LGCA) and Ngorongoro Conservation Area (NCA; Marsden et al. 2012; Lyamuya, unpublished data). Wild dog survival in LGCA and NCA for several decades (see methods), yet failure to recolonize the SNP, suggests that certain ecological factors may be of vital importance for subordinate African wild dogs to realize their ecological niche. Habitat heterogeneity results in differential use of different habitat types by top carnivores (e.g. Mills & Gorman 1997) and certain habitats may therefore have a lower risk, acting as competition refuges (Durant 1998). As a species with low competitive abilities, wild dogs are dependent on respite from competition in order to maximise fitness and persist as viable populations.

We hypothesised that, in the presence of interspecific competition, the availability of competition refuges would directly affect the probability of localised wild dog persistence. Habitat characteristics in the LGCA and NCA landscapes may therefore provide a greater availability competition refuges than the SNP landscapes. To quantify the differences between these two areas we developed a species distribution model based on habitat selection by the extant LGCA-NCA wild dog population. The model's spatial extent enveloped the greater Serengeti-Mara Ecosystem, allowing us to investigate the distribution of suitable habitat across the entire region. We incorporated variables documented to drive variation in Serengeti lion densities as we were particularly interested in determining the distribution and ecological characteristics of competition refuges. Since wild dogs spend a disproportionately large amount of time in the small core area of a territory (Creel & Creel 2002; Jackson et al. submitted (a)), risk avoidance behaviour should result in the selection of comparatively low-risk habitat, i.e. competition refuges, for intensively utilised (core) areas.

We predicted that core areas of the reintroduced wild dog packs' ranges would be located in habitat predicted as highly suitable by the SDM, thereby identifying habitat constituting competition refuges. Distances between consecutive locations (step lengths) are shorter in core areas than step lengths in less-intensively utilised areas (Parker 2009). We therefore additionally predicted that step lengths in packs' core areas should be shorter and located in habitat predicted to be highly suitable. In contrast, step lengths in less intensively utilised areas would be greater and associated with lower suitability values from the SDM. Finally, if interspecific competition was a major driver of the wild dog population decline, then habitat providing relief from competition should be scarce within the initial 3000 km<sup>2</sup> study area where wild dogs were studied from 1967 until their disappearance (Frame et al. 1979). In combination these components would provide a unique insight into spatially explicit factors affecting intra-guild coexistence which are currently not considered in conservation planning for African wild dogs.

## **Methods**

### *Study area*

The Serengeti-Mara Ecosystem (Fig. 1) encompasses over 30 000 km<sup>2</sup> of wildlife-dominated land in northern Tanzania and south western Kenya. The Serengeti National Park (SNP) forms the heart of the system (14763 km<sup>2</sup>) and is bordered to the east by the Loliondo Game Controlled Area (LGCA; ca. 4000 km<sup>2</sup>) and south east by the Ngorongoro Conservation Area (NCA; ca. 8300 km<sup>2</sup>). Smaller areas forming part of the ecosystem include Ikorongo (602km<sup>2</sup>), Grumeti (411km<sup>2</sup>) and Maswa Game Reserves (2200km<sup>2</sup>) to the west and the Masai Mara National Reserve in the north (Kenya). Siana communal lands, bordering LGCA to the north, were also included. The SNP, LGCA and NCA formed the focal study areas. The SNP is free of livestock and human settlements, while the LGCA and NCA in contrast are

mixed land use areas. Pastoral Maasai are the dominant tribe in the area, followed by the Sonjo. Wildlife moves freely between the contiguous areas as there are no barriers separating them. Herbivore density and diversity in the SNP, LGCA and NCA were found to be similar (Maddox 2003). Furthermore, there was no significant difference between lion densities in the three areas, while spotted hyenas were more abundant inside SNP (Maddox 2003).

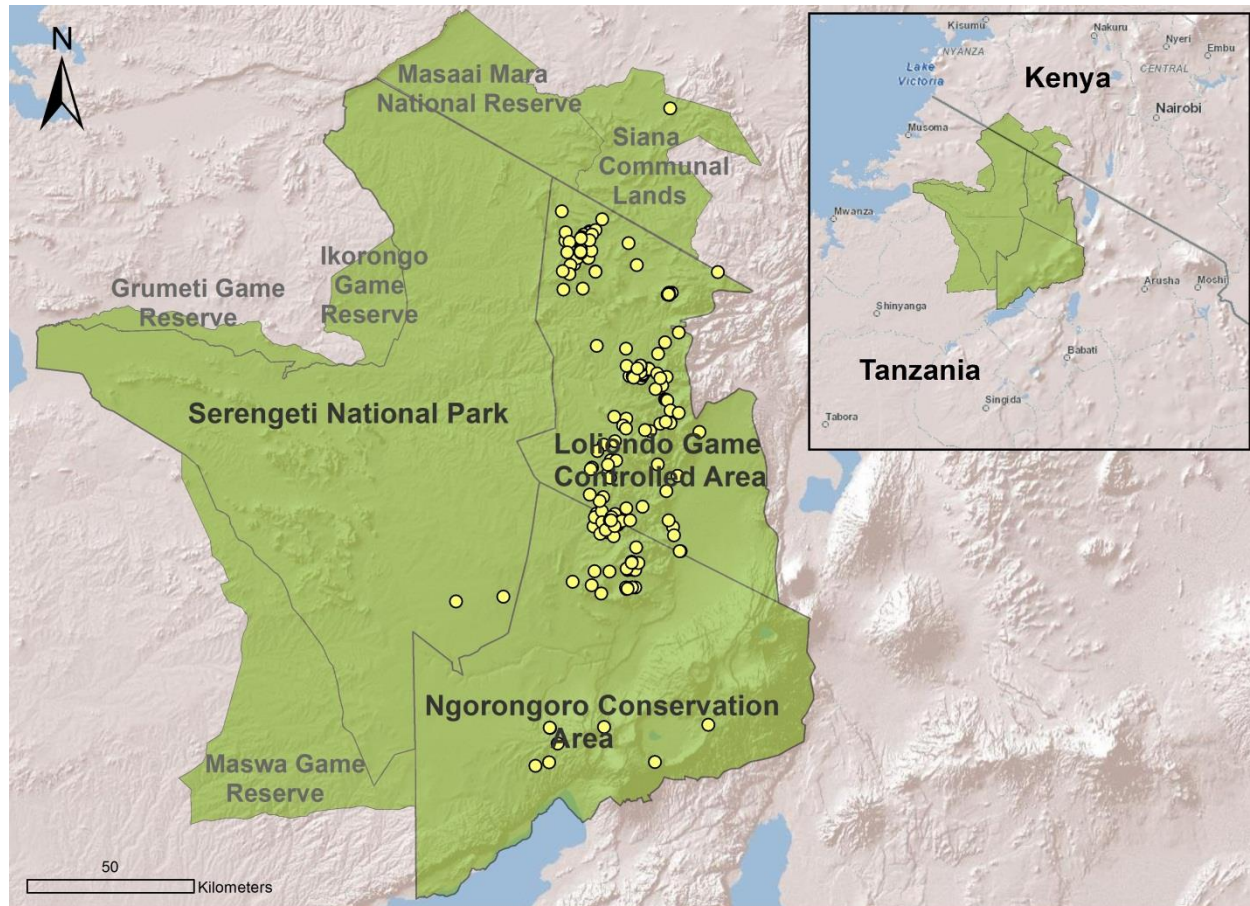


**Figure 1.** The greater Serengeti–Mara Ecosystem in northern Tanzania and southern Kenya. The focal areas for our study were the Serengeti National Park, Loliondo Game Controlled Area and the Ngorongoro Conservation Area. Yellow circles denote wild dog occurrence records used in the species distribution model.

The history of the LGCA wild dog population is not well documented, but local Maasai report regular wild dog sightings for several decades (R. Lyamuya et al., unpublished data) which is corroborated by recent genetic evidence (Marsden et al. 2012). Monitoring has revealed a population of approximately 130 animals in eight to ten packs (Masenga 2011) and wild dogs were the carnivore species responsible for the most livestock losses in the LGCA (Lyamuya et al., in press).

#### *Species Distribution Model*

We used a database of wild dog occurrence records, predominantly from LGCA and NCA (see below), recorded between 2005 and 2009 by a wild dog research team (Masenga 2011) to develop a species distribution model (SDM). The database consisted of 465 occurrence records. Since habitat selection by dispersing wild dogs may differ greatly from resident packs (Jackson et al. Paper V, this thesis)), we only

used occurrence data of known resident packs located within the map area ( $n = 223$ ). The majority of these were located within LGCA (60.5%;  $n = 135$ ) and NCA (38.1%;  $n = 85$ ; Fig.1).

We used Maxent (Phillips et al. 2006) to develop the SDM. This correlative modelling approach is favourable due to its use of presence-only data and has performed well when compared to alternative techniques (Elith et al. 2006). A species' potential distribution is modelled using occurrence records and a set of environmental predictor variables, where the distribution of maximum entropy is determined subject to the constraint that the expected value of each environmental variable under this estimated distribution matches its empirical average (Phillips et al. 2006). Models were produced using default parameters in Maxent (version 3.3.3; feature selection automatic; regularisation multiplier at unity; maximum iterations 500; convergence threshold  $10^{-5}$ ; and random test percentage at zero) and five-fold cross validation. The region from which background samples are drawn has been shown to be important for model performance (Anderson & Raza 2010). We used the entire study area (Fig. 1) as wild dogs are expected to be able to access this whole region.

#### *Environmental predictor variables*

Lions have been studied for more than 40 years in the Serengeti ecosystem (Mosser et al. 2009). At the broad scale, lion density is positively correlated with prey density (Hopcraft et al. 2005; Mosser et al. 2009). Prey abundance is primarily determined by access to water and dry season rainfall (Mosser et al. 2009). At a finer scale, lions select habitat with good cover and physical features such as erosion gullies along water courses which are preferential for hunting (Hopcraft et al. 2005). Lion density and preferred lion habitat are thus strongly influenced by rivers (Hopcraft et al. 2005; Mosser et al. 2009) and lion density is inversely related to distance from rivers (Mosser et al. 2009). The risks lions pose to wild dogs are well documented (e.g. Creel & Creel 1996), as is their avoidance of high lion density areas (e.g. Mills & Gorman 1997) and lions whenever encountered (Webster et al. 2012). In areas with a high river density, wild dogs would have difficulty avoiding lions in both time and space. In contrast, areas with few rivers would allow wild dogs to utilise large parts of the landscape, but selectively avoid the most risky riverine habitats. Variations in river density promote landscape heterogeneity and facilitate spatial and temporal avoidance.

Based on the mean Akaike weights for univariate models investigating the association between various landscape variables and adult female lion density in SNP, the three highest ranked variables were dry season rainfall, distance to river confluences and distance to rivers (Mosser et al. 2009). To account for variability in lion densities across landscapes in the SDM we thus included dry season rainfall (June to October; as per Mosser et al. 2009) and river density as environmental predictor variables. In addition, denser vegetation cover is selected by lions for hunting (Hopcraft et al. 2005) and we thus included vegetation cover as a predictor variable. Finally, terrain ruggedness was included to represent spatial and topographical heterogeneity in the ecosystem. Wild dogs favour rugged terrain while it is avoided by lions (Mills & Gorman 1997; van Dyk & Slotow 2003) and wild dogs select rugged terrain during denning as part of a risk avoidance strategy (Jackson et al. submitted (b)). A terrain ruggedness layer was derived from a 90 m digital elevation model (DEM). A spatial filter was applied to determine the standard deviation around each focal grid cell. Since each grid cell value is altitude, increased ruggedness would be characterised by increased variation in the values of neighbouring grid cells. This difference can be quantified by calculating the standard deviation around each grid cell to provide a terrain ruggedness index (TRI). For this analysis, we selected a grid cell neighbourhood of  $15 \times 15$  grid cells around each focal grid cell from which the TRI value was calculated. Although occurrence records were located in LGCA and NCA, habitat suitability was evaluated for the entire Serengeti-Mara ecosystem given that the spatial extent of environmental predictor variables covered the greater region.

**Table 1.** Environmental predictor variables used in the species distribution model.

| Variable                                       | Source                                      | Reference                                                        |
|------------------------------------------------|---------------------------------------------|------------------------------------------------------------------|
| Dry season rainfall                            | WorldClim (1km x 1km)                       | Hijmans et al. 2005                                              |
| River density<br>(calculated from river layer) | Serengeti GIS and Data Centre               | <a href="http://www.serengetidata.org">www.serengetidata.org</a> |
| Vegetation Cover                               | Serengeti GIS and Data Centre               | <a href="http://www.serengetidata.org">www.serengetidata.org</a> |
| Terrain Ruggedness<br>(derived from DEM)       | Digital elevation model<br>(90m resolution) | Jarvis et al. 2008                                               |

#### *Wild dogs ranging data inside the SNP*

During 2012, two wild dog packs were reintroduced and released in SNP. Both packs were released from the same enclosure in the west of the SNP. The first pack ("Pack 1") was released on 28 August 2012 (n = 11 individuals) and the second ("Pack 2") on 23 December 2012 (n = 15 individuals). Two adult females in each pack were fitted with satellite global positioning system (GPS) collars (African Wildlife Tracking, Pretoria, South Africa). Collars were programmed to provide a minimum of eight daily GPS locations per pack. We used GPS data for a ten month period (1 September 2012 – 30 May 2013) for Pack 1 and six months for Pack 2 (1 January – 30 June 2013). We were limited to these time periods as Pack 1 had left the study area by the end of May 2013 and Pack 2 denned (within SNP) in July 2013 thereby restricting space use to the vicinity around the den.

#### *Evaluating the model*

The SDMs performance was evaluated using the area under the curve (AUC) statistic. Most predictive models lack independent quantitative data for model evaluation. GPS collar data from the reintroduced packs (entirely independent from the location records used to build the SDM) were used to evaluate how actual habitat selection related to the model's predictions. Although we only had GPS collar data from two wild dog packs, the well-established natural avoidance behaviour (e.g. Webster et al. 2012) allowed us to use the 431 days' worth of data within the map area to test the model output and specifically confirm whether or not habitat identified as highly suitable was in fact likely to represent competition refuges.

##### *i) Linking model predictions to competition refuges*

Step lengths between consecutive wild dog locations increase with increasing proximity from the frequented core area; i.e. distances in the core area are short compared to those in less intensively utilised areas (Parker 2009). Furthermore, a disproportionally large amount of time is spent in the comparatively small core areas (Creel & Creel 2002; Jackson et al. submitted (a)). Since wild dogs avoid lions whenever encountered (Webster et al. 2012), frequented areas are expected to represent some of the safest parts of their territory with low risk of encountering lions.

If habitat predicted as highly suitable by the SDM functions as competition refuges, then: i) GPS locations within core areas should be associated with higher quality habitat than locations in less-frequented areas, and ii) average distances moved between consecutive positions should be the shorter within core rather than less-frequented areas. If both of these predictions are supported then it

provides strong evidence that the SDM does in fact identify competition refuges. This would also elucidate whether wild dog habitat selection in the SNP is largely driven by risk avoidance.

Due to extensive periodic exploratory behaviour of Pack 1, conventional home range analyses (e.g. kernel density estimates) were not suitable to determine areas differing in utilisation intensity. Recurrent use of specific habitat patches over several months would be characterised by a clustered distribution of GPS locations. Consequently, short distances between locations would be indicative of intensively utilised patches (i.e. core areas) while larger distances would identify less intensively utilised areas. Core areas were delineated by the distribution of any daily resting locations (DRLs; a single daily GPS location indicating a packs midday resting location) that were less than 500m from one another. Since these were not necessarily consecutive DRLs, it reveals areas where two or more DRLs were less than 500m of each other. DRLs that were between 500m < 1000m from one another represent areas utilised regularly, between 1000m < 2000m correspond to moderately utilised areas, and areas of low utilisation were categorised as 2000m < 3000m. We refer to these utilisation classes as: < 500m = “intensively utilised”, 500m < 1000m = “highly utilised”, 1000m < 2000m = “moderately utilised”, and 2000m < 3000m = “rarely utilised”.

Serengeti lion density is inversely correlated to distance from rivers (Mosser et al. 2009). We fitted linear models to determine which factors affected wild dog’s step length and proximity to rivers for each wild dog location record (n = 431) in R (R Development Core Team 2012). Predictor variables included were terrain ruggedness, vegetation cover, river density and altitude. Distance to rivers and step length were square root transformed and terrain ruggedness were  $\log_{10}$  transformed to meet assumptions of normality. Furthermore, we used hierarchical partitioning, an analytical form of multiple regression which ranks the relative importance of various factors while alleviating problems associated with multicollinearity (Mac Nally 2000; Olea et al. 2010), to identify the factors with the greatest effect on the wild dog distance to rivers. We used the “hier.part” package (Walsh and Mac Nally 2008) in R to run the hierarchical partitioning. All figures were produced in Sigmaplot v12.0 (Systat Software Inc, London, UK).

#### *Former wild dog study area*

A study area of 3000 km<sup>2</sup>, centred on Naabi Hill, was selected when the Serengeti wild dog study commenced in 1967 (Frame et al. 1979; Fig. 2). To determine the extent of suitable habitat we generated 300 random points within this area (i.e. an average of one point per 10 km<sup>2</sup>). The SDM suitability values associated with each random point were extracted. A Mann-Whitney rank sum test was used to contrast these to the SDM values associated with all the DRL data (431 days in total) for Packs 1 and 2, regardless of how intensively areas might have been utilised.

## **Results**

The SDM identified large contiguous areas of highly suitable habitat in the LGCA and NCA. Highly suitable habitat within the SNP was far more limited and patchy in distribution, yet the frequented areas of the reintroduced wild dogs largely coincided with these areas of high suitability. The SDM performed well with mean AUC values following five-fold cross validation for training records being 0.942 and test data AUC equal to 0.926. When using the independent wild dog GPS collar data to test the model, the AUC value was 0.862. Predictor variable contribution: terrain ruggedness = 50.5%, dry season rainfall = 28%, river density = 20.1% and vegetation cover = 1.5%. Rugged terrain, in the form of undulating mountainous terrain in the LGCA and NCA and ridges and hills in the western parts of the SNP, had the greatest contribution in the SDM and the distribution thereof closely mirrored areas predicted to be highly suitable for wild dogs (Figures 2 and 3).

The largest contiguous patches of highly suitable habitat are located within the LGCA and NCA (Fig. 2). Within the SNP, highly suitable habitat is located in the western parts, but in addition to having slightly lower values, is distributed in narrow strips (ridges) and embedded in a matrix of relatively high-risk habitat (Fig. 2). Areas frequented by the wild dog packs, evident as clusters in Figures 2 and 3, showed a remarkable match with habitat predicted to be highly suitable. Pack 1 ranged widely compared to Pack 2. Pack 1 had two areas that were frequented for extended periods; one to west (alongside Pack 2) and another in the LGCA in the north east.

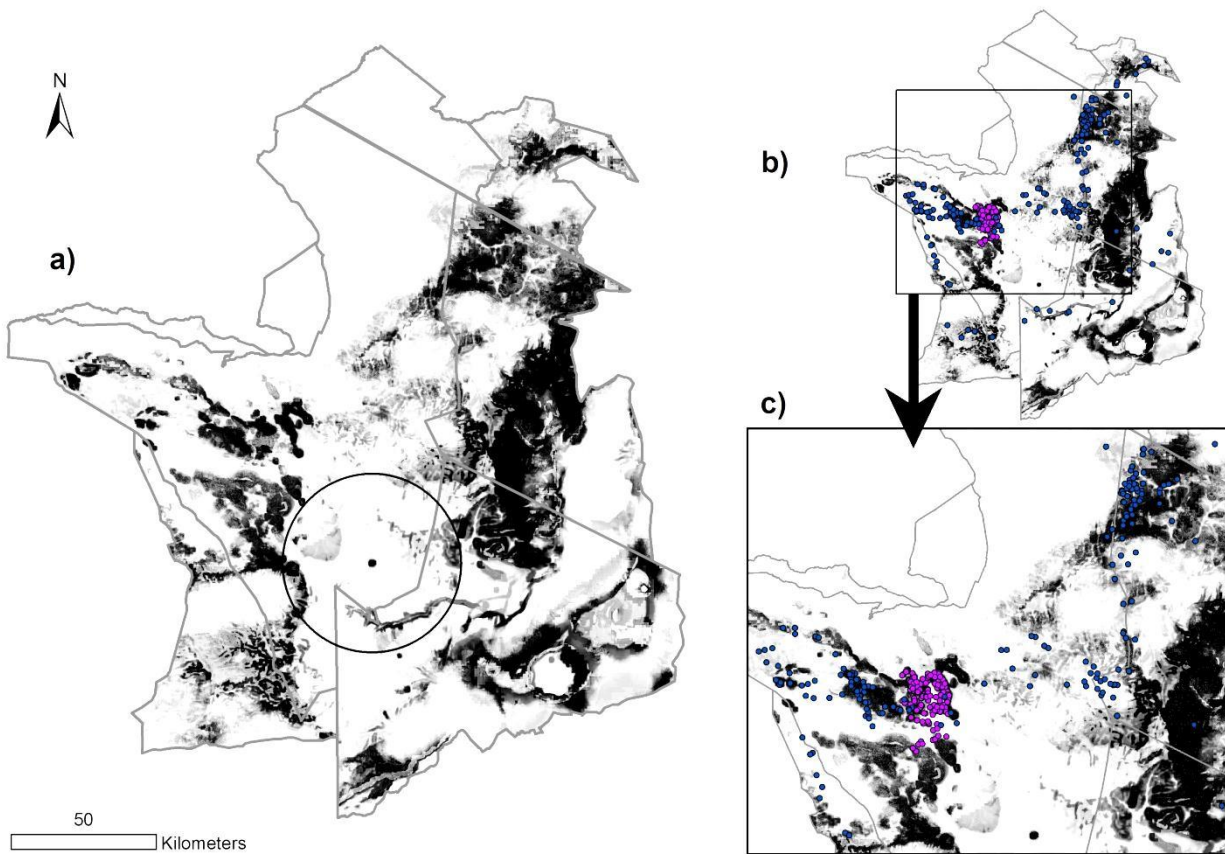


**Figure 2.** Habitat predicted as highly suitable by the species distribution model shown in black, while white areas indicate highly unsuitable habitat. Model values shown are the average following five-fold cross validation. Insert a) shows the model output for the entire study area as well as the location of the original 3000 km<sup>2</sup> study area (Frame et al. 1979), indicated by the black circle. Ranging behaviour of the two reintroduced wild dog packs are illustrated in insert b) and the most utilised part of the study area is magnified in insert c). Pack 1 = dark blue circles; Pack 2 = purple circles.

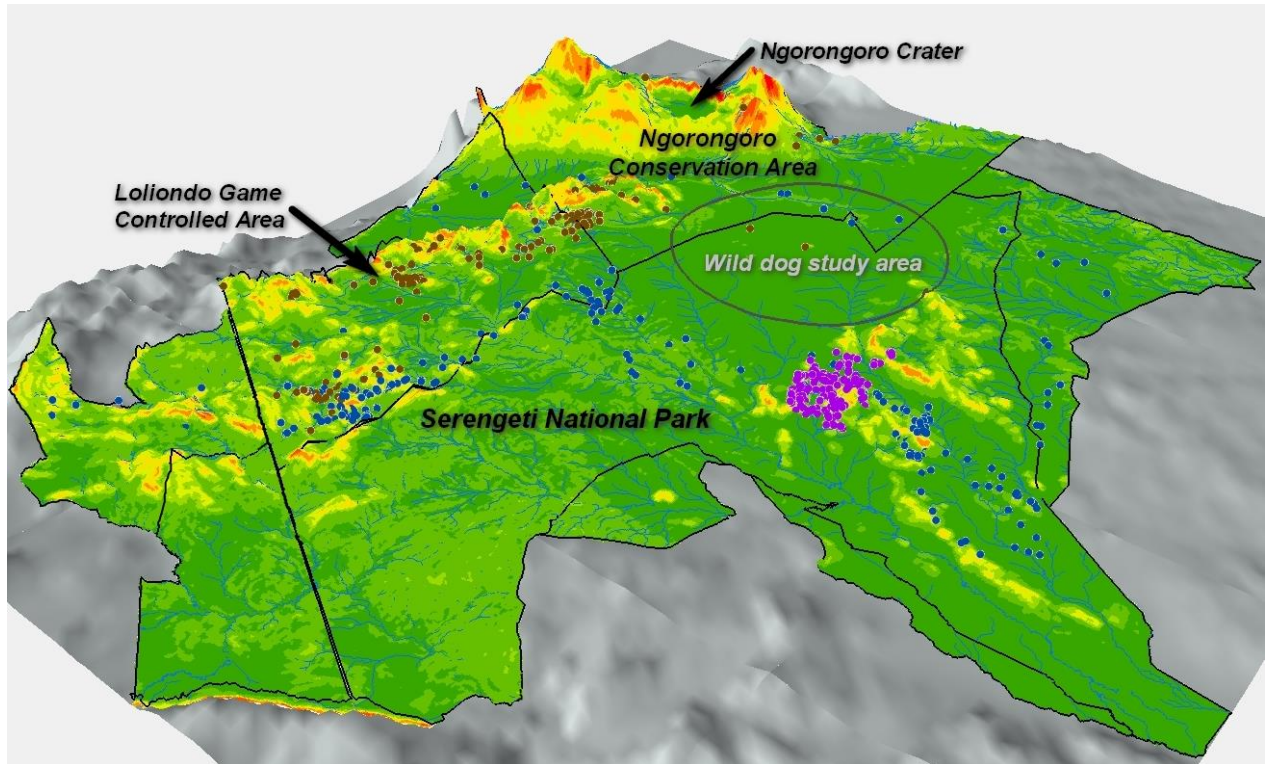


**Figure 3.** A three-dimensional image where terrain ruggedness values have been overlaid onto a digital elevation model, viewed from the north-west. Warmer colours indicate areas with a greater ruggedness and rivers are drawn in blue. The occurrence records used to build the species distribution model are shown in brown. Daily midday resting locations, indicating the preference for rugged terrain, are shown in blue for Pack 1 and purple for Pack 2. The lack of rugged terrain within the former (1967-1992) wild dog study area (indicated by the circle; Frame et al. 1979) is apparent.

Both packs' intensively utilised habitat was associated with significantly greater SDM values than moderately and rarely utilised habitats (Fig. 4; ANOVA; Pack 1:  $H = 14.901$ ,  $df = 3$ ,  $P = 0.002$ ; Pack 2:  $H = 17.005$ ,  $df = 3$ ,  $P = <0.001$ ). Additionally, Pack 1's step lengths between DRLs were significantly shorter in intensively utilised areas when compared to moderately and rarely utilised areas (Fig. 4; ANOVA;  $H = 19.231$ ,  $df = 3$ ,  $P = <0.001$ ). Although the data for Pack 2 followed a similar pattern with mean step lengths increasing with proximity from the intensively utilised area, it was only significantly greater than the moderately utilised areas (Mann-Whitney rank sum test,  $U = 1140.00$ ,  $T = 2466.00$ ,  $P = 0.040$ ). The negative relationship between step length and utilisation intensity is consistent with other studies (Parker 2009) and confirms that our method of distinguishing between varying intensities of use was adequate for the purposes of our analyses. Given the high SDM values and shorter step lengths in the intensively utilised areas, our stipulated criteria for the identification of competition refuges are met.

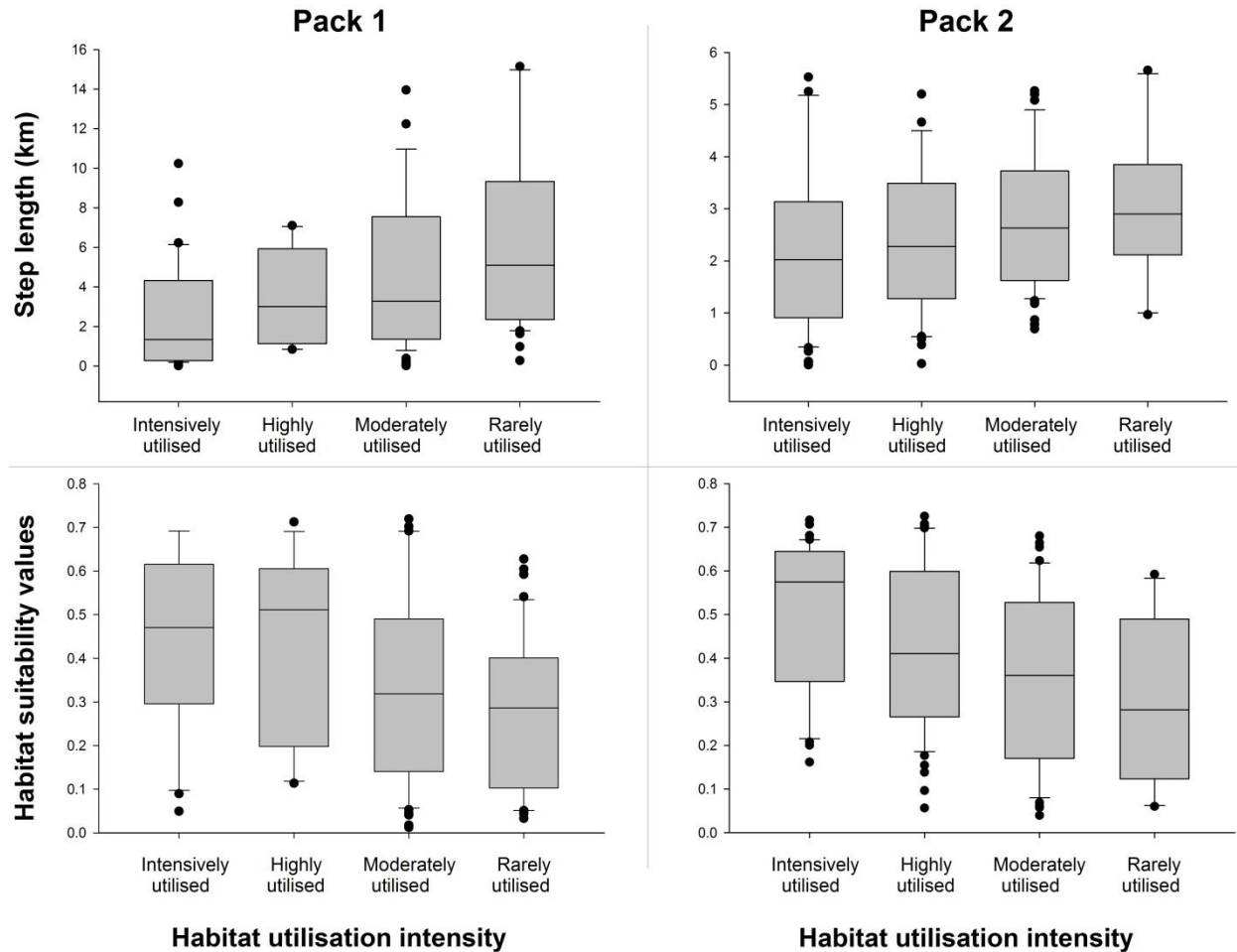


**Figure 4.** Box-plots indicating the variation in step lengths between consecutive daily resting locations (km) and predicted habitat suitability values from the species distribution model. Wild dog location records were separated into four groups based on how intensively parts of the study area were utilised, ranging from the frequented core areas (500m) through to rarely used peripheral patches (3km). Number of locations that met the selection criteria for the groups: Pack 1, n = 151; pack 2, n = 178. Certain outliers are not displayed due to scaling of the plots.

The linear model identified that terrain ruggedness was positively associated with the wild dog pack's proximity to rivers and was the most important explanatory variable. A Pearson product moment correlation revealed a highly significant relationship between distance to rivers and terrain ruggedness ( $r = 0.49$ ,  $P < 0.001$ ). In more rugged areas, the distance to rivers increased, yet there was no significant relationship with river density. A linear model with step length as the response variable indicated that terrain ruggedness was important, but not river density. A Pearson product moment correlation indicated a significant negative relationship between step length and terrain ruggedness ( $r = -0.17$ ,  $P = 0.021$ ) and a significant positive relationship between step length and river density ( $r = 0.21$ ). Step length therefore increases with increasing river density, but decreases as terrain ruggedness increases.

Table 1. Linear models investigating the factors affecting wild dog packs' A) distance to rivers ( $R_{adj} = 0.32$ ,  $F = 26.2$ ,  $DF = 408$ ,  $P < 0.001$ ) and B) step length ( $R_{adj} = 0.27$ ,  $F = 26.2$ ,  $DF = 408$ ,  $P < 0.001$ ).

|                              | Estimate | SE   | t     | P      |
|------------------------------|----------|------|-------|--------|
| <b>A. Distance to rivers</b> |          |      |       |        |
| (Intercept)                  | 55.37    | 6.71 | 8.25  | <0.001 |
| Terrain ruggedness           | 9.84     | 0.84 | 11.70 | <0.001 |
| River density                | -0.08    | 0.02 | -4.12 | <0.001 |
| Altitude                     | -0.02    | 0.00 | -4.03 | <0.001 |
| Dry season rainfall          | -0.34    | 0.16 | -2.16 | 0.032  |
| Vegetation cover             | -0.63    | 0.68 | -0.92 | 0.36   |
| Pack2 relative to pack 1     | -1.17    | 1.55 | -0.75 | 0.45   |
| <b>B. Step length</b>        |          |      |       |        |
| (Intercept)                  | 2.62     | 0.46 | 5.64  | <0.001 |
| Terrain ruggedness           | -0.08    | 0.06 | -1.37 | 0.17   |
| River density                | 0.00     | 0.00 | 0.72  | 0.48   |
| Altitude                     | 0.00     | 0.00 | 4.14  | <0.001 |
| Dry season rainfall          | -0.08    | 0.01 | -6.87 | <0.001 |
| Vegetation cover             | -0.06    | 0.05 | -1.21 | 0.23   |
| Pack2 relative to pack 1     | -0.49    | 0.11 | -4.53 | <0.001 |

With distance to rivers as the response variable, the hierarchical partitioning analyses confirmed the strong influence of terrain ruggedness on the distribution of wild dogs, with river density having the second greatest independent effect (Fig. 5).

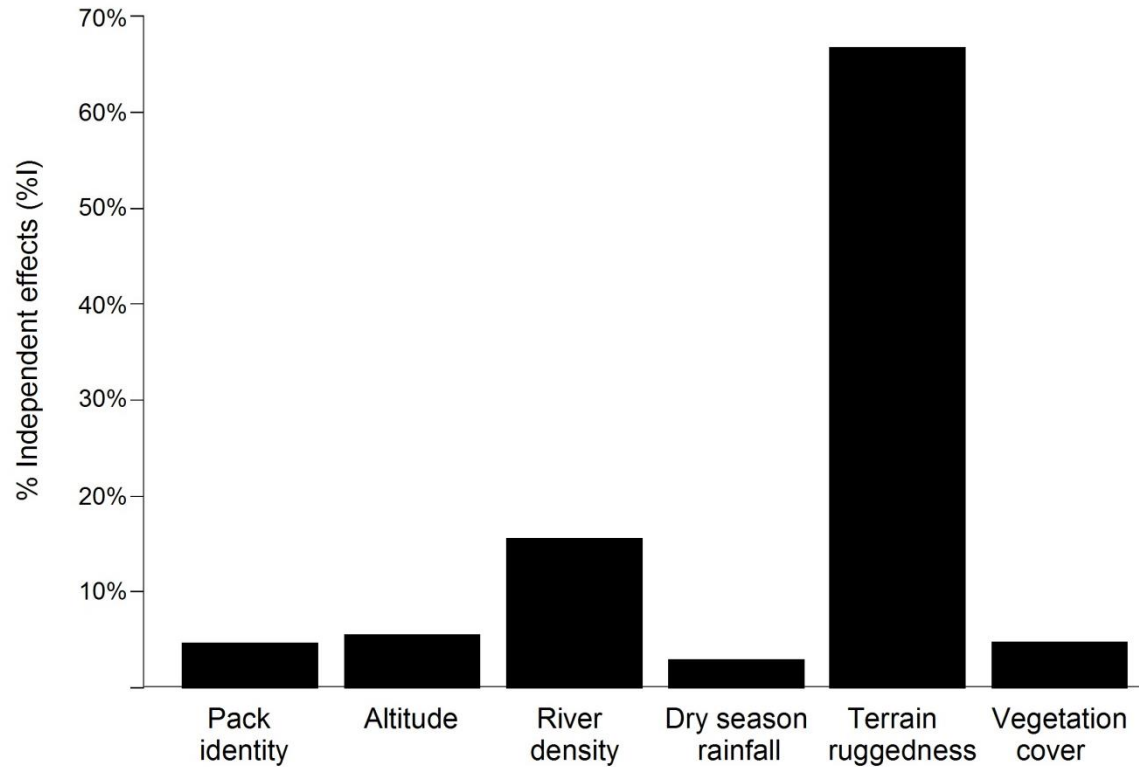


**Figure 5.** Results from the hierarchical partitioning analysis assessing the relatively independent effect of each variable in explaining the distance to rivers for the free-ranging wild dog packs.

#### *Habitat suitability within former wild dog study area*

The model clearly illustrated that the original study area was dominated by habitat that had a low suitability value (Fig. 2). The SDM suitability values associated with 300 random locations within the former study area was contrasted to all the daily resting location data for Packs 1 and 2, regardless of how intensively areas were utilised (Fig. 6). The habitat suitability in this area were significantly lower than both pack's data (Mann-Whitney rank sum test,  $U = 22218.00$ ,  $T = 66769.00$ ,  $P < 0.001$ ). This indicates that the vast majority of the area has very little habitat which could function as competition refuges, greatly increasing the probability of negative competitive encounters. Although five of Pack 1's DRLs were located within the former study area, confirming that the area was accessible to the reintroduced wild dogs, the pack only made a single foray through the area and never returned.

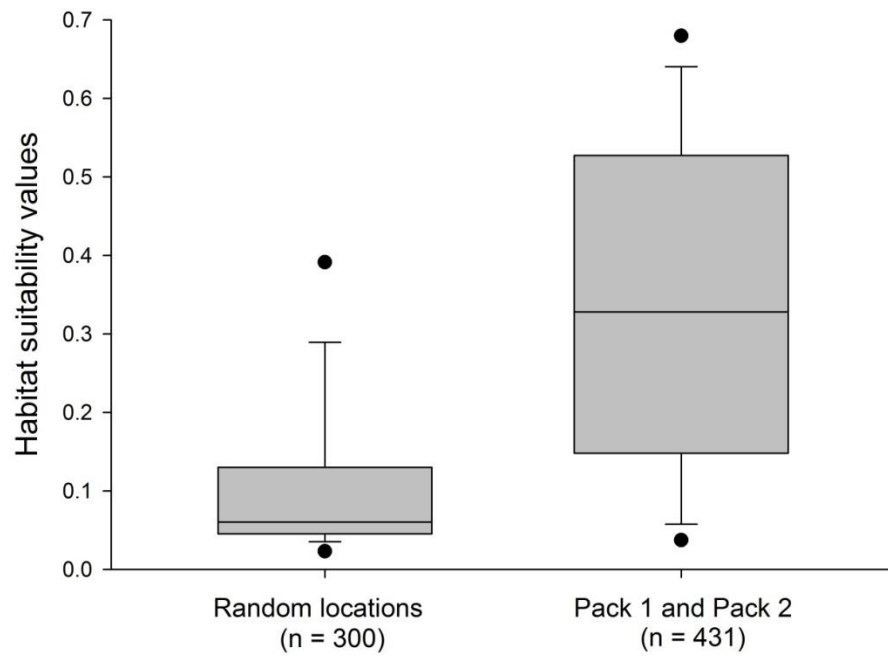


**Figure 6.** Habitat suitability values associated with all the location records for two wild dog packs ranging freely in the Serengeti-Mara Ecosystem. These are contrasted with 300 randomly located points within the original 3000 km<sup>2</sup> study area (Frame et al. 1979). Outliers indicated by 5<sup>th</sup> and 95<sup>th</sup> percentiles.

## Discussion

### *Habitat heterogeneity, ecological niches and interspecific avoidance*

Top predators can be adversely affected by other guild members (Caro & Stoner 2002) through processes such as harassment (Creel & Creel 1996), kleptoparasitism (Cooper 1991), intra-guild predation (Palomares & Caro 1999), and avoidance of competing predators (Fuller & Keith 1981). Mechanisms enabling wild dogs to occur sympatrically with dominant competitors evolved in large, heterogeneous ecosystems (Creel et al. 2001). Here the densities of competing large carnivores, prey, and the availability of diverse habitat types varied spatially and temporally and could be exploited in varied fitness-maximising strategies. Wild dogs have developed the anatomical and physiological ability to rapidly cover large distances. Heterogeneous landscapes and the associated variations in competitor and resource densities may thus be equally important (or more so) to their survival as other physical, behavioural or life history traits. It has been proposed that wild dogs occupy large territories in order to be afforded some degree of spatial and temporal avoidance of the dominant competitors (Creel & Creel 2002). Although the threat posed by lions and hyenas is well documented, mechanisms facilitating coexistence have never been explored, in particular identifying the ecological characteristics of competition refuges. Our data clearly illustrates that in a topographically diverse landscape, rugged terrain provides competition refuges for a subordinate carnivore. This is supported by data from other ecosystems indicating that habitat composed of rugged terrain is lion's least preferred habitat type but most preferred habitat type for wild dogs (Mills & Gorman 1997). Since rugged terrain is generally avoided by lions but utilised by wild dogs (Mills & Gorman 1997; van Dyk & Slotow 2003), such habitat has the ability to facilitate refuge from interspecific competition.

Habitat selection is an adaptive behaviour allowing animals to utilise habitat attributes differently as part of fitness-maximising strategies (Thomas & Taylor 2006). The model prediction accurately matched habitat intensively utilized by the reintroduced wild dog packs. The core areas were located in rugged habitat identified as highly suitable, where the wild dog packs moved significantly shorter distances. In contrast the lower quality areas, where risk of inter-specific competition is far higher, were traversed far more quickly. Although Parker (2009) did not take landscape features and their associated risk of encountering lions or hyenas into account, the clear association of the cores area coinciding with the safest "refuges" could also be a contributing factor to the shorter movements. The shorter step lengths indicate that more time is spent in habitat types which provide respite from competition. Our data also showed that by actively selecting rugged terrain, wild dogs increased the distance to rivers which represents the preferred lion habitat along river courses. To our knowledge, this is the first study using a species distribution model to investigate spatially-explicit factors affecting interspecific competition.

### *Original wild dog study area*

A study area of 3000km<sup>2</sup>, centred on Naabi Hill, was selected when the Serengeti wild dog study commenced in 1967 (Frame et al. 1979; Fig. 2). This area is dominated by open grasslands. Even when the study area was expanded to 5200km<sup>2</sup> six years later, which included 1000km<sup>2</sup> of *Acacia* woodlands, the focal area "*was selected because the open vegetation and even terrain were conducive to sighting and following wild dogs*" (Frame et al. 1979). Given the role of rugged terrain as competition refuges, it

is now evident that the 25 year study of wild dogs on the Serengeti plains was located in poor quality habitat (Figs. 2 and 3) which exposed wild dogs to interspecific competition. Lion and hyena numbers were relatively low when the study commenced (see Ginsburg et al. 1995). In the presence of minimal competition, wild dog populations can increase rapidly (Woodroffe 2011) while lion and hyena populations take far longer to recover from low densities (Smuts 1978). However, two decades later when the wild dogs disappeared, lion numbers had almost doubled (Packer et al. 2005) and the hyena population had increased by 150% (Burrows et al. 1994). We therefore postulate that prior to the start of the study, in the presence of low levels of competition, wild dogs expanded their range into the SNP from more suitable habitats in the vicinity of LGCA and NCA. Similarly, elk (*Cervus canadensis*) utilised optimal foraging areas in the absence of predation risk, but altered their habitat selection behaviour following the reintroduction of a wolf (*Canis lupus*) population into Yellowstone National Park (Fortin et al. 2005).

While significant increases in lion and hyena populations probably drove the gradual wild dog population decline, outbreaks of disease resulted in periodic crashes (Gascoyne et al. 1993). However, disease was (and still is) present in the two areas where wild dogs persisted (e.g. Lembo et al. 2008). Furthermore, since outbreaks of disease have the potential to affect vast areas of the ecosystem, it is probable that the LGCA-NCA wild dog population were also infected by the same outbreaks that affected the SNP packs. This is particularly likely as domestic dogs, the reservoir host for both CDV and rabies in the ecosystem (Alexander & Appel 1994; Lembo et al. 2008), are resident in the LGCA and NCA, but not the SNP.

By 1992, the studied wild dog population within SNP was reported as having gone extinct (Ginsburg et al. 1995). However, local inhabitants who report that wild dogs have been resident in LGCA since at least the 1950's (Lyamuya et al. unpublished data). Furthermore, recent genetic evidence indicates that the extant LGCA-NCA population originated from the same genetic population as the pre-extinction SNP wild dogs and not through recolonisation from other populations (Madsen et al. 2012). This indicates that the studied SNP population was in fact merely a component of a far larger wild population and confirms that the Serengeti wild dog population, as a whole, never went extinct.

By restricting the wild dog study area to open areas with even terrain, researchers did not document wild dog population sizes, densities or fluctuations in the more suitable parts of the ecosystem in LGCA and NCA (Madsen et al. 2012). Our SDM puts the genetic evidence (Madsen et al. 2012) into a spatial context, and in combination illustrate that the "Serengeti extinction" (Burrows et al. 1994; Ginsburg et al. 1995) was merely a range contraction into more suitable habitat which provided refuge from competition. This is further supported by the fact the large LGCA-NCA wild dog population has not recolonized the adjoining SNP. The comprehensive study by Ginsburg et al. (1995) noted that all explanations of the local "extinction" only addressed proximate factors, and that a real understanding of threats to wild dog populations would only emerge if the ultimate causes were identified. Although the authors stated that it was unlikely that this would ever be revealed, we believe that our findings, more than 20 years after the reported extinction and 45 years after the start of the wild dog studies, offer the most parsimonious explanation of the ultimate cause of the wild dog population decline. Most

importantly, we identify fundamental issues of importance to the conservation management of the species across its entire range.

### *Conservation implications*

The plight of the African wild dog is complicated. They require large protected areas to halt their decline and these are limited in number. Wild dogs are considered as habitat generalists, but as a weaker competitor they require habitat providing suitable refugia for them to survive sympatrically with the dominant lions and hyenas. Our results illustrate how a huge national park, with an abundance of prey, may have limited suitable wild dog habitat. In isolation from the surrounding wildlife areas, and in the presence of current lion and hyena densities, it is unlikely that the SNP alone would be able to support a viable wild dog population. In contrast, the far smaller LGCA may have a greater capacity to conserve wild dogs due to its rugged terrain. Conservation planning may aim to specifically address the large number of wild dogs being killed in the LGCA (Masenga et al. 2013).

Reintroductions of wild dogs have formed a major part of conservation efforts, particularly in South Africa (Davies-Mostert et al. 2009). It has been argued that reintroductions of the endangered wild dog should be conducted in areas with low lion density due to their negative impact on wild dog populations (Creel 2001). Our findings indicate that it is not merely lion density that is important, but the availability of competition refuges. Feasibility studies for potential reintroductions as well as the IUCN Canid Specialist Group reintroduction guidelines should therefore take landscape features into account.

### **Acknowledgements**

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## PAPER V

# Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa

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## Abstract

In fragmented landscapes, connectivity between subpopulations is vital for species' persistence. Various techniques are used to assess the degree of connectivity between habitat patches, yet their performance is seldom evaluated. Models are regularly based on habitat selection by individuals in resident populations, yet dispersers may not require habitat which supports permanent residence. Using a database of African wild dog (*Lycaon pictus*) occurrence records in north-eastern South Africa (n = 576), we developed and compared ecological niche models (ENM) for wild dogs packs and dispersers. In addition to the dispersal ENM, we used least cost path (LCP) and current flow models to assess connectivity. Results were further validated using occurrence records (n = 339) for cheetah (*Acinonyx jubatus*). The ENM for wild dog packs identified large but isolated patches of suitable habitat, while the disperser ENM had greater suitability values for areas in between highly suitable patches. Without disperser-specific data, models omitted large areas which were confirmed to have provided connectivity. Although models derived from a potentially subjective cost layer have been criticised, the current flow model outperformed the other connectivity techniques and provided the most meaningful predictions for conservation planning. We identified five priority conservation areas for wild dogs, two of which had a greater feasibility for recolonisation. The scarcity of disperser-specific data promotes models using habitat data for resident individuals but the debated shortcomings thereof are illustrated here. Our study provides insights into the performance of these frequently employed techniques and how they may affect conservation management decisions.

**Key words:** carnivores, Circuitscape, cheetah, current flow, ecological niche model, habitat fragmentation, least cost path (LCP), Maxent, metapopulation.

## Introduction

Identifying and maintaining connectivity between key habitats has become increasingly important in conservation planning (e.g. Wilcove et al. 1998; Fahrig 2003; Cushman 2006). However, the validity and biological relevance of the various methods used to derive linkages are debated (Beier et al. 2008; Cushman et al. 2009; Richard & Armstrong 2010; Carroll et al. 2012). Identifying and creating corridors based on empirical observations of dispersing individuals is one of the most reliable ways of designing connectivity networks (Hilty and Merenlender 2004; Graves et al. 2007). However, the required dispersal data is lacking for most species (Fagan & Calabrese 2006) and inferences of habitat suitability based on habitat selected by individuals within resident populations may not accurately represent habitat required for dispersal (Carroll et al. 2012).

In the absence of disperser-specific habitat selection data, the most common connectivity analysis method involves delineating corridors (Adriaensen et al. 2003). This is frequently performed using algorithms which determine the path between two predetermined points that have the lowest accumulative cost, a technique referred to as least-cost path (LCP) analysis (Adriaensen et al. 2003). This method implicitly assumes that a dispersing animal has a perfect knowledge of the landscape and bases movement decisions on this (Carroll et al. 2012). In contrast, the more recent current flow models assume that dispersers have no knowledge of the landscape more than one step ahead (Newman 2005) and have also been shown to be highly correlated with genetic distance in several plant and animal populations (McRae et al. 2008; Lee-Yaw et al. 2009). Unlike the linear paths calculated by LCP analyses, the zones identified by current flow modelling provide alternative linkages which may be important under changing climate, land-use change or environmental catastrophes (McRae et al. 2008; Carroll et al. 2012). Due to a lack of appropriate data, the effectiveness of corridors in providing connectivity is usually assessed subjectively (Beier et al. 2008).

Mammalian carnivores are particularly vulnerable to local extinction in fragmented landscapes because of their large ranges, low population densities, and persecution by humans (Noss et al. 1996; Woodroffe & Ginsberg 1998; Cardillo et al. 2005). Since carnivores play a pivotal ecological role and their status can be indicative of landscape connectivity, they can serve as a focal species to assess the degree of connectivity across large areas (Dobson et al. 2006).

In South Africa, the endangered African wild dog (*Lycaon pictus*) is the rarest large carnivore with fewer than 450 free-ranging animals remaining (WAG-SA meeting minutes 2013). The only unmanaged population inhabiting a protected area occurs in the Kruger National Park while the remainder of the country's protected populations are scattered among several smaller reserves (Davies-Mosert et al. 2009). The small reserves are intensively managed as a meta-population by periodically translocating individuals among geographically isolated reserves (Davies-Mosert et al. 2009). Although 20 000 km<sup>2</sup> in size, the Kruger National Park at present supports a population of only 181 animals while 162 wild dogs are distributed among eight meta-population reserves (WAG-SA meeting minutes 2013). Wild dogs occur at low densities even in protected populations (Creel & Creel 2002) and their highly dynamic populations are prone to large-scale fluctuations (Fuller et al. 1992), making connectivity between populations vital. The species remains threatened and since meta-population reserves have limited potential to support additional packs, conservation planning needs to assess the best possible long-term solution that would maximise the species' survival probability.

Almost a third of South Africa's wild dog population ranges outside the boundaries of formally protected areas (Lindsey et al. 2004). Despite high rates of mortality, wild dogs have the potential to disperse several hundreds of kilometres through human-dominated landscapes, find mates and form packs

(Davies-Mostert et al. 2012). Sightings of wild dogs located outside of extant populations infer some level of connectivity to a source population. Maintaining connectivity is vital for immigration, emigration and gene flow, and may serve as an important conservation strategy for wild dogs in southern Africa (Davies-Mostert et al. 2009, 2012). Areas where wild dogs regularly occur are therefore of great conservation significance and could be regarded as priority conservation areas as they represent landscapes suitable for wild dog recolonisation (Davies-Mostert et al. 2009). While initial recolonisation could potentially be accelerated through reintroduction programs, connectivity to source populations is envisaged as the mechanism ensuring population viability (Lindsey et al. 2005a).

Given the global need to accurately identify habitats providing connectivity, we set out to evaluate the effectiveness of different methodologies. Using an extensive database of wild dog occurrence records, which importantly included records for both packs and dispersing groups, we aimed to: 1) evaluate the differences between ecological niche models (ENM) derived from occurrence data of packs and dispersing individuals; 2) test the functionality of corridors identified by the three different methods (maximum entropy, LCP, and current-flow) and evaluate the performance of these techniques; and 3) using an ecological niche model derived from records of wild dog packs identify priority conservation areas with some degree of connectivity to source populations. Lastly, distribution records for cheetah (*Acinonyx jubatus*) were used to investigate the applicability of the priority conservation areas and corridors to another wide-ranging carnivore of conservation concern.

## Methods

### *Study area*

The north-eastern part of South Africa has the greatest number of wild dogs occurring outside of protected areas (Lindsey et al. 2004) and was therefore used to define the extent of our study area (c. 192000km<sup>2</sup>; Fig. 1). The region is dominated by the savanna biome, with the grassland biome present in the south and along the upper Drakensberg escarpment (Mucina & Rutherford 2006). The location of major towns and cities are shown in Fig. 1.



**Figure 1.** Study Area located in north-eastern South Africa where potential wild dog source populations are illustrated in black: 1 - Madikwe Game Reserve (750km<sup>2</sup>), 2 - Pilanesburg National Park (572km<sup>2</sup>), 3 - Marakele National Park (670km<sup>2</sup>), 4 - Northern Tuli Game Reserve (Botswana; 720km<sup>2</sup>), 5 - Venetia Limpopo Nature Reserve (330km<sup>2</sup>), 6 - the greater Kruger National Park (21400km<sup>2</sup>; comprised of the Kruger National Park and the Balule, Klaserie, Umbabat, Sabie Sand, Sabi Sabi, Manyeleti and Timbavati Game Reserves). The Drakensberg escarpment, separating the higher inland plateau from the lower-lying eastern region, is indicated by the dashed line.

#### *Occurrence records*

Wild dog sightings outside protected areas (n=576; 1996–2011) were sourced from Lindsey et al. (2004) and a database maintained by the Endangered Wildlife Trust, South Africa. Data were collected almost exclusively via reports to researchers or questionnaire surveys. Due to lack of precise coordinates in most instances, locations of sightings were recorded at the central point of a property they were recorded on or the nearest 5 arc-minute (0.083 degree) grid vertices. The precision of occurrence records was presumed to have little influence on the modelling work since wild dogs' cusorial habits would allow them to cover the distance introduced by any potential location error in less than an hour (Creel & Creel 2002). At the extent of the entire map area, the locations indicate the approximate location of wild dogs fairly accurately and are consequently valuable for conservation planning and model evaluation. To evaluate model outputs (below), we used a dataset of 339 occurrence records for cheetah. These records (2000-2010) were collected in the same manner as the wild dog records and obtained from the Endangered Wildlife Trust, South Africa.

To investigate whether dispersing wild dogs and wild dog packs utilised different habitats, occurrence data were sorted into two groups. Although individuals may disperse in large groups, dispersing groups usually number 1-8 individuals (McNutt 1996). Records documenting 1-8 individuals within a group (n =

426) were used to represent dispersing animals. Groups of nine or more animals (n=150, range 9–35) were consequently defined as “packs”. Sample sizes for these records do not include more than one presence record at any specific location and are all located within the map area.

*Ecological niche model: habitat selection by wild dog packs and dispersers*

Factors that influence species distributions differ in their relative importance during different life stages. More specifically, habitat that facilitates dispersal may not meet the ecological requirements necessary to support permanent residence (Carroll et al. 2012) and dispersing wild dogs will keep moving in search of mates. Assessing connectivity based on habitat selected by resident individuals, which is common and even advocated (Huck et al. 2011), may underestimate the extent and distribution of functional corridor habitat.

To gain an insight into this potential shortcoming, we used the two groups of occurrence records to assess whether habitat selection by wild dog packs and dispersers differed, mapping the distribution of each. Ecological niche models for i) dispersing wild dogs and ii) wild dog packs were developed using Maxent (Phillips et al. 2006). This correlative modelling approach is beneficial given its use of presence-only data and has performed favourably even with few occurrence records (Jackson & Robertson 2011) and when compared to other methods (Elith et al. 2006). Using occurrence records and a set of environmental predictor variables, Maxent estimates a species’ ecological niche by determining the distribution of maximum entropy, subject to the constraint that the expected value of each environmental variable under this estimated distribution matches its empirical average (Phillips et al. 2006). Models were produced using default parameters in Maxent (version 3.3.3; feature selection automatic; regularisation multiplier at unity; maximum iterations 500; convergence threshold 10–5; and random test percentage at zero) and five-fold cross validation. Factors affecting carnivore movement across landscapes are largely governed by land cover type, human population density and main road density (Merrill et al. 1999; Carroll et al. 2012). We used these predictor variables (Table 1) which were processed in ArcMap 10 (ESRI).

**Table 1.** Predictor variables used in the ecological niche model.

| Variable                    | Source                                                                                                         | Comments                                       |
|-----------------------------|----------------------------------------------------------------------------------------------------------------|------------------------------------------------|
| 1. Land cover               | National Landcover Classification for South Africa (2000)                                                      | all original classes used                      |
| 2. Human population density | Environmental Potential Atlas,<br>Department of Environmental Affairs and Tourism, RSA                         | all original classes used                      |
| 3. Main road density        | Derived from Main Roads, Environmental Potential Atlas<br>Department of Environmental Affairs and Tourism, RSA | calculated line density<br>of main roads layer |

Areas identified as having a high probability of occurrence by the models therefore indicate habitat that largely meets the ecological requirements of a) dispersing individuals or b) packs. Since dispersers are usually single sex groups in search of mates (McNutt 1996) they cover great distances in search of members of the opposite sex (Davies-Mostert et al. 2012). Habitat identified as suitable for this group may therefore specifically have a low resistance to movement, facilitating connectivity. For example, varied land uses involving agriculture or livestock production would not be expected to pose a significant barrier to movement, while urbanised landscapes would. In contrast to dispersers, packs may be relatively more sedentary and suitable habitat would therefore infer that ecological requirements

necessary to support permanent residence are met as well as some level of connectivity to a source population. Consequently, the output for the wild dog pack model may be useful for identifying priority conservation areas (below).

#### *Assessing connectivity*

The Maxent model for dispersers (described above) provides an indication of habitat functioning as corridors between the various source populations. In addition to this ecological niche model, we assessed habitat connectivity across the study area using current-flow analysis and by least-cost paths (LCP). These two methods were performed using Circuitscape (McRae et al. 2008) and Linkage Mapper (McRae & Kavanagh 2011), respectively. Both current flow and LCP techniques require a resistance layer and a set of focal nodes between which connectivity is calculated.

The resistance layer was created from the three predictor variables listed in Table 1. In addition to these, a fourth layer representing steep mountain slopes was included (see supplementary material). In particular, certain sections of the Drakensberg escarpment in north-eastern South Africa (see Fig. 1) present a barrier to movement. This natural barrier was incorporated into the weighted layer using a 90m digital elevation model (DEM; srtm90). The standard deviation for each cell was calculated in ArcMap (ESRI). This was done using a square cell neighbourhood area comprising 3 cells in height and in width, thus indicating variations in altitude at a very fine scale (2.49 km x 2.49 km). The highest values correspond to the steepest parts of the escarpment. The minimum value which represented a barrier to movement was determined by visual assessment using contour lines corresponding with the steepest parts of the escarpment. This also resulted in certain steep sections of other mountain ranges in the study area being exposed, such as the Waterberg. This process did not result in saddles between the steepest parts being incorporated into the steep slope category, so these natural corridors are adequately represented in the cost layer. The four layers were weighted and added (see supplementary material) using the “weighted sum” function in ArcMap10 (ESRI). The classes within each predictor variable were assigned weights ranging from 1 to 10, with 1 having the least resistance to movement. Since human populations and their associated activities represent the greatest threats and barriers to wild dogs (Woodroffe & Ginsburg 1999), this layer received a weighting of 10, while land cover, main road density and steep mountain slopes received a weighting of 5 (see supplementary material).

Connectivity was assessed between protected areas that were home to resident packs of wild dogs during the time period when GPS records were collected (Fig. 1). These are the only sources of wild dogs that are formally protected and thus have a reasonable chance of persisting into the future. While sources could exist outside protected areas, these animals are vulnerable to persecution and their long-term survival is not ensured. Reserves included were the greater Kruger National Park (including Balule, Klaserie, Umbabat, Sabie Sand, Sabi Sabi, Manyeleti and Timbavati Game Reserves), Venetia Limpopo Nature Reserve, Madikwe Game Reserve, Pilanesberg National Park, Marakele National Park and the Northern Tuli Game Reserve (located in Botswana, bordering South Africa and Zimbabwe, with recorded dispersal events into South Africa and Zimbabwe (Davies-Mosert et al. 2012)).

#### *Evaluation of the circuit flow output*

The current flow connectivity analysis uses the resistance layers to assess connectivity between the designated source populations and is thus derived independently from wild dog occurrence records. In the circuit flow output, areas predicted to provide greater ease of movement, and thus facilitate connectivity, have greater cell values. Consequently, if the model accurately reflects areas that would have facilitated wild dog movement from source populations, the occurrence records should be located within grid cells that, on average, have greater values than the values associated with a set of randomly generated points. We created a set of 300 random points in ArcMap which were distributed throughout

the map area, but not located inside any of the source populations. Furthermore, to determine whether the current flow connectivity network may be of importance to other threatened carnivores, we overlaid the 339 cheetah occurrence records onto the current flow connectivity map. The current flow grid cell values were extracted to each random point and to the wild dog and cheetah occurrence records. Analysis of variance (ANOVA) was conducted to compare current flow values associated with the random points, cheetah and wild dog packs and wild dog dispersers.

#### *Identifying priority conservation areas*

Since a large proportion of South Africa's wild dog population occur outside of protected areas, this portion of the population are of great significance in the conservation of the endangered species (Davies-Mostert et al. 2009). Priority conservation areas, which we define here as landscapes suitable for re-establishing wild dog populations or ensuring survival of existing populations, would need to be large, relatively ecologically intact, spatially contiguous and interspersed with minimal amounts of human activities which are incompatible with large carnivores (Woodroffe & Ginsburg 1999). Given the importance of immigration and emigration for population viability, habitats for permanent occupation would additionally need to have some degree of connectivity to a source population.

The Maxent model using occurrence records for wild dog packs identifies areas with the greatest potential to support a resident population. The small grid cell size used in the Maxent model (0.83km x 0.83km) results in habitat suitability maps being expressed at a fine scale. Grid cell values range from zero (highly unsuitable) to one (highly suitable). Contiguous suitable habitat is therefore characterised by several neighbouring grid cells with values that are close to one. At a landscape scale, as opposed to a local scale, mean habitat suitability at a coarser resolution (e.g. 5km x 5km) would be more informative of landscape level habitat quality. This will facilitate the identification of large contiguous areas which are required to support one or more packs and could be assessed further in an attempt to identify priority conservation areas.

To assess landscape level-habitat quality, we performed a spatial filter on the output from the Maxent wild dog pack model. A filter was applied to calculate the mean grid cell values around focal grid cells. The filter calculated the mean value of the grid cells surrounding each focal cell using a kernel of 10x10 grid cells in size (equivalent to 8.3km x 8.3km = 68.9km<sup>2</sup>). To identify the distribution of the highest quality landscapes, we used the grid cell values and selected only the highest 10% of all the cells. The selection of the highest quality regions delineates high quality habitat patches which vary greatly in size. Priority conservation areas should be able to support at least a single resident wild dog pack. Although it has been proposed that protected areas as small as 200 km<sup>2</sup> may be suitable for wild dog reintroduction in South Africa (van Dyk & Slotow 2003), we used a more conservative minimum area requirement of 500 km<sup>2</sup> which is still relatively small. Consequently, all high quality habitat patches smaller than 500 km<sup>2</sup> were excluded from subsequent analysis.

The viability of potential priority conservation areas, although all larger than 500 km<sup>2</sup>, could vary greatly and would be influenced by factors such as patch size, perimeter-area ratio (indication of risk of edge effects), degree of fragmentation by main roads, and extent of existing protected areas (percentage covered). These factors were calculated for each potential priority conservation area, in addition to the degree of connectivity, since they would assist in quantifying the potential and viability of priority conservation areas.

## Results

### *Habitat selection by wild dog packs and dispersers*

Evaluating the ENMs performance using the area under the curve (AUC) statistic indicated that the wild dog pack model performed better than the disperser model, with variation in the permutation importance of the three predictor variables. Mean values following five-fold cross validation for wild dog packs: training AUC = 0.881; test AUC = 0.850; predictor variable permutation importance: main road density = 47.9%, land cover = 36.9%, human population density 15.2%. Disperser model: training AUC = 0.776; test AUC = 0.750; predictor variable permutation importance: land cover = 36.9%, main road density = 32.7%, human population density 30.4%.

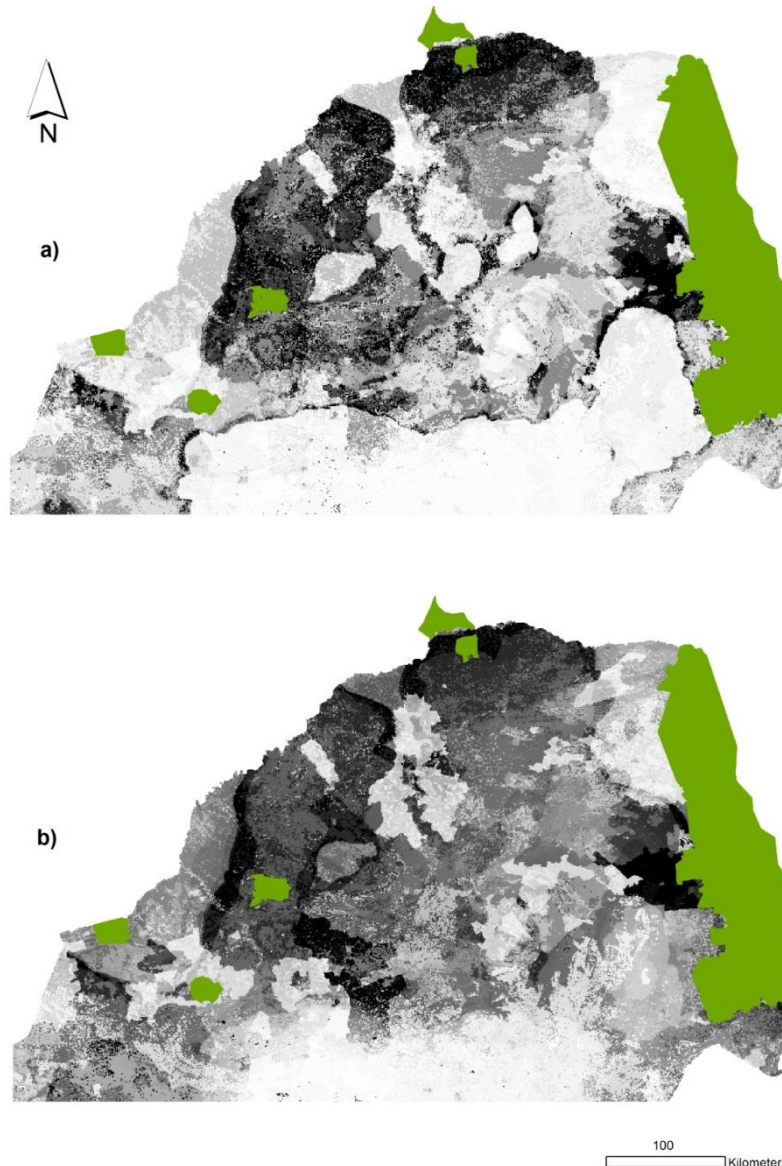


**Figure 2.** Areas identified as potentially suitable to support a) resident wild dog packs and b) wild dog dispersal. Black = most suitable; white = totally unsuitable. Protected areas which served as potential source populations are shown in green.

The Maxent model for dispersing wild dogs (Fig. 2b) was noticeably more general than that for the wild dog packs (Fig. 2a), as larger areas of higher suitability were identified. Values associated with training records used in the wild dog pack model (mean = 0.56) were significantly greater than those in the dispersal model (mean = 0.52;  $P = 0.038$ ; Mann-Whitney rank sum test; U-statistic = 21879.0). A histogram (Fig. 3) with ten classes between zero and one indicated that values associated with dispersal records were more evenly distributed than the pack records, with a peak (19.6%) between 0.4 and 0.5. The values for pack records were distributed more towards the higher suitability classes, peaking (28.5%) between 0.6 and 0.7. Furthermore, a comparison of Shannon diversity values using a t test (Hutcheson 1970), which accounts for both abundance and evenness of the distribution of records across the ten classes, indicated a significant difference between the two groups ( $P = 0.033$ ,  $t = 2.15$ ,  $df = 200.35$ ). The quality of habitats utilised by dispersing individuals thus varied greatly compared to resident packs.

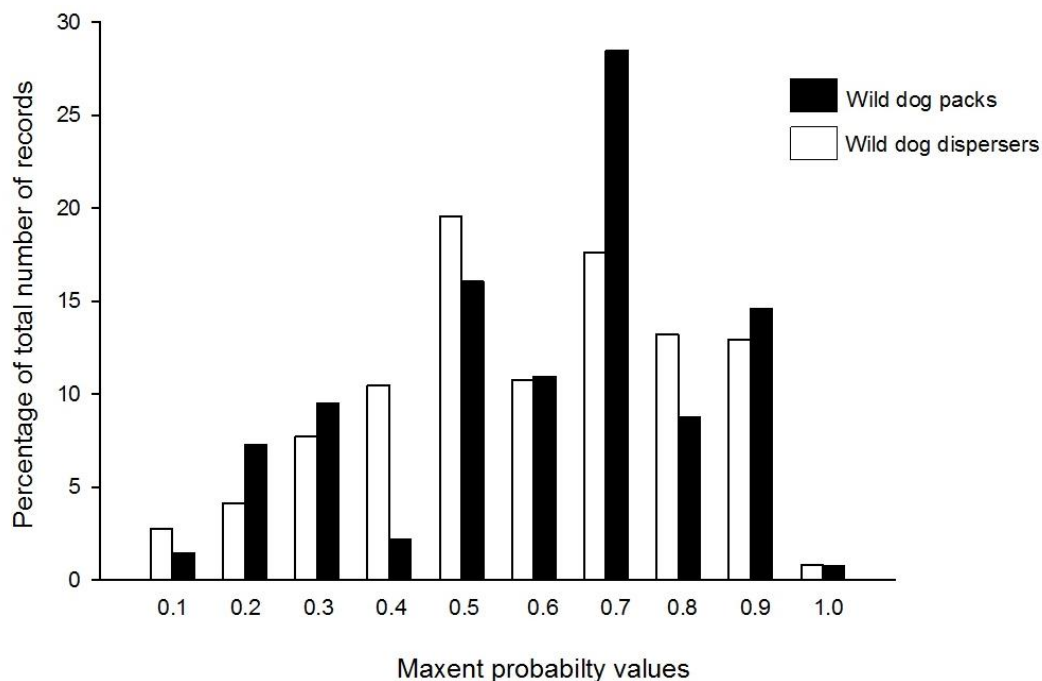


**Figure 3.** Histogram indicating the distribution of probability values extracted from Maxent models associated with occurrence records for wild dog packs and dispersers in each of the two models. Highly suitable habitat has a higher value.

#### *Habitat connectivity*

The current flow model (Fig. 4) had some similarities to the Maxent disperser model (Fig. 2b), but is far easier to interpret. The linkages identified by the least cost path model were located within areas identified as providing connectivity by the current flow model, but the single paths result in the omission of extensive areas which provide connectivity (as confirmed by occurrence records and as predicted by the current flow model). Notably, the areas highlighted as providing connectivity by the current flow model largely captured the wild dog and cheetah distribution records.

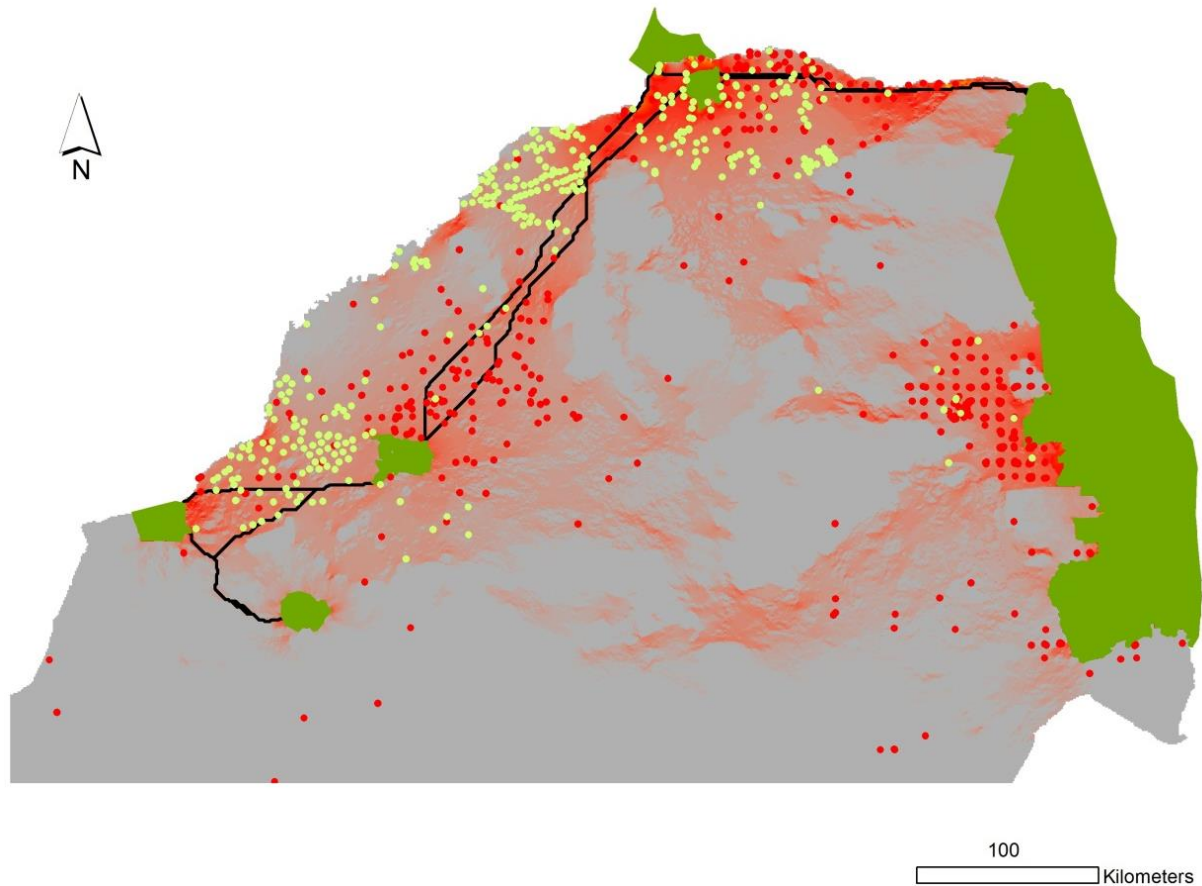


**Figure 4.** Connectivity between source populations based on current flow modelling. The GPS records of wild dog occurrence are shown in red and cheetah in green. Although these GPS records were not used in the model, they are largely contained within the areas predicted to facilitate connectivity (darker red = more suitable; source populations in green).

The ANOVA indicated a significant difference between the current flow values associated with cheetah, wild dog packs, wild dog dispersers and the random points in the study area ( $H = 244.9$ ,  $df = 4$ ,  $P = <0.001$ ). The pairwise multiple comparison procedure using Dunn's method revealed that the current flow values associated with the cheetah and both wild dog groups were significantly greater than those for the random locations ( $P = <0.05$ ), but there was no difference among the cheetah and wild dog groups (Fig 5). The wild dog and cheetah location data were therefore associated with significantly higher current flow values than the random samples, thus indicating the model's biological relevance and good performance.

We hypothesized that wild dog dispersers would utilise a broader variety of habitat qualities than packs. The data in Fig. 5 indicates that, in addition to a lower median value, the spread of current flow values (which translates to habitats) within the disperser group is far greater than that recorded within the pack group, supporting our hypothesis.

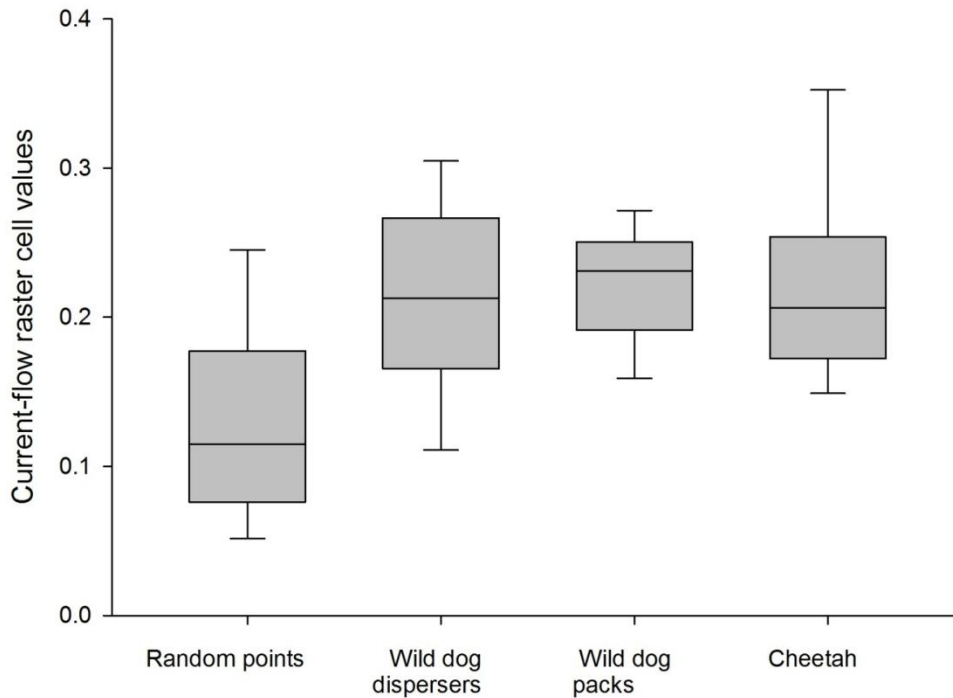


**Figure 5.** The raster grid cell values from the current flow model linked to the locations of random points, wild dog dispersers, wild dog packs and cheetah across the study area.

#### *Priority Conservation Areas*

The criteria used to identify priority conservation areas yielded five areas greater than 500 km<sup>2</sup> in size (Fig. 6). These patches ranged from 537 to 5215 km<sup>2</sup> in size (Table 2). Of the 576 wild dog and 339 cheetah location records, 311 (54%) and 139 (41%) fall within these five regions, respectively. Of the 311 wild dogs records, 191 (61.4%) were dispersers and 120 (38.6%) were packs. Evaluating the feasibility of the five focal conservation areas can be aided by a graphical display of their proximity to source populations, degree of connectivity, extent of existing unpopulated protected areas, fragmentation due to main roads and the distribution of occurrence records (Fig. 6).

**Table 2.** Characteristics of the five focal areas (Fig. 6) and the number of wild dog occurrence records occurring within each.

| Focal area | Size (km <sup>2</sup> ) | Perimeter-Area ratio | % covered by PA | Main roads (km) | Km road / km <sup>2</sup> | Number of wild dog records |
|------------|-------------------------|----------------------|-----------------|-----------------|---------------------------|----------------------------|
| 1          | 5215                    | 9.1                  | 21              | 237             | 0.045                     | 105                        |
| 2          | 4316                    | 5.1                  | 9               | 116             | 0.027                     | 39                         |
| 3          | 3139                    | 6.4                  | 60              | 190             | 0.061                     | 178                        |
| 4          | 2969                    | 4.8                  | 12              | 97              | 0.033                     | 7                          |
| 5          | 537                     | 3.2                  | 0               | 24              | 0.045                     | 1                          |

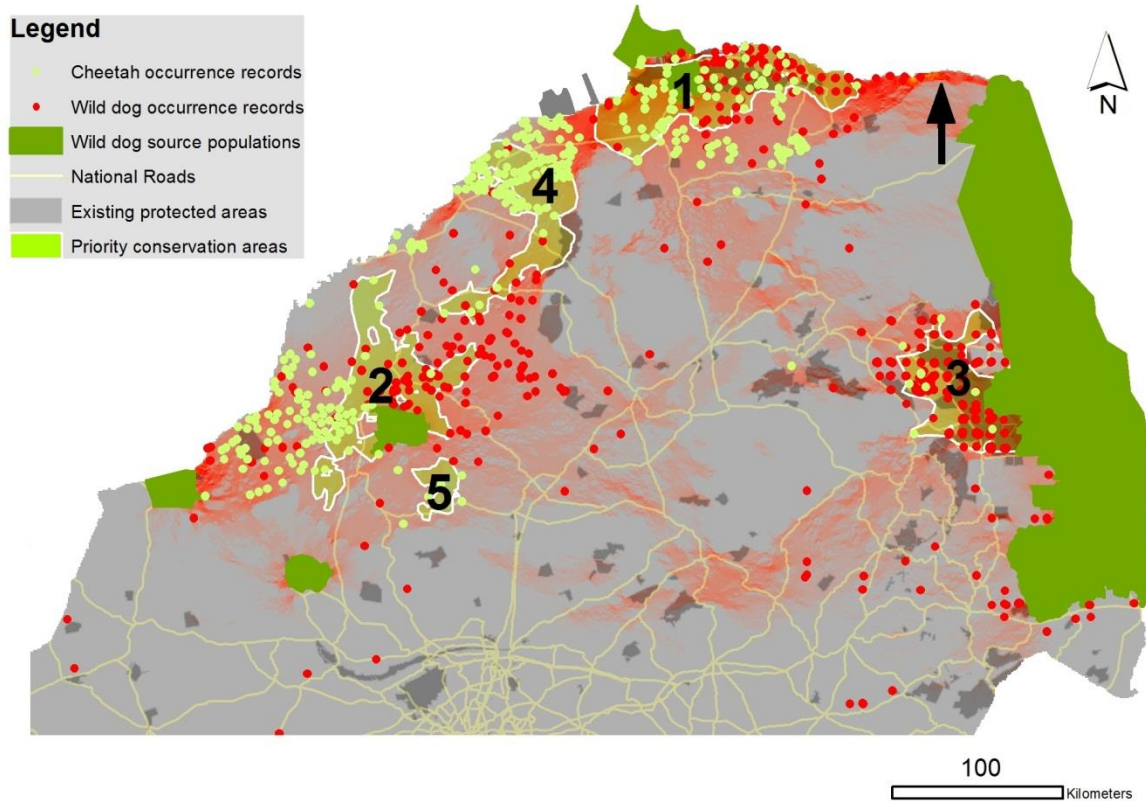


**Figure 6.** The five priority conservation areas (numbered) are shown in light green and encapsulated by a white line. These are overlaid onto the current flow connectivity network (in red) indicating the potential connectivity between the priority conservation areas and source populations (dark green). Existing protected areas shown in dark grey. Wild dog occurrence records are shown as red dots, cheetah as light green dots, with major national roads in yellow. The black arrow indicates an important corridor providing connectivity between the Kruger National Park and the northern parts of the study area.

## Discussion

### *Identifying suitable habitat for resident and dispersing wild dogs*

While habitat selection data of resident animals may be available for many taxa, it is rarely available for dispersing individuals. This is an important consideration in modelling work since habitat which facilitates movement between patches or populations may lack key features and resources required for long-term occupancy (Carroll et al. 2012). As a consequence, connectivity models based on ecological information from resident animals may lead to inaccurate conclusions. Most notably, such models may not identify habitat that facilitates movement, thereby overestimating the degree of habitat fragmentation. Failure to detect corridor habitat precludes these key areas from receiving conservation attention, further exacerbating isolation. Although studies have documented how dispersing carnivores use lower quality habitat than resident conspecifics (e.g. Palomares et al. 2000), we could not find any literature specifically comparing models derived with separate empirical data for dispersers and residents and our results thus provide insights into this debated issue.

Modelling and contrasting wild dog habitat suitability based on occurrence records associated with wild dog packs and disperser groups indicated that dispersing individuals were less habitat-specific. These results also confirm that our differentiation of wild dog packs and dispersing groups based on documented patterns of group size sufficed for the purposes of our analyses. In the wild dog pack model, large patches of highly suitable habitat were isolated, separated by extremely unsuitable regions (Fig. 2a). In contrast, predictions for wild dog dispersers identified habitat linking the highly suitable patches, indicating some level of connectivity (Fig. 2b). This habitat facilitated wild dog movement (as confirmed by occurrence records) and was also identified to provide linkage by both the LCP and current flow models. Huck et al. (2011) argue that the shift in habitat selection for dispersing animals arises primarily as a result of necessity and not actual active selection and that data from resident individuals may be more appropriate for establishing dispersal corridors. Using empirical data, our study illustrates the short-comings of such an approach; using wild dog pack data for corridor determination did not identify habitat which did in fact provide connectivity for dispersing wild dogs. Overlooking these corridors in an initial conservation planning phase would preclude them from receiving the adequate conservation attention, impeding effective conservation planning. Flexibility in selecting conservation areas is important in conservation planning (Margules & Pressey 2000) and using pack data alone would reduce the number of land parcels identified as suitable, thereby limiting the options for implementing corridors.

#### *Insights into the performance of alternative habitat connectivity models*

It has been argued that using expert opinion to assign costs to predictor variables in order to create a cost layer is subjective and not based on sound biological grounds (Ray & Burgman 2006; Huck et al. 2011). We created and used a cost layer in both the LCP and current flow models. The current flow model resulted in a good spatial match between occurrence records and landscapes predicted to facilitate linkage, validating the model's performance. Furthermore, the values associated with the independent occurrence data were significantly greater than would be expected by chance, indicating that the model accurately predicted areas that would support both wild dog and cheetah movement. The data linked to wild dog dispersers showed a lower mean value and far greater spread than data for resident packs, explicitly indicating how dispersing individuals use habitat of variable suitability that would not necessarily support permanent residence. Since the occurrence records confirmed the use of the identified habitat by both these species, the same corridors may be important in providing connectivity for other species in the region.

Testing the performance of the relatively new current flow methodology has to date not been possible due to a lack of disperser occurrence records (Carroll et al. 2012). Our evaluation and results therefore provide strong support for the performance of the current flow methodology. Since habitat selection data for dispersing individuals is often lacking for species of conservation concern, this technique may be particularly useful in conservation planning. Although assumptions regarding obstacles to a species' movement may be subjective, in our case it resulted in a useful model that is directly beneficial to conservation planning. The Maxent model for dispersing wild dogs has some similarities to the current flow model, but interpreting habitat providing linkage is more difficult. While the LCP did traverse habitat which was utilised by wild dogs, the current flow model considers all possible routes between predefined patches and is thus biologically more realistic and comprehensive. Although the LCP linkages were captured by the current flow model, the distribution of wild dog and cheetah records (Fig. 4) indicate that the LCP greatly underestimates habitat facilitating connectivity, unlike the current flow model.

### *Identifying priority conservation areas*

Wild dogs occurring outside of protected areas in South Africa need to be prioritized in future conservation initiatives (Davies-Mostert et al. 2009). In particular, restoration should attempt to promote connectivity as the natural movement it facilitates increases population viability (Davies-Mostert et al. 2009). Dispersing wild dogs will travel through unfavourable habitat, but pack formation and persistence is restricted to areas of higher quality and is dependent on individuals finding mates. The regular occurrence of wild dogs will decrease the negative mate-finding Allee effect within a given area. In addition, increasing distance between areas is negatively correlated with connectivity for carnivores (Ferreras 2001). Consequently, selecting the most viable potential recolonisation site will depend largely on these factors.

The five priority conservation areas represent the most feasible areas to potentially re-establish populations of African wild dogs within their historical range, or ensure survival of existing animals. Apart from accommodating additional packs, these areas may serve as stepping stones between existing wild dog populations, reducing anthropogenic mortality risks and increasing the probability of dispersing animals successfully finding mates and forming packs (Davies-Mostert et al. 2012). Areas 1 and 3 (Fig. 6) have the greatest number of occurrence records (86% of records occurring within the five areas), the most favourable perimeter-area ratio, and the largest extent of currently protected areas. Importantly, both areas are large and well connected to source populations; Area 1 is connected to the Tuli Block (Botswana) and parts of southern Zimbabwe which are home to resident and transient wild dogs, while Area 3 is directly alongside the greater Kruger National Park ecosystem and the wild dog population it supports. The wild dogs occurring here are consequently managed as part of the greater Kruger National Park population and including this area in conservation planning for wild dogs would increase the area available to the population's conservation. Although 60% of Area 3 is protected, it also has the highest density of main roads which represents a serious mortality risk to wild dogs (Woodroffe & Ginsburg 1999). Furthermore, Area 1 is relatively close to the Kruger National Park with the shortest route between the two being identified as suitable dispersal habitat. Consequently, maintaining this ecological corridor between the two (indicated by an arrow in Fig. 6) is of vital importance. For the purposes of connectivity between populations this corridor could be viewed as a priority conservation area.

In comparison to Areas 1 and 3, Areas 2, 4 and 5 are generally less suitable for attempting to re-establish a self-sustained wild dog population. This is due largely to a far lower incidence of wild dog presence which will limit gene flow and decrease the likelihood of pack formation. Fewer wild dogs are attributable to the increased distance from large source populations and, as indicated by the connectivity analysis, the greater degree of isolation given limited suitable dispersal habitat to these areas. The scarcity of lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) increases the potential suitability of those areas, given that those species are major competitors for wild dogs (Creel & Creel 2002).

Future conservation efforts in these areas would need to take specific factors into account to realise the areas true conservation potential. Prey availability would be assumed to be sufficient given the semi-natural state of much of the suitable areas and given the high frequency of wildlife ranching in those areas. Despite the ecological suitability of the areas, high rates of anthropogenic induced mortality would negate the viability of otherwise suitable areas. Due to a lack of relevant data, land use could not be incorporated into our models. Even if a region is ecologically intact, land uses associated with low predator tolerance such as livestock farming and game ranching directly influence a region's suitability for re-establishing a wild dog population or transient dispersing animals. Increased mortality due to deliberate killings of wild dogs (Thorn et al. 2013) will hamper population establishment and persistence

and greatly reduce the probability of dispersing individuals successfully moving between populations. The knowledge of conservation officials familiar with these regions and land use practices will be helpful in refining conservation strategies. In particular, tolerance by land owners would need to be addressed and suitable initiatives implemented (Lindsey et al. 2005a). These may include establishing research projects where researchers could actively engage with land owners. In addition to listening to complaints, the information provided by fieldworkers may improve general attitudes and tolerance. The formation of conservancies, where fences between neighbouring game ranches are removed to form larger wildlife areas, may be particularly preferable (Lindsey et al. 2011). In the larger areas, game ranchers are more tolerant of large predators and are more positive to their recolonisation (Lindsey et al. 2011). Both Areas 1 and 3 are comprised of a large proportion of informally (private) protected areas where land use would be expected to be compatible with large carnivores. Since ecotourism is the main form of utilisation within these areas, the reintroduction of wild dogs may be received particularly favourably as they are attractive to tourists (Lindsey et al. 2005b).

Expanding conservation areas based on the requirements of single species is unlikely to be a realistic proposition. The most viable areas and the linkages between them would not only be of importance to wild dogs. Our use of cheetah occurrence data supported this assumption and indicates how other species of conservation concern may also benefit should these areas receive more conservation attention. Furthermore, wild dogs and cheetah are large carnivores near the top of the trophic level. Should these areas successfully support populations of these and other large carnivore species, it would indicate that the lower trophic levels were in place and that the greater ecosystem was functioning, and thereby acting as an umbrella species and aiding the conservation of biodiversity in general (Dalerum et al. 2008).

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## Supplementary material

**Table 1.** Environmental predictor variables, and their respective weights, which were used to create the cost layer used in the connectivity analyses.

| Variable                 | Classes and class weights                       | Source                                | Layer weight |
|--------------------------|-------------------------------------------------|---------------------------------------|--------------|
| Land cover               | <i>a.</i> Natural vegetation = 1                | National land cover map               | 5            |
|                          | <i>b.</i> Degraded = 1                          |                                       |              |
|                          | <i>c.</i> Cultivation = 4                       |                                       |              |
|                          | <i>d.</i> Water bodies = 10                     |                                       |              |
|                          | <i>e.</i> Plantations = 4                       |                                       |              |
|                          | <i>f.</i> Mines = 10                            |                                       |              |
| Human population density | <i>a.</i> 0-5 people per km <sup>2</sup> = 1    | Environmental potential atlas         | 10           |
|                          | <i>b.</i> 5-10 people per km <sup>2</sup> = 2   |                                       |              |
|                          | <i>c.</i> 10-25 people per km <sup>2</sup> = 4  |                                       |              |
|                          | <i>d.</i> 25-50 people per km <sup>2</sup> = 7  |                                       |              |
|                          | <i>e.</i> 50-100 people per km <sup>2</sup> = 9 |                                       |              |
|                          | <i>f.</i> >100 people per km <sup>2</sup> = 10  |                                       |              |
| Main road density        | <i>a.</i> 0 – 3 = 1                             | Environmental potential atlas         | 5            |
|                          | <i>b.</i> 3,1 – 7 = 2                           |                                       |              |
|                          | <i>c.</i> 7,1 – 10 = 4                          |                                       |              |
|                          | <i>d.</i> 10,1 – 18,5 = 6                       |                                       |              |
|                          | <i>e.</i> 18,6 – 30,155 = 10                    |                                       |              |
| Steep mountain slopes    | <i>a.</i> Steep slopes = 10                     | Derived from 90m DEM (see text above) | 5            |
|                          | <i>b.</i> All other areas = 0                   |                                       |              |